REVIEW

Heterothermy, body size, and locomotion as ecological predictors of migration in mammals

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ABSTRACT

1. Migration is ubiquitous among animals and has evolved repeatedly and independently. Comparative studies of the evolutionary origins of migration in birds are widespread, but are lacking in mammals. Mammalian species have greater variation in functional traits that may be relevant for migration. Inter-specific variation in migration behaviour is often attributed to mode of locomotion (i.e., running, swimming, flying) and body size, but traits associated with the evolutionary precursor hypothesis, including geographic distribution, habitat, and diet, could also be important predictors of migration in mammals. Furthermore, mammals vary in thermoregulatory strategies and include many

heterothermic species, providing an alternative strategy to avoid seasonal resource depletion.

2. We tested the evolutionary precursor hypothesis for the evolution of migration in mammals and tested predictions linking migration to locomotion, body size, geographic distribution, habitat, diet, and thermoregulation. We compiled a dataset of 722 species from 27 mammalian orders and conducted a series of analyses using phylogenetically informed models.
3. Swimming and flying mammals were more likely to migrate than running mammals, and larger species were more likely to migrate than smaller ones. However, heterothermy was common among small running mammals that were unlikely to migrate. High-latitude swimming and flying mammals were more likely to migrate than high-latitude running mammals (where heterothermy was common), and most migratory running mammals were herbivorous. Running mammals and frugivorous bats with high thermoregulatory scope (greater capacity for heterothermy) were less likely to migrate, while insectivorous bats with high thermoregulatory scope were more likely to migrate.
4. Our results indicate a broad range of factors that influence migration, depending on locomotion, body size, and thermoregulation. Our analysis of migration in mammals provided insight into some of the general rules of migration, and we highlight opportunities for future investigations of exceptions to these rules, ultimately leading to a comprehensive understanding of the evolution of migration.

Key words: body size, evolutionary precursor hypothesis, heterothermy, hibernation, mammals, movement ecology, thermoregulatory scope.

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Text for Graphical Abstract

Migration is a strategy for animals to avoid seasonal resource depletion. Migration is common in animals and studies of migration in birds are widespread. By contrast, there are fewer studies for mammals. In contrast to birds, mammals have three primary modes of locomotion (i.e., running, swimming, flying) and they vary in size by several orders of magnitude, live in varied geographic areas, habitats, and have highly variable diets. Finally, mammalian species vary considerably in their heterothermic ability, i.e., the use of hibernation and torpor to avoid seasonal resource depletion. We compiled a dataset of 722 species from 27 mammalian orders and examine the effects of various behavioural and ecological predictors on migration. Overall, swimming and flying mammals were more likely to migrate than running mammals, and larger species were more likely to migrate than smaller ones. However, heterothermy was common among small running mammals that were unlikely to migrate. High-latitude swimming and flying mammals were more likely to migrate than high-latitude running mammals (where heterothermy was common), and most migratory running mammals were herbivorous. Our results provide insight into some of the general rules of migration and highlight a body-size mediated trade-off between migration and hibernation.

INTRODUCTION

Among the 'grand challenges in migration biology' is the challenge to integrate migration biology across species as well as with other biological disciplines (Bowlin et al. 2010). Migration is a ubiquitous strategy used by a wide diversity of taxa to cope with seasonal and spatial variation in resource availability (McGuire & Fraser 2014). The evolution of migration is highly convergent, and, in many cases, migration has evolved without apparent phylogenetic constraints (Alerstam et al. 2003). In simple terms, migration is expected to evolve when the benefits outweigh the costs. The benefits of migration for animals include taking advantage of seasonal resource availability and avoiding seasonal resource limitation (Fryxell et al. 1988), avoiding disease (Altizer et al. 2011), and evading predation (Furey et al. 2018). Migration is costly in terms of time and energy, and may expose animals to risk of predation or other mortality factors such as extreme weather (Newton 2007). In many systems, migration is energetically demanding, and optimal migration theory suggests minimising energy costs of activity is one of three major selective forces, along with time and predation risk, that are responsible for variation in migration behaviour across individuals and species (Alerstam & Lindström 1990, Hedenström & Alerstam 1997). Energetic demands are especially important to consider among endotherms that maintain high body temperatures under variable environmental conditions (Wikelski et al. 2003). Therefore, the evolution of migration is frequently considered in terms of cost and capacity.

Birds are among the most-well studied migrants, in terms of empirical research output for a wide range of clades (Bauer & Klaassen 2013), as well as hypotheses which explain the evolutionary origins of migration (Rappole et al. 2003, Zink 2011). For instance, the ‘evolutionary precursor hypothesis’ suggests that species that rely on more variable habitats or rely on more variable food sources are more likely to evolve long-distance migration than those exploiting more stable food sources in more stable habitats (Levey & Stiles 1992). Alternatively, the ‘stepping-stone hypothesis’ predicts that migratory species evolved from sedentary ancestors living in seasonal environments (Cox 1985). With multiple hypotheses to consider, several researchers have evaluated these hypotheses and, in some cases, contrasted the predictions of multiple hypotheses within a taxonomic group to determine which is best supported. For example, the evolutionary precursor hypothesis is supported by multiple studies of New World passerines (Levey & Stiles 1992, Chesser & Levey 1998), but a study of birds in the family Motacillidae found better support for the stepping-stone hypothesis (Outlaw & Voelker 2006). With additional study, the evolutionary precursor hypothesis has been refined, yielding the ‘resource variability hypothesis’ (Boyle & Conway 2007). The tradition of developing and testing competing hypotheses has provided insights into the important underlying factors involved in the comparative evolution of migration in birds. However, equivalent hypothesis testing frameworks are lacking for other vertebrate clades.

Compared with birds, the evolution of migration in mammals has received comparatively little research attention. There are several factors (related and not mutually exclusive) which complicate the development of broad hypotheses for the evolution of migration in mammals: mode of locomotion, body size, and thermoregulatory capacity. While most birds move via powered flight, mammals use three major forms of locomotion: running, flying, or swimming. Without the body size restrictions posed by flight (Norberg & Norberg 2012), terrestrial and aquatic mammals range in body size by several orders of magnitude, resulting in animals that either cannot migrate, or do not need to migrate. Among running mammals, body size constrains the ability to migrate. Larger mammals have greater capacity to travel long distances, while although theoretically small running mammals could migrate, the benefits of seasonal movements are negligible given they are unable to travel far enough to escape environment conditions that motivate migration. Mode of locomotion is also related to the energetic cost of migration; running mammals face the greatest energetic cost per unit distance, while swimming mammals spend the least amount of energy, and the cost of locomotion scales with body size (Schmidt-Nielsen 1972). Thus, small running mammals (e.g., rodents) cannot travel sufficient distances to escape seasonal weather challenges and must adopt alternative strategies to cope with seasonal resource limitation.

