

# *The decoupled nature of basal metabolic rate and body temperature in endotherm evolution*

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*Title:* The decoupled nature of basal metabolic rate and body temperature in endotherms evolution

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22 The origin of endothermy in birds and mammals are iconic events in vertebrate  
23 evolution. Endotherms can maintain their body temperature ( $T_b$ ) over a wide range  
24 of ambient temperatures ( $T_a$ ) using primarily the heat generated continuously by  
25 their high basal metabolic rates ( $BMR$ )<sup>1</sup>. There is also an important positive  
26 feedback loop in that  $BMR$  itself is influenced by  $T_b$ <sup>1-3</sup>. Owing to this, many  
27 ecologists and evolutionary physiologists posit that the evolution of  $BMR$  and  $T_b$   
28 must have been coupled during the radiation of endotherms<sup>3-5</sup>, changing with  
29 similar trends<sup>6-8</sup>. However, colder historical environments might have imposed  
30 strong selective pressures on  $BMR$  to compensate for increased rates of heat loss and  
31 to keep  $T_b$  constant<sup>9-12</sup>. Thus, adaptation to cold  $T_a$  via  $BMR$  increases could have  
32 decoupled  $BMR$  from  $T_b$  and caused different evolutionary routes to the modern  
33 diversity in these traits. Here we show that  $BMR$  and  $T_b$  were decoupled in ~ 90% of  
34 mammalian and in ~ 36 % of avian phylogenetic branches. Mammalian  $BMR$   
35 evolved with rapid bursts but without any long-term directional trend, whereas  $T_b$   
36 evolved mostly at a constant rate and towards colder bodies from a warmer-bodied  
37 ancestor. Avian  $BMR$  evolved predominantly at a constant rate – again with no  
38 trend, whereas  $T_b$  evolved with much greater rate heterogeneity than  $BMR$  and  
39 there has been adaptive evolution towards colder bodies. Furthermore, rapid shifts  
40 leading to both  $BMR$  increases and decreases were linked to abrupt changes  
41 towards colder  $T_a$  but only in mammals. Our results suggest that natural selection  
42 effectively exploited the diversity of mammalian  $BMR$  under diverse, often adverse  
43 historical thermal environments.

45 Phylogenetic statistical methods<sup>13, 14</sup> now provide us with the opportunity to formally test  
46 whether  $BMR$  has been linked to  $T_b$  or  $T_a$  throughout the evolution of birds and mammals.  
47 By accommodating for and identifying heterogeneity in the rate of phenotypic evolution  
48 these methods can detect and reconstruct accurate historical evolutionary processes<sup>15</sup>.  
49 Evaluation of the evolutionary coupling between  $BMR$  and  $T_b$  has direct consequences for  
50 several longstanding ecological and evolutionary theories (including the Metabolic  
51 Theory of Ecology) which assume coupling<sup>2-8</sup>.

52  
53 We first quantified and compared rates for  $BMR$  and  $T_b$  evolution along each branch of  
54 the time-calibrated phylogenetic trees of birds and mammals (henceforth *branch-wise*  
55 *rates*,  $r$ ; see Methods).  $r$  measures how fast a trait evolved along an individual

phylogenetic branch ( $r$  is a rate scalar by which the background rate is multiplied to increase or decrease the pace of evolution). If  $BMR$  and  $T_b$  were coupled during the evolution of endotherms, the amount of change along phylogenetic branches in both traits should be positively associated – where  $r$  is high in  $BMR$  we expect it to be high in  $T_b$  (Fig. 1 b). We tested this prediction against alternative evolutionary scenarios. Firstly, we cannot make any inferences about coupling or decoupling where there is no rate heterogeneity for both  $BMR$  and  $T_b$  ( $r = 1$  for all branches in the tree for both traits; Fig. 1a). Secondly, we infer decoupled evolution if both traits show rate heterogeneity, but the magnitudes of  $rs$  are negatively correlated (*i.e.* branches evolving at a high rate for  $BMR$  are evolving at a low rate for  $T_b$ , and vice-versa, Fig. 1c). We suggest this scenario implies decoupled evolution because a negative correlation most likely implies that one trait tends to be conserved whilst the other evolved rapidly. Thirdly, we infer decoupled evolution if only one trait shows rate heterogeneity while the other evolved at a constant rate (Fig 1d and e) or if both traits show heterogeneity but the *branch-wise rates* are not associated (Fig 1f).

