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Abstract. Physiological regulation of body temperature, set at a high level, is one of the key features of endothermic homeotherms, such as birds and mammals. However, many mammals and some birds have evolved the ability for temporal down-regulation of core body temperature. We investigated how variation in environment temperature and habitat primary productivity determine variation in daily body temperature down-regulation among mammalian species. Nearly half of the variation in minimum daily body temperature among species was explained by variation in both primary productivity and environmental temperature. Mammals expressing low minimum body temperature inhabited regions of low annual temperature with wide daily and seasonal temperature variation. Simultaneously, those regions were characterized by low productivity and low seasonality in productivity. Furthermore, regions characterized by a high level of among-year variation in environmental temperature, but not in primary productivity, were inhabited by species with low minimum body temperature, but only by those adapted to relatively humid conditions. Our results suggest that daily heterothermy can be selectively advantageous in the environmental circumstances when high energetic demands for maintaining endothermic homeothermy, physiological regulation of a high and stable body temperature, cannot be supported. The results corroborate the hypothesis that mammals that have evolved daily down-regulation of body temperature may have higher chances of surviving extinction events caused by climatic changes. Therefore, daily heterothermy adaptation in contemporary mammals represents a mechanism for surviving the ongoing global warming.

Key words: climatic adaptation, climate change, heterothermy, thermoregulation, physiological performance, torpor

Introduction

Physiological regulation of body temperature is a key aspect of mammalian and avian biology (McNab 1978, Lovegrove 2017, Rezende et al. 2020). Maintaining high and stable body temperature over fluctuating environmental conditions, known as endothermic homeothermy, has probably contributed to the ecological and evolutionary success of birds and mammals (Nespolo et al. 2011). However, many mammals and some birds, can temporarily abandon their strict temperature regulation, typically maintained above 30 °C (Ruf & Geiser 2015, Nowack et al. 2020). Temporal heterothermy, down-regulation of body temperature, can be selectively advantageous in

the circumstances when high energetic demands for maintaining endothermic homeothermy, a physiologically regulated high and stable body temperature, cannot be fulfilled (Hetem et al. 2016, Dammhahn et al. 2017, Lovegrove 2017).

The high and stable core body temperature of endothermic homeotherms provides an optimal environment for enzymatic reactions, enables development of a complex nervous system, and allows a high reproductive rate, among other benefits (Nespolo et al. 2011, Preußner et al. 2017). However, homeothermic endothermy is energetically expensive, an endothermic mammal consumes five times more food than an ectothermic tetrapod of similar size (Pough 1980, McNab 2009). Temporal down-regulation of metabolic processes can reduce such costs, but it results in intra-individual body temperature variation observed, for instance, in hibernating and daily torpid mammals (Hetem et al. 2016, Dammhahn et al. 2017, Lovegrove 2017). The evolution of metabolic suppression, the physiological trait associated with heterothermy, is directly linked to energy conservation (Lovegrove 2000a). The adaptive benefits of temporal heterothermy are reduction of energy and water usage when those resources are unavailable or limited (Tieleman & Williams 1999, Vuarin & Henry 2014) and may have led to repeated evolution of heterothermy in mammals (Geiser 2008). It has been suggested that temporal heterothermy allowed mammalian lineages to survive the Cretaceous-Paleogene extinction event (Lovegrove 2017), with extinction risk potentially reduced in contemporary heterothermic mammals (Geiser & Turbill 2009). Hence, it was concluded that a heterothermic strategy can be beneficial if endothermic homeothermic animals are exposed to changing, fluctuating or unpredictable environmental conditions (Geiser & Brigham 2012, Dammhahn et al. 2017). Nevertheless, how environmental variation affects heterothermy is still debatable (Vuarin & Henry 2014, Levesque et al. 2016, Dammhahn et al. 2017).

Intra-individual temperature variation, or heterothermy, is a physiological strategy in which animals can adjust their body temperature depending on resource availability and ambient temperature (Bligh & Johnson 1973, Boyles et al. 2011, Geiser & Brigham 2012, Vuarin & Henry 2014). How multiple environmental variables simultaneously affect the level of heterothermy is still unclear (Vuarin & Henry 2014, Dammhahn