Heterothermy is a thermoregulatory strategy used by many mammals (Boyles et al. 2013), but comparatively few birds (McKechnie & Lovegrove 2002, Brigham et al. 2012, Wolf et al. 2020), to reduce exposure to seasonal resource constraints. Heterothermic organisms use torpor, which is a controlled reduction in body temperature and metabolic rate over a range of ambient temperatures, to conserve energy (Geiser 2004). Heterothermy exists along a continuum in mammals ranging from species capable of small to extreme reductions in body temperature (Boyles et al. 2013). In the context of migration, heterothermy could be an important factor that has not been widely considered for birds (but see Wojciechowski & Pinshow 2009), and, at least for some species, heterothermy is a ‘logical’ (*sensu* Ruf & Geiser 2015) alternative to migration to avoid seasonal resource limitation. Migrants and non-migrants therefore possess different, but potentially equally effective, strategies for avoiding seasonal limitations in resource availability.

Migration and heterothermy are non-mutually exclusive species-specific solutions to the same ecological problem, although torpor is more-or-less phylogenetically constrained to mammals (Ruf & Geiser 2015). However, morphological and physiological limitations may dictate whether a species is migratory, heterothermic, or both. Metabolic scaling predicts that certain combinations of body size and locomotion will favour long-distance movement (Alexander 2002, Hein et al. 2012), while other combinations should favour heterothermy (Geiser 1998). In mammals, migration is more energetically favourable for larger species (Avgar et al. 2013), and heterothermy is more energetically favourable for smaller species (Boyles et al. 2013). While morphology and physiology can constrain the evolution of migration and heterothermy in mammals through effects of body size, locomotion is also inherently linked to morphology and is therefore an important constraint. Predictably, the costs and benefits associated with migration in mammals are therefore highly dependent on locomotion and body size (Avgar et al. 2013), as well as on the heterothermic capacity of a given species.

Mammals provide a unique opportunity to address the evolutionary origins of migration. Like birds, mammals are endotherms, have diverse foraging niches and species with geographic ranges around the world. But unlike birds, mammals range in body size by several orders of magnitude, exist along a thermoregulatory continuum, and have three distinct forms of locomotion. Comparisons of the evolution of birds and mammals may be informed by these differences, i.e., thermoregulatory continuum and variation in capacity to move long distances as a function of locomotion. A particularly important question about the evolution of migration in mammals is how the functional diversity of locomotion and body size affects whether a species is predisposed to be migratory, heterothermic, or both.

To evaluate ecological correlates of migration in mammals, we had three main objectives. First, we evaluated relationships between locomotion, body size, and phylogeny and migration in mammals, and tested two predictions (Table 1):

P_1: We predicted a higher percentage of swimming migrants than flying migrants, and a higher percentage of swimming and flying migrants than running migrants, because long-distance movement is less energetically costly for flying and swimming mammals than for running mammals (Schmidt-Nielsen 1972, Alerstam et al. 2003, Gnanadesikan et al. 2017). We also predicted a higher percentage of swimming migrants than flying migrants, because, even when accounting for body size, swimming is less energetically expensive over long distances than flying (Alexander 2002).

P_2: We predicted that larger swimming and running, but not flying mammals, are more likely to migrate than smaller mammals, because of the energetic constraints associated with long-distance movement for smaller swimming and running, but not flying, mammals (Alerstam et al. 2003, Gnanadesikan et al. 2017).

Second, we evaluated the evolutionary precursor hypothesis in mammals and examined relationships between habitat, latitude, and diet and migration, and tested two predictions (Table 1):

P_3: We predicted that, when accounting for phylogeny and locomotion, mammals living at higher latitudes and in more ephemeral habitats are more likely to migrate than those at lower latitudes and in more stable habitats (cf. birds: Newton & Dale 1996).

P_4: We predicted that, when accounting for phylogeny and locomotion, mammals with diets associated with seasonality (e.g., frugivory and insectivory) are more likely to migrate than those with more stable food sources (Alerstam & Enckell 1979, Boyle & Conway 2007).

Third, we evaluated the relationship between migration and heterothermy in mammals, and tested one prediction (Table 1):

P_5: We predicted that, when accounting for phylogeny and locomotion, mammals capable of heterothermy, i.e., torpor and hibernation, are less likely to migrate than those not capable of heterothermy, because heterothermy could represent an alternative strategy to migration for some mammals.

METHODS

Data collection

To test our predictions (Table 1), we reviewed the primary literature and compiled a list of mammals known to migrate. We supplemented our findings from the primary literature using Nowak (1991). Species were designated as either migratory or non-migratory; partial migrants were considered to be migratory. We also designated species as migratory regardless of the distance travelled during migration, thus including elevational migrants as migratory species in our dataset. Migration is not defined by distance, as outlined by Dingle and Drake (2007). Elevational migration is an example of migration where distance travelled is relatively short (McGuire & Boyle 2013), but it represents a seasonal migration as does a long-distance continental scale migration (e.g. Mysterud 1999). Sedentary and nomadic species, as well as species that have one-off long-distance dispersal events, consistent year-round home ranges, or year-round reproduction, were considered to be non-migratory.

We considered mode of locomotion, body mass, latitude, diet, and habitat as factors that may predict migration in mammals. We quantified thermoregulatory strategy with thermoregulatory scope, measured as mean body temperature minus minimum body temperature, and extracted these data for 560 mammal species from Boyles et al. (2013). Species were considered as one of terrestrial, aerial, or aquatic. We used a published database of body mass (g) for mammals (Smith et al. 2003) and $\log_{10}$-transformed mass for subsequent analysis. Mean latitude for each species was obtained from International Union for the Conservation of Nature (IUCN) Red List of Threatened Species spatial data (IUCN 2012). We calculated the centroid coordinate (latitude, longitude) for each species-specific two-dimensional shapefile (i.e., geospatial vector data of points on a map) and calculated weighted mean latitude based on the area of each shapefile vector (i.e., larger shapefile vectors were weighted more heavily). We used absolute latitude for analysis, assuming that seasonality increases with latitude, regardless of hemisphere. To evaluate diet, we categorised each species in our dataset as carnivorous (including sanguivores), frugivorous (including nectarivores), herbivorous, insectivorous, or omnivorous based on the primary literature following Nowak (1991). We identified the primary habitat classification for each species in our dataset using the IUCN's habitat classification scheme (IUCN 2012). Habitat classifications for species in our dataset included forest (boreal, temperate, and Tropical), grassland (savanna and temperate), shrubland (temperate and Tropical), tundra, fresh water (rivers, lakes, and wetlands), and marine (coastal, pelagic, and coastal-pelagic).

