Metabolism constrains bird and mammal ranges and predicts shifts in response to climate change

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Abstract

30 **Aim**

We test whether physiological constraints on maximum metabolic rate and the factor by which

32 endotherms can elevate their metabolism (metabolic expansibility) govern cold range limits for mammal

and bird species.

34 **Location**

Global

36 **Methods**

We examine metabolic expansibility at the cold range boundary (ME_{CRB}) and its trait predictors and then

38 use ME_{CRB} to project range shifts for 210 mammal and 61 bird species.

Results

40 We find evidence for metabolic constraints: the distributions of metabolic expansibility at the cold range

boundary peak at similar values for birds (2.7) and mammals (3.2). The right skewed distributions

42 suggest some species have adapted to elevate or evade metabolic constraints. Mammals exhibit greater

skew than birds, consistent with their diverse thermoregulatory adaptations and behaviors. Mammal

44 and bird species that are small and occupy low trophic levels exhibit high levels of ME_{CRB}. Mammals with

high ME_{CRB} tend to hibernate or use torpor. Predicted metabolic rates at the cold range boundaries

46 represent large energetic expenditures (>50% of maximum metabolic rates). We project species to shift

their cold range boundaries poleward by an average of 3.9° latitude by 2070.

48 **Main conclusions**

Our analysis suggests that metabolic constraints provide a viable mechanism for projecting cold range

50 boundaries and range shifts in response to climate change for endotherms.

Keywords: distribution, endotherm, metabolic scope, metabolic expansibility, range limit, thermal

52 neutral zone

54 **INTRODUCTION**

Environmental temperatures govern the performance and energy use, and ultimately the abundance

56 and distribution, of animals (Bozinovic *et al.*, 2011). Performance and energetic constraints provide a

powerful basis for projecting responses to climate change because the constraints should extrapolate

58 better into novel environments than statistical correlations (Radeloff *et al.*, 2015). Models translating

environmental conditions into the body temperatures of ectotherms and quantifying limitations on

60 performance and activity durations can robustly predict patterns of abundance and distribution

(Kearney & Porter, 2009; Buckley *et al.*, 2010). The translation is more complex for endothermic animals

62 because they can use endogenous heat production to maintain their body temperatures under a wide

range of environmental thermal conditions if available resources and physiological capacities are

64 sufficient (Boyles *et al.*, 2011; McNab, 2012). Thus, few mechanistic approaches predict endotherm

distributions (but see examples reviewed in Boyles *et al.*, 2011). Several recent examples employ

66 biophysical models to estimate metabolic constraints, activity limitations, and water balance for focal

endotherms (Kearney *et al.*, 2016; Mathewson *et al.*, 2017).

68

Fundamental physiological constraints on metabolism limit maximum metabolic rate and the factor by

70 which endotherms can elevate their metabolism (Humphries *et al.*, 2004; Stager *et al.*, 2015). An initial

test of metabolic constraints (Root, 1988) suggested that the cold range boundaries of passerine birds in

72 North America coincided with winter metabolic rates at the cold range boundary being elevated by a

factor of 2.5 over basal rates, but subsequent analyses (Repasky, 1991; Canterbury, 2002) have

74 questioned the generality of metabolic constraints due to the limited biological, distributional, and

environmental data available or poor fit between range boundaries and temperature isotherms.

76

Physiological measurements indicate metabolic constraints and adaptations. Seasonal cold associated

78   with either climate variability [Climate Variability Hypothesis (Janzen, 1967; Stevens, 1989; Ghalambor

et al., 2006)] or seasonal temperature extremes [Cold Adaptation Hypothesis (Swanson & Garland Jr,

80   2009)] is expected to select for increased metabolic capacity. Maximum cold-induced metabolic rate

(M_{sum}) is greater in cold environments (Wiersma *et al.*, 2007) and is phylogenetically conserved

82   (Swanson & Garland Jr, 2009; Stager *et al.*, 2015). Extensions of classic work examining how animals

adapt to regulate heat (Scholander *et al.*, 1950; Scholander, 1955) find that adaptation to environmental

84   conditions alters both basal metabolic rate (BMR) and heat conductance in birds and mammals (Fristoe

et al., 2015). Birds and mammals with more poleward range limits that experience colder minimum

86   temperatures can tolerate colder temperatures without elevating metabolism (Khaliq *et al.*, 2015).

88   Here we leverage extensive metabolic, distribution, and phylogenetic datasets (Khaliq *et al.*, 2014;

Fristoe *et al.*, 2015) to test the viability of using metabolic constraints to project bird and mammal

90   distributions. Specifically, we estimate the factor by which metabolism is elevated at the cold range

boundaries (metabolic expansibility, ME_{CRB}). We expect the distribution of ME_{CRB} to be normal and

92   strongly peaked if the cold range edges of birds and mammals are limited by the capacity of their

metabolic systems to maintain approximate temperature homeostasis. A peaked distribution would

94   indicate similar limits to ME_{CRB} across birds and mammals that differ substantially in geographic

distribution, habitat, traits, and life history. However, positive skew in the distribution could reflect

96   species that are metabolically adapted to or able to evade cold conditions. Species may evade extreme

temperatures by adjusting activity times (e.g., diurnality) or the maintenance of body temperatures

98   (e.g., use of hibernation or torpor) or by selecting favorable microclimates. We hypothesize that

because mammals use strategies to evade full exposure to winter cold (e.g., hibernation, use of

100 subnivean space) to a much greater degree than birds (Swanson, 2010; Williams *et al.*, 2014; Ruf &

Geiser, 2015), that mammals will show both greater skew in the density distribution of ME_{CRB} and more

102   values of ME_{CRB}/Msum approaching or exceeding unity than birds.

104   We test whether physiological, behavioral and ecological traits (body size, nocturnality, torpor use, diet) associated with adaptation or evasion correspond to higher ME_{CRB} values. Body size influences the

106   ability to use potential microclimates as well as metabolic rates and thermal inertia. Trophic levels influence the seasonal availability of food and metabolic rate (McNab, 2008, 2009). We also examine

108   the conservatism of traits and metabolic expansibility at the cold range boundary (ME_{CRB}) across the phylogeny. Finally, evidence for metabolic constraints suggests that (in the absence of adaptation or

110   acclimation) species will follow thermal isoclines through climate change. We thus project ranges and range shifts in response to predicted climate change.

