RESEARCH ARTICLE

Functional Ecology — BRITISH ECOLOGICAL SOCIETY

Mass-independent maximal metabolic rate predicts geographic range size of placental mammals

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Abstract

1. Understanding the mechanisms driving geographic range sizes of species is a central issue in ecology, but remarkably few rules link physiology with the distributions of species. Maximal metabolic rate (MMR) during exercise is an important measure of physiological performance. It sets an upper limit to sustained activity and locomotor capacity, so MMR may influence ability to migrate, disperse and maintain population connectivity. Using both conventional ordinary least squares (OLS) analyses and phylogenetically generalized least squares (PGLS), we tested whether MMR helps explain geographic range size in 51 species of placental mammals.

2. Log body mass alone (OLS r^2 = .074, p = .053; PGLS r^2 = .016, p = .373) and log MMR alone (OLS r^2 = .140, p = .007; PGLS r^2 = .061, p = .081) were weak predictors of log range size.

3. However, multiple regression of log body mass and log MMR accounted for over half of the variation in log range size (OLS R^2 = .527, p < .001). The relationship was also strong after correcting for the phylogenetic non-independence (PGLS R^2 = .417, p < .001).

4. In analyses restricted to rodents (34 species), neither log body mass alone (OLS r^2 = .004, p = .720; PGLS r^2 = .003, p = .77) nor log MMR alone was useful in predicting log geographic range size (OLS r^2 = .008, p = .626; PGLS r^2 = .046, p = .225), but multiple regressions of log body mass and log MMR accounted for roughly a third to a half of the variation in log range size (OLS R^2 = .443, p < .001, PGLS R^2 = .381, p < .001).

5. Mass-independent MMR is a strong predictor of mass-independent geographic range size in placental mammals. The ability of body mass and MMR to explain nearly 50% of the variation in the geographic ranges of mammals is surprising and powerful, particularly when neither variable alone is strongly predictive.

6. A better understanding of MMR during exercise may be important to understanding the limits of geographic ranges of mammals, and perhaps other animal groups.

KEYWORDS
aerobic capacity, biogeography, energetics, macrophysiology, MMR, VO$_2$max

1 | INTRODUCTION

Species vary enormously in geographic range size, from salamanders that occupy a single mountain peak (e.g. *Plethodon neomexicanus*), to mammals and birds whose ranges include major parts of several continents (e.g. *Canis lupus* and *Tyto alba*). While environmental variables are often invoked as delimiters of geographic ranges (Brown, Stevens, & Kaufman, 1996; McNab, 2002; Ohlemuller et al., 2008; Pigot, Owens, & Orme, 2010; Root, 1988), comparatively little is known about how physiological capacities (e.g. thermal tolerances or metabolic rates) affect geographic range sizes (Bozinovic, Calosi, & Spicer, 2011; Bozinovic & Rosenmann, 1989; Rezende, Bozinovic, & Garland, 2004; Swanson & Bozinovic, 2011). Despite more than a century of study, biologists have discovered few rules that link physiological characteristics of species with their geographic distributions (Lomolino, Riddle, Whittaker, & Brown, 2010). Until recently, progress has been limited because ecophysiologists and biogeographers have seldom collaborated to explore broad scale geographic patterns in physiology (Chown, Gaston, & Robinson, 2004; Gaston et al., 2009; Lovegrove, 2000). But as researchers strive to incorporate physiological mechanisms into species distribution models (Kearney & Porter, 2009), the prospect is for rapid progress.

Recent decades have seen intense interest in understanding how energy metabolism impacts ecology (Brown, Gillooly, Allen, Savage, & West, 2004). Still much remains to be learned about how organismal capacities and tolerances influence survival, reproduction, foraging, dispersal and ultimately species distributions (Araujo et al., 2013; Bozinovic, Ferri-Yanez, Naya, Araujo, & Naya, 2014; Lyons, Shepard, & Kozak, 2016). Maximal metabolic rate (MMR) during exercise may be a crucial determinant of species distributions because MMR sets an upper limit for sustaining vigorous activity, such as locomotion. Hence, MMR may affect the ability to widely forage, to maintain large territories, to migrate and to disperse, thereby influencing population connectivity (and metapopulation dynamics) and ultimately, geographic ranges. We tested whether MMR predicts geographic range size of placental (eutherian) mammalian species. We report what may be a new macrophysiological insight: in mammals, geographic range size is strongly correlated with mass-independent MMR in placental mammals.