Phylogenetic analysis

To account for species' relatedness, we superimposed our dataset over a mammalian phylogenetic tree (Fritz et al. 2009) and pruned species from the tree until only those from our dataset remained, accounting for cases where species' names may have changed. Phylogenetic signal (λ) accounts for the relatedness of two species and considers the likelihood a given trait has evolved so that two closely related species are more similar than any random pair of species (Blomberg et al. 2003). Thus, species that have recently diverged are more similar, and should have more similar traits, than more distantly related species (Blomberg et al. 2003). We used phylogenetic least squares models in the R package 'ape' (Paradis et al. 2017) to estimate λ using maximum likelihood methods (Blomberg et al. 2003). Values of λ range from 0 to 1, where 0 represents no phylogenetic signal and 1 represents trait data that is fully explained by phylogeny. Intermediate values of λ indicate that phylogeny is corrected in the model (Pagel 1999, Freckleton et al. 2002). We used the R package 'ggtree' to visualise phylogenetic data (Yu et al. 2017).

Statistical analysis

All statistical analyses were conducted in R (R Core Team 2019). We assessed the role of candidate variables on the presence or absence of migration in mammals using three series of models. We first tested for collinearity among our candidate variables using variance inflation factors (VIFs), and used body mass, latitude, diet, habitat, and locomotion as predictor variables in our initial models. Our first series of models tested the effects of locomotion and body mass on the presence or absence of migration in all mammals in our dataset (n = 722). These models are hereafter referred to as 'combined models'. For our second series of models we separated running (n = 556), flying (n = 98), and swimming (n = 68) mammals, and tested the effects of body mass, latitude, diet, and habitat on the presence or absence of migration for each group. For all models, VIF < 5, so we did not remove any variables (Appendix S1). These models are hereafter referred to as the 'locomotion models'. For our third series of models, we used a subset of our dataset for which information on thermoregulatory scope was available (Boyles et al. 2013). For these models, we only included running (n = 258) and flying (n = 42) species, because all aquatic species were strictly homeothermic. Because we were interested in the effects of thermoregulatory scope on migration, we parameterised a smaller number of biologically relevant models. For each series of models, we included body mass and latitude as independent covariates and thermoregulatory scope in separate interactions with diet and habitat, respectively. We removed habitat from all running mammal models because VIF = 9.5, while VIFs < 5 for all flying mammal models (Appendix S1). These models are hereafter referred to as the 'heterothermy models'. Phylogenetically corrected logistic regression models are not widely developed, so we followed Ives and Garland (2010) and used the presence or absence of migration (i.e., a binomial variable) as the dependent variable for all models.

We used the Akaike Information Criterion for small sample sizes (AIC_C) as a model selection approach, and calculated Akaike weight (w_i), and cumulative Akaike weight ($accw_i$) to determine the relative strength of each model (Symonds & Moussalli 2010). We retained all models with $\Delta AIC_C < 2.0$.

RESULTS

We compiled a dataset including 722 species from 27 orders of mammals (Fig. 1). Migration is widespread among mammals: 22% (159/722) of species from one third (9/27) of orders were deemed migratory. Only two mammalian orders (Dermoptera and Paucituberculata) were not included in our analysis.

Combined models

The percentage of migratory species varied across modes of locomotion as predicted by P_1, with migration observed in only 9.7% (54/556) of running mammals, but in 50% (49/98) of flying and 81% (55/68) of swimming mammals. A model including the interaction between body mass and locomotion was best supported, indicating that the effect of body mass differs among the three modes of locomotion (Table 2; Appendix S2). Consistent with P_2, larger running and swimming mammals are more likely to migrate than smaller species, while for flying mammals, larger species were only slightly more likely to migrate than smaller species (Fig. 2A). In the top model, $\lambda = 0.28$, suggesting that migration in running mammals is at least partially explained by phylogeny.

Locomotion models

For running mammals, the top model included body mass and latitude as important predictors of migration (Table 2; Appendix S3). Although latitude was included in the top model, we found limited support for P_3, with no effect of latitude or habitat on the likelihood of migration for running mammals (Fig. 2B; Table 2). Although diet did not appear in the top model (Table 2), 85% (46/54) of all migratory running mammals were herbivorous, providing some support for P_4. In the top model, $\lambda = 0.50$, suggesting that migration in running mammals is at least partially explained by phylogeny.

For flying mammals, the top models included body mass, habitat, and latitude as important predictors of migration (Table 2; Appendix S3). In contrast to P_2, larger bats were more likely to migrate than smaller bats (Fig. 2A), while in support of P_3, bats at higher latitudes were more likely to migrate than those at lower latitudes (Fig. 2B). In addition, 65% (32/49) of migratory bats inhabited temperate and boreal forests, while 53% (36/49) of non-migratory bats inhabited Tropical forests. In contrast to P_4, the percentage of insectivorous and frugivorous species was approximately equal for migratory and non-migratory species, where 51% (38/74) of insectivores were migratory and 49% (36/74) were non-migratory and 63% (10/16) of frugivores were migratory and 37% (6/16) were non-migratory. In the top model, $\lambda = 0$, suggesting that migration in flying mammals is not explained by phylogeny.

For swimming mammals, the top model included only body mass, although latitude and diet appeared in other top models (Table 2; Appendix S3). In support of P_2, larger swimming mammals were more likely to migrate than smaller swimming mammals (Fig. 2A). Consistent with P_3, species living at higher latitudes were also more likely to migrate than those at lower latitudes (Fig. 2B), and, although diet was in a top model, 96% of swimming mammals were carnivorous (the only herbivorous swimming mammals were Sirenia). In the top model, $\lambda = 0$, suggesting that migration in swimming mammals is not explained by phylogeny.

Heterothermy models

For our heterothermy models, we identified the presence of migration in 6.5% of running (17/258) and 52% of flying (22/42) mammals, which are similar percentages to our larger dataset, i.e., 9.7% (54/556) of running mammals and 50% (49/98) of flying mammals. Top models for running mammals included an interaction between thermoregulatory scope and diet, where the effect of thermoregulatory scope differed between herbivores and other diet types, while body mass and latitude were also in top models (Table 2; Appendix S4). Consistent with P_5, running mammals with lower thermoregulatory scope (less heterothermic species) were more likely to migrate than running mammals with higher thermoregulatory scope (Fig. 3A). For flying mammals, the top model included an interaction between thermoregulatory scope and diet, where the effect of thermoregulatory scope differed between frugivorous and insectivorous species, as well as body mass (Table 2; Appendix S4; Fig. 3). We found mixed support for P_5 in bats, where frugivorous bats with lower thermoregulatory scope were more likely to migrate than those with higher scope (Fig. 3B), while insectivorous bats with higher thermoregulatory scope were more likely to migrate than those with lower scope (Fig. 3C). In the top model for running mammals, $\lambda = 1.0$, suggesting that, when heterothermy is accounted for, migration in running mammals was fully explained by phylogeny. By contrast, in the top model for flying mammals, $\lambda = 0$, suggesting that, when heterothermy is accounted for, migration in flying mammals is not explained by phylogeny.