112

MATERIALS AND METHODS

114   We estimated the factor by which metabolism is elevated at the cold range boundaries (as in Root, 1988). We calculated metabolic rate (ml O_2 h^{-1}) at the cold range boundary as $MR_{CRB} = (T_{lc} - T_{min})C +$

116   BMR, where T_{lc} is the lower critical temperatures bounding the lower limit of the thermal neutral zone (TNZ); T_{min} is the coldest environmental temperatures (see below) at the cold range boundary; BMR is

118   basal metabolic rate (ml O_2 h^{-1}), and C is thermal conductance (ml O_2 h^{-1} $°C^{-1}$) (figure 1). We calculated metabolic expansibility at the cold range boundary as $ME_{CRB}=MR_{CRB}$ /BMR. We focus on cold range

120   boundaries because they are more likely governed by metabolic constraints than are warm range boundaries (see discussion); at warm range boundaries the capacity for evaporative cooling may be

122   more limiting than the associated metabolic costs and minimal endogenous heating is favored (Tieleman & Williams, 2000; McKechnie *et al.*, 2016b). Our estimates of ME_{CRB} are approximate in that

124   they do not account for additional factors such as use of solar radiation, convective heat loss,

microclimate variation, and microhabitat selection (Porter & Kearney, 2009).

126

Data

128   We restricted our analysis to resident (non-migratory) species. We omitted species on islands and those

with latitudinal range limits constrained by continental boundaries. We additionally restricted our

130   analysis to cold range boundaries with temperatures below the T_{lc} (omitted 1% of species). Accounting

for these constraints and limitations on available physiological data, we analyzed 210 and 61 cold range

132   boundaries for mammal and bird species, respectively.

134   For species distribution data, we used the IUCN range maps for mammals (Patterson *et al.*, 2005) and

the BirdLife range maps for birds (BirdLife International and NatureServe, 2014). We calculated

136   temperatures at the range boundaries (T_{min} and T_{max}) using BIO5 (max temperature of warmest month)

and BIO6 (min temperature of coldest month) at 5 minute resolution from the WorldClim dataset

138   (Hijmans *et al.*, 2005). Data are interpolated from air temperature at weather stations (generally 2m

high). Trait data are insufficient to account for microhabitat use (e.g., burrows or under snow), but our

140   trait analysis does provide some indication of exposure to air temperatures. We extracted the grid cells

at the northern and southern extremes of the species' distribution for each 5-minute longitudinal band.

142   We quantified the degree to which range boundaries follow temperature isoclines as the standard

deviation and median absolute deviation (mad, R function mad) of cells along the range boundaries.

144   Subsequently, we estimated T_{min} and T_{max} as the median of the grid cells along the cold and warm range

boundaries, respectively. We checked that minimum and maximum temperatures were sufficiently

146   constant across the range boundaries for our results to be robust to our selection of the median (figure

S1). Current data are normals for 1950-2000 and future data are downscaled global climate model

148   (GCM) projections from CMIP5 (IPCC Fifth Assessment) averaged over 2061-2080. We examined output

from both the HadGEM2-AO and CCSM4 models assuming a midrange greenhouse gas concentration

150   scenario (Representative Concentration Pathway RCP6.0, indicates a $6W/m^2$ increase in radiative forcing

in 2100 relative to pre-industrial values, http://cmip-pcmdi.llnl.gov/cmip5/). Data were accessed using

152   the getData function in the R package raster.

154   The bounds of the TNZ (T_{lc} and T_{uc}, °C) and body temperature (T_b, °C), were compiled from the literature

by Khaliq et al. (2014). We incorporated data compiled for additional species (Canterbury, 2002; Riek &

156   Geiser, 2013; Bozinovic *et al.*, 2014). We used BMR data from Fristoe et al. (2015) and McNab (2008,

2009) after assessing whether the data met criteria for data quality (see below). We extracted Msum

158   data (Msum = BMR + maximum thermogenic capacity) for 20 mammal and 6 bird species from existing

compilations (Rezende *et al.*, 2004; Lovegrove, 2005; Swanson & Garland Jr, 2009; Stager *et al.*, 2015).

160   Those MR values reported in watts were converted to oxygen consumption assuming a factor of 179 ml

O_2 h^{-1} W^{-1}, which corresponds to lipid metabolism (Schmidt-Nielsen, 1997). Minimum conductance was

162   estimated as the absolute value of the slope of the line connecting T_{lc} at BMR to T_b when metabolic rate

is 0: $Cmin=|(0-BMR)/(T_b-T_{lc})|$(Fristoe *et al.*, 2015). We use units of oxygen consumption for metabolism

164   and conductance to align with previous analyses (Fristoe *et al.*, 2015).

166   Analysis of the quality of the data compiled in Khaliq et al. (2014) identified issues with T_{uc} but not T_{lc}

(McKechnie *et al.*, 2016a). Some T_{uc} data are of lesser quality due to small sample sizes or weak

168   measurement protocols (McKechnie *et al.*, 2016a), so we only use the T_{uc} data for a coarse analysis

mentioned in our discussion. We omitted T_{uc} measurements that were found to be of poor quality ["No

170   UCT" or "NA-" categories; we kept values based on low sample sizes due to the tentative nature of our

analyses] (McKechnie *et al.*, 2016a). We revisited the source papers to assess whether the T_{lc} data were

172   calculated from valid BMR measurements. We used the following criteria to assess data quality for BMR: measurements were made during the rest phase on inactive individuals in a postabsorptive state. We

174   additionally recorded whether individuals measured were field-collected (or the first generation reared in a laboratory or zoo in a small number of cases) and the location of field collection, as individuals

176   collected far from the range boundary may lack adaptations and acclimation present near the range boundary. We assessed the influence of these quality criteria on our results as described below.