As  $BMR$ , body mass ( $Mass$ ),  $T_b$ , and  $T_a$  are at least to some extent correlated in extant birds and mammals, and such correlations may vary between orders<sup>16</sup>, we estimated the *branch-wise rates* for  $BMR$  and  $T_b$  while accounting for their covariates across extant species using the *phylogenetic variable-rates regression* model<sup>17</sup> (henceforth *variable-rates*; Methods). This approach allows for simultaneous estimation of both an overall relationship between, for instance,  $BMR$  as a function of  $Mass$  and  $T_b$  across extant species, and any shifts in rates ( $r$ ) that apply to the phylogenetically structured residual

variance in the relationship. In both birds and mammals, the *variable-rates* model significantly fits the data better than the *constant-rate regressions*, which assume a single rate across all branches (Methods; Table S1 to S8). The best fitting *variable-rates* model for mammalian *BMR* includes both *Mass* and  $T_b$  with a single slope for each trait estimated across all orders (Table S1 and S2). For mammalian  $T_b$ , the best fitted model includes *Mass* and *BMR* as covariates, also with a single slope across all orders (Table S3 and S7). In birds, the best model for *BMR* includes only *Mass* with a single slope for all orders (Table S4). Finally, the best fitted model for avian  $T_b$  includes *Mass* only in Columbiformes (Table S6).

The *branch-wise rates* estimated in the best fitting models shows that mammalian *BMR* evolved at a constant rate ( $r = 1$ ) in just 11.2% of branches and at faster rates ( $r > 1$ ) in 88.8% of branches (Fig. 2a). Mammalian  $T_b$  evolved at a constant rate in 70.3% of branches and faster rates in 29.7% of branches (Fig. 2b). In birds, *BMR* evolved at a constant rate in 90.5% of branches and at faster rates in 9.5% of branches (Fig. 2d). Avian  $T_b$  evolved at a constant rate in 69 % of branches and at faster rates in 31% (Fig. 2e). When the *branch-wise rates* for *BMR* and  $T_b$  were compared, we found that in mammals, both traits evolved at a constant rate in 10.6% of branches (Fig. 3a consistent with Fig. 1a). In 60.2% of branches only one trait evolved at faster rates while the other trait diverged at a constant rate. This indicates that *BMR* and  $T_b$  evolved in a decoupled fashion along these branches (Fig. 3a consistent with Fig. 1d, e). We found that 29.2% of branches had an increased rate in both *BMR* and  $T_b$ . However, the magnitudes of the *branch-wise rates* were not significantly correlated ( $p_{\text{MCMC}}$  [% of posterior distribution

crossing zero] = 9%; Table S9; Fig. 3a consistent with Fig 1f). This also suggests decoupled evolution in those branches – likely because of distinct selection pressures acting on *BMR* and *T<sub>b</sub>*. On the other hand, both traits evolved at a constant rate in 63.8% of branches for birds (Fig. 3c consistent with Fig. 1a). In 32% of branches only one trait evolved at fast rates while the other trait diverged at a constant rate (Fig. 3c consistent with Fig. 1d, e). In the remaining 4.2% of branches, both traits evolved at faster rates, but the *r* magnitudes were not statistically correlated ( $p_{\text{MCMC}} = 16.9\%$ , Table S10, Fig. 3c consistent with Fig. 1f).

