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

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

2   evolution

3

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21

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

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

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

56   phylogenetic branch (r is a rate scalar by which the background rate is multiplied to

57   increase or decrease the pace of evolution). If BMR and T_b were coupled during the

58   evolution of endotherms, the amount of change along phylogenetic branches in both traits

59   should be positively associated – where r is high in BMR we expect it to be high in T_b

60   (Fig. 1 b). We tested this prediction against alternative evolutionary scenarios. Firstly, we

61   cannot make any inferences about coupling or decoupling where there is no rate

62   heterogeneity for both BMR and T_b ($r = 1$ for all branches in the tree for both traits; Fig.

63   1a). Secondly, we infer decoupled evolution if both traits show rate heterogeneity, but the

64   magnitudes of rs are negatively correlated (*i.e.* branches evolving at a high rate for BMR

65   are evolving at a low rate for T_b, and vice-versa, Fig. 1c). We suggest this scenario

66   implies decoupled evolution because a negative correlation most likely implies that one

67   trait tends to be conserved whilst the other evolved rapidly. Thirdly, we infer decoupled

68   evolution if only one trait shows rate heterogeneity while the other evolved at a constant

69   rate (Fig 1d and e) or if both traits show heterogeneity but the *branch-wise rates* are not

70   associated (Fig 1f).

71

72   As BMR, body mass (*Mass*), T_b, and T_a are at least to some extent correlated in extant

73   birds and mammals, and such correlations may vary between orders[16], we estimated the

74   *branch-wise rates* for BMR and T_b while accounting for their covariates across extant

75   species using the *phylogenetic variable-rates regression* model[17] (henceforth *variable-*

76   *rates*; Methods). This approach allows for simultaneous estimation of both an overall

77   relationship between, for instance, BMR as a function of *Mass* and T_b across extant

78   species, and any shifts in rates (r) that apply to the phylogenetically structured residual

79 variance in the relationship. In both birds and mammals, the *variable-rates* model

80 significantly fits the data better than the *constant-rate regressions*, which assume a single

81 rate across all branches (Methods; Table S1 to S8). The best fitting *variable-rates* model

82 for mammalian *BMR* includes both *Mass* and T_b with a single slope for each trait

83 estimated across all orders (Table S1 and S2). For mammalian T_b, the best fitted model

84 includes *Mass* and *BMR* as covariates, also with a single slope across all orders (Table S3

85 and S7). In birds, the best model for *BMR* includes only *Mass* with a single slope for all

86 orders (Table S4). Finally, the best fitted model for avian T_b includes *Mass* only in

87 Columbiformes (Table S6).

88

89 The *branch-wise rates* estimated in the best fitting models shows that mammalian *BMR*

90 evolved at a constant rate ($r = 1$) in just 11.2% of branches and at faster rates ($r > 1$) in

91 88.8% of branches (Fig. 2a). Mammalian T_b evolved at a constant rate in 70.3% of

92 branches and faster rates in 29.7% of branches (Fig. 2b). In birds, *BMR* evolved at a

93 constant rate in 90.5% of branches and at faster rates in 9.5% of branches (Fig. 2d).

94 Avian T_b evolved at a constant rate in 69 % of branches and at faster rates in 31% (Fig.

95 2e). When the *branch-wise rates* for *BMR* and T_b were compared, we found that in

96 mammals, both traits evolved at a constant rate in 10.6% of branches (Fig. 3a consistent

97 with Fig. 1a). In 60.2% of branches only one trait evolved at faster rates while the other

98 trait diverged at a constant rate. This indicates that *BMR* and T_b evolved in a decoupled

99 fashion along these branches (Fig. 3a consistent with Fig. 1d, e). We found that 29.2% of

100 branches had an increased rate in both *BMR* and T_b. However, the magnitudes of the

101 *branch-wise rates* were not significantly correlated (p_{MCMC} [% of posterior distribution

102   crossing zero] = 9%; Table S9; Fig. 3a consistent with Fig 1f). This also suggests

103   decoupled evolution in those branches – likely because of distinct selection pressures

104   acting on *BMR* and T_b. On the other hand, both traits evolved at a constant rate in 63.8%

105   of branches for birds (Fig. 3c consistent with Fig. 1a). In 32% of branches only one trait

106   evolved at fast rates while the other trait diverged at a constant rate (Fig. 3c consistent

107   with Fig. 1d, e). In the remaining 4.2% of branches, both traits evolved at faster rates, but

108   the *r* magnitudes were not statistically correlated (p_{MCMC} = 16.9%, Table S10, Fig. 3c

109   consistent with Fig. 1f).