et al. 2017). It was observed in hibernating mammals that metabolic rate reduces in response to decreased environmental temperature (Geiser 2004, Heldmaier et al. 2004). As a consequence, their body temperature also declines, as well as their overall energy expenditure (Geiser 1988). Surprisingly, little empirical evidence exists confirming that environmental temperature can predict body temperature down-regulation in daily heterotherms (Nespolo et al. 2010). Some evidence indicates that a decrease in ambient temperature can induce torpor intensity in some species of birds and mammals (Nowack et al. 2017, 2020). For example, in the lesser hedgehog tenrec (*Echinops telfairi*) daily torpor bounds were longer and minimum skin temperature was lower under a fluctuating versus constant temperature experimental condition (Dausmann et al. 2020). Daily heterothermy level, estimated from body temperature variation of free-ranging wood mice (*Apodemus flavicolis*) during a central European winter, was negatively related to minimum daily environmental temperatures (Boratyński et al. 2018). However, experimental results suggest that environmental temperature can interact with habitat productivity in controlling expression of heterothermic physiology in mammals, complicating the temperature dependence pattern (Nespolo et al. 2010). Laboratory studies confirmed that food shortage alone can induce heterothermy. The euthermic Chilean mouse-opossum (*Thylamys elegans*) showed daily fluctuations in body temperature, decreasing body temperature and entering torpor, only when food was absent (Bozinovic et al. 2005). Likewise, when pale kangaroo mice (*Microdipodops pallidus*) were provided with food in excess, animals did not enter torpor, but otherwise the torpor intensity increased with decreasing experimental temperature (Brown & Bartholomew 1969). The probability of entering torpor in sugar gliders (*Petaurus breviceps*) reflected differences in weather patterns, food availability and thermoregulatory costs in relation to ambient temperature (Körtner & Geiser 2000). These results from intraspecific experiments suggest that environmental temperature fluctuation, in combination with habitat productivity, can influence conditions in which evolution of the daily heterothermic strategy is promoted in otherwise homeothermic animals. However, the hypothesis that variation of daily heterothermy observed among mammalian species is predicted by both temperature and productivity has yet to be evaluated.

The main aim of this work was to estimate the relative contribution of thermal environment and energetic limitation caused by variation in habitat productivity on the expression of daily minimum body temperature among mammalian species. It was hypothesized that the level of daily heterothermy is determined by variation of ambient temperature (Brown & Bartholomew 1969, Körtner & Geiser 2000). Specifically, lower average and higher amplitude of daily and seasonal temperature fluctuations can stimulate temporal expression of a low body temperature in mammals, resulting in an increased heterothermy level. It was also hypothesized that the level of daily heterothermy is determined by variation in habitat productivity. Lower average and higher amplitude of seasonal variations in habitat productivity can stimulate expression of temporal body temperature down-regulation, when resources in the environment are too scarce to fulfil high energetic demands for homeothermic endothermy. High among-year fluctuations in ambient temperature and food availability could select for adaptive strategies to compensate for unpredictability in the environment, resulting in the evolution of daily heterothermic strategies. We tested the above hypotheses using comparative data for mammalian species known to express daily heterothermic physiology (Ruf & Geiser 2015, Nowack et al. 2020). In particular, we tested if and how variation in habitat productivity and environmental temperature predict variation in minimum body temperature. We predicted that species with daily heterothermy adaptation will inhabit regions with both low environmental temperature and productivity and high variation in environmental predictors. Due to food and water limitations, e.g. in deserts and semi-deserts, thermal and energetic processes can have differential consequences between arid and humid adapted species. As a consequence, and because of allometric scaling of multiple physiological traits, we evaluated how species body mass and aridity adaptation influence the covariation between minimum body temperature and environmental predictors.

Material and Methods

Comparative data

Minimum core body temperature (BT_{min} °C) and body mass (g) data for mammals expressing daily heterothermy was obtained from recent reviews (Ruf & Geiser 2015, Nowack et al.

2020). Environmental variables were derived for geographic distributions of terrestrial mammals obtained from Digital Distribution Maps (IUCN 2020). Environmental temperature variables (BIO1, BIO2 and BIO4) were derived from a historical climate data repository (Fick & Hijmans 2017) at a resolution of 2.5 minutes (downloaded on 30 October 2020). The range polygons for each species were used to clip the rasters of the variables and to estimate the median and standard deviations for each species. Environmental temperature variables in subsequent analyses included the annual median temperature (T_M) and its standard deviation (T_{SD}; among-year variation in temperature), median diurnal temperature range (T_R) and temperature seasonality (T_S). Normalized difference vegetation index (NDVI; the difference between near-infrared and red reflectance divided by their sum, with densely vegetated areas represented by higher values) was derived for the years 1982-2015 (National Center for Atmospheric Research Staff 2018, https://staff.ucar.edu/browse/orgs/NCAR, downloaded on 13 November 2020). Bimonthly measurements of NDVI were used to estimate the averages and standard deviations of primary productivity for each year. The mean and standard deviation of the average primary productivity across the years, and mean of within years standard deviations of primary productivity were estimated to summarize NDVI data (Fig. S1). Indices of annual primary productivity (P_M; median of annual productivity), among-year variation in productivity (P_{SD}; median of standard deviation of annual productivity) and seasonality of productivity (P_S; median of within years standard deviations) were calculated from summarized NDVI data and species ranges. Species were classified as inhabiting relatively arid or humid environments based on aridity index data (species with average aridity index < 0.5 were classified as arid and humid if average aridity index ≥ 0.5); Trabucco & Zomer 2019). Records deviating markedly from the distributions of the data on trait paired regression plots, five for BT_{min} (*Elephantulus rozeti*, *Microcebus berthae*, *Microcebus myoxinus*, *Tarsipes rostratus* and *Vespadelus vulturnus*) and two for T_M (*Apodemus peninsulae* and *Phodopus sungorus*), were excluded from analyses as outliers, resulting in complete records for 81 mammalian species (Supplementary online material: data). A trimmed mammalian phylogeny (topology with branch lengths: http://vertlife.org/phylosubsets/; Upham et al. 2019) was used in comparative analyses.