2 | MATERIALS AND METHODS

We analysed data for maximal metabolic rates, geographic range sizes and body sizes of 51 species of placental mammals: six artiodactyls, 11 carnivores and 34 rodents. We gathered published data on MMR of mammals from an extensive literature search. Our literature search strove to capture all the data on MMR for terrestrial placental mammals. Additional MMR data exist for at least nine marsupial (metatherian) species and one monotreme (prototherian). However, many of these species have suffered extensive range contractions due to anthropogenic activities (Van Dyck & Strahan, 2008), which could limit our ability to uncover underlying ecological rules. Others possessed metabolic rates that were outliers compared to the overall mammal dataset. Hence, we restricted our analysis to only placental mammals.

We checked all MMR and body mass data back to the original sources with the consequence that actual values used in our analyses sometimes differ from those reported in other reviews (Dlugosz et al., 2013; Koteja, 1987; Weibel, Bacigalupe, Schmitt, & Hoppeler, 2004; see supporting information for MMR and mass data). Note the taxonomic names for some species have changed since the original publication, and we report the updated names. In some cases there were measurements under a variety of conditions or more than one original data source for a species, so it was necessary to choose which MMR and mass to use. With one exception (see below), we chose the highest MMR reported for a particular study. When more than one original source reported MMR data for the same species, we selected the higher MMR relative to body mass as follows. Firstly, choosing which MMR was higher for a given mass required an allometric calculation because, due to the strong effect of mass on MMR, MMR of animals that differ in mass cannot be compared directly. To adjust for mass differences, we calculated the ratio of the observed MMR to MMR predicted by assuming that MMR scaled with mass 0.84 (Dlugosz et al., 2013). A higher ratio indicates that an animal's MMR is higher compared to its mass than a lower ratio indicates. For example both Macmillen and Hinds (1992) and Dlugosz et al. (2013) measured MMR of *Dipodomys ordii*. The ratio of observed MMR to the allometrically predicted MMR was higher for the animals studied by Macmillen and Hinds (1992) so we used the MMR data from that paper instead of the data from Dlugosz et al. (2013). The magnitude of these differences was small so the effect of these choices was trivial in the overall outcomes we report. One exception is that in the case of the lion *Panthera leo* we used data for the larger individuals that were measured, not the more commonly reported data for the animals when they were younger and smaller. We did this to use the mass data that were closer to the adult mass of the species. We excluded data for (1) domesticated and laboratory species and (2) species that primarily locomote by swimming or flying. In the former case, domesticated species have likely undergone either deliberate or unintentional selection that may have influenced their MMRs and establishing a natural geographic range for these taxa is also problematic. In the latter case, MMR is likely to differ with locomotor mode so we only used data for MMR elicited via running. We also excluded data for the pronghorn *Antilocapra americana*, because that species was a very large statistical outlier (studentized residual > |3|) in analyses of both log MMR predicted from log mass and in a multiple regression predicting log range size from log mass and log MMR.

We also analysed the data for rodents alone. This monophyletic group has smaller body size and generally lacks the cursorial specializations of artiodactyls and carnivores. In analyses with rodents alone, the capybara *Hydrochoerus hydrochaeris* was a large statistical outlier (studentized residual > |3|) in the regression predicting log range from log mass and log MMR. For simplicity in comparing

across models, we excluded both the pronghorn and capybara from all analyses, yielding a final dataset of 51 species of placental mammals of which 34 species were rodents.

We obtained geographic range data from the IUCN Global Mammal Assessment (http://www.iucnredlist.org/initiatives/mammals/description), which contains estimates of the current geographic ranges of the world's mammals provided in the Global Mammal Assessment (Schipper et al., 2008). We used ARC GIS v9 (ESRI) to re-project the geographic range of each species onto an equal area projection, and then we recorded the total area of each species' range.

We performed ordinary least squares (OLS) regressions on the log transformed MMR, body mass and range size data using SAS version 9.3 (SAS Institute). We used regressions to test the relationship between log range size and (1) log body mass alone, (2) log MMR alone and (3) log body mass and log MMR. We also ran models including a log MMR by log body interaction. The interaction term was not significant for all placental mammals (p = .28) or for rodents alone (p = .91). We log transformed the data to improve homogeneity of the variance of residuals in regressions and so that the transformed relationship better approximated linearity. We tested residuals from these analyses for deviations from normality (Shapiro Wilk test), and we tested for misspecification (including heteroscedasticity) with the 1st and 2nd moment specification test in SAS Proc Reg.