178

        Diet, habitat, and nocturnality data were extracted from Elton Traits (Wilman *et al.*, 2014). Data on

180   whether a species uses torpor or hibernation were extracted from McNab (2008, 2009) and Ruf and Geiser (2015). A "torpor" trait was assigned a value of 1 if the species uses either torpor or hibernation

182   and 0 otherwise. Data on relevant thermoregulatory traits such as body shape, insulation, and fur or feather properties were inadequate to include the traits in the analysis.

184

        Analyses

186   We examine the distribution of ME_{CRB} estimates across birds and mammals to assess evidence for a metabolic constraint. We assessed skewness and kurtosis of the ME_{CRB} distribution using the skewness

188   metric and D'Agnostino skewness test and Geary metric and Bonett-Seier test in the R moments package. We tested for unimodality in the distributions using Hartigans' dip statistic in the R diptest

190   package. To test whether ME_{CRB} varies systematically with T_{min} or T_{max}, we constructed null models for ME_{CRB} by randomizing T_{min} or T_{max} among species and calculating the median and mean ME_{CRB} values.

192   We repeated the randomization 1000 times.

194   We then used regressions to assess whether species' traits indicating adaptation to or evasion of cold temperatures can explain variation in ME_{CRB}. We used model selection based on AICc (dredge function)

196   and model averaging (model.avg function in R package MuMIn) to conclude that the best models

        omitted interactions between the predictor variables (mass, diet, nocturnality, torpor). Accounting for

198   phylogeny did not alter our results, so we report phylogenetic analyses in appendix S1.

200   We used thermal isoclines (consistent with species maintaining a constant ME_{CRB} in the absence of

        acclimation or adaptation) to project species' distribution in both current and future environments. We

202   restricted predicted distributions to observed west and east longitudinal extents since we have no basis

        for predicting longitudinal distributions. We identified all pixels with T_{min} warmer than the predicted

204   physiological lower temperature limit (based on species-specific observed ME_{CRB}). We removed pixels

        predicted to be thermally habitable that were geographically isolated from other habitable pixels from

206   our prediction using the clump function in the R package raster. We omitted all clumps with areas less

        than 5% of the area of the largest clump, because the core of the predicted distribution is most

208   representative of latitudinal extents. We further restricted our predicted distribution to clumps

        overlapping with the latitudinal extent of the observed species range. We then quantified the median

210   latitude of grid cells along the cold range edges.

212   **RESULTS**

        Metabolic expansibility at the cold range boundary

214   Our analysis of bird and mammal species with disparate geographic distributions, habitats, traits, and

        life histories suggest that winter temperatures and the ability to elevate metabolism to maintain body

216   temperatures constrain cold range boundaries (Fig. 2). Cold range boundaries of both mammals

        (sd=4.6°, mad=3.9° of median T_{min}) and birds (sd=4.6°, mad=3.3° of median T_{min}) approximately follow

218   temperature isoclines (Fig. S1 in the Supporting Information). Translating this thermal variability into

        metabolic consequences, the median standard deviations represent a change in metabolic rate of

220     $12.4 \pm 12.2\%$ (mean ± sd) for mammals and $10.8 \pm 7.8\%$ for birds. The distributions of metabolic

expansibility, ME_{CRB}, are peaked and peaks occur at similar values for birds and mammals. The bird

222   distribution has a slight dip at the peak of the density distribution, which we attribute to limited sample

size in the absence of evidence for non-unimodality (Hartigans' dip test: $D=0.05$, $p=0.3$). We thus

224   estimate the peak value as the mean of the two subpeaks. The density distribution of ME_{CRB} peaks at

2.72 for birds (median=3.21, mean ± sd= 3.28 ± 1.63) and at a slightly higher value (3.17, median=3.63,

226   mean ± sd= 4.64 ± 3.35) for mammals. ME_{CRB} values fall outside the 95% confidence intervals of the null

model estimated by randomization for both mammals (median: 3.53-3.54, mean:4.55-4.56) and birds

228   (median: 2.63-2.64, mean:3.16-3.17). The previous value found for birds (2.5 x BMR; Root, 1988) was

similar to our estimate of the peak of the distribution.

230

We assessed whether ranges may be constrained more strongly by maximum metabolic capacity (M_{sum})

232   rather than the factorial capacity for elevating metabolism over BMR (ME_{CRB}). Among the limited data

available for our focal species (N=20 mammal and 6 bird species), M_{sum} is on average 5.0 times BMR

234   (median 5.4, 25th to 75th percentile= 4.0 to 6.3). The density distribution of the ratio of MR_{CRB} to M_{sum}

peaks at 0.7 (median=0.88, mean ± sd =0.96 ± 0.44, Fig. 3).

236

The right skewed distributions of ME_{CRB} (Fig. 2) suggest that some species have evolved the capacity to

238   maintain a higher ME_{CRB} or to evade the constraints of cold temperatures via torpor, microclimate

selection, or movement. The distribution for mammals is more skewed (2.54) than that for birds (1.06),

240   but both exhibit significant positive skew (D'Agnostino test, mammals: $z=9.52$, $p<10^{-15}$; birds: $z=3.22$,

$p<0.001$). Only mammals exhibit significantly more kurtosis than expected under normality (Bonett-

242   Seier test, mammals: Geary metric: 0.78, $z=10.20$, $p<10^{-15}$; birds: Geary metric: 0.66, $z=0.78$, $p=0.2$).

244   We next assess whether traits that allow organisms to maintain high metabolism or evade cold

temperature can explain the skewed distribution. Mammalian traits (mass, diet, nocturnality, and use of

246   torpor or hibernation) account for a substantial portion of variation in ME_{CRB} (r^2=0.29, $F_{[7,171]}$=11.2,

$p<0.001$); mammal species that are relatively small (t=-4.36, $p<0.001$) and use torpor or hibernation

248   (t=4.99, $p<0.001$) tend to have higher ME_{CRB} (Fig. 2, Table S1). Diet also significantly influences ME_{CRB},

with granivores having higher ME_{CRB} than mammals consuming other diets (F=2.44, $p<0.05$, ANOVA,

250   Table S3). Bird traits (mass, diet, and nocturnality) likewise account for a substantial portion of variation

in ME_{CRB} (r^2=0.28, $F_{[6,54]}$=4.9, $p<0.001$); birds that are small (t=-2.82, $p<0.05$) tend to have higher ME_{CRB}.