DISCUSSION

Numerous hypotheses have been proposed to explain the evolutionary origins of migration in birds. In mammals, migration is widespread across taxa, and a range of factors influence whether or not a given species is migratory (Avgar et al. 2013, Gnanadesikan et al. 2017). Our analysis further corroborates the ubiquity of migration. Migratory species were identified in nine of 27 mammalian orders, highlighting the repeated and convergent evolution of migration. This same pattern is observed in other taxa (e.g., birds; Cox 1985, Chesser & Levey 1998), but mammals are highly variable in terms of ecological, physiological, and biomechanical traits. Mammals are therefore an important taxonomic group for examining the evolution of migration, and the evolution of migration is driven by the capacity for long-distance movement (mode of locomotion, body size), the availability of alternative strategies (heterothermy), and the environmental necessity of migration (evolutionary precursor hypothesis).

We found mixed support for existing hypotheses and our results highlight the complex nature of the evolution of migration in mammals. Foremost among the drivers of the complexity associated with migration are the biomechanical and bioenergetic bases for the evolution of migration in mammals. Simply put, species that are capable of travelling longer distances (greater body mass) and can do so in a more energetically efficient manner (flying and swimming) are more likely to migrate (Hedenström 2003). Nearly all of our results were context-dependent based on body size and locomotion, resulting in mixed support for the evolutionary precursor hypothesis.

Swimming mammals are more likely to migrate than flying and running mammals, while flying mammals are more likely to migrate than running mammals (P_1). Many running mammals are small, and, based on biomechanical constraints, they face physiological and morphological constraints with respect to migration. Larger running, swimming, and flying species are more likely to migrate than smaller species for each locomotion type (P_2); the energetic constraints of movement for larger organisms are lower than those of smaller organisms, an allometric relationship that is consistent for running and swimming (Hein et al. 2012). An exception is bats, where the positive effect of body size on the probability of migration is counter to existing research on birds (Alerstam et al. 2003) and counter to our expectation. A potential explanation is that the largest bat species, i.e. flying foxes (Pteropodidae), tend to have a higher propensity for migration (Popa-Lisseanu & Voigt 2009), not because they are large, but rather because they are frugivorous and rely on seasonal or ephemeral resources. Our findings, in combination with the biomechanical constraints associated with long-distance movement, suggest that body mass is arguably the most important predictor of migration in mammals.

Flying and swimming, but not running, mammals that live at higher latitudes were more likely to migrate (P_3). Temperate, boreal, and Arctic species encounter greater variation in seasonal resource abundance than Tropical species, and the probability of migration reflects this trend. The relationship between latitude and migration was strongest for swimming mammals, where nearly all non-migrants were low-latitude species. One explanation is that migration is ubiquitous among high-latitude swimming mammals due to seasonal pulses of resources in summer followed by either constraints to food resources or ice coverage in winter (e.g. Pomerleau et al. 2012). Meanwhile, bats at high latitudes invariably migrate and/or hibernate to avoid winter resource limitations (e.g., Humphries et al. 2004, Norquay et al. 2013, Boyles et al. 2016). By contrast, the lack of relationship between latitude and migration for running mammals is presumably related to alternative strategies used by high-latitude species, including hibernation (see below; Williams et al. 2014) or the ability to tolerate periods when resources are unavailable (e.g., Brigham & Geiser 2012). Our results clearly highlight that, due to extreme fluctuations in resource availability, flying and swimming species living at higher latitudes are more likely to migrate than running species at higher latitudes.

We posit that heterothermy is an alternative to migration in mammals. Specifically, we found that thermoregulatory scope was an important predictor of migration (P_5), but our results were context-dependent. Specifically, running mammals with low thermoregulatory scope, e.g., ungulates, are more likely to migrate than running mammals with higher thermoregulatory scope, e.g., rodents. These results confirm that non-migrants are more likely to hibernate or use torpor to avoid seasonal resource limitation. This relationship is dependent on body size; many running mammals with relatively high thermoregulatory scope are small, whereas many running mammals with relatively low thermoregulatory scope are large (Boyles et al. 2013). Migration and heterothermy therefore have potential to be alternative strategies for small, but not large, running mammals. Although many running mammals either migrate or hibernate, some running mammals tolerate periods of low resource abundance by maintaining normal body temperature and taking advantage of thermally insulated dens, burrows, or nests (e.g., Brigham & Geiser 2012). Thus, running mammals employ one of three strategies to avoid seasonal limitations in resource abundance: 1) migrate (typically larger species); 2) hibernate (typically smaller species); or 3) tolerate (large and small species).

For flying mammals, we observed an interaction between thermoregulatory scope and diet. Frugivorous bats with low thermoregulatory scope were more likely to migrate, while insectivorous bats with high thermoregulatory scope were more likely to migrate. These findings are not entirely surprising because most frugivorous bats are, in general, larger than insectivores, and are thus more likely to migrate (see above). Moreover, frugivores tend to live in the Tropics and are thus less likely to hibernate or use torpor (Stawski et al. 2014), but are more likely to migrate (see also Bisson et al. 2009). By contrast, most temperate and boreal bat species are insectivorous, hibernating species, some of which also migrate. Specifically, many temperate hibernating bats are regional migrants that move between summer colony roost sites and nearby hibernacula (Popa-Lisseanu & Voigt 2009, Norquay et al. 2013, Green et al. 2021), thus migrating to facilitate hibernation. The inverse also occurs: using heterothermy to facilitate migration. Many bats use torpor during migration, especially insectivorous species (Cryan & Wolf 2003, McGuire et al. 2014), a phenomenon known as 'torpor-assisted migration' (McGuire et al. 2014) which enables migrating bats to use torpor to save both time and energy.