Because these data come from three ecologically and morphologically distinct mammal clades (rodents, artiodactyls and carnivores), and because taxa often share traits due to common ancestry, we used phylogenetic generalized least squares (PGLS) to analyse the data accounting for phylogeny (Revell, 2010). We used the "CAPER" package v05.20 (Revell, 2012) in v3.4.0 (R Core Team, 2017) for PGLS analyses, except see below for methods relating to partial R-squares in PGLS. We constructed a tree (and branch lengths) with cytochrome b sequence (mtDNA) data from GenBank, but resolved polytomies and corrected imperfect relationships based on those established in the literature (details of phylogeny construction, phylogenetic tree and references in online supporting materials). In parallel with the OLS analyses, we ran PGLS analyses to test the relationship between log range size and (1) log body mass alone, (2) log MMR alone and (3) log body mass and log MMR. We also ran PGLS models including a log MMR by log body mass interaction. The interaction term was not significant for all placental mammals (p = .37) or for rodents alone (p = .85).

There are complexities associated with the calculation and interpretation of R^2 in generalized least squares (GLS) models (Buse, 1973; Ives, 2017; Symonds & Blomberg, 2014). Accordingly for PGLS models, although we report the overall model R^2 from caper, we recognize that the interpretation of such R^2 may differ from the R^2 for OLS models. In addition, insofar as we know the methods and software for calculating partial or semi-partial R^2 are not well-established for PGLS. Hence to visualize the size-corrected relationship and provide an indication of the magnitude of the mass-adjusted (partial) effect of MMR in the PGLS multiple regression, we took two approaches. First, to visualize the data, we calculated the residuals from PGLS regressions of (1) log range with log mass and

(2) log MMR with log mass, following the methodology described for size-correction in Revell (2009). Then we plotted the residuals as deviations of the observations minus the predicted values from the PGLS fitted regressions (Figure 1).

Second, for the PGLS multiple regression, we calculated the partial R^2 for log MMR (adjusted for mass) following Ives (2017). Ives (2017) suggested three alternative forms for partial R^2, and he made the point that different experts might not agree on which of them is the most intuitive, so we report all three of the partial R^2 calculations he suggested. These partial R^2 were calculated using the R code associated with Ives (2017).

3 | RESULTS

### 3.1 | Placental mammals – conventional analyses

For the 51 species of placental mammals, log body mass alone was a relatively weak, and borderline significant predictor of log geographic range size (β = 0.186, r^2 = .074, p = .053; Figure 2). Log MMR alone was a somewhat stronger predictor of log geographic range size (β = 0.293, r^2 = .140, p = .007; Figure 2). As would be expected from the strong allometric scaling of metabolic rate, log body mass and log MMR were highly correlated (β = 0.862, r^2 = .976, p < .001; Figure 2). The residuals from this regression deviated significantly from normality, but a robust regression (SAS Proc Robustreg) confirmed a highly significant correlation with a similar slope (β = 0.837, r^2 = .685, p < .001).

Not only were log MMR alone and log body mass alone significant predictors of log range size, jointly the two variables explained about half the of the variance in log range size (R^2 = .527, p < .001). In this multiple regression log MMR (β = 3.39, p < .001) and log mass (β = −2.73, p < .001) were both significant predictors of log geographic range size.

Because multiple regression adjusts each predictor for other predictors in the regression, the significance of log MMR when log mass is included in the regression indicates that residual log MMR, (i.e. mass-independent MMR; Hayes & Shonkwiler, 1996), correlates with the mass-independent geographic range size of mammals. The squared partial correlation between log MMR and log geographic range shows that after accounting for the effects of log body mass on log MMR and on log geographic range size, log MMR accounts for nearly half the variation in log geographic range size (partial r^2 = .489, Figure 1). The squared semi-partial r^2 = .453 indicates that the mass-independent log MMR accounts for a similar amount of variation in log range size. The corresponding values for log mass are partial r^2 = .450, semi-partial r^2 = .387.