110

111   As rapid bursts in *BMR* evolution were not coupled with those in T_b evolution, we

112   evaluated the alternative hypothesis postulating that *BMR* evolved in response to T_a. This

113   hypothesis suggests that colder environments increase the rate of heat lost from

114   organisms which is subsequently compensated by *BMR* increases[9-12]. These *BMR*

115   increases could have occurred over long periods of time because of global cooling[18] -

116   generating a long-term directional trend in *BMR* during the radiation of mammals and

117   birds. This expectation is in line with the Plesiomorphic-Apomorphic Endothermy

118   Model[6-8] (PAE Model). By assuming that *BMR* and T_b are coupled in endotherms and that

119   they both can be used as a proxy of the degree of endothermy, the PAE model predicts a

120   general tendency towards higher endothermic levels through time (from basoendothermic

121   ancestors, Methods) associated with the Cenozoic global cooling. Global cooling is not

122   the only source of variation in T_a. Long-term directional increases in *BMR* might have

123   also been driven by historical dispersals of endotherms towards higher latitudes[19]. In

124   either case, if a long-term decrease in T_a drove adaptation via *BMR* elevation, and T_b

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 ($p_{MCMC} = 0\%$; 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

148   decrease in T_a. We conducted Bayesian phylogenetic regressions between extant values

149   of these two variables (in turn) and the *path-wise rates* (sum of *branch-wise rates* along

150   branches in the path from the root of the tree to each terminal species, Methods)[15]. We

151   found a negative effect of *path-wise rates* on T_a across all mammals (Fig. 4b; Table S14),

152   which supports a long-term directional trend towards habitats with lower T_a over time.

153   However, we did not find evidence for any trend in mammalian *BMR* evolution – *BMR*

154   increases and decreases were equally likely in our sample (Table S14). Our results

155   suggest that in colder environments, where resources were available to fuel metabolic

156   elevation, selection favoured higher mammalian *BMR*[20]. Another possibility might be that

157   *BMR* increase was a correlated response to direct selection on other physiological traits,

158   like maximal metabolic capacities for thermogenesis, whose benefits outweigh the

159   energetic cost of *BMR* elevation[20]. Otherwise, selection may have always favoured *BMR*

160   decreases under an ever colder environment[20].

161

162   In contrast to mammals, most avian branches that experienced rapid shifts in T_a did not

163   show evidence of coupled changes in *BMR* – 68.4% of branches had fast rates of T_a

164   evolution but a constant rate of *BMR* evolution (Fig. 3d consistent with Fig. 1d, e).

165   Moreover, the small fraction of branches where *BMR* evolved at fast rates (9.5%) were

166   not linked to rapid shifts in T_a (Fig. 3d consistent with Fig. 1f; Table S13). Avian *BMR*

167   did not show a positive evolutionary trend despite the fact they also experienced colder

168   environments over time (Fig. 4d; Table S15). Birds might not have responded to colder

169   temperatures by changes in their *BMR* because their lower thermal conductance might

170   have helped them retain internal heat[9]. Alternatively, other physiological strategies, such

171   as torpor, may have been selected for under colder environments[21].

172

173   Finally, we found a negative effect of *path-wise rates* on T_b in both mammals (Fig. 4a;

174   Table S14) and birds (Fig. 4c; Table S15). This suggest that – on average – endotherms

175   evolved towards colder bodies from warmer-bodied ancestors. These directional models

176   predict a mean T_b of 35.3 °C and 40.4 °C in the most recent common ancestor (MRCA)

177   of mammals and birds respectively (Fig. 4a, c), suggesting that early birds and mammals

178   were mesoendotherm rather than basoendotherms (Methods). This result does not support

179   that ancestral mammals could not attain $T_b > 30$ °C owing to the elevated metabolic rates

180   necessary to compensate heat loss in cold environments[22]. However, if the T_b-T_a

181   differential (ΔT) determines how hot early mammals were, we expect that the mammalian

182   MRCA with a T_b of 35.3 °C could survive in an environment warm enough to have a low

183   ΔT. Our model describing the negative trend in T_a predicts that the MRCA of mammals

184   lived in an environment with 23 °C on average (Fig. 4b), resulting in a ΔT of 15.3 °C.