252   Birds that eat invertebrates or plants and seeds exhibit higher ME_{CRB} than those consuming other diets

(F=7.85, $p<0.01$, ANOVA). Limited phylogenetic signal in mammal and bird ME_{CRB} (Fig. S3) arises largely

254   from conservatism of predictor traits (appendix S1). Phylogenetic regressions do not substantially

deviate from linear regressions (Table S1, appendix S1).

256

Data quality

258   In our full dataset for mammal ME_{CRB}, the following proportions of species with data met our BMR

quality control criteria: 93.9% [58.6% including NA (not available) values as not meeting quality criteria]

260   were measured during the resting phase, 70.0% (42.9% including NA values) were postabsorptive, and

81.2% were wild-caught (70.0% including NA values) (Table S2). Of the quality criteria, only whether the

262   mammal species was live-trapped or captive was a significant predictor of ME_{CRB} (resting phase:

$F_{[1,82]}$=1.53, p=0.22; postabsorptive: $F_{[1,82]}$=0.04 p=0.84; wild caught: $F_{[1,82]}$=5.15, $p<0.05$). However,

264   restricting the dataset to wild-caught species does not substantially alter the peak value of metabolic

expansibility (peak= 3.27, mean= 4.72, median= 3.75). The trait predictors of ME_{CRB} remain similar when

266   considering only wild-caught individuals (Table S3).

268   In our full dataset for bird ME_{CRB}, the following proportions of species with data met our BMR quality

criteria: 93.0% (86.9% including species without data) were measured during the resting phase, 88.9%

270   (52.4% including species without data) were postabsorptive, and 68.9% were wild-caught (50.8%

including species without data) (Table S2). Similar to mammals, of the quality criteria only whether the

272   bird species was live-trapped or captive was a significant predictor of ME_{CRB} (resting phase: $F_{[1,32]}=0.00$,

p=0.94; postabsorptive: $F_{[1,32]}=0.68$ p=0.42; wild caught: $F_{[1,32]}=6.90$, p<0.05). However, restricting the

274   dataset to wild-caught species did not substantially alter the peak value of ME_{CRB} (peak= 2.60, mean=

3.07, median= 3.11). The trait predictors of ME_{CRB} remained similar, but some predictors lose

276   significance, when considering only wild-caught individuals (Table S3).

278   The measured individuals were collected throughout the species' range with average positions near the

center of the range for both mammals (median and mean from range edge: 10.3° and 13.4° latitude,

280   47.2% and 49.4% of the species' latitudinal range) and birds (median and mean from range edge: 18.3°

and 20.4° latitude, 50.8% and 49.9% of the species' latitudinal range). Neither distance metric is a

282   significant predictor of ME_{CRB} in mammals (distance: $F_{[1,142]}=0.27$, p=0.60; percent: $F_{[1,142]}=0.10$, p=0.76)

or birds (distance: $F_{[1,29]}=0.12$ p=0.73; percent: $F_{[1,29]}=0.39$ p=0.54). Collection locations have a median

284   elevation of 275m (25th and 75th quantiles: 39 to 849m, based on collection coordinates and Google

Maps Elevation API). Thus, few of the physiological measurements reflect metabolic adaptation to high

286   elevation.

288   **Range shifts**

We forecast potential range shifts by examining how metabolic constraints will shift through climate

290   change. For example, North American rodent species differ in their metabolic constraints, the extents of

their current distribution, and the projected range expansion as a result of climate change (Fig. 4 for

292   projections using the HadGEM2-AO model; Fig. S4 for CCSM4 model projections). The quality of the

range projections vary across species (Figs. S5-S8). We predict that most mammals and birds will shift

294   their cold range boundaries poleward through climate changes (Fig. 4). We project a similar magnitude

of cold range boundary shifts for mammals (mean=3.77°, median=2.58°) and birds (mean=4.20°,

296   median=3.63°). Numerous species are projected to shift their cold range boundary poleward by 6°

latitude (75% quantile) and some species are predicted to shift by as much as 22° (Fig. 4).

298

DISCUSSION

300   Our analysis supports a mechanism underlying observations that endotherms track thermal isotherms

through climate change (Tingley *et al.*, 2009; Chen *et al.*, 2011). However, many observed range shifts

302   have been idiosyncratic in extent and direction (Gibson-Reinemer & Rahel, 2015). Filtering the range

shifts through the lens of metabolic constraints may resolve some discrepancies. Our data are

304   consistent with the poleward range edges of both birds and mammals being constrained by the factor

by which they can elevate their metabolism above basal rates (perhaps resulting from a constraint on

306   maximum metabolic rates). The constraint may result from either direct physiological limitations on

metabolism, such as the ability to sustain high rates of thermogenesis over prolonged periods, or

308   limitations on energy acquisition. The rates of ME_{CRB} that we find for birds (peak of distribution=2.7) are

similar to a previous value (2.5) for a more taxonomically and geographically restricted analysis (Root,

310   1988).

312   We find a slightly higher peak of the ME_{CRB} distribution for mammals (3.2). The distribution of ME_{CRB} is

right skewed, more so for mammals than for birds. The greater skew in the mammal ME_{CRB} distribution

314   is consistent with the prominent use of hibernation and protected microclimates (e.g., burrows, dens,

subnivean space) during winter in mammals, but lesser use of these options to avoid cold thermal

316   environments in birds (Swanson, 2010; Ruf & Geiser, 2015). These adjustments have the effect of

rendering the thermal conditions encountered at the ME_{CRB} as less extreme than the actual ambient

318   conditions, which results in an overestimation of the thermal isocline followed by the cold range

boundary. In addition, differences in the mechanisms of thermoregulation between mammals and birds

320   may contribute to the difference in ME. Cold-adapted mammals have well developed capacities for non-

shivering thermogenesis through brown fat, but birds lack brown fat and although they may possess

322   some muscular non-shivering thermogenesis, muscular shivering appears to be the primary mechanism

of heat production in birds (Mezentseva *et al.*, 2008).