As rapid bursts in *BMR* evolution were not coupled with those in *T<sub>b</sub>* evolution, we evaluated the alternative hypothesis postulating that *BMR* evolved in response to *T<sub>a</sub>*. This hypothesis suggests that colder environments increase the rate of heat lost from organisms which is subsequently compensated by *BMR* increases<sup>9-12</sup>. These *BMR* increases could have occurred over long periods of time because of global cooling<sup>18</sup> - generating a long-term directional trend in *BMR* during the radiation of mammals and birds. This expectation is in line with the Plesiomorphic-Apomorphic Endothermy Model<sup>6-8</sup> (PAE Model). By assuming that *BMR* and *T<sub>b</sub>* are coupled in endotherms and that they both can be used as a proxy of the degree of endothermy, the PAE model predicts a general tendency towards higher endothermic levels through time (from basoendothermic ancestors, Methods) associated with the Cenozoic global cooling. Global cooling is not the only source of variation in *T<sub>a</sub>*. Long-term directional increases in *BMR* might have also been driven by historical dispersals of endotherms towards higher latitudes<sup>19</sup>. In either case, if a long-term decrease in *T<sub>a</sub>* drove adaptation via *BMR* elevation, and *T<sub>b</sub>*

125 followed the same trajectory (as assumed by the PAE model) we expect to find a positive  
126 correlation between the *branch-wise rates* of *BMR* and the *branch-wise rates* of  $T_a$ . With  
127 this in mind, we also expect a positive trend towards higher *BMR* and  $T_b$  values from  
128 basoendothermic ancestors and a negative trend towards lower  $T_a$  from warmer ancestral  
129 environments. We used the *variable-rates* model to estimate the *branch-wise rates* for  $T_a$   
130 whilst accounting for latitude since, generally,  $T_a$  decreases from the equator to the poles  
131 (Methods; Table S11).

132  
133 The *variable-rates* model significantly improved the fit to the  $T_a$  data over the *constant-*  
134 *rate* regression model in both mammals and birds (Table S11). In 21.2% of mammalian  
135 branches  $T_a$  evolved at a constant rate, and with rate heterogeneity in the remaining  
136 78.8% – including 72.2% of branches with faster rates and 6.6% with slower rates ( $r < 1$ ,  
137 Fig. 2c). This indicates that most ancestral mammalian lineages (72.2%) faced abrupt  
138 historical changes in their  $T_a$ , while far fewer lineages (6.6%, mostly bats) survived and  
139 continued existing in similar thermal environments. In birds, 77.6% of branches show  
140 faster rates of  $T_a$  change, 22.1% show changes at a constant rate, and in only a single  
141 branch the  $T_a$  changed at a slower rate (Fig. 2f).

142  
143 When *branch-wise rates* of mammalian *BMR* and  $T_a$  evolution were compared, we found  
144 that they were coupled in 74.9% of branches ( $p_{\text{MCMC}} = 0\%$ ; Table S12; Fig. 3b, consistent  
145 with Fig. 1b). To evaluate further if  $T_a$  decreases were linked to *BMR* increases in the  
146 74.9% of mammals where both traits were coupled (i.e. to ascertain the direction of  
147 change), we evaluated the expected positive trend in *BMR* as a response to the long-term



decrease in  $T_a$ . We conducted Bayesian phylogenetic regressions between extant values of these two variables (in turn) and the *path-wise rates* (sum of *branch-wise rates* along branches in the path from the root of the tree to each terminal species, Methods)<sup>15</sup>. We found a negative effect of *path-wise rates* on  $T_a$  across all mammals (Fig. 4b; Table S14), which supports a long-term directional trend towards habitats with lower  $T_a$  over time. However, we did not find evidence for any trend in mammalian *BMR* evolution – *BMR* increases and decreases were equally likely in our sample (Table S14). Our results suggest that in colder environments, where resources were available to fuel metabolic elevation, selection favoured higher mammalian *BMR*<sup>20</sup>. Another possibility might be that *BMR* increase was a correlated response to direct selection on other physiological traits, like maximal metabolic capacities for thermogenesis, whose benefits outweigh the energetic cost of *BMR* elevation<sup>20</sup>. Otherwise, selection may have always favoured *BMR* decreases under an ever colder environment<sup>20</sup>.