185   This ancestral ΔT is very conservative compared with the ΔTs observed in extant

186   mammals. For example, there are small mammals that achieve T_b higher than 39 °C (e.g.

187   *Microdipodops pallidus*[16]) that can survive in environments of 11 °C[19] ($\Delta T = 28$ °C).

188   Also, some larger mammals have stable T_b even in extreme environmental conditions –

189   the Artic hare (*Lepus arcticus*) can maintain its T_b of 38 °C[16] in temperatures as low as -

190   12 °C[19] ($\Delta T = 50$ °C).

191

192   Taken together, our results reveal that *BMR* was not coupled with T_b across the evolution

193   of endothermic species. As environments became colder, mammals survived by changing

194   their *BMR*, while birds likely survived owing to their high thermal insulation. Evaluating

195   the isolated and/or combined effect of environmental variables on physiological attributes

196   has implications for evidence-based projections for the future[23]. In this sense, the

197   previously unappreciated complexity, interplay and decoupled nature in the evolutionary

198   history of *BMR*, T_b and T_a might point to undetected resilience of endotherms in the face

199   of modern global challenges.

200

201   **Figure legends.**

202

203   **Figure 1. Possible evolutionary scenarios between *BMR* and T_b given their *branch-**

204   **wise rates* (*r*) in a bivariate space**. Grey colours represent the constant background rate

205   ($r = 1$). Red colours represent rates faster than the background rate ($r > 1$) and blue

206   colours represent rates slower than the background rate ($r < 1$), which might be related to

207   past events of positive[17] and stabilizing selection[29] respectively. Point fill colours

208   represent *BMR* rates and point outline colours represent T_b rates.

209

210   **Figure 2. *Branch-wise rates* (*r*) of *BMR*, T_b, and T_a on the mammalian and avian**

211   **phylogeny.** Silhouettes courtesy of Phylopic/Apokryltaros (vectorized by T. Michael

212   Keesey), Becky Barnes, Doug Backlund et al., Emily Willoughby, Enoch Joseph et al.,

213   Estelle Bourdon, Ferran Sayol, FunkMonk, Jon Hill (Photo by DickDaniels), L. Shyamal, Lip

214   Kee Yap (modified), Mathew Callaghan, Matt Martyniuk, nicubunu, Pearson Scott

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

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

217 https://creativecommons.org/licenses/by/3.0/;

218 https://creativecommons.org/licenses/by-sa/3.0/.

219

220 **Figure 3. *Branch-wise rates* (*r*) of *BMR*, *T*$_b$, and *T*$_a$ in bivariate space for mammals**

221 **(a, b) and birds (c, d).** Bayesian GLS analyses indicates that only fast *branch-wise rates*

222 for *BMR* and slow-fast *branch-wise rates* of T_a were statistically correlated in mammals

223 (p_{MCMC} = 0; n = 602 branches; black line).

224

225 **Figure 4. Mammals (a, b) and birds (c, d) evolved towards both colder *T*$_b$ and *T*$_a$**

226 **over their evolutionary history.** *Path-wise rates* had a significant negative effect in

227 mammalian and avian T_b (p_{MCMC} = 4% and 3%; n = 502 and 367 species) and in

228 mammalian and avian T_a (p_{MCMC} = 0 and 0; n = 2922 and 6142 species), both supporting

229 a negative macroevolutionary trend[15]. Transparent and dark lines indicate the posterior

230 distribution of slopes and the mean slope respectively, estimated from the Bayesian

231 PGLS (Methods).

232

233 **Methods.**

234 **Data**. We used a time-calibrated phylogenetic tree of extant mammals (n = 3321)[24], and

235 the body mass (*M*), basal metabolic rate (*BMR*), and body temperature (*T*$_b$) taken from

236 Clarke et al.[16] (n = 632). After identifying species in the tree that have trait information,

237   we obtained a final mammalian dataset of 502 species, which includes representatives

238   from 15 orders (SI).