324

The limited data on maximum cold-induced metabolic capacity (M_{sum}) provide additional support for a

326   metabolic constraint. We estimate that thermoregulation at the cold range boundary requires a

substantial proportion (>50%) of the potential metabolic capacity for thermogenesis of the species. This

328   supports the existence of a metabolic constraint on range boundaries and suggests that species use a

substantial portion of their maximum metabolic capacity to thermoregulate. The right skewed

330   distribution (and instances where MR_{CB}/M_{sum} >1) suggests that some species use torpor or hibernation

or evade the coldest temperatures through habitat and microclimate selection (Fig. 3). Because M_{sum} is a

332   flexible trait correlated with environmental conditions (Rezende *et al.*, 2004; Swanson, 2010), ratios

approaching or exceeding one may also result from M_{sum} measurement occurring for populations in

334   warmer climates than those at the cold range boundary. Correlations between M_{sum} and environmental

temperatures have been previously documented for rodents (Rezende *et al.*, 2004; Bozinovic *et al.*,

336   2011) and birds (Swanson, 2010; Stager *et al.*, 2015).

338   We identify traits associated with high values for ME_{CRB}, which may be adaptations to or consequences

of inhabiting cold environments. Body mass is an important factor that influences ME_{CRB}. Smaller

340   mammals, which tend to exhibit greater ME_{CRB}, may be able to evade cold temperatures through

seeking shelters or selecting favorable microclimates. Alternatively, the ability to use torpor or

342   hibernation enables mammals to inhabit colder environments. Mammals using torpor tend to be small,

which may contribute to the relationship between mass and ME_{CRB} (Ruf & Geiser, 2015). Small

344   mammals may also be able to meet the resource requirements or store energy to maintain high

metabolism through cold periods (due to the low per-organism, or total, metabolic rate stemming from

346   their small size) (Humphries *et al.*, 2004; Angilletta *et al.*, 2010). Mammals at lower trophic levels

(herbivores and invertebrate consumers) tend to exhibit higher ME_{CRB}. These species tend to have lower

348   BMR (Khaliq *et al.*, 2014, 2015) and their food sources may be more consistently available.

350   Lower mass-specific rates of heat production and heat loss (conductance) and smaller surface area to

volume ratios favor larger body sizes in colder environments (i.e., Bergmann's hypothesis, Ashton *et al.*,

352   2000). Regardless, birds' and mammals' body sizes are diverse across climates (Khaliq *et al.*, 2014;

Fristoe *et al.*, 2015). An analysis of regression residuals suggests that adaptations to cold environments

354   in birds and mammals results in increased BMR and reduced conductance (Fristoe *et al.*, 2015). Our

analysis suggests that greater values of ME_{CRB} (perhaps associated with selection for higher M_{sum}) enable

356   small birds and mammals to inhabit cooler environments. Birds from cold climates tend to exhibit

higher M_{sum} (Stager *et al.*, 2015). We identify traits (small body size, use of torpor or hibernation, diet)

358   that may enable the elevated ME_{CRB}.

360   We omit analysis of warm range boundaries because we estimated that 61% and 45% of mammal and

bird species with unconstrained warm range boundaries, respectively, do not experience T_{max} values

362   exceeding their T_{uc}. We note that these values are likely an overestimate because they do not account

for heat associated with solar radiation or heat extremes, but they do suggest a greater viability for

364   using metabolic constraints to project cold range boundaries. Our estimates of metabolic expansibility at

the warm range boundry (for species with $T_{max} > T_{uc}$, following methodology for ME_{CRB}) approximate 1,

366   highlighting the physiological challenges of heat dissipation (Weathers, 1981). At warm range

boundaries, the capacity for evaporative cooling may be more limiting than the associated metabolic

368   costs and minimal endogenous heating is favored (Tieleman & Williams, 2000; McKechnie et al., 2016b).

Evaporative cooling poses a risk of dehydration in response to short term heat stress (McKechnie et al.,

370   2012) and presents a challenge for longer term water balances (Kearney et al., 2016). Additionally,

other biotic factors such as species interactions and resource or habitat constraints often constrain

372   warm range boundaries (Sexton et al., 2009).

374   The observation that many species do not currently face metabolic constraints at their warm range

boundaries suggests that direct temperature effects on metabolism resulting from climate change may

376   predominately expand cold range boundaries rather than contract warm range boundaries. However,

the increase in extreme heat events associated with climate change will likely result in range

378   contractions via thermal stress (McKechnie & Wolf, 2009; Buckley & Huey, 2016). Range contractions at

warm range boundaries may primarily result from indirect effects (e.g., species' interactions), which

380   often predominate in climate change responses (Tylianakis et al., 2008; Walther, 2010).

382   Assuming species follow thermal isoclines due to metabolic constraints, we project that species will shift

their cold range boundaries poleward by an average of 3.9° latitude with numerous species shifting by 6°

384   (75% quantile). Our analyses suggest that hibernation and torpor are important determinants of cold

range boundaries. Climate change will also likely alter the energetics of hibernation, which may amplify

386   poleward range shifts (Humphries et al., 2002). Many bird and mammal species rely on seasonal

migration to obtain resources to meet seasonal energetic demands; considering the costs and benefits

388   of such movements will be important to forecasting responses to climate change among migratory birds

and mammals (which we excluded from our analysis) (Robinson *et al.*, 2009). Shifting activity times may

390   also function to modify estimates of range shifts (Levy *et al.*, 2012).