3.2 | Placental mammals – phylogenetic analyses

As for the OLS analyses, for the PGLS analyses log body mass alone was not a significant predictor of log geographic range size (β = 0.115, r^2 = .016, p = .373, λ = 0.576; Figure 2). Log MMR alone was a marginally stronger predictor of log geographic range size,
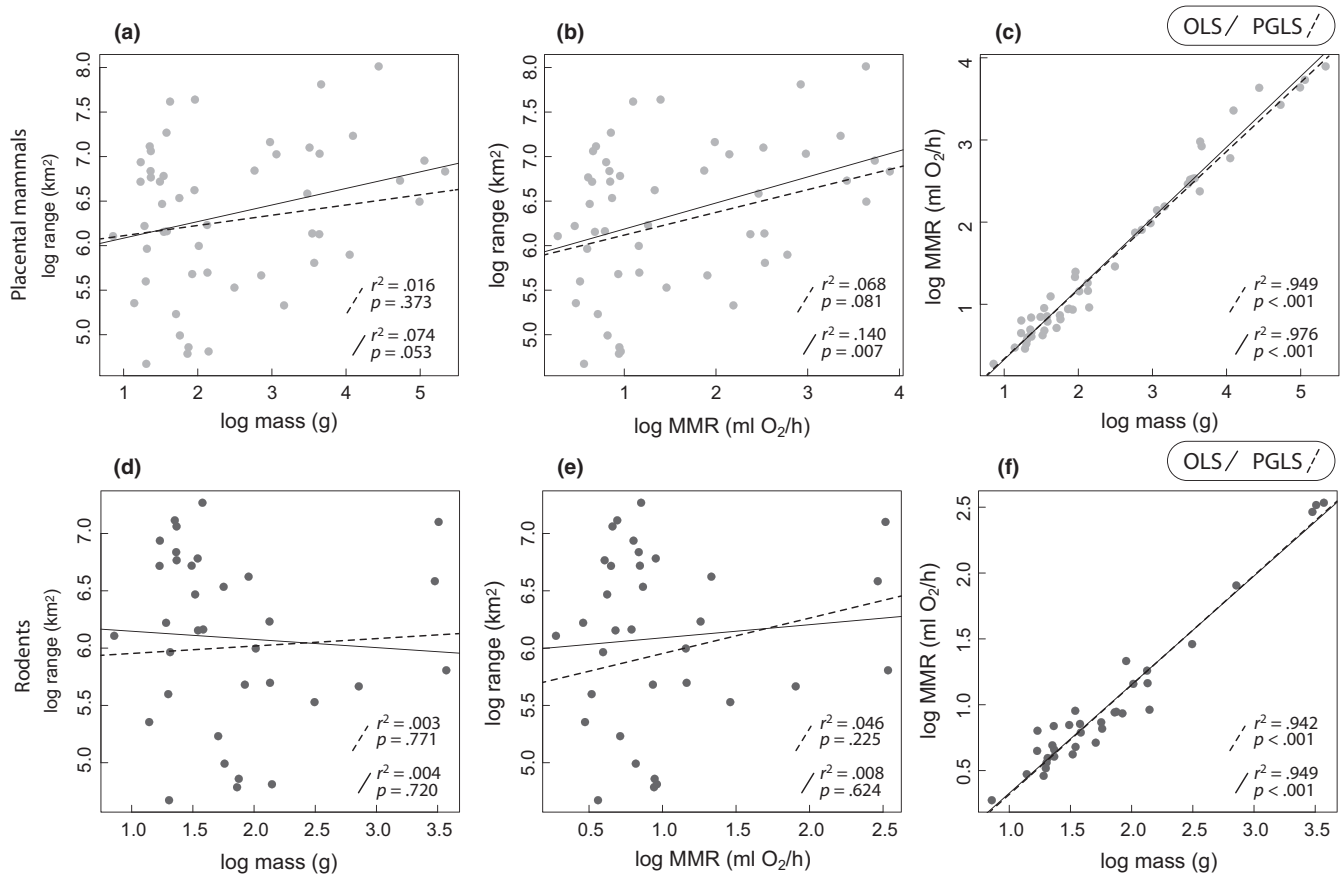
FIGURE 1 Bivariate plots for placental mammals (top panels) and rodents only (bottom panels). Each panel contains ordinary least squares (OLS) and phylogenetically generalized least squares results plotted against the raw data. From left to right plots are log geographic range size vs. log body mass (a and d), log geographic range size vs. log maximal metabolic rate (MMR) (b and e) and log MMR vs. log body mass (c and f)

but still not significant ($\beta = 0.259$, $r^2 = .061$, $p = .081$, $\lambda = 0.584$; Figure 2). However, log body mass and log MMR were again highly correlated ($\beta = 0.847$, $r^2 = .949$, $p < .001$, $\lambda = 0.788$; Figure 2).