In contrast to past work in birds (Boyle & Conway 2007) and our prediction (P_3), habitat was not an important factor for predicting migration in mammals. Most running and flying mammals occupy forests, and similar percentages of migrants and non-migrants live in forests, suggesting that, unlike in birds, open habitat does not predict migration in mammals. One possible drawback of our analysis is the broad-scale categories we used as proxies for habitat. Specifically, the concept of 'open' or ephemeral habitats was described by Boyle and Conway (2007) as forest canopy, edges, or non-forested areas. Making a distinction between discrete habitats within an ecosystem (such as forest edge or canopy) was not possible in our broad analysis. Our measure of habitat was relatively coarse and was based on ecosystem-scale classifications. Ideally, measures of habitat would be continuous, and would account for some form of environmental variation that potentially drives migration, e.g., availability of emergent vegetation in ungulates, or flying insect abundance for insectivorous bats. We suggest that future studies should be more narrowly focussed within groups of closely related species and populations to identify specific, high-resolution habitat metrics that predict the probability of migration (Allen et al. 2016). For example, the role of habitat as a driver of migration may be most relevant in partially migratory populations, which we considered as migratory in our analysis (Shaw & Levin 2011).

We found partial support for our prediction that diet would influence migration (P_4). The evolutionary precursor hypothesis posits that habitat and diet are important predictors of migration in birds, where, for instance, frugivorous birds living in open habitats are more likely to migrate than forest-dwelling insectivorous birds (Boyle & Conway 2007). In mammals, research suggests that the relationship between migration and diet is equivocal (Gnanadesikan et al. 2017), even though diet is an important predictor of migration in birds. For running mammals, diet was an important predictor of migration: 85% of running migrants were herbivores. Herbivory is inherently linked to the availability and dispersion of plants, and, in extreme or seasonal environments, variation in the availability of plant forage could drive the evolution of migration, at least for large running mammals. Our results therefore support previous work which described migration in large terrestrial herbivores as ubiquitous (Fryxell et al. 1988).

Depending on locomotion, phylogenetic signal either did not explain any variation in migration, as was the case in flying and swimming species, or it explained most of the variation in migration, as was the case for running species. Intuitively, running mammals have more diverse functional traits, especially body size, than flying and swimming mammals. Thus, the phylogenetic signal detected for running mammals is presumably related to diversity in migration at higher levels of organisation. Specifically, running mammals are spread across at least 24 orders, while all flying mammals are contained within a single order and swimming mammals are spread across three orders. Given that phylogenetic signal was low in most models, the evolution of migration appears to largely be driven by key functional traits rather than by phylogenetic inertia within certain clades (for similar results in birds, see Helbig 2003).

CONCLUSION AND FUTURE DIRECTIONS

Migration is widespread in animals, and our results contribute to existing literature suggesting there is no single explanation for the evolution of migration. Our integration of thermoregulation as a predictor of migration highlights heterothermy as an alternative to migration for small mammals. Due to variation in biophysical energetics associated with body size and locomotion, our findings also suggest that predicting migration in mammals is not straightforward, but rather that the convergent evolution of migration in mammals occurred as a result of many selective pressures (Avgar et al. 2013). Our inclusion of thermoregulation within the evolutionary ecology of mammalian migration fulfils the integrative challenge highlighted among the ‘grand challenges in migration biology’ (Bowlin et al. 2010). Our study was conducted at the species level, but species-level patterns are in fact the cumulative result of decisions made by individual animals (Dingle & Drake 2007).

Within the framework linking migration and thermoregulation, future work can examine the ecological and physiological factors associated with migratory decisions for individuals and populations to assess potential for intra-specific variation in the relationship between migration and thermoregulation (Table 3). Migration is a diverse phenomenon; it is possible to describe many types of migration, and there are clearly a variety of drivers of the evolution of migration. This notion is captured by Dingle and Drake (2007), who highlight that that the ‘classic’ examples of migration may be exceptions, as opposed to the rule. We have conducted a broad analysis to investigate general ‘rules’ of migration across all mammals, but we suggest that investigations of exceptions to the general migration paradigm will be valuable next steps. Studies of more targeted taxonomic groups that exemplify exceptions to the broader patterns will contribute to a thorough and detailed understanding of migration.

Our analysis here presents migration and heterothermy as alternative strategies, but the torpor-assisted migration hypothesis indicates that heterothermy is a key aspect of migration for bats (Table 3; McGuire et al. 2014). In another potential exception, most studies consider direct drivers of the evolution of migration for a particular focal group, but the migratory coupling hypothesis (Table 3) suggests that migration in some species is coupled to drivers of migration in another species (e.g., predators that migrate with migratory prey; Gnanadesikan et al. 2017, Furey et al. 2018). These are examples of potential exceptions to general migration rules that can be studied within more focused taxonomic groups. Bottom-up taxa-specific explanations for the evolution of migration that combine other adaptations (e.g., torpor for bats) to explain migratory patterns complement taxonomically broad top-down approaches such as that presented here. In Table 3, we highlight several future opportunities where investigations of systems that may be considered exceptions (often within more taxonomically focused groups) could provide key insights into broader patterns of the evolution of migration. We have addressed some of the challenges in migration biology (Bowlin et al. 2010) by presenting a broad comparative analysis of migration and integrating behavioural, ecological, and physiological mechanisms as drivers of the evolution of migration in mammals. As future studies integrate the exceptions to the rule, we can continue to develop a comprehensive understanding of the evolutionary drivers of migration, a behaviour that is critically important to mammals throughout the phylogenetic tree and throughout the planet.

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Table 1. Summary of predictions, results, and conclusions associated with each variable. Results are presented as stand-alone findings, but nearly all traits are confounded by one or more other traits. In these cases, confounded traits are highlighted in the Discussion.

Variable	Prediction	Expectation	Result	Conclusion
Locomotion	P_1	**Running:** less likely to migrate than swimming and flying mammals.	9.7% of running species migrate.	Supported
		Flying: more likely to migrate than running, but not swimming, mammals.	50% of flying species migrate.	Supported
		Swimming: more likely to migrate than running and flying mammals.	81% of swimming species migrate.	Supported
Body size	P_2	**Running:** larger species more likely to migrate.	Larger species more likely to migrate.	Supported
		Flying: no effect of body mass.	Larger species more likely to migrate.	Not supported
		Swimming: larger species more likely to migrate.	Larger species more likely to migrate.	Supported
Latitude	P_3	Higher latitude species are more likely to migrate than lower latitude species.	**Running:** No difference across latitudes.	Not supported
			Flying: higher latitude species more likely to migrate.	Supported
			Swimming: higher latitude species more likely to migrate.	Supported
Habitat	P_3	Species living in more ephemeral habitats, e.g., temperate, boreal, or tundra habitats, are more likely to migrate.	**Running:** no effect of habitat on the likelihood of migration.	Not supported
			Flying: 65% of migratory bats inhabited temperate or boreal forests; 53% of non-migratory bats inhabited tropical forests.	Supported
			Swimming: no effect of habitat on the likelihood of migration.	Not supported
Diet	P_4	Species with diets associated with seasonality, e.g., herbivory, frugivory, or insectivory, are more likely to migrate.	**Running:** 85% of running migrants herbivorous.	Supported
			Flying: the percentage of insectivores and frugivores among migrants and non-migrants approximately equal.	Not supported
			Swimming: 96% of all swimming mammals carnivorous.	Not modelled
Thermoregulatory scope	P_5	Species with higher thermoregulatory scope are less likely to migrate.	**Running:** species with high thermoregulatory scope do not migrate.	Supported
			Flying: frugivorous bats with high thermoregulatory scope less likely to migrate; insectivorous bats with high thermoregulatory scope more likely to migrate.	Mixed support

