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Accepted Version

Avaria-Llautureo, J., Hernández, C. E., Rodríguez-Serrano, E. and Venditti, C. ORCID: https://orcid.org/0000-0002-6776-2355 (2019) The decoupled nature of basal metabolic rate and body temperature in endotherm evolution. Nature, 572. pp. 651-654. ISSN 0028-0836 doi: 10.1038/s41586-019-1476-9 Available at https://centaur.reading.ac.uk/85675/

To link to this article DOI: http://dx.doi.org/10.1038/s41586-019-1476-9

Publisher: Nature Research

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

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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 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 *r*s 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[16], 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[17] (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_{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_b. 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_{MCMC} = 16.9%, Table S10, Fig. 3c consistent with Fig. 1f).

As rapid bursts in *BMR* evolution were not coupled with those in T_b evolution, we evaluated the alternative hypothesis postulating that *BMR* evolved in response to T_a. This hypothesis suggests that colder environments increase the rate of heat lost from organisms which is subsequently compensated by *BMR* increases[9-12]. These *BMR* increases could have occurred over long periods of time because of global cooling[18] - 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[6-8] (PAE Model). By assuming that *BMR* and T_b 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_a. Long-term directional increases in *BMR* might have also been driven by historical dispersals of endotherms towards higher latitudes[19]. In either case, if a long-term decrease in T_a drove adaptation via *BMR* elevation, and T_b

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

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

When *branch-wise rates* of mammalian *BMR* and T_a evolution were compared, we found that they were coupled in 74.9% of branches ($p_{\mathrm{MCMC}} = 0\%$; Table S12; Fig. 3b, consistent with Fig. 1b). To evaluate further if T_a decreases were linked to *BMR* increases in the 74.9% of mammals where both traits were coupled (i.e. to ascertain the direction of 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)[15]. 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*[20]. 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[20]. Otherwise, selection may have always favoured *BMR* decreases under an ever colder environment[20].

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[9]. Alternatively, other physiological strategies, such as torpor, may have been selected for under colder environments[21].

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[22]. However, if the T_b-T_a differential (ΔT) 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 ΔT. Our model describing the negative trend in T_a predicts that the MRCA of mammals lived in an environment with 23 ºC on average (Fig. 4b), resulting in a ΔT of 15.3 ºC. This ancestral ΔT is very conservative compared with the ΔTs observed in extant mammals. For example, there are small mammals that achieve T_b higher than 39 °C (e.g. *Microdipodops pallidus*[16]) that can survive in environments of 11 °C[19] ($\Delta T = 28$ ºC). 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[16] in temperatures as low as -12 °C[19] ($\Delta T = 50$ °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[23]. 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[17] and stabilizing selection[29] 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 Keesey), 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: https://creativecommons.org/licenses/by/3.0/; https://creativecommons.org/licenses/by-sa/3.0/.

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[15]. 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)[24], and the body mass (*M*), basal metabolic rate (*BMR*), and body temperature (T_b) taken from Clarke et al.[16] (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.[19]. This tree was inferred from the samples of trees provided by Jetz et al[25]. Data for *BMR*, T_b, and *Mass* were obtained from Fristoe et al[9]. 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[26], 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.[19] 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.[19]). 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.

Finally, to evaluate the endothermic levels for the MRCA of mammals and birds proposed by Lovegrove[7, 8], we followed his categorization of endothermic species as basoendotherms ($T_b^{\text{Birds}} < 40.4$ ºC; $T_b^{\text{Mammals}} < 35.0$ ºC), mesoendotherma (40.4 ºC ≤ $T_b^{\text{Birds}} \leq 42.5$ ºC; 35 ºC ≤ $T_b^{\text{Mammals}} \leq 37.9$ ºC), and supraendotherms ($T_b^{\text{Birds}} > 42.5$ ºC; $T_b^{\text{Mammals}} > 37.9$ ºC).

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

We estimated the *r* values of *BMR*, T_b, and T_a evolution using the *phylogenetic variable-rates regression* model in a Bayesian framework[17]. 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[27]. 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[28] 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 β 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[13]. 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.

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

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 β (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.

Acknowledgments: We thank Ciara O'Donovan, Joanna Baker, Manabu Sakamoto and Ana N. Campoy for helpful discussion on the manuscript. We also thank to three anonymous reviewers who made valuable contributions. Andrew Clarke kindly supplied data for mammals and birds. This work was part of the J.A-LL. PhD thesis, supported by the CONICYT Doctoral Fellowships #21130943. CV was supported by the Leverhulme Trust (RPG-2013-185 and RPG-2017-071). C.E.U and E.R.S were supported by FONDECYT grants #1170815 and #1170486.

Authors contribution. J.A-LL., C.E.U., E.R.S, and C.V., contributed to all aspect of this work.

Author information: We have no competing interests.

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).

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