Despite the fact that log MMR alone and log body mass alone were not significant predictors of log range size, collectively these two variables were good predictors of log geographic range size ($R^2 = .417$, $p < .001$, $\lambda = 0.217$). In this PGLS multiple regression, log MMR ($\beta = 3.05$, $p < .001$) and log mass ($\beta = -2.46$, $p < .001$) were both significant predictors of log geographic range size. Overall, the conclusions from the PGLS analyses and the OLS analyses were highly consistent (Figures 1 and 2).

3.3 | Rodents only – conventional analyses

For the 34 species of rodents, log body mass alone was not a significant predictor of log geographic range size ($\beta = -0.071$, $r^2 = .004$, $p = .720$; Figure 2), and log MMR alone was not a significant predictor of log geographic range size ($\beta = 0.115$, $r^2 = .008$, $p = .624$; Figure 2). As would be expected from the strong allometric scaling of metabolic rate, log body mass and log MMR were highly correlated ($\beta = 0.824$, $r^2 = .949$, $p < .001$ Figure 2).

While neither log MMR alone nor log body mass alone were significant predictors of log range size, the two variables jointly explained a substantial fraction of the variance in log range size ($R^2 = .443$, $p < .001$). In the multiple regression log MMR ($\beta = 3.88$, $p < .001$) and log mass ($\beta = -3.27$, $p < .001$) were both significant predictors of log geographic range size.

For rodents only, the squared partial correlation between log MMR and log geographic range shows that after accounting for the effects of log body mass on log MMR and on log geographic range size, log MMR accounts for nearly half the variation in log geographic range size (partial $r^2 = .441$; Figure 1). The squared semi-partial $r^2 = .439$ indicates that the mass-independent log MMR accounts for a similar amount of variation in log range size. The corresponding values for log mass are partial $r^2 = .439$, semi-partial $r^2 = .436$.