Table 2. Summary of results from three phylogenetic least square model sets. Combined Models tested the effect of locomotion and body mass on migration in 722 mammalian species. Locomotion Models tested the effects of body mass, latitude, habitat, and diet on migration in mammals (*n* = 556 running mammals; *n* = 98 flying mammals; *n* = 68 swimming mammals), and Heterothermy Models tested the effects of thermoregulatory scope in combination with the same set of variables on migration in running (*n* = 258) and flying mammals (*n* = 42). AIC_C = Akaike Information Criterion for small sample sizes, ΔAIC_C = difference in AIC_C between top models, w_i = Akaike weight, $accw_i$ = cumulative Akaike weight, Model λ = phylogenetic signal where values of λ range from 0 to 1, where 0 represents no phylogenetic signal and 1 represents trait data that is fully explained by phylogeny.

Combined Models	**AIC_C**	**ΔAIC_C**	**w_i**	**$accw_i$**	**Model λ**
~locomotion + log(mass) + locomotion*log(mass)	298.68	0	0.95	0.95	0.28
~locomotion + log(mass)	304.55	5.87	0.05	1.00	0.25
Locomotion Models					
Running mammals					
~log(mass) + latitude	–73.7	0	0.922	0.922	0.50
Flying mammals					
~log(mass) + habitat	133.8	0	0.425	0.425	0
~log(mass) + habitat + latitude	135.8	2.0	0.179	0.604	0
Swimming mammals					
~log(mass)	56.88	0	0.264	0.264	0
~log(mass) + diet	58.19	1.31	0.152	0.416	0
~log(mass) + latitude	58.43	1.55	0.135	0.551	0
Heterothermy Models					
Running mammals					
~thermoregulatory scope*diet + log(mass)	–204.72	0	0.629	0.629	1.0

~thermoregulatory scope*diet + log(mass) + latitude	–203.10	1.62	0.309	0.938	1.0
Flying mammals					
~thermoregulatory scope*diet	48.03	0	0.490	0.490	0

Table 3. Suggested opportunities for future studies to test exceptions to the general 'rules' of migration in a comparative context.

Opportunity	Description	Potential focal group	Example
Intra-specific variation in migration	Our analysis focuses on migration of species, but many aspects of migration vary among populations and among individuals within populations. Understanding the drivers of variation will contribute to a broader understanding of the evolution and ecology of migration.	Partial or differential migration systems	Elk *Cervus elaphus* are partial migrants (Hebblewhite & Merrill 2011). The determinants of whether to migrate, or not, are related to predator risk and the availability of forage, both of which vary among migratory and non-migratory individuals in the population. However, in this population, fitness is equivalent for both groups.
Integrating alternative strategies	Our review presents heterothermy and migration as alternative strategies, but torpor-assisted migration describes a strategy where heterothermy is integral to migration	Bats	Silver haired bats *Lasionycteris noctivagans* use torpor to save energy at stopover sites during migration (McGuire et al. 2014).
Exceptions to established migration patterns	'Green wave surfing' – tracking high-quality forage – is a well-established pattern that is common among many species of ungulates. However, not all species follow this pattern, and investigations of species that adopt different migration strategies could be particularly revealing	Ungulates	In a study of multiple populations of ungulates, including bison *Bison bison*, elk *Cervus elaphus*, bighorn sheep *Ovis canadensis*, moose *Alces alces*, and mule deer *Odocoileus hemionus*, seven of the ten populations timed migration to coincide with peak forage biomass, but some species and populations migrate either ahead of, or behind, the 'green wave' (Merkle et al. 2016).
Degrees of separation	Studies of migration typically consider drivers that directly impact the focal species or group. But the migratory coupling hypothesis suggests that migration in some groups may be coupled to migration in another group. Understanding migration in one group may require understanding the drivers of migration in the	Carnivores	Grizzly bears *Ursus arctos* exploit migration of Pacific salmon *Oncorhynchus* sp. along river systems (Deacy et al. 2016). Additional examples are provided by Furey et al. (2018).

	coupled group, such as predators that migrate in response to migratory prey		
Climate-related exceptions	Seasonal resource limitation as a result of predictable climate variation underlies migration in many taxa. Responses in years of exceptional climate, such as El Niño or La Niña years, might reveal the degree to which migration is a facultative response	Marine mammals	Migratory patterns of grey whales *Escrichtius robustus* in the Pacific Ocean are altered during La Niña years, suggesting the possibility that whales travelled farther to access warmer water (Gardner & Chavez-Rosales 2000).