239

240   For birds, we used the consensus time-calibrated tree from Rolland et al.[19]. This tree was

241   inferred from the samples of trees provided by Jetz et al[25]. Data for *BMR*, T_b, and *Mass*

242   were obtained from Fristoe et al[9]. After matching this database with the phylogenetic

243   tree, we obtained a final sample of 164 species which includes representatives from 21

244   orders (SI). The dataset used to evaluate evolutionary trends in T_b (see below) is from

245   Clarke & Rothery[26], which contains 367 species with phylogenetic information.

246

247   Data for ambient temperature (T_a) and latitude for extant mammals and birds was

248   extracted from Rolland et al.[19] These datasets include 2922 species of mammals and 6142

249   species of birds which have phylogenetic information. The T_a for extant endothermic

250   species is the temperature of environments in which birds and mammals inhabit today –

251   measured as the mean ambient temperature for the mid-point latitude of each species

252   distribution (Rolland et al.[19]). The T_a at which a species exists today may not be a

253   heritable trait *per se*. However, the evolution of T_a can still be inferred using phylogenetic

254   methods since habitat selection reflects species adaptations (traits) to some characteristics

255   of the environment. This interrelationship should leave phylogenetic signal in the T_a at

256   which endothermic species live. Accordingly, we found significant phylogenetic signal in

257   the T_a of both mammals ($\lambda_{PosteriorMean} = 0.77$; Bayes Factor = 665) and birds ($\lambda_{PosteriorMean} =$

258   0.8; Bayes Factor = 1404). Furthermore, the phylogenetic signal for T_a is very high ($\lambda=1$)

259   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[7, 8], we followed his categorization of endothermic species as

263 basoendotherms ($T_b^{\text{Birds}} < 40.4$ ºC; $T_b^{\text{Mammals}} < 35.0$ ºC), mesoendotherma (40.4 ºC $\leq$

264 $T_b^{\text{Birds}} \leq 42.5$ ºC; 35 ºC $\leq T_b^{\text{Mammals}} \leq 37.9$ ºC), and supraendotherms ($T_b^{\text{Birds}} > 42.5$ ºC;

265 $T_b^{\text{Mammals}} > 37.9$ ºC).

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 (σ^2_b) 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 ($\sigma^2_b\,r$). 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

282   We estimated the r values of BMR, T_b, and T_a evolution using the *phylogenetic variable-*

283   *rates regression* model in a Bayesian framework[17]. This model is designed to

284   automatically detect shifts in the rate of trait evolution across phylogenetic branches

285   while accounting for a relationship with another trait or traits across extant species

286   values. This approach allows for simultaneous estimation of both an overall relationship

287   between, for instance, BMR as a function of $Mass$ and T_b across extant species, and any

288   shifts in rates (r) that apply to the phylogenetically structured residual variance in the

289   relationship. As residual variance is explained by shifts in rate across phylogenetic

290   branches we can, for example, determine how much BMR has changed in the past (r)

291   after accounting for their covariation with $Mass$ and T_b in the present (the relationship

292   between the values across extant species). Thus, if the amount of BMR change along

293   individual phylogenetic branches were coupled with the amount of change of T_b, then we

294   should find the r values of BMR to be positively associated with the r values of T_b. The

295   *branch-wise rates* for T_b evolution can be estimated while accounting for its covariation

296   with other traits or factor across extant species. Previous studies on the association

297   between BMR and T_b using extant species values alone have not evaluated the association

298   in evolutionary terms even when they use phylogenetic method.