392   Our analysis of a taxonomically and geographically diverse dataset suggests that metabolic constraints

provide a viable mechanism for projecting the poleward range boundaries of endotherms. We hold that

394   the Scholander-Irving model we employ provides a useful approximation of metabolism, but highlight

several considerations that may improve upon the analyses. We estimate metabolic costs assuming

396   homeothermy, but accumulating data suggest that endotherms represent a continuum of heterothermy

(Boyles *et al.*, 2013). Consideration of the occurrence of torpor/hibernation in the present study likely

398   only partially accounted for deviations from thermoregulation due to T_b variation. Many endotherms

seasonally acclimatize their insulation, behavior, and physiology (Boyles *et al.*, 2011; Bozinovic *et al.*,

400   2011). Some metabolic estimates in our database are specific to the cold season, but we did not fully

account for acclimatization. A comparison of BMR and field metabolic rates (FMR) for small mammals

402   failed to find support for intrinsic limitations on metabolism and low FMRs in very cold climates

indicated acclimatization including behavioral avoidance (Humphries *et al.*, 2005). Over longer time

404   periods, adaptation may alter morphology or metabolic constraints (Boyles *et al.*, 2011). Behavioral

strategies for buffering cold include sheltering, huddling, basking, and microclimate selection (Angilletta

406   *et al.*, 2010). Despite these complications, metabolic constraints provide an initial step towards

generalizable and mechanistic projections of endotherm responses to climate change.

408

414

Data accessibility

416   Data and scripts will be available from a repository upon publication. Data and scripts for the analysis are currently available at github.com/lbuckley/tnz. Data are temporally uploaded as an appendix.