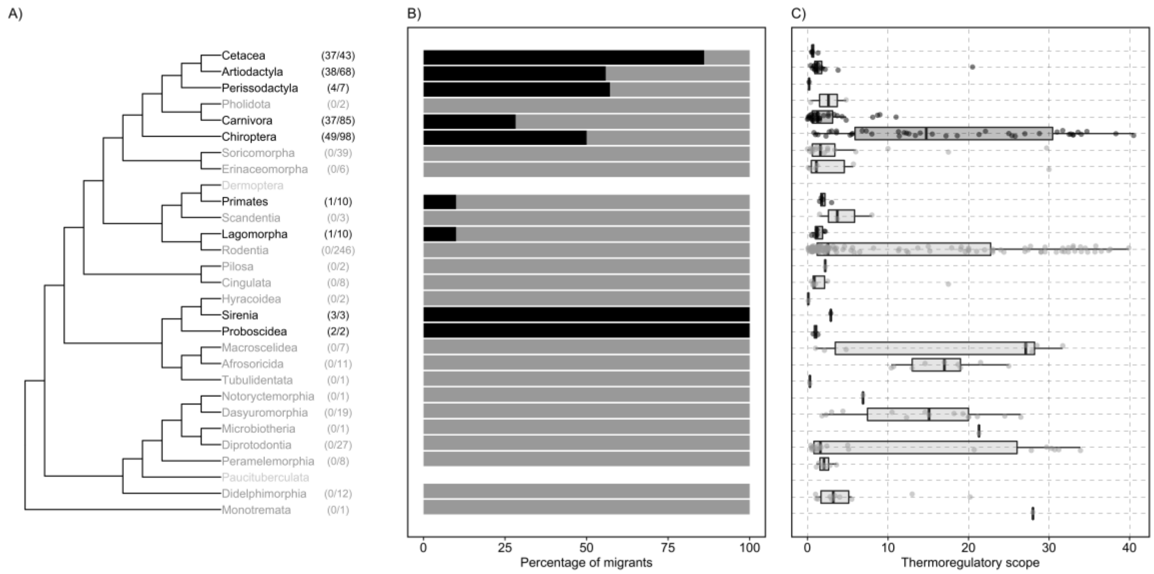

Fig. 1. A) Phylogenetic tree of 29 mammalian orders obtained from 'the Catalogue of Life' (Roskov et al. 2015), where black print represents orders with at least one migratory species, dark grey print represents orders with no migratory species, and orders with light grey print have no species in our database. Numbers in parentheses are the number of migratory species and the total number of species for which we determined migratory or non-migratory behaviour in each order. B) Bar chart displaying percentages of migratory species: black represents migratory species and dark grey represents non-migratory species. C) Box plots displaying the distribution of thermoregulatory scope for 29 mammalian orders: black boxes represent orders with at least one migratory species and dark grey boxes represent orders with no migratory species. Points show the distribution of data, thick dark lines represent the median, upper and lower edges of each box represent the interquartile range (25% and 75% of data), and whiskers represent the upper and lower quantiles (2.5% and 97.5% of data).

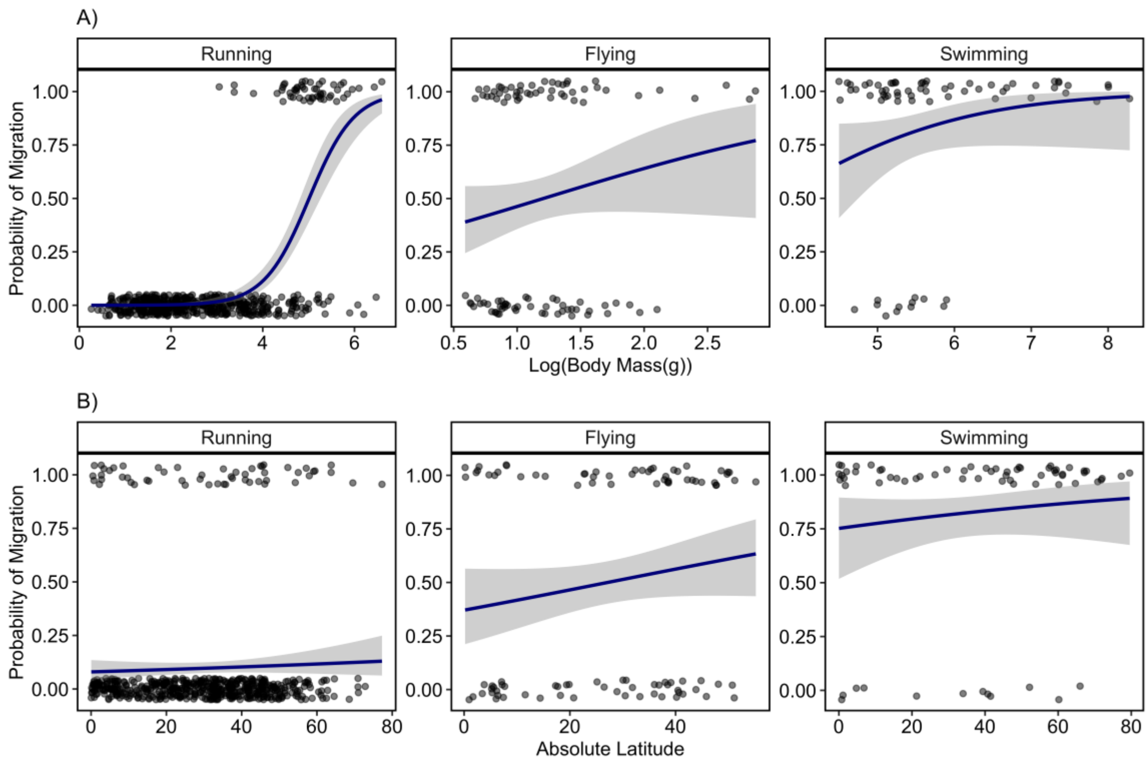

Fig. 2. Logistic regression-derived relationships between probability of migration and body mass (A) and latitude (B) for: running mammals (left; *n* = 556), flying mammals (centre; *n* = 98), and swimming mammals (right; *n* = 68). Each data point represents a species that either migrates or does not migrate; data points are jittered to visualise the distribution of data. Running, flying, and swimming mammals with higher body mass are more likely to migrate than those with lower body mass (A). Flying and swimming mammals found at higher latitudes are more likely to migrate than those found at lower latitudes (B).