In contrast to mammals, most avian branches that experienced rapid shifts in  $T_a$  did not show evidence of coupled changes in *BMR* – 68.4% of branches had fast rates of  $T_a$  evolution but a constant rate of *BMR* evolution (Fig. 3d consistent with Fig. 1d, e). Moreover, the small fraction of branches where *BMR* evolved at fast rates (9.5%) were not linked to rapid shifts in  $T_a$  (Fig. 3d consistent with Fig. 1f; Table S13). Avian *BMR* did not show a positive evolutionary trend despite the fact they also experienced colder environments over time (Fig. 4d; Table S15). Birds might not have responded to colder temperatures by changes in their *BMR* because their lower thermal conductance might

have helped them retain internal heat<sup>9</sup>. Alternatively, other physiological strategies, such as torpor, may have been selected for under colder environments<sup>21</sup>.

Finally, we found a negative effect of *path-wise rates* on  $T_b$  in both mammals (Fig. 4a; Table S14) and birds (Fig. 4c; Table S15). This suggest that – on average – endotherms evolved towards colder bodies from warmer-bodied ancestors. These directional models predict a mean  $T_b$  of 35.3 °C and 40.4 °C in the most recent common ancestor (MRCA) of mammals and birds respectively (Fig. 4a, c), suggesting that early birds and mammals were mesoendotherm rather than basoendotherms (Methods). This result does not support that ancestral mammals could not attain  $T_b > 30$  °C owing to the elevated metabolic rates necessary to compensate heat loss in cold environments<sup>22</sup>. However, if the  $T_b - T_a$  differential ( $\Delta T$ ) determines how hot early mammals were, we expect that the mammalian MRCA with a  $T_b$  of 35.3 °C could survive in an environment warm enough to have a low  $\Delta T$ . Our model describing the negative trend in  $T_a$  predicts that the MRCA of mammals lived in an environment with 23 °C on average (Fig. 4b), resulting in a  $\Delta T$  of 15.3 °C. This ancestral  $\Delta T$  is very conservative compared with the  $\Delta T$ s observed in extant mammals. For example, there are small mammals that achieve  $T_b$  higher than 39 °C (e.g. *Microdipodops pallidus*<sup>16</sup>) that can survive in environments of 11 °C<sup>19</sup> ( $\Delta T = 28$  °C). Also, some larger mammals have stable  $T_b$  even in extreme environmental conditions – the Artic hare (*Lepus arcticus*) can maintain its  $T_b$  of 38 °C<sup>16</sup> in temperatures as low as -12 °C<sup>19</sup> ( $\Delta T = 50$  °C).

Taken together, our results reveal that *BMR* was not coupled with  $T_b$  across the evolution of endothermic species. As environments became colder, mammals survived by changing their *BMR*, while birds likely survived owing to their high thermal insulation. Evaluating the isolated and/or combined effect of environmental variables on physiological attributes has implications for evidence-based projections for the future<sup>23</sup>. In this sense, the previously unappreciated complexity, interplay and decoupled nature in the evolutionary history of *BMR*,  $T_b$  and  $T_a$  might point to undetected resilience of endotherms in the face of modern global challenges.

#### Figure legends.

**Figure 1. Possible evolutionary scenarios between *BMR* and  $T_b$  given their branch-wise rates ( $r$ ) in a bivariate space.** Grey colours represent the constant background rate ( $r = 1$ ). Red colours represent rates faster than the background rate ( $r > 1$ ) and blue colours represent rates slower than the background rate ( $r < 1$ ), which might be related to past events of positive<sup>17</sup> and stabilizing selection<sup>29</sup> respectively. Point fill colours represent *BMR* rates and point outline colours represent  $T_b$  rates.