418

Biosketch

420   The research team is interested in the broad scale implications of physiology. The team integrates expertise in bird physiology (Swanson), bird and mammal macroecology (Khaliq and Hof), and energetic

422   modelling (Buckley).

424   **Supporting Information**

Appendix S1. Phylogenetic analysis.

426   Appendix S2. Data description.

Appendix S3. Data.

428   Table S1. Regression model results.

Table S2. Summary of data quality.

430   Table S3. Regression model results for live trapped animals.

Figure S1. Comparison of range edge temperature metrics.

432   Figure S2. Metabolic expansibility at the warm range edge.

Figure S3. Phylogenetic conservatism of metabolic expansibility and mass.

434   Figure S4. Range projections using CCSM4 climate projections.

Figure S5-S8. Range projections for all species.

436

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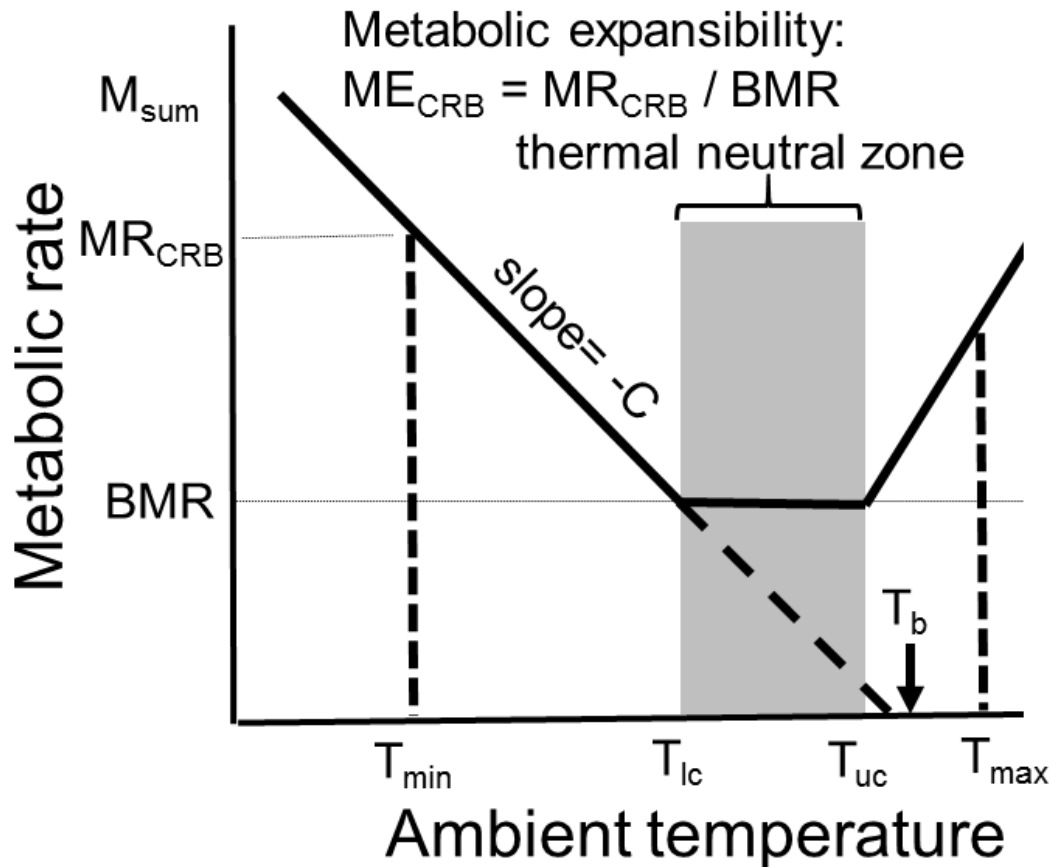
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568   **Figure 1**. How ambient temperature governs metabolic rate. The thermal neutral zone [bounded by lower (T_{lc}) and upper (T_{uc}) critical temperatures] is the range of temperatures over which endotherms
570   are able to maintain their basal metabolic rate (BMR). We use the minimum (T_{min}) and maximum (T_{max}) ambient temperatures across a species' range to estimate sustained metabolic rate at the range
572   boundary (MR_{CRB}). We calculate metabolic expansibility (ME_{CRB}) as MR_{CRB}/BMR and depict maximum metabolic capacity (M_{sum}). Thermal conductance (C) is calculated as the slope of the line terminating at
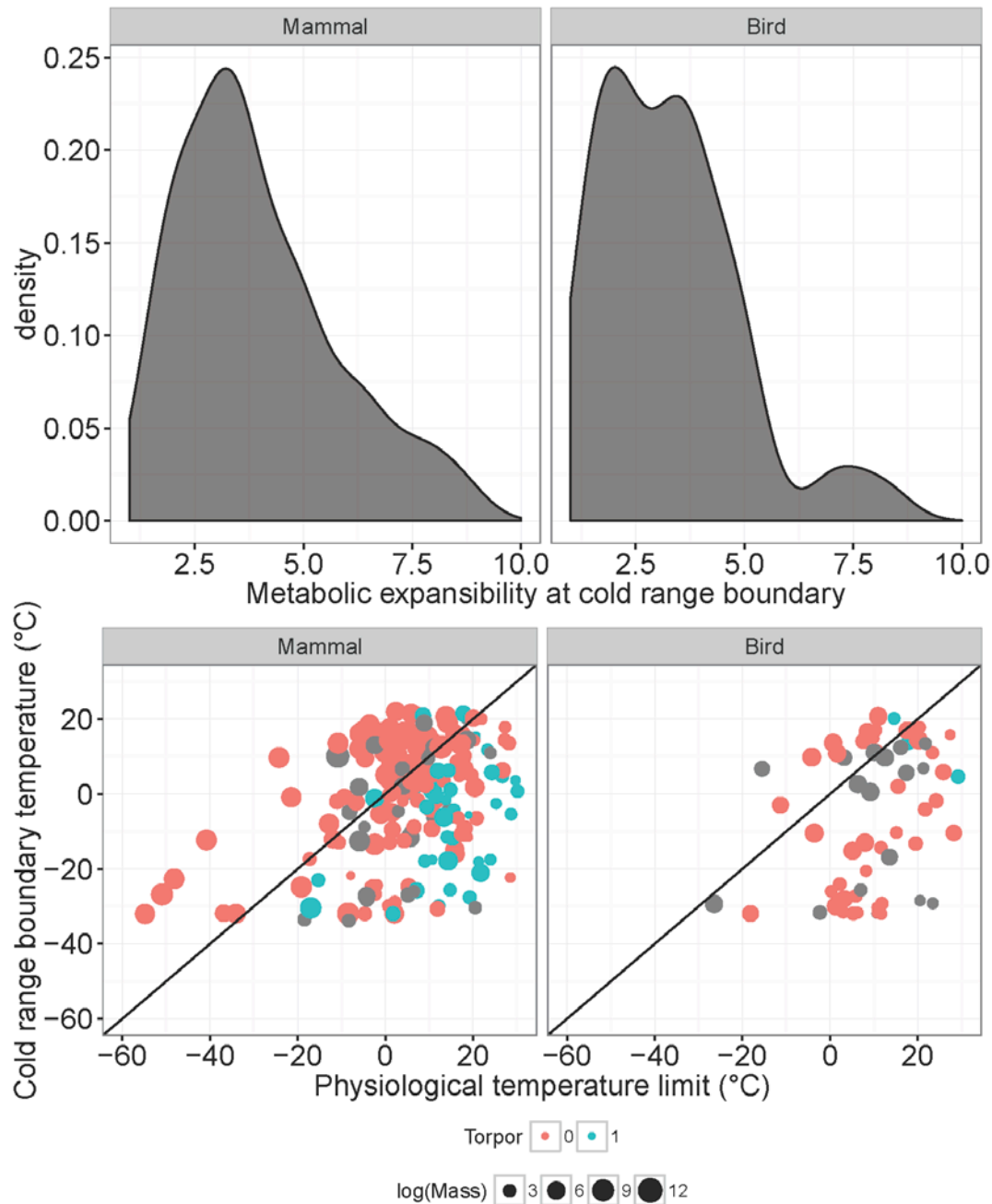574   body temperature (T_b).

