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Climate and foraging mode explain interspecific variation in snake metabolic rates

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The energy cost of self-maintenance is a critical facet of life-history strategies. Clarifying the determinant of interspecific variation in metabolic rate (MR) at rest is important to understand and predict ecological patterns such as species distributions or responses to climatic changes. We examined variation of MR in snakes, a group characterized by a remarkable diversity of activity rates and a wide distribution. We collated previously published MR data ($n = 491$ observations) measured in 90 snake species at different trial temperatures. We tested for the effects of metabolic state (standard MR (SMR) versus resting MR (RMR)), foraging mode (active versus ambush foragers) and climate (temperature and precipitation) while accounting for non-independence owing to phylogeny, body mass and thermal dependence. We found that RMR was 40% higher than SMR, and that active foragers have higher MR than species that ambush their prey. We found that MR was higher in cold environments, supporting the metabolic cold adaptation hypothesis. We also found an additive and positive effect of precipitation on MR suggesting that lower MR in arid environments may decrease dehydration and energetic costs. Altogether, our findings underline the complex influences of climate and foraging mode on MR and emphasize the relevance of these facets to understand the physiological impact of climate change.

1. Introduction

Understanding metabolic adaptation has attracted considerable scientific interest [1,2]. Whole organism metabolic rate (MR) is an integrative parameter of biochemical kinetics that can be related to major traits such as growth, survival and reproduction [3–5]. In this context, energy requirement for self-maintenance (i.e. either standard or resting MR, designated hereafter as SMR and RMR [6]) is a crucial facet of life-history variation both at the individual and species level [2,4]. Variations in MR are primarily driven by allometric factors (body size) and temperature dependence (Arrhenius relationship) [7] but are also functionally related to life-history strategies (fast versus slow pace of life [8]) and to climatic conditions [9,10]. Therefore, MR ultimately correlates with major ecological traits such as species distribution and responses to climatic change [5,9,11].

Important interspecific variation exists in resting energy requirements. For example, endothermic vertebrates (i.e. birds and mammals) have an elevated metabolism at rest which is essential to support high maximal MR and sustain prolonged activity (i.e. aerobic scope model [12]). This metabolic specialization has profound implications from subcellular (e.g. ATP production by mitochondria) to the whole organism level (e.g. muscle performance, activity level) [13]. Substantial variation in MR also exists depending on ecological traits such as foraging mode, energy intake capacity or diet [14]. For instance, among ectotherms, sustained locomotor performances in active foragers are usually associated

with higher MR compared with sit-and-wait species as demonstrated in arthropods [15], fishes [16], amphibians [17] and reptiles [6,18].

Interspecific variation in MR can also be related to environmental gradients and reflect climatic adaptation [9,19]. Notably, when measured at the same body temperature, species from cold climates (high altitude or latitude) usually display higher MR than those from warmer climates. The slope between MR and temperature can also be steeper under cold climates [20]. This difference in MR-temperature relationship is described as the metabolic cold adaptation (MCA [21]), and appears essential to complete the life cycle and perform critical activities despite thermal constraints. Although this hypothesis is still debated [22,23], it has received substantial empirical support in most taxa (i.e. negative relationships between MR and environmental temperature) such as in insects [10], fishes [22], amphibians [24], reptiles [25], birds [26] and mammals [27].

Conversely, the determinants of MR in warm climates are relatively rather overlooked [26,28]. Lower MR in warm climates can be beneficial, for example, in limiting energy expenditure but also dehydration through lowered rates of ventilatory water loss [29]. The influence of water availability on MR variation is crucial in the context of climate change that involves both changes in temperature and precipitation regimes. Several studies previously examined the influence of global warming on species functional traits [30,31], but the impacts of aridity changes are currently overlooked [32].

Snakes (more than 3000 species [33]) represent particularly relevant models to clarify the influence of climatic conditions and foraging modes on MR. Snakes typically have limited energy requirements associated with important fasting capacities. Their body temperature is closely influenced by environmental thermal conditions and also behavioural thermoregulation. As ectotherms, there is an exponential increase in MR with body temperature [34]. Snakes are widely distributed from deserts and tropics to boreal climates, thereby allowing the exploration of climatic influences [25,35]. Finally, their diversity in life-history strategies provides a unique opportunity to investigate variation in MR notably according to foraging modes that range from sit-and-wait to active predation [18].