Statistical analyses

Species and environmental variables were $\log_{10}$ transformed, centred and scaled to improve normality of their residual variances and to place variation on the same scale. Because environmental variables were correlated (Table S1) principal component analysis was conducted to reduce multicollinearity between seven environmental predictors (T_M, T_{SD}, T_R, T_S, P_M, P_{SD} and P_S). Principal components (proportion of explained variable by component > 0.05, eigenvalue > 1) were extracted with varimax rotation (with "principal" command in the psych R package). Calculated principal components were used in the subsequent analysis. Differences between arid- and humid-adapted species (Fig. 1) for studied variables were tested with ordinary (OLS) and phylogenetic (PGLS) generalized least squares regressions. Associations between BT_{min} and principal components were tested with PGLS (phylolm R package; Rezende & Diniz-Filho 2012). The significance of the principal components on BT_{min} was tested, with body mass as covariate and a binomial factor of aridity adaptation, distinguishing arid- from humid-adapted species. To test if size of species and their adaptation to aridity influenced response to environmental predictors, two-way interactions between environmental predictors with aridity factor and body mass were tested. The goodness-of-fit of the models were evaluated with the Akaike information criterion (AIC) and alternative phylogenetic regression R-squared values for PGLS analyses (Ives 2019). Finally, a backward step-wise selection method was applied on a full model, including all the above listed terms, and the model was simplified by removing the least significant interaction terms.

Results

Environmental predictors, calculated for the distribution ranges of 81 mammalian species (Fig. 1), were pairwise correlated (Pearson's product-moment correlation; |r|: 0.05-0.76; Table S1) and varied between arid- and humid-climate species (Fig. 2, Table S2). Neither body temperature (mean = 18.7, median = 17.9, range = 7.7-31.0 °C) nor body mass (mean = 335.4, median = 27.0,
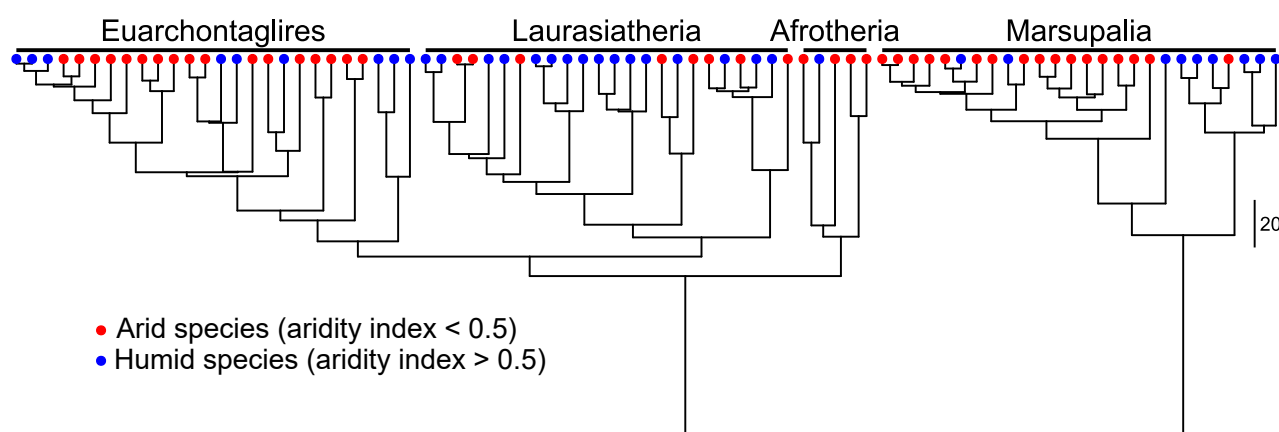