3.4 | Rodents only – phylogenetic analyses

As for the rodent only OLS analyses, for the PGLS analyses log body mass alone was not a significant predictor of log geographic range size ($\beta = 0.065$, $r^2 = .003$, $p = .77$, $\lambda = 0.435$; Figure 2). Log
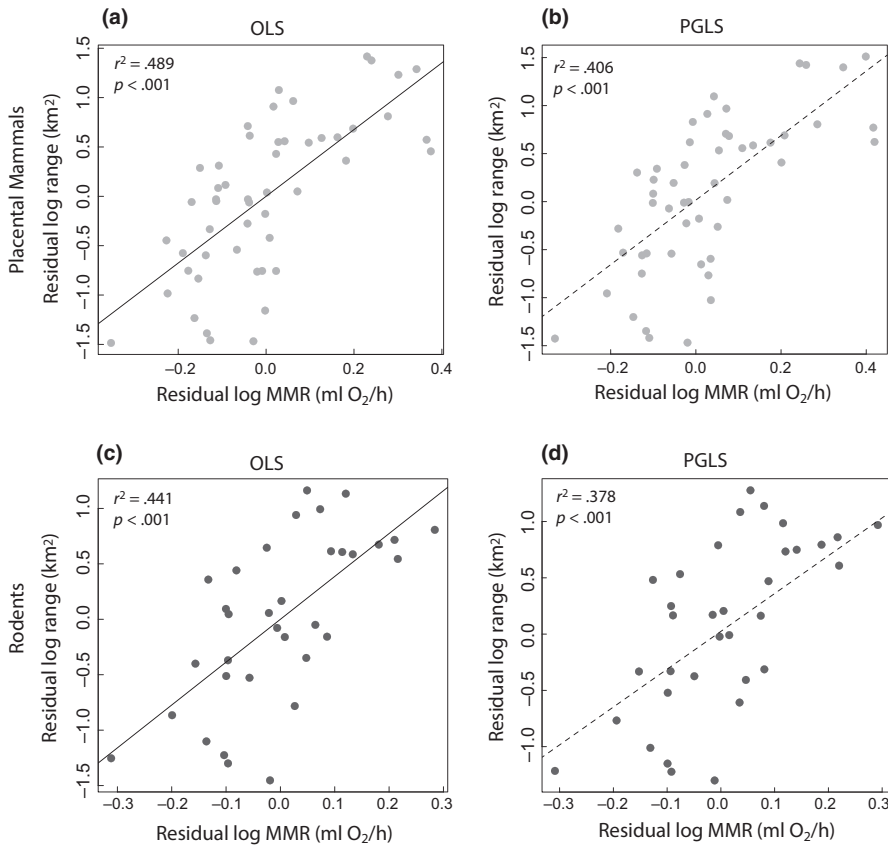
FIGURE 2 Residual log geographic range size from regression on log body mass plotted against residual maximal metabolic rate (MMR) from regression on log body mass. For ordinary least squares (OLS) regressions, these residual plots depict the partial correlations of log range with log MMR, both adjusted for log mass. For phylogenetically generalized least squares (PGLS) regression, methods for partial r^2 are not well-established and there is more than one possible partial r^2. The PGLS residuals are plotted only as a visualization aid. The partial r^2s for the PGLS analyses were calculated following Ives (2017). The PGLS partial r^2s for MMR were $r^2_{ls} = .254$, $r^2_{ce} = .258$, $r^2_{lr} = .328 =$ for placental mammals and $r^2_{ls} = .300$, $r^2_{ce} = .315$, $r^2_{lr} = .338$ for rodents only. The panels are (a) OLS residuals for placental mammals; (b) PGLS residuals for placental mammals; (c) OLS residuals for rodents only; (d) PGLS residuals for rodents only

MMR alone was a slightly stronger predictor of log geographic range size, but still not significant ($\beta = 0.311$, $r^2 = .046$, $p = .225$, $\lambda = 0.468$; Figure 2). However, log body mass and log MMR were again highly correlated ($\beta = 0.830$, $r^2 = .942$, $p < .001$, $\lambda = 0.167$; Figure 2).

Despite the fact that log MMR alone and log body mass alone were not significant predictors of log range size, collectively these two variables were good predictors of log geographic range size ($R^2 = .381$, $p < .001$, $\lambda = 0.255$). In this PGLS multiple regression, log MMR ($\beta = 3.38$, $p < .001$) and log mass ($\beta = -2.78$, $p < .001$) were both significant predictors of log geographic range size. Overall, the conclusions from the PGLS analyses and the OLS analyses were highly consistent (Figures 1 and 2).

4 | DISCUSSION

We provide novel insight into the determinants of geographic range size in placental mammals. Species with high mass-independent MMR (i.e. residual MMRs that were positive) possess greater geographic ranges than species with low mass-independent MMR. This intriguing finding suggests that mass-independent MMR is not just an important physiological variable, but a variable with major consequences for ecological and biogeographic patterns and processes. What might account for this relationship? Several physiological factors contribute to aerobic endurance, and MMR is among the most important of those factors (Joyner & Coyle, 2008; Levine,

2008). Across mammals, athletic species have higher MMR for their mass (Weibel et al., 2004). In addition, artificial selection experiments indicate that both mice and rats with high MMR for their mass have greater endurance (Meek, Lonquich, Hannon, & Garland, 2009; Wisloff et al., 2005), and in *Peromyscus californicus*, mass-independent MMR correlated with endurance (Andrew, Saltzman, Chappell, & Garland, 2016). While studies on more species are warranted, and interspecific comparative studies on endurance (and its possible link to MMR) are sorely needed, it seems quite plausible that both MMR and mass-independent MMR are correlated with endurance in mammals. If mass-independent MMR affects activity and locomotion, then high mass-independent MMR might also enable species to disperse and/or migrate greater distances, thereby enabling them to occupy larger distributional ranges (Baselga, Lobo, Svenning, Aragon, & Araujo, 2012; Hein, Hou, & Gillooly, 2012; Jetz, Freckleton, & McKechnie, 2008). Via effects on movement, high MMR might also influence the ability of species to maintain genetic connectivity through landscape-level metapopulation dynamics. Furthermore, because geographic ranges are not static over time (Gaston, 2009), species with high mass-independent MMRs might have larger geographic range sizes because they are better able to colonize newly available habitat and avoid range contractions (Anderson et al., 2009).