**Figure 2. Branch-wise rates ( $r$ ) of *BMR*,  $T_b$ , and  $T_a$  on the mammalian and avian phylogeny.** Silhouettes courtesy of Phylopic/Apokryltaros (vectorized by T. Michael Keeseey), Becky Barnes, Doug Backlund et al., Emily Willoughby, Enoch Joseph et al., Estelle Bourdon, Ferran Sayol, FunkMonk, Jon Hill (Photo by DickDaniels), L. Shyamal, Lip Kee Yap (modified), Mathew Callaghan, Matt Martyniuk, nicubunu, Pearson Scott

Foresman, Prin Pattawaro et al., Rebecca Groom, Sarah Werning, T. Michael Keesey

(after Joseph Wolf), Yan Wong, Steven Traver. Silhouette licence links:

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**Figure 3. Branch-wise rates ( $r$ ) of  $BMR$ ,  $T_b$ , and  $T_a$  in bivariate space for mammals**

**(a, b) and birds (c, d).** Bayesian GLS analyses indicates that only fast *branch-wise rates* for  $BMR$  and slow-fast *branch-wise rates* of  $T_a$  were statistically correlated in mammals ( $p_{MCMC} = 0$ ;  $n = 602$  branches; black line).

**Figure 4. Mammals (a, b) and birds (c, d) evolved towards both colder  $T_b$  and  $T_a$**

**over their evolutionary history.** *Path-wise rates* had a significant negative effect in mammalian and avian  $T_b$  ( $p_{MCMC} = 4\%$  and  $3\%$ ;  $n = 502$  and  $367$  species) and in mammalian and avian  $T_a$  ( $p_{MCMC} = 0$  and  $0$ ;  $n = 2922$  and  $6142$  species), both supporting a negative macroevolutionary trend<sup>15</sup>. Transparent and dark lines indicate the posterior distribution of slopes and the mean slope respectively, estimated from the Bayesian PGLS (Methods).

## **Methods.**

**Data.** We used a time-calibrated phylogenetic tree of extant mammals ( $n = 3321$ )<sup>24</sup>, and the body mass ( $M$ ), basal metabolic rate ( $BMR$ ), and body temperature ( $T_b$ ) taken from Clarke et al.<sup>16</sup> ( $n = 632$ ). After identifying species in the tree that have trait information,

we obtained a final mammalian dataset of 502 species, which includes representatives from 15 orders (SI).

For birds, we used the consensus time-calibrated tree from Rolland et al.<sup>19</sup>. This tree was inferred from the samples of trees provided by Jetz et al.<sup>25</sup>. Data for *BMR*,  $T_b$ , and *Mass* were obtained from Fristoe et al.<sup>9</sup>. After matching this database with the phylogenetic tree, we obtained a final sample of 164 species which includes representatives from 21 orders (SI). The dataset used to evaluate evolutionary trends in  $T_b$  (see below) is from Clarke & Rothery<sup>26</sup>, which contains 367 species with phylogenetic information.

Data for ambient temperature ( $T_a$ ) and latitude for extant mammals and birds was extracted from Rolland et al.<sup>19</sup>. These datasets include 2922 species of mammals and 6142 species of birds which have phylogenetic information. The  $T_a$  for extant endothermic species is the temperature of environments in which birds and mammals inhabit today – measured as the mean ambient temperature for the mid-point latitude of each species distribution (Rolland et al.<sup>19</sup>). The  $T_a$  at which a species exists today may not be a heritable trait *per se*. However, the evolution of  $T_a$  can still be inferred using phylogenetic methods since habitat selection reflects species adaptations (traits) to some characteristics of the environment. This interrelationship should leave phylogenetic signal in the  $T_a$  at which endothermic species live. Accordingly, we found significant phylogenetic signal in the  $T_a$  of both mammals ( $\lambda_{\text{PosteriorMean}} = 0.77$ ; Bayes Factor = 665) and birds ( $\lambda_{\text{PosteriorMean}} = 0.8$ ; Bayes Factor = 1404). Furthermore, the phylogenetic signal for  $T_a$  is very high ( $\lambda=1$ ) in birds and mammals, when estimated using the median- $r$  scaled tree.