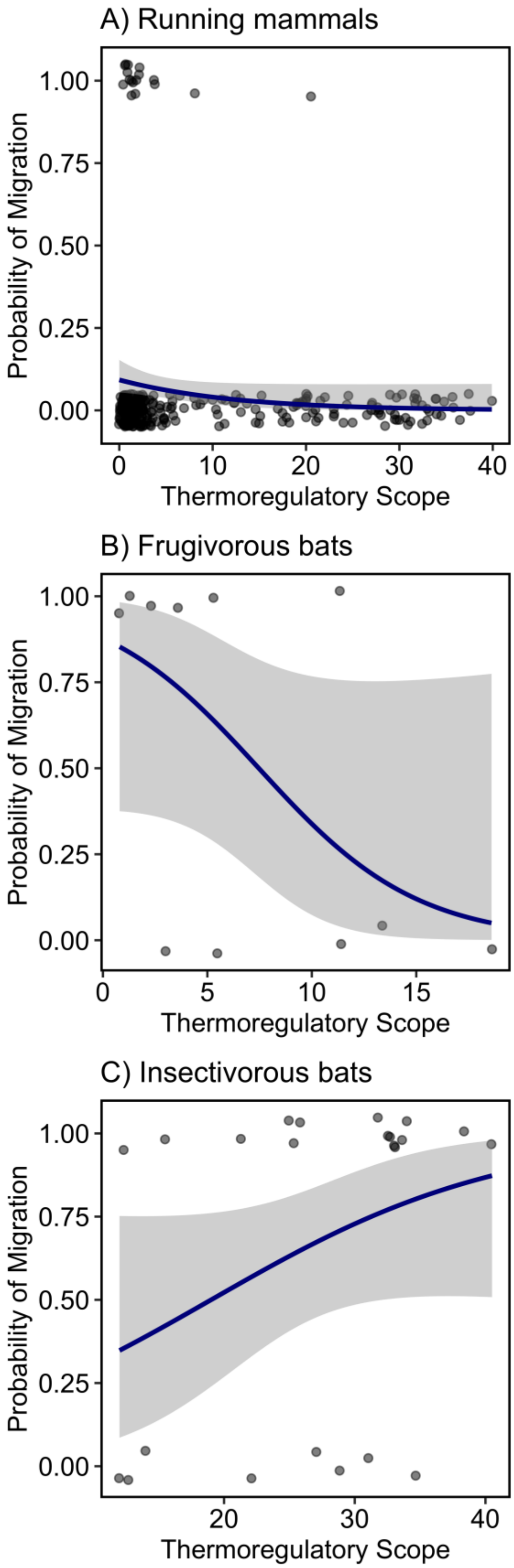

Fig. 3. Logistic regression-derived relationships between probability of migration and thermoregulatory scope for running mammals (A; *n* = 258), frugivorous bats (B; *n* = 11), and insectivorous bats (C; *n* = 23). Running mammals with higher thermoregulatory scope are less likely to migrate than running mammals with lower thermoregulatory scope (A). Frugivorous bats with higher thermoregulatory scope are also less likely to migrate than frugivorous bats with lower thermoregulatory scope (B), whereas insectivorous bats with higher thermoregulatory scope are more likely to migrate than insectivorous bats with lower thermoregulatory scope (C). Each data point represents a species that either migrates or does not migrate; data points are jittered to visualise the distribution of data.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.

Appendix S1. Summary of Variance Inflation Factors (VIFs) for the global models in each of the five model sets in our analyses.

Appendix S2. Summary of the top Combined Model.

Appendix S3. Summary of the top Locomotion Model.

Appendix S4. Summary of the top Heterothermy Models.

Appendix S1: Summary of Variance Inflation Factors (VIFs) for the global models in each of the five model sets in our analyses. Note, the only instance where VIFs indicated multi-collinearity among variables was the habitat variable in the Heterothermy Model for running models and this variable was removed for all subsequent analyses. Asterisks in the table denote instances where VIFs dictated removal of a variable from subsequent analyses.

Model	**Locomotion group**	**Variance Inflation Factor**				
		Mass	**Latitude**	**Diet**	**Habitat**	**Thermoregulatory scope**
Locomotion	Running	1.47	3.29	1.21	4.62	–
Locomotion	Flying	1.60	2.68	2.08	2.71	–
Locomotion	Swimming	1.09	1.00	1.07	1.14	–
Heterothermy	Running	1.97	6.94	2.04	9.41*	1.52
		1.44	2.00	1.62	–	1.25
Heterothermy	Flying	1.62	3.51	4.21	3.41	4.28

Appendix S2: Summary of the top *Combined Model* (n = 722), which included locomotion (categories flying, running, and swimming), log-transformed body mass, and an interaction between locomotion and body mass (see Table 2 for model selection results).

Combined models	**Coefficient ± SE**	**t-value**	**p-value**
Intercept	0.04 ± 0.16	0.26	0.79
Locomotion[1]			
-Running	–0.25 ± 0.14	–1.69	0.09
-Swimming	0.33 ± 0.31	1.05	0.29
log(mass)	0.26 ± 0.07	3.45	**0.0006**
log(mass)*locomotion[1]			
-log(mass)*Running	–0.17 ± 0.07	–2.17	**0.03**
-log(mass)*Swimming	–0.21 ± 0.09	–2.23	**0.03**

[1]Reference category is flying mammals.

Appendix S3: Summary of the top *Locomotion Model*. The top running model included log-transformed body mass and latitude (n = 556), the top flying model included log-transformed body mass and habitat (n = 98), and the top swimming model included log-transformed body mass (n = 68). See Table 2 for model selection results.

Group of mammals	Variables	Coefficient ± SE	t-value	p-value
Running	Intercept	–0.27 ± 0.11	–2.43	**0.01**
	log(mass)	0.09 ± 0.014	6.71	**<0.0001**
	Latitude	0.002 ± 0. 0007	3.77	**0.0001**
Flying mammals	Intercept	–0.40 ± 0.22	1.84	0.07
	log(mass)	0.28 ± 0.11	2.60	0.01
	Habitat[1]			
	-Grassland	0.23 ± 0.38	0.60	0.54
	-Temperate forest	–0.08 ± 0.20	–0.40	0.68
	-Temperate shrubland	–0.52 ± 0.28	–1.81	0.07
	-Tropical Forest	0.44 ± 0.21	–2.09	**0.03**
Swimming mammals	Intercept	0.23 ± 0.30	0.76	0.44
	log(mass)	0.10± 0.05	1.99	**0.05**

[1]Reference category is boreal forest.

Appendix S4: Summary of the top *Heterothermy Models*. The top running model included log-transformed body mass, thermoregulatory scope, diet, and the interaction between diet and thermoregulatory scope (n = 258) and the top flying model included thermoregulatory scope, diet, and the interaction between diet and thermoregulatory scope (n = 42). See Table 2 for model selection results.

Group of mammals	Variables	Coefficient ± SE	t-value	p-value
Running mammals	Intercept	–0.17 ± 0.21	–0.81	0.42
	log(mass)	0.05 ± 0.017	2.73	**0.007**
	Thermoregulatory scope	0.001 ± 0.005	0.34	0.73
	Diet[1]			
	-Frugivore	–0.52 ± 0.16	–3.37	**0.0009**
	-Herbivore	0.09 ± 0.10	0.86	0.39
	-Insectivore	0.05 ± 0.09	0.58	0.56
	-Omnivore	0.09 ± 0.10	0.86	0.39
	Thermoregulatory scope : Diet[1]			
	-Thermoregulatory scope : Frugivore	0.02 ± 0.009	2.26	**0.02**
	-Thermoregulatory scope : Herbivore	–0.0012 ± 0.006	–0.22	0.83
	-Thermoregulatory scope : Insectivore	–0.0009 ± 0.005	–0.17	0.87
	-Thermoregulatory scope : Omnivore	–0.0016 ± 0.006	–0.30	0.77
Flying mammals	Intercept	0.90 ± 0.22	4.00	**0.0004**
	Thermoregulatory scope	–0.05 ± 0.02	–2.01	**0.05**
	Diet[2]			
	-Insectivore	–0.83 ± 0.39	–2.11	**0.04**
	Thermoregulatory scope : Diet[2]			
	-Thermoregulatory scope : Insectivore	0.07 ± 0.03	2.59	**0.01**

[1]Reference category is carnivore.
[2]Reference category is frugivore.