Fig. 1. Phylogenetic relatedness among the 81 mammalian species studied (after: Upham et al. 2019).
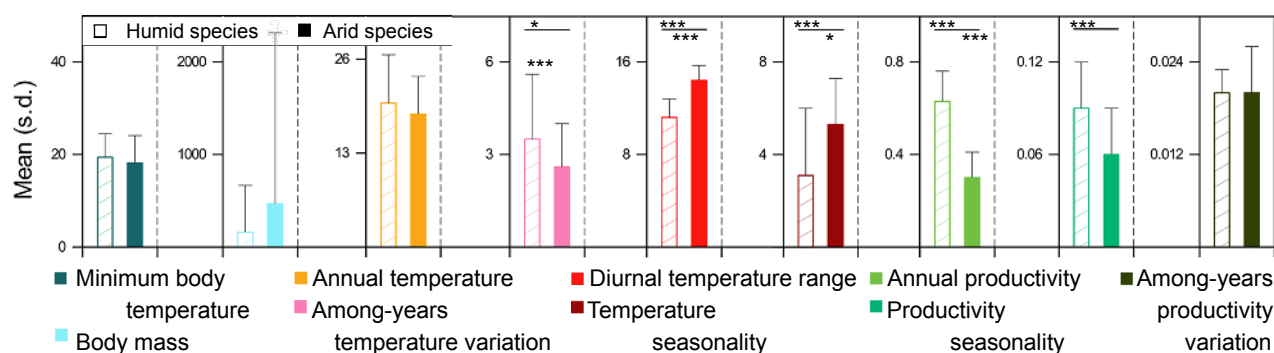

Fig. 2. Mean and standard deviations of studied variables and differences between arid and non-arid climate species (Table S2). *$P < 0.05$ and ***$P < 0.0001$ indicate significant differences as tested with ordinary (above) and phylogenetic (below lines) generalized least squares.
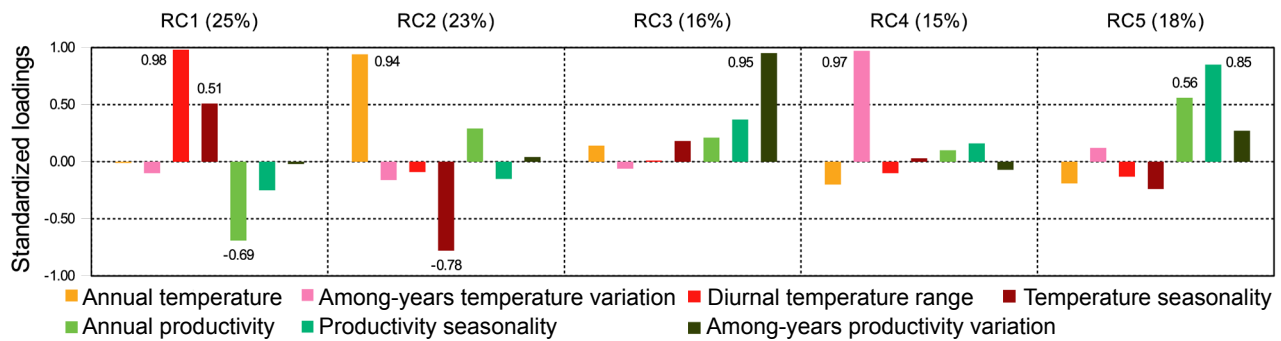
Fig. 3. Summary of rotated principal component analysis of environmental predictors calculated from species ranges of 81 mammals. Percentages of explained variation in environmental variables by the rotated principal components (RCs) and standardized loadings (> 0.50) of environmental variable to the components (Table S3) are presented.

Table 1. Parameter estimates for phylogenetically generalized least squares (PGLS) analyses of environmental variables and body mass predicting minimum body temperature in mammals (λ = 0.849, AIC = 207.02, n = 81). Arid factor stands for (0) humid- (aridity index > 0.5) or (1) arid-climate species (aridity index < 0.5), and RC stands for rotated principal components (Fig. 3). Interpretation of standard regression R-squared are uncertain in PGLS analyses, thus alternative values are provided: R_{ls}^2 = 0.52, R_{ce}^2 = 0.55, R_{lr}^2 = 0.42 (Ives 2019). Left panel presents results from an analysis including the non-significant terms of body mass and RC3, which are excluded (-) from the analysis presented in the right panel.