Previous studies have investigated the determinant of MRs in squamates focusing notably on the influences of lifestyle [6,18]. Yet, we emphasize that additive influences of climatic conditions and phylogeny on MR have not been considered to date. In this study, we investigated the effects of foraging mode combined with climate (temperature and precipitation) on MR in 90 species of the main snake clades. We constituted a dataset based on MR at rest (SMR and RMR) measured at different trial temperatures (T_{trial}) including phylogenetic proximity among species [36]. In this context, we hypothesized that snake MR should be explained by the combined influences of lifestyle (foraging mode) and climate and we tested the following predictions:

(i) to sustain higher aerobic activity, species that actively hunt their prey (active foragers) should have higher MR than species that wait in ambush [6,18];
(ii) according to the MCA hypothesis, MR (corrected for body mass and T_{trial}) should negatively correlate with environmental temperature because higher MR in cold climates compensates for lower average body temperature [21]; and
(iii) because low MR helps to limit the rate of water loss, snake MR (corrected for body mass and T_{trial}) should

be positively correlated with precipitation, so that species from arid climates should display lower rates of water loss than species from humid climates [26,37].

2. Material and methods

(a) Dataset

We reviewed the published literature on snake oxygen consumption (VO_2), which is an indirect measure of whole organism MR [38] to compile the dataset (90 species from 76 studies; electronic supplementary material, table S1). We only extracted VO_2 values collected when individuals were post-absorptive and inactive and we assessed metabolic state (i.e. SMR or RMR) following the previously established classification [6]. That is, RMR is measured during the active period of the daily cycle (daytime for most snake species), while SMR is measured during the inactive period of the daily cycle (night for most snake species) [6]. VO_2 values were either given in the text, derived from allometric equations ($VO_2 = a \times Mass^b$) provided within each study, or extracted from figures using a specific software (PLOTDIGITIZER v. 2.6.6) when neither values nor equations per species were provided in text [39–41], because these three methods did not affect snake VO_2 (all $p > 0.360$). When authors measured carbon dioxide production (VCO_2), we used the respiratory quotient of post-absorptive uricotelic carnivores (RQ = 0.72), to estimate snake VO_2: $VO_2 = VCO_2/RQ$. Data were collected at various T_{trial} ranging from 5 to 35°C leading to a total of 491 observations (electronic supplementary material, table S1). We also included data obtained from eight species (electronic supplementary material, table S1), for which we used a closed-system respirometry to measure snake SMR at three T_{trial} (10°C, 20°C and 30°C) (for details in methods, see [25]).

(b) Foraging mode assignment

Snakes are characterized by a continuum in foraging mode ranging from sit-and-wait to active predation. For simplicity, we used a categorical approach and assigned to each species a foraging mode. We used supplementary information from [42] as a basis and we completed the dataset with published data and personal experience. Species that are known to rely mainly on sit-and-wait strategies (e.g. most viperids or boids) were classified as 'ambush' predators, whereas species relying on important movement for resource acquisition (e.g. most colubrids, natricines or lamprophids) were classified as 'active' foragers (electronic supplementary material, table S1).

(c) Climatic conditions

We used the mean annual temperature and total annual precipitation (obtained from http://en.climate-data.org) to approximate thermal conditions (T_{clim}) and total precipitation (P_{total}) experienced at the locality of origin described in the study. When locality was lacking, (e.g. not provided or captive animals), we randomly chose a locality within species geographical range (see the electronic supplementary material, table S1 for all localities) because this procedure did not impact the following results. Although large-scale climatic variables do not permit us to address microclimatic variation and actual body temperature, they reflect contrasted thermal environment that can correlate with physiological adaptations [43]. Preliminary analyses showed that T_{trial} used in the different studies were related to local T_{clim} because MR was usually measured in an ecologically relevant thermal range. That is, species from cold climates were measured in relatively cold T_{trial} as compared to species from warm climates (generalized linear models, $T_{clim} \sim T_{trial}$: $F_{5,387} = 7.1$, $p < 0.001$).