260

261 Finally, to evaluate the endothermic levels for the MRCA of mammals and birds  
262 proposed by Lovegrove<sup>7, 8</sup>, we followed his categorization of endothermic species as  
263 basoendotherms ( $T_b^{\text{Birds}} < 40.4\text{ °C}$ ;  $T_b^{\text{Mammals}} < 35.0\text{ °C}$ ), mesoendotherma ( $40.4\text{ °C} \leq$   
264  $T_b^{\text{Birds}} \leq 42.5\text{ °C}$ ;  $35\text{ °C} \leq T_b^{\text{Mammals}} \leq 37.9\text{ °C}$ ), and supraendotherms ( $T_b^{\text{Birds}} > 42.5\text{ °C}$ ;  
265  $T_b^{\text{Mammals}} > 37.9\text{ °C}$ ).

266

267 **Inferring the *branch-wise rates* of evolution.** We identified heterogeneity in the rate of  
268 evolution along phylogenetic branches (*branch-wise rates*) by dividing the rate into two  
269 parameters: a background rate parameter ( $\sigma_b^2$ ) which assumes changes in the trait of  
270 interest (e.g. *BMR*) are drawn from an underlying Brownian process, and a second  
271 parameter,  $r$ , that identifies a branch-specific rate shift. A full set of *branch-wise rates* are  
272 estimated by adjusting the lengths of each branch in a time-calibrated tree (stretching or  
273 compressing a branch is equivalent to increasing or decreasing the phenotypic rate of  
274 change relative to the underlying Brownian rate of evolution). *Branch-wise rates* are  
275 defined by a set of branch-specific scalars  $r$  ( $0 < r < \infty$ ) which transform each branch in  
276 order to optimize the phenotypic rate of change to a Brownian process ( $\sigma_b^2 r$ ). If  
277 phenotypic change occurred at accelerated (faster) rates along a specific branch of the  
278 tree, then  $r > 1$  and the branch is stretched. Decelerated (slower) rates of evolution are  
279 detected by  $r < 1$  and the branch is compressed. If the trait evolves at a constant rate  
280 along a branch, then the branch will not be modified (*i.e.*  $r = 1$ ).

281

We estimated the  $r$  values of  $BMR$ ,  $T_b$ , and  $T_a$  evolution using the *phylogenetic variable-rates regression* model in a Bayesian framework<sup>17</sup>. This model is designed to automatically detect shifts in the rate of trait evolution across phylogenetic branches while accounting for a relationship with another trait or traits across extant species values. This approach allows for simultaneous estimation of both an overall relationship between, for instance,  $BMR$  as a function of  $Mass$  and  $T_b$  across extant species, and any shifts in rates ( $r$ ) that apply to the phylogenetically structured residual variance in the relationship. As residual variance is explained by shifts in rate across phylogenetic branches we can, for example, determine how much  $BMR$  has changed in the past ( $r$ ) after accounting for their covariation with  $Mass$  and  $T_b$  in the present (the relationship between the values across extant species). Thus, if the amount of  $BMR$  change along individual phylogenetic branches were coupled with the amount of change of  $T_b$ , then we should find the  $r$  values of  $BMR$  to be positively associated with the  $r$  values of  $T_b$ . The *branch-wise rates* for  $T_b$  evolution can be estimated while accounting for its covariation with other traits or factor across extant species. Previous studies on the association between  $BMR$  and  $T_b$  using extant species values alone have not evaluated the association in evolutionary terms even when they use phylogenetic method.

We evaluated 24 *phylogenetic variable-rates regression models* and 24 *phylogenetic constant-rate regression models* (Table S1 to S8). Regression model selection was conducted using Bayes Factors ( $BF$ ) via marginal likelihoods estimated by stepping stone sampling.  $BF$  is calculated as the double of the difference between the log marginal-likelihood of the complex model and the simple model. By convention,  $BF > 2$  indicates