	β_{PGLS} (SE)	t	P	β_{PGLS} (SE)	t	P
Intercept	–0.34 (0.66)	–0.52	0.61	–0.36 (0.68)	–0.53	0.60
Arid (0,1)	0.38 (0.30)	1.26	0.21	0.45 (0.30)	1.50	0.14
Body mass	0.21 (0.12)	1.70	0.093	-	-	-
RC1	–0.26 (0.15)	–1.71	0.091	–0.33 (0.15)	–2.14	0.035
RC2	0.27 (0.11)	2.37	0.020	0.28 (0.11)	2.47	0.016
RC3	0.13 (0.10)	1.37	0.18	-	-	-
RC4	–0.35 (0.15)	–2.30	0.024	–0.34 (0.16)	–2.19	0.032
RC5	0.38 (0.12)	3.30	0.001	0.47 (0.11)	4.36	< 0.0001
Arid*RC4	0.57 (0.18)	3.22	0.002	0.53 (0.18)	2.96	0.0041

range = 2.0-9000.0 g) significantly differed between arid- and humid-climate species (*P* > 0.25; Fig. 2). Environmental predictors moderately correlated with BT_{min} (|r| < 0.38, *P* > 0.001) and body mass (|r| < 0.17, *P* > 0.15; Table S1). In simple univariate analysis, body mass positively correlated with BT_{min} (β_{PGLS} (SE) = 0.28 (0.13), t = 2.16, *P* = 0.034).

Five rotated principal components explained 97% of the variation among the studied species in seven environmental predictors derived for the species distribution ranges (Fig. 3; Table S3). The first component (RC1) was primarily loaded by diurnal temperature range, annual productivity and temperature seasonality. The second component (RC2) was loaded by annual temperature and temperature seasonality. Third (RC3) and fourth (RC4) components were loaded by among-year variation, either in productivity or in temperature,

respectively. The fifth component (RC5) was loaded by annual productivity and productivity seasonality (Fig. 3).

Phylogenetic generalized least squares analysis showed that variation in BT_{min} among 81 mammalian species was significantly predicted by environmental variables, explaining around 50% of the variation in BT_{min} (Table 1, Table S4). Among-year variation in primary productivity (RC3) did not correlate with BT_{min} (β_{PGLS} (SE) = 0.13 (0.10), t = 1.37, *P* = 0.18) and among species variation in body mass has only weakly associated with BT_{min} (β_{PGLS} (SE) = 0.21 (0.12), t = 1.70, *P* = 0.093). The negative trend of RC1 on BT_{min} (β_{PGLS} (SE) = –0.26 (0.15), t = –1.71, *P* = 0.091) was significant (β_{PGLS} (SE) = –0.33 (0.15), t = –2.14, *P* = 0.035) after step-wise backward reduction of insignificant effects of RC3 and body mass (Table 1). BT_{min} was
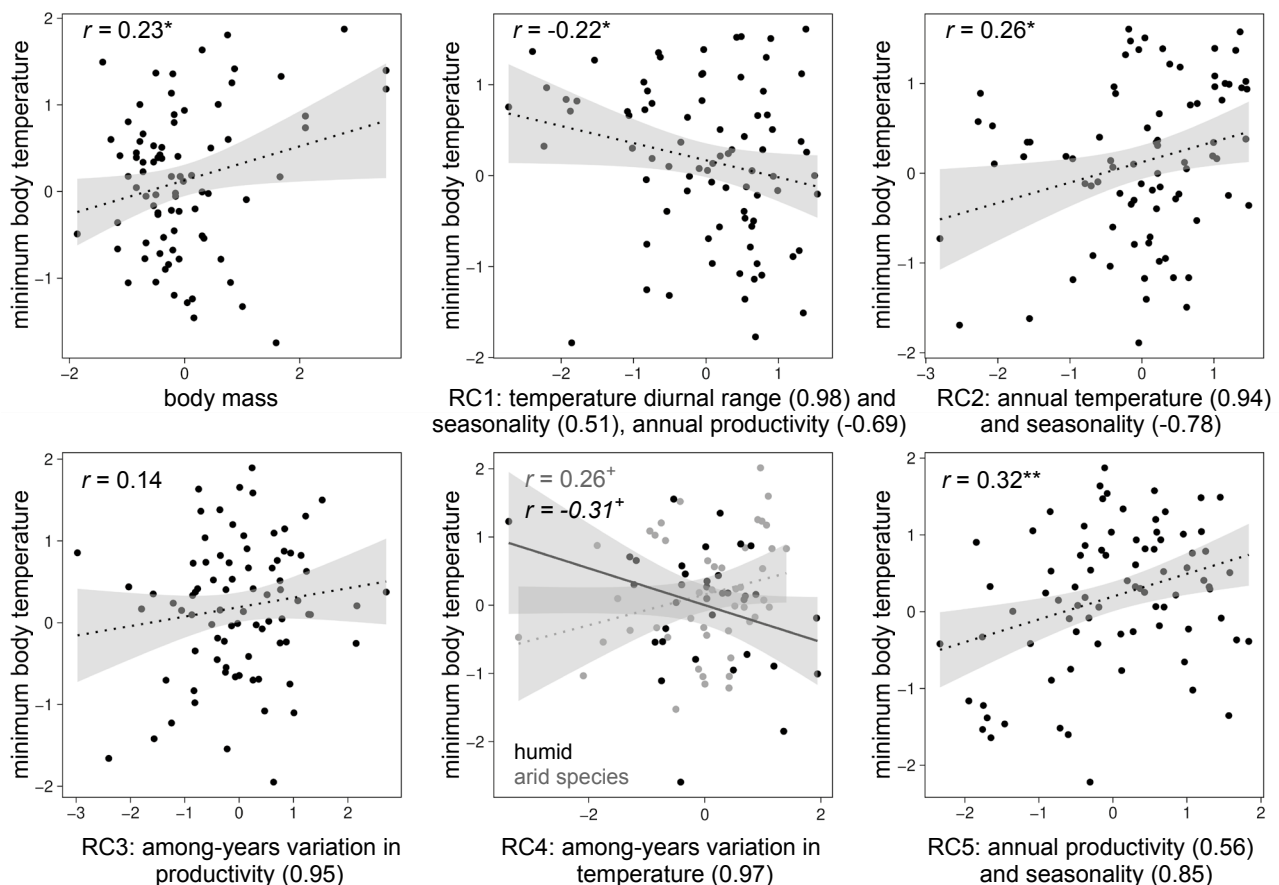
Fig. 4. Bivariate plots for the relationships between traits from multivariate phylogenetically generalized least squares (PGLS) results (lines ± confidence intervals) plotted against the raw data (dots). Residuals of species minimum body temperature are plotted against body mass and principal components calculated from environmental predictors (Fig. 1). Residuals of minimum body temperature were calculated from PGLS regression of minimum body temperature on predictors in the multivariate PGLS analysis (Table 1), except the predictor plotted on the given panel. Presented are Pearson's product-moment correlations (r; **P < 0.01, *P < 0.05, ⁺P < 0.08). X-axis logged and includes values of standardized loading of environmental variables to the principal components for variables with loading > 50% (Fig. 2).