3
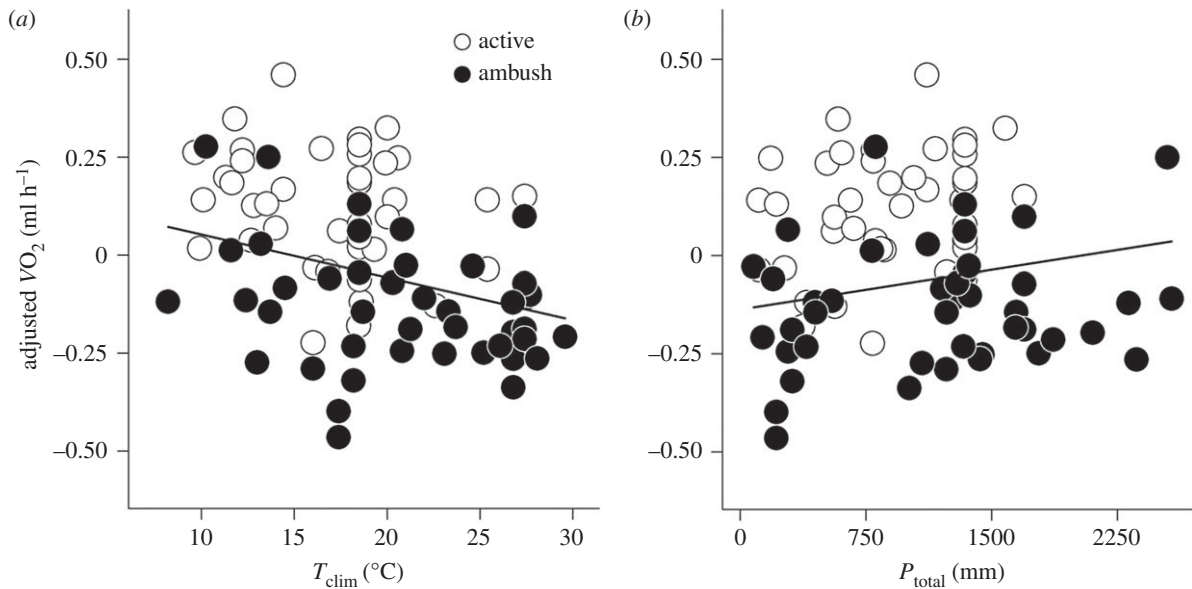
Figure 1. Effects of climatic conditions on VO_2 adjusted for body mass and T_{trial} (species VO_2 coefficients derived from a mixed model including fixed effects of body mass and T_{trial}, random effect of species as a random factor, and phylogenetical signal set to $\lambda = 0.2$). (a) Negative relationship between VO_2 and habitat temperature T_{clim} and (b) positive relationship between VO_2 and total precipitation P_{total}.

(d) Statistical analysis

All statistics were performed with R software (R Development Core Team, v. 3.2.0, http://cran.r-project.org/). VO_2 and mass were $\log_{10}$ transformed to achieve normal distributions. We built a mixed effect model (package coxme [44]) initially designed from pedigree analyses to test for the effects of body mass, T_{trial}, respirometry method (closed versus open-flow system), metabolic state (RMR or SMR), foraging mode, climatic conditions (T_{clim} and P_{total} at the locality) on snake VO_2. We accounted for multiple VO_2 measures by treating species as random factor. Phylogenetic relationships between species were included in this model using a recent molecular-based study [36] (electronic supplementary material, figure S1). We excluded four species that were not in the phylogeny from [36]: *Dasypeltis inornata*, *Helicops modestus*, *Pseudonaja nuchalis*, and *Philodryas chamissonis* (electronic supplementary material, table S1). To determine the influence of phylogenetic relationships on VO_2, we adjusted the scaling-factor for the correlation of the residual error (λ, the coefficient that applies on branch length) (package ape, [45]). For $\lambda = 1$, traits follow a constant-variance model of evolution equivalent to a Brownian motion model, while for $\lambda = 0$, trait evolution is supposedly independent between species corresponding to an ordinary least square model [46]. For $0 < \lambda < 1$, phylogeny covariance among species is overestimated and supposes different levels of phylogenetic signal [46]. Figures were obtained after extracting VO_2 coefficients for each species in the global model.

3. Results

(a) Influence of phylogenetical signal, body mass, T_{trial}, metabolic state and respirometry method

Log likelihood ratio tests showed that the final model was obtained for $\lambda = 0.2$ (see the electronic supplementary material, table S2).

VO_2 was significantly positively influenced by mass ($\beta = 0.86 \pm 0.02$, $z_{1,490} = 45.2$, $p < 0.001$) and T_{trial} ($\beta = 0.04 \pm 0.00$, $z_{1,490} = 36.7$, $p < 0.001$). We found a significant influence of metabolic state ($\beta = 0.06 \pm 0.02$, $z_{1,490} = 3.1$, $p = 0.002$) with

RMR being on average 39.87% higher than SMR. In turn, MR was not influenced by respirometry method ($\beta = 0.05 \pm 0.02$, $z_{1,490} = 1.9$, $p = 0.058$).