Particularly for birds and mammals, most previous attempts to link geographic distributions to physiology have focused on thermal tolerances or closely related energetic traits, such as metabolic rate, ability to generate heat, or, for fossorial mammals, ability to

dissipate heat (Bozinovic et al., 2011; McNab, 1979, 2002). For example the so-called climatic variability hypothesis suggests that species inhabiting environments with greater climatic variation should have broader thermal tolerances (or else they could not survive there). Because climatic variation could be correlated with latitude, this greater variation in climate could lead to correlations between physiological tolerances and latitude (Naya, Spangenberg, Naya, & Bozinovic, 2012), and thereby might underlie other macroecological patterns, such as Rapoport's rule (Bozinovic & Naya, 2015). However, we do not think such associations can explain the striking relationship we found between mass-independent MMR and geographic range size.

We studied MMR elicited by exercise, not thermal tolerances. MMR elicited by cold exposure is clearly related to thermal conditions, but MMR elicited by exercise is not. Cold acclimation and seasonally colder thermal environments both lead to substantially higher MMR elicited by cold exposure (Chappell & Hammond, 2004; Hayes, 1989; Rezende et al., 2004), but cold exposure does not have that same effect on MMR elicited by exercise (Chappell & Hammond, 2004; Kristan & Hammond, 2004). Hence our findings are novel because we are not proposing an explanation based on thermal tolerance. Rather we propose that among species of placental mammals, a higher exercise capacity appears to enable those species to have a larger geographic range.

While high MMR is associated with larger geographic range size in this study, curiously, higher MMR was not associated with larger home-range size in mammals (Albuquerque, Sanchez, & Garland, 2015). One possible explanation for that finding is that the home-range data contained too much measurement error to detect a relationship (Albuquerque et al., 2015). The fact that mass-independent MMR influences geographic range size but not home-range size is intriguing, and it suggests that further investigation into the mechanisms leading to these associations might be highly informative. In addition it would be valuable to determine whether similar patterns occur in other clades, including ectotherms.

The association between MMR and geographic range size also has potential conservation implications. In mammals, larger geographic ranges are associated with lower extinction risk (Cardillo et al., 2008). Numerous studies have explored the relationships between geographic range size, energetics (e.g. trophic level) and extinction risk. For example in mammals the primary productivity required to support an individual varied significantly across the Red List of Threatened Species categories of the International Union for the Conservation of Nature (Boyer & Jetz, 2012). Unsurprisingly, mammals that were endangered tended to have smaller range sizes than species that were not threatened. In addition, it has recently been proposed that both small and large mammals with high, mass-independent, basal metabolic rates may be at greater risk for extinction (Agosta, Bernardo, Ceballos, & Steele, 2013). Our analyses suggest yet another possibility, if high mass-independent MMR leads to larger range size, and if larger range sizes reduce extinction risk, then high mass-independent MMR might be associated with a lower extinction risk.

Previous work looking at energetic associations between metabolic rates and biogeography has almost exclusively focused on BMR, not MMR. Mass-independent BMR (i.e. residual BMR from regression on mass) was correlated ($r^2 = .02$, $p < .001$) with geographic range size for a large ($n = 574$ species) sample of mammals (Agosta et al., 2013). For rodents only, the correlation ($r^2 = .05$, $p < .001$) was a bit higher. By comparison, the predictive power of mass-independent MMR that we found was an order of magnitude higher (semi-partial correlation of mass-independent MMR with geographic ranges size had an $r^2 = .451$ for all mammals, and for rodents only the semi-partial correlation of mass-independent MMR with geographic ranges size had an $r^2 = .435$). Likewise, MMR seems to be more important than BMR for understanding energetic trade-offs with immune function and energetic impacts on growth (Downs, Brown, Wone, Donovan, & Hayes, 2016; Downs et al., 2013). BMR is measured much more frequently than MMR because MMR is much more challenging to measure. Nevertheless, biologists seeking to integrate energetic information into their understanding of ecology should recognize that MMR may be as useful and ecologically relevant to study as BMR.