299

300   We evaluated 24 *phylogenetic variable-rates regression models* and 24 *phylogenetic*

301   *constant-rate regression models* (Table S1 to S8). Regression model selection was

302   conducted using Bayes Factors (BF) via marginal likelihoods estimated by stepping stone

303   sampling. BF is calculated as the double of the difference between the log marginal-

304   likelihood of the complex model and the simple model. By convention, $BF > 2$ indicates

305   positive evidence for the complex model, *BF* 5-10 indicates strong support, and *BF* > 10

306   are considered very strong support[27]. We inferred the *r* values of *BMR* and T_b with the

307   *phylogenetic variable-rates regression models* that best fit the data for our samples of

308   mammals and birds (Table S7 and S8). We also estimated the *r* values for T_a after

309   accounting for the effect of latitude of species distribution (Table S11) and, consequently,

310   we accounted for the geographic variation of T_a across extant species distributions. We

311   used BayesTraits v3.0[28] to detect the magnitude and location of *r* in a Bayesian Markov

312   chain Monte Carlo (MCMC) reversible-jump framework, which generates a posterior

313   distribution of trees with scaled branches lengths according to the rate of evolution. There

314   is no limit or prior expectation in the number of the *r* branch-scalars, *r* numbers vary

315   from zero (no branch is scaled) to *n,* where *n* is the number of branches in the

316   phylogenetic tree. Regarding the values of each *r* parameter, we used a gamma prior,

317   with $\alpha = 1.1$ and β parameter rescaled in order to get the median of the distribution equal

318   to one. With this setting, the numbers of rate increases and decreases proposed is

319   balanced[13]. We ran 50,000,000 iterations sampling every 25,000 to ensure chain

320   convergence and independence in model parameters in *BMR* and T_b analyses. We

321   discarded the first 25,000 iterations as burn in. For the T_a analysis in mammals we ran

322   200,000,000 iterations sampling every 100,000, and we discarded the first 100,000

323   iterations as burn in. For T_a analysis in birds we ran 400,000,000 iterations discarding the

324   first 100,000,000 as burn in, and we sampled every 200,000. Regression coefficients

325   were judged as significant according to a calculated p_{MCMC} value for each posterior of

326   regression coefficients: where < 5% of samples in the posterior distribution crossed zero,

327   this indicates that the coefficient is significantly different from zero.

328

Testing the relationship between the *branch-wise rates* of evolution. We first

estimated the consensus branch-scaled tree for *BMR* and T_b from the posterior sample of

branch-scaled trees obtained with the *phylogenetic variable-rates regression model*. The

consensus branch-scaled tree was generated by using the median *r* from the posterior

distribution. We evaluated the correlation between the *r* values for *BMR* and T_b using a

Bayesian GLS regression in BayesTraits v3.0. The same analyses were conducted to

evaluate the correlation between *branch-wise rates* for *BMR* and T_a. We used a uniform

prior for the β (slope coefficient) ranging from -100 to 100. We ran 50,000,000 iterations

sampling every 25,000 to ensure chain convergence and independence in model

parameters. Significance of regression coefficients were determined as above.

Detecting trends. We evaluated the direction of change in *BMR*, T_b, and T_a across all

mammals and birds using the *path-wise rates* of these variables (Table S15 and S16).

Path-wise rate is the sum of all the *branch-wise rates* along the path of a species, which

lead from the root (the MRCA) to the tips of the tree, and it accounts for the total changes

the species has experienced during its evolution[15]. If high *path-wise rates* have

disproportionately been associated with trait increases or decreases, we expect to find that

species with greater *path-wise rates* will have high or low trait values in the present. For

instance, if ancestral mammals experienced progressively colder environmental

temperatures owing to climate change or colonization of colder habitats as they were

evolving from their MRCA, we expect a negative correlation between the *path-wise rate*

of T_a and the T_a of extant species. We performed six Bayesian PGLS regressions in

351   BayesTraits 3.0 to evaluate the relationship between *BMR, T_b, T_a* and their *path-wise*

352   *rates* (Table S15 and S16). We used a uniform prior for the β (slope coefficients) ranging

353   from -100 to 100 to allow all possible values to be equally likely. Finally, we ran

354   50,000,000 iterations sampling every 25,000 to ensure chain convergence and

355   independence in model parameters. Significance of regression slopes were determined as

356   above.

357

358   **End notes.**

359   **Supplementary Information** is linked to the online version of the paper at

360   www.nature.com/nature.

361

369

374

Data availability statement. Correspondence and request for materials should be

addressed to J.A-LL. (jorgeavariall@gmail.com) or C.V. (c.d.venditti@reading.ac.uk).

377

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