576

Figure 2. The density distribution of metabolic expansibility, ME_{CRB} (the factor by which metabolic rate at the cold range edge is elevated over basal metabolic rate) peaks at similar values for birds and mammals (a). We examine interspecific variation in ME_{CRB} by (b) plotting the physiological temperature limit predicted by assuming the mode of ME_{CRB} and the observed temperatures at the cold range boundaries. Mammals and birds that are small (symbol size) and use torpor or hibernation (color, 1=use, gray=no data) tend to be found in environments colder than predicted assuming the mode ME_{CRB} (i.e., they have higher ME_{CRB}).
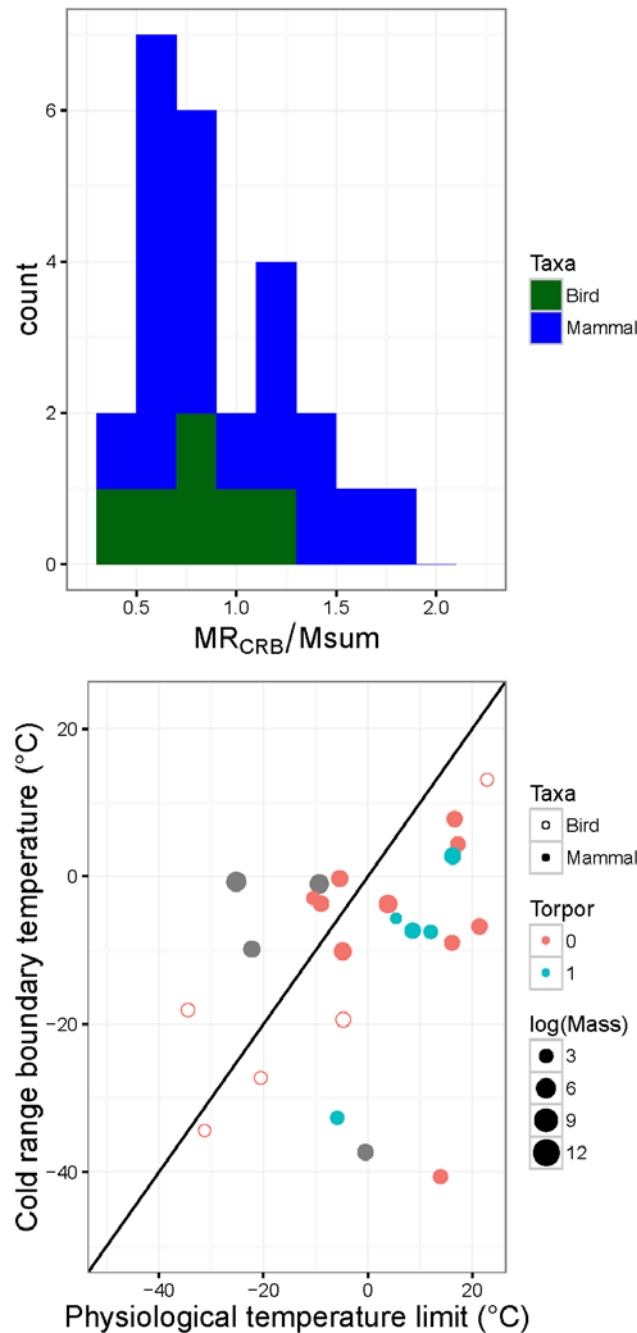
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Figure 3. A histogram (a) of the ratio of maximum metabolic capacity (M_{sum}) to estimated metabolic rate
588   at the cold range boundary (MR_{CRB}) suggests the high energetic demands of thermoregulation. We
examine interspecific variation in the ratio (MR_{CRB} / M_{sum}) by plotting the observed temperatures at the
590   cold range boundaries against the physiological temperature limit corresponding to MR_{CRB} = 0.7 M_{sum} (b).
We depict mammals (filled circles) and birds (hollow circles), mass (symbol size), and use of torpor or
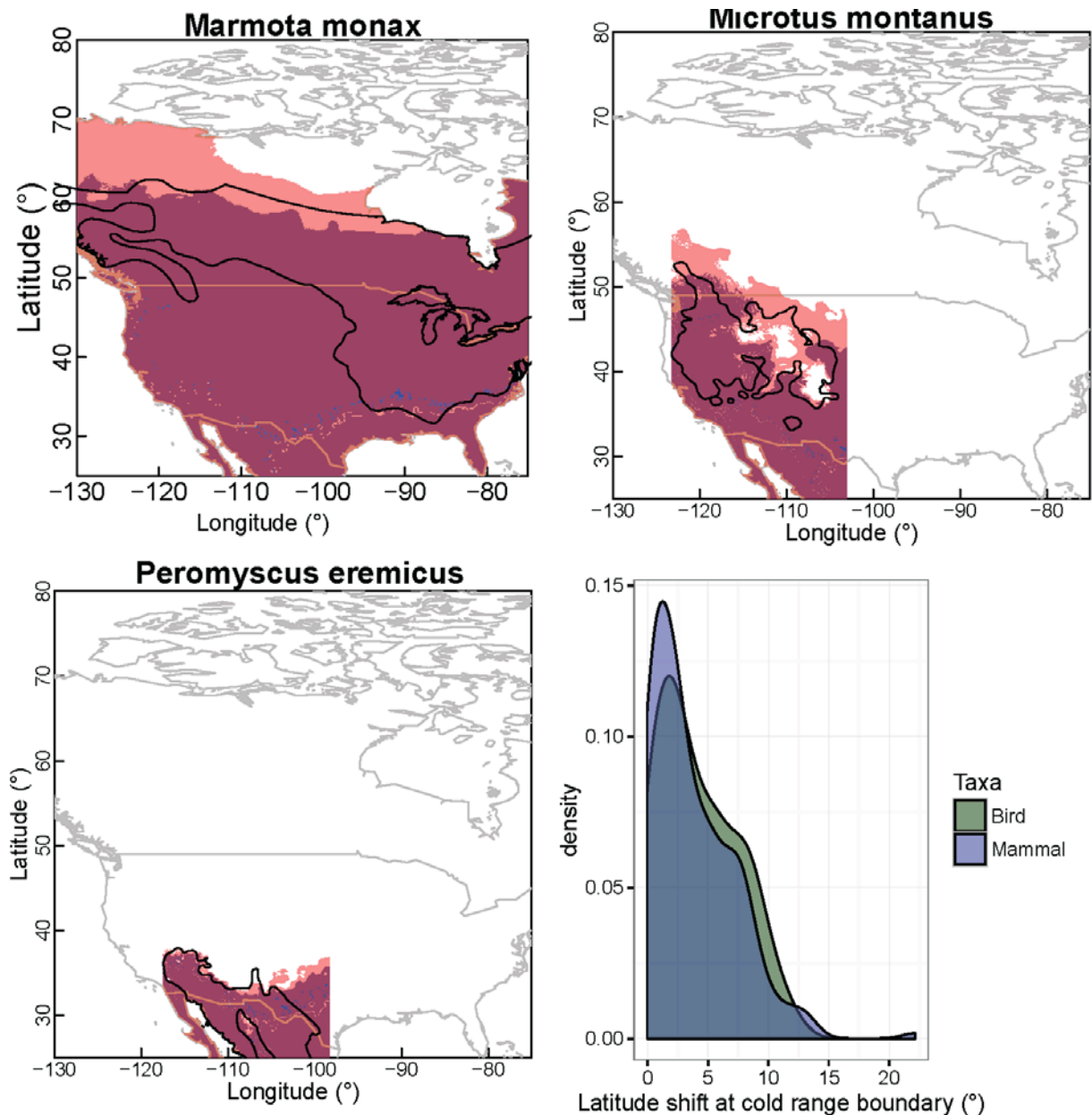592   hibernation (color, 1 indicates use).

Figure 4. We depict observed cold range boundaries (black polygons: IUCN range maps) and those projected based on metabolic constraints for exemplar North American rodents in current (blue: 1950-2000) and predicted future (red: 2061-2080 from HadGEM2-AO model) climates (a – c). Purple shading indicates portions of the projected range occupancy that persists through climate warming. We note few areas of range contraction (blue). The species differ in the extent of their current distribution and the projected range expansion as a result of climate change (a, *Marmota monax*, groundhog; b, *Microtus montanus*, montane vole; and c, *Peromyscus eremicus*, cactus mouse). Projected based on metabolic constraints indicate that the majority of mammals (purple) and birds (green) will shift their cold range boundary modestly poleward through climate changes (d). However, numerous species are projected to shift their cold range boundary poleward by 10° latitude and some species are projected to shift by as much as 22°.