In the future as we attempt to identify physiological correlates of range size and other ecological variables, it would be useful to consider how representative (i.e. biased or unbiased) our samples may be. Very few species have had their MMR measured while comparatively many more species have had their BMR measured. Neither the species for which BMR have been measured nor those for which MMR have been measured is a random sample of the species of extant mammals. Hence, whatever patterns emerge in studies, such as ours, will need to be revisited as larger and potentially more representative datasets becomes available. Given the challenges inherent in getting animals to locomote at maximal effort while being physiologically monitored, it may be a considerable time before such additional data become available for MMR. While this report is novel with respect to MMR and geographic range size, the relationship between body size and geographic range size has been studied previously (Angielczyk, Burroughs, & Feldman, 2015; Arita, Robinson, & Redford, 1990; Brown et al., 1996; Diniz-Filho, Carvalho, Bini, & Torres, 2005; Gaston & Blackburn, 1996). The distributions of body mass and range size in birds and mammals tends to inhabit triangular spaces(Boyer & Jetz, 2012; Brown & Maurer, 1987) such that animals with high mass are constrained to have a large range size (with a small range size being precluded). In contrast animals with low mass can have diverse ranges sizes, from small to large. More recently (Agosta & Bernardo, 2013) suggested that the smallest size mammals (i.e. those below modal body mass) may also have smaller range size, such that maximum range size, at least for mammals, would be an intermediate value. If true that would result in a modification to the triangular constraint space at lower body sizes. The evidence for at least a roughly triangular range size constraint space is robust (Boyer & Jetz, 2012). Our analyses suggest that whatever constraints may exist on the range size relationship with mass, they are not sufficient to preclude a strong correlation between mass-independent MMR and range size, at least in the sample of mammals we studied.

The weak relationship that we found between log mass and log geographic range size ($r = .27$, $p = .053$) is similar to correlations reported previously for vertebrates. For example the correlation between body mass and geographic range size was weak in (1) 70 species of North American carnivores ($r = .30$, $p = .011$; Diniz-Filho et al., 2005), (2) 100 species of Neotropical forest mammals ($r = .32$, $p < .01$; Arita et al., 1990), (3) 391 species of North American land birds ($r = .08$, $0.05 < p < .10$; Brown et al., 1996) and (4) 148 species of Anseriformes ($r = -.15$, $p > .05$; Gaston & Blackburn, 1996). More recently, Agosta and Bernardo (2013) suggested that for mammals above modal size there was a positive correlation ($r = .22$, $p < .001$) between body mass and geographic range size but for mammals below mean modal size there was a negative correlation $r = -.15$, $p < .001$). Although that study was based on a remarkably comprehensive sample ($n = 3,268$ species) of mammals, and the relationships they observed were highly statistically significant, body mass explained only a small fraction (<5%) of the variation in geographic range size. Overall, these studies suggest that, by itself, body mass is not a strong predictor of geographic range size in endothermic vertebrates.

The scarcity of MMR data for wild mammals might limit its general use for predicting species range size. However, we hope that our analyses will stimulate interest in the influence of MMR and other physiological attributes on the ecology and biogeography of animals. Ideally, physiological ecologists will not only collect new MMR data from a larger sample of taxa, but will also consider incorporating MMR and other physiological data to investigate landscape-level patterns. Despite the scarcity of existing data on MMR for wild mammals, we suggest that mass-independent MMR may have profound ecological consequences. While it will require more extensive sampling before the generality of our results can be supported or refuted, we posit that if the strong association between mass-independent MMR and geographic range size proves general, it might form the basis for a new "macrophysiological rule".

AUTHOR'S CONTRIBUTIONS

J.P.H. conceived the study, collected body size and MMR data from the literature and wrote the manuscript; M.B.A. conceived the study, collected the range size data and contributed to the manuscript; C.R.F. collected the phylogenetic data and contributed to the manuscript; J.P.H. and C.R.F. carried out the statistical analyses. All authors gave approval for publication of the final version and agree to be held accountable for the content herein.

COMPETING INTERESTS

We have no competing interests.

DATA ACCESSIBILITY

Phylogenetic data supporting this article are available at TreeBase S22185. The MMR, mass, and geographic range data are in the supporting materials and are available via Dryad Digital Repository https://doi.org/10.5061/dryad.08c4c (Hayes, Feldman & Araújo, 2018).

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