negatively related to diurnal temperature range and seasonality, and positively related to annual productivity (Fig. 4). The positive effects of RC2 (β_{PGLS} (SE) = 0.27 (0.11), t = 2.37, P = 0.020) and RC5 (β_{PGLS} (SE) = 0.38 (0.12), t = 3.30, P = 0.0015) translate into positive associations with annual temperature, annual productivity and productivity seasonality, and to a negative association between temperature seasonality and BT_{min} (Fig. 4).

The direction of the relationship between BT_{min} and among-year variation in environmental temperature (RC4) differed between arid- and humid-climate species, as indicated by a significant interaction (Arid*RC4: Fig. 4; Table 1). Subsequent analyses (PCA and PGLS) were performed on data sets constrained to either arid- (AI < 0.5) or humid climate species (AI ≥ 0.5). Minimum body temperature was negatively related to among-year variation in environmental temperature in humid-climate species (β_{PGLS} (SE) = –0.42 (0.15),

t = –2.83, P = 0.0086, λ = 0.849, AIC = 103.4, n = 35); the positive trend in arid-climate species did not achieve significance (β_{PGLS} (SE) = 0.13 (0.13), t = 1.05, P = 0.30, λ = 0.614, AIC = 123.6, n = 46; Tables S5, S6). None of the detected associations were affected by body mass, with interactions between body mass and environmental predictors on BT_{min} non-significant ($|\beta_{PGLS}| < 0.16$, $|t| < 1.18$, P > 0.24).

Discussion

Physiological regulation of core body temperature is a key characteristic of endothermic animals (Ruben 1995, Lovegrove 2017). As a vital aspect of their biology, precise temperature regulation is sometimes postulated to have facilitated the ecological and evolutionary success of birds and mammals (Koteja 2000, Lovegrove 2017). However, there is growing recognition of deviations from tight homeothermic regulation in many lineages of mammals, resulting in the evolution of the

capacity to temporarily abandon homeothermy, such as daily heterothermy (Geiser 1988, Boyles et al. 2011, Geiser & Brigham 2012, Dammhahn et al. 2017). The phylogenetic analysis presented here showed that minimum body temperature can be determined by environmental predictors (Table 1). Variation in primary productivity and thermal environment together explained around half of the observed variation among studied species in minimum body temperature. In particular, low primary productivity and narrow seasonality in productivity predicted the low minimum body temperature observed in some species. At the same time, low environmental temperature and wide daily and seasonal variation in temperature predicted low minimum body temperature. Interestingly, among-year variation in primary productivity had a negligible influence on variation among species minimum body temperature. In contrast, among-year variation in environmental temperature had the opposite effect on minimum body temperature between mammals inhabiting relatively arid and relatively humid areas.