positive evidence for the complex model,  $BF$  5-10 indicates strong support, and  $BF > 10$  are considered very strong support<sup>27</sup>. We inferred the  $r$  values of  $BMR$  and  $T_b$  with the *phylogenetic variable-rates regression models* that best fit the data for our samples of mammals and birds (Table S7 and S8). We also estimated the  $r$  values for  $T_a$  after accounting for the effect of latitude of species distribution (Table S11) and, consequently, we accounted for the geographic variation of  $T_a$  across extant species distributions. We used BayesTraits v3.0<sup>28</sup> to detect the magnitude and location of  $r$  in a Bayesian Markov chain Monte Carlo (MCMC) reversible-jump framework, which generates a posterior distribution of trees with scaled branches lengths according to the rate of evolution. There is no limit or prior expectation in the number of the  $r$  branch-scalars,  $r$  numbers vary from zero (no branch is scaled) to  $n$ , where  $n$  is the number of branches in the phylogenetic tree. Regarding the values of each  $r$  parameter, we used a gamma prior, with  $\alpha = 1.1$  and  $\beta$  parameter rescaled in order to get the median of the distribution equal to one. With this setting, the numbers of rate increases and decreases proposed is balanced<sup>13</sup>. We ran 50,000,000 iterations sampling every 25,000 to ensure chain convergence and independence in model parameters in  $BMR$  and  $T_b$  analyses. We discarded the first 25,000 iterations as burn in. For the  $T_a$  analysis in mammals we ran 200,000,000 iterations sampling every 100,000, and we discarded the first 100,000 iterations as burn in. For  $T_a$  analysis in birds we ran 400,000,000 iterations discarding the first 100,000,000 as burn in, and we sampled every 200,000. Regression coefficients were judged as significant according to a calculated  $p_{MCMC}$  value for each posterior of regression coefficients: where  $< 5\%$  of samples in the posterior distribution crossed zero, this indicates that the coefficient is significantly different from zero.



328

329 **Testing the relationship between the *branch-wise rates* of evolution.** We first  
330 estimated the consensus branch-scaled tree for *BMR* and  $T_b$  from the posterior sample of  
331 branch-scaled trees obtained with the *phylogenetic variable-rates regression model*. The  
332 consensus branch-scaled tree was generated by using the median  $r$  from the posterior  
333 distribution. We evaluated the correlation between the  $r$  values for *BMR* and  $T_b$  using a  
334 Bayesian GLS regression in BayesTraits v3.0. The same analyses were conducted to  
335 evaluate the correlation between *branch-wise rates* for *BMR* and  $T_a$ . We used a uniform  
336 prior for the  $\beta$  (slope coefficient) ranging from -100 to 100. We ran 50,000,000 iterations  
337 sampling every 25,000 to ensure chain convergence and independence in model  
338 parameters. Significance of regression coefficients were determined as above.

339

340 **Detecting trends.** We evaluated the direction of change in *BMR*,  $T_b$ , and  $T_a$  across all  
341 mammals and birds using the *path-wise rates* of these variables (Table S15 and S16).  
342 *Path-wise rate* is the sum of all the *branch-wise rates* along the path of a species, which  
343 lead from the root (the MRCA) to the tips of the tree, and it accounts for the total changes  
344 the species has experienced during its evolution<sup>15</sup>. If high *path-wise rates* have  
345 disproportionately been associated with trait increases or decreases, we expect to find that  
346 species with greater *path-wise rates* will have high or low trait values in the present. For  
347 instance, if ancestral mammals experienced progressively colder environmental  
348 temperatures owing to climate change or colonization of colder habitats as they were  
349 evolving from their MRCA, we expect a negative correlation between the *path-wise rate*  
350 of  $T_a$  and the  $T_a$  of extant species. We performed six Bayesian PGLS regressions in

BayesTraits 3.0 to evaluate the relationship between  $BMR$ ,  $T_b$ ,  $T_a$  and their *path-wise* rates (Table S15 and S16). We used a uniform prior for the  $\beta$  (slope coefficients) ranging from -100 to 100 to allow all possible values to be equally likely. Finally, we ran 50,000,000 iterations sampling every 25,000 to ensure chain convergence and independence in model parameters. Significance of regression slopes were determined as above.

#### **End notes.**

**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Author information:** We have no competing interests.

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375 **Data availability statement.** Correspondence and request for materials should be  
376 addressed to J.A-LL. (jorgeavariall@gmail.com) or C.V. (c.d.venditti@reading.ac.uk).

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