It was predicted that mammals exposed to warmer temperatures would express lower levels of heterothermy than those inhabiting colder areas (Nowack et al. 2017, Boratyński et al. 2018, Dausmann et al. 2020). Indeed, our analyses showed that higher annual environmental temperature (the main contributor to the second principal component: Fig. 3) resulted in higher minimum body temperature in the studied mammals (Fig. 4, Table 1). However, in addition to annual temperature we found that the parameters determining temperature variability substantially contributed to explained variation in minimum body temperature. A wide diurnal temperature range (main contributor to the first principal component: Fig. 3) was observed in areas inhabited by mammals with relatively low minimum body temperature (Fig. 4). Also, wide seasonal temperature variation (the main contributor to both the first and second principal components) was observed in areas inhabited by mammals with relatively low minimum body temperature (Fig. 4). Therefore, it can be postulated that lower annual environmental temperatures and wider amplitude of daily and seasonal temperature fluctuations are associated with the evolution of mechanisms for temporal down-regulation of body temperature in mammals. Interestingly, the effects of annual temperature level and daily temperature range contributed independently to variation in

minimum body temperature. These environmental predictors were not correlated (Table S1) and contributed to two independent environmental principal components, both important predictors of mammalian daily heterothermy (Fig. 3). This statistical independence suggests that variation in the two predictors can lead to the origin of heterothermy independently, and when occurring simultaneously can reinforce evolutionary and physiological responses in exposed organisms. Consequently, areas of wide daily temperature variation and low annual environmental temperatures, such as relatively cold arid and semi-arid regions, and high-altitude regions around equator, are particularly anticipated to host mammals expressing daily heterothermy physiology (Geiser & Turbill 2009, McKechnie & Mzilikazi 2011, Okrouhlík et al. 2021).

Among-year variation in environmental temperature has a contrasting effect for mammals inhabiting relatively arid and relatively humid regions (Fig. 4, Table 1). This effect was strong in mammals from relatively humid areas (Tables S5, S6), predicting a lower level of minimum body temperature in species inhabiting regions with wide among-year variation in environmental temperature (Fig. 4). It has been previously hypothesized that an increased level of heterothermy, in otherwise homeothermic animals, could be a mechanism facilitating species to survive extreme climatic changes (Boyles et al. 2011, Geiser & Brigham 2012). The negative and strong covariation between minimum body temperature and among-year variation in environmental temperature is the first quantification of the relationship that supports the hypothesis. Our comparative results suggest that endothermic animals inhabiting areas with greater levels of temperature unpredictability have evolved temporal suspension of homeothermy, which could facilitate their survival during thermally harsh and unpredictable conditions. Such a mechanism seems not to operate in species inhabiting arid regions, where other environmental factors, such as the low level of primary productivity (Tables S5, S6), in addition to environmental temperature variation, are limiting to physiological and population responses (Lovegrove 2000b, Barros et al. 2018).

Daily heterothermy levels may be influenced by resource availability determined by variation in habitat productivity (Brown & Bartholomew 1969, Bozinovic et al. 2005, Nespolo et al. 2010). Low

primary productivity may stimulate expression of temporal body temperature down-regulation, when resources in the environment are too scarce to fulfil the high energetic demands of homeothermic endothermy. Indeed, we established that low annual environmental productivity (a contributor to the second and fifth principal components: Fig. 3) predicted a low level of minimum body temperature in some mammals (Fig. 4, Table 1). Seasonality in primary productivity was positively correlated with its annual level (and also contributed to the fifth principal component: Fig. 3), suggesting that seasonal variation in productivity is higher in more productive areas. Together, the annual level and seasonality in productivity had the strongest positive association with minimum body temperature among mammals (Table 1). Annual productivity was negatively correlated with diurnal temperature range and temperature seasonality (and contributed to the same, first, principal component: Fig. 3). These environmental predictors, low annual productivity and wider temperature variation, set climatic conditions that promoted the occurrence of heterothermy in mammals (Fig. 4). In contrast, among-year variation in primary productivity was the poorest predictor of variation in minimum body temperature observed among the studied mammals. Thus, it can be concluded that a certain minimum level of primary productivity is needed to support energetically costly homeothermic endothermy and, whenever such condition is not fulfilled and species experience wide temperature fluctuations, heterothermic strategy is expected to evolve. Despite more than three orders of magnitude in body mass variation in our data the environmental effects on daily heterothermy were not associated with the body size of the studied mammals. We recognise that our results are derived only from 81 mammalian species, thus we do not provide overwhelming evidence for the absence of the effects of body mass on environmental constraints to daily heterothermy. However, if this result is representative it suggests that environmental predictors impose relatively similar selective forces on daily temperature regulation between large and small mammalian species.

Conclusions

Animals collect and transform energy from the environment and allocate it to physiological processes and ultimately to fitness (Boratyński & Koteja 2009, Boratyński et al. 2010, Dammhahn et

al. 2017, Boratyński & Szafrańska 2018, Boratyński 2020, Desforges et al. 2020, Pettersen et al. 2020). We showed that the environmental predictors of primary productivity and environmental temperature, can determine the minimum body temperature observed in mammals. Minimum body temperature results from down regulation of physiological processes that can indicate the intensity of expressed heterothermy (Brown & Bartholomew 1969, Körtner & Geiser 2000). Thus, our results provide evidence that a physiological strategy to save energy, daily heterothermy, is expected to evolve in mammals (Fig. 2, Table 1). Among-year variation in environmental temperature, irrespectively of among-year variation in habitat productivity, strongly predicted low minimum body temperature observed among mammalian species. This result supports the hypothesis that mammals that evolved daily body temperature down-regulation may experience a greater chance of surviving extinction arising from environmental temperature changes (Lovegrove 2000b, Boyles et al. 2011). Our results suggest that such a mechanism does not apply in arid-adapted fauna, reinforcing our understanding of their sensitivity to habitat and climatic alterations (Brito et al. 2016). At the same time, an overall decreased level of primary productivity was a strong predictor of low minimum body temperature, confirming that heterothermy emerges when energetic requirements to support endothermic homeothermic regulation cannot be fulfilled (Rezende et al. 2020). To conclude, our results clearly show that low minimum body temperature is promoted by certain environmental conditions. In particular, organisms expressing low minimum body temperatures are predicted to inhabit regions of low but variable environmental temperature, and a low level and narrow seasonality in environmental productivity. Further research will verify whether results for minimum body temperature are confirmed by direct estimates of daily body temperature fluctuations, related to behavioural performance, locomotory activity, metabolic and food consumption rates (Boratyński et al. 2020, Nowack et al. 2020).

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Supplementary online material

Fig. S1. Raster workflow of estimated NDVI statistics. The figure presents steps of how between-year variation in productivity was estimated. Step 1: estimation of per pixel summary statistics (mean or SD) from 24 raster layers per year (two per month). Step 2: estimation of summary statistics as in Step 1 for the years 1982-2015 resulting in 34 raster layers, one for each year. Step 3: estimation of per pixel summary statistics (mean or SD) from the 34 raster layers produced in Step 2, resulting in one raster layer. Step 4: extracting values from the single raster layer produced in Step 3 that overlap species distributions (shapefile polygons from IUCN terrestrial mammal dataset) to estimate median values within the range of the species. Summary statistics for NDVI estimated at each step for variables used in this study, medians of: averages of yearly

means (PM: Step 1 mean, Step 3 mean, Step 4 median), averages of yearly SDs (PS: Step 1 SD, Step 3 mean, Step 4 median) and average SDs of yearly means (PSD: Step 1 mean, Step 3 SD, Step 4 median).

Table S1. Correlation matrix of variables for 81 studied mammalian species. BT_{min} and BM refer to minimum core body temperature and body mass, respectively. Bioclimatic variables include annual median (TM) and standard deviation (TSD) of environmental temperature (BIO1), median diurnal temperature range (TR; BIO2) and temperature seasonality (TS; BIO4). Indices of yearly levels of primary productivity (PM; median of yearly averages), among year variation in productivity (PSD; median of standard deviations of yearly averages) and seasonality of productivity (PS; median of within years standard deviations) were calculated from NDVI data and species ranges. *$P \leq 0.05$, **$P \leq 0.001$.

Table S2. Differences in studied variables between arid (factor level = 1) and non-arid species (level = 0). Results for ordinary (OLS) and phylogenetic (PGLR) generalized least squares.

Table S3. Results from rotated principal component analysis of environmental predictors calculated from species ranges of 81 mammals. Percentages of explained variation in environmental variables by the rotated principal components (RCs) and standardized loadings of environmental variables to the given components are presented. The main environmental predictor loadings to the components are indicated in bold.

Table S4. Model selection procedure applied in the study. The full model included the factors aridity, body mass, five principal components and two-way interactions. The predictors "reduced predictor" refers to a predictor included in the above model (see "statistics of reduced predictor") but excluded in the given analysis.

Table S5. Results from two rotated principal component analysis of environmental predictors calculated from species ranges of 46 arid and 35 non-arid mammals. Percentages of explained variation in environmental variables by the rotated principal components (RCs) and standardized loading of environmental variable to the given components are presented.

Table S6. Parameter estimates for two phylogenetically generalized least squares (PGLS) analyses of environmental variables predicting minimum body temperature in arid ($R_{ls}^2 = 0.50$, $R_{ce}^2 = 0.47$, $R_{lr}^2 = 0.41$) and non-arid mammals ($R_{ls}^2 = 0.44$, $R_{ce}^2 = 0.44$, $R_{lr}^2 = 0.31$).

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