(b) Influence of foraging mode and climatic conditions

We found a significant influence of foraging mode ($\beta = 0.31 \pm 0.04$, $z_{1,490} = 7.7$, $p < 0.001$) with species that actively hunt their prey having VO_2 (adjusted for body mass and T_{trial}) 28% higher than sit-and-wait foragers. Finally, we found that VO_2 (adjusted for body mass and T_{trial}) was negatively influenced by T_{clim} ($\beta = -8.03 \times 10^{-3} \pm 2.57 \times 10^{-3}$, $z_{1,490} = -3.1$, $p = 0.002$; figure 1a) and positively influenced by P_{total} ($\beta = 6.7 \times 10^{-5} \pm 2.97 \times 10^{-5}$, $z_{1,490} = 2.2$, $p = 0.024$; figure 1b).

4. Discussion

We demonstrated that foraging mode, climate (temperature and precipitation) independently contribute to explain interspecific variation in snake MR. Our results show that active foragers have higher maintenance requirements than species relying on sit-and-wait strategies, and that MR is negatively correlated to temperature but positively correlated to precipitation. To our knowledge, this is the first empirical demonstration of combined effects of foraging mode and climate on MRs in snakes.

We found a weak phylogenetic signal ($\lambda = 0.2$) suggesting that the phylogeny describing residual covariance was nearly a star with little hierarchical structure. This results contrast with others studies on ecological correlates of MRs in ectotherms that have detected a more important contribution of phylogeny [47]. Although our finding may be owing to a strong covariation pattern between phylogeny and foraging mode in snakes, we emphasize that other phylogenetically informed analyses in this group have led to similar weak phylogenetic signals [42,48]. Such contrasts among lineages clearly warrant further explorations [49].

Factors affecting MR are multiple, including allometry, thermal dependence but also life-history strategies and environmental gradients. Coefficients for mass-scale and T_{trial} were highly similar with those previously reported [6]. The approximately 40% difference between RMR and SMR is also consistent with these previous findings. This considerable source of variation underlines the critical importance of reporting the metabolic state to permit comparative studies. In support of our first prediction, we found that active foragers have higher MR (either standard or resting) than species relying on a sit-and-wait strategy. Similar effects of foraging mode on MR have been reported in several species [6,18,50]. A close relationship between resting and maximal MR is expected [51]. While high MR is costly [4], active species benefit from high MR at rest owing to enhanced maximal MR and sustained activity capacities. A previous meta-analysis in snakes also showed that active foragers have a higher proportion of red blood cells to optimize oxygen delivery [42]. Our results also provided support to the MCA hypothesis [21], with a counter gradient variation between MR and environmental temperature. Therefore, species from cold climates have higher MR than species from warm ones when accounting for T_{trial}. Ectotherms primarily rely on behavioural means to regulate body temperature and optimize performance (e.g. locomotion, digestion, immunity, reproduction) [34]. Under cold climates, elevated MR provides a positive compensation to efficiently perform these physiological functions despite low ambient temperatures and reduced thermal opportunities [34]. Higher MR can result from both adaptation and physiological plasticity such as thermal acclimation to local conditions [52]. While our study does not permit us to separate their relative contribution the trends detected cannot be solely attributed to acclimation and probably reflect climatic adaptations [20,25].

The negative relationship between MR and temperature may also involve a specific response to warm climates for energy saving strategies. That is, higher ambient temperatures probably translate in higher mean body temperature and lower MR may contribute to minimize energy costs of self-maintenance [21]. Concomitantly, a lower MR may limit the production of reactive oxygen species and oxidative damage [53], and the rate of dehydration through lower respiratory water loss [29]. In this perspective, our results support a positive effect of precipitation on snake MR at rest which is consistent with previous studies in vertebrates [26,37,54]. Arid or xeric environments are typically characterized by limited access to energy and water resources [55]. At the individual level, diverse responses help in limiting the dehydration rate when access to water is limited, which include physiological (e.g. metabolic depression [56]) or behavioural adjustments (e.g. shift in thermoregulation [57]; change in activity level [58]). Therefore, species exposed to arid conditions might benefit from lower MR to limit the risk of dehydration through lower pulmo-cutaneous water loss [29,59]. Aridity probably correlates with other parameters such as primary productivity and reduced MR at rest may therefore also reflect limiting energy availability. However, a recent comparative analysis in birds showed that precipitation *per se* and not primary production drive metabolic adaptations [26]. Further studies are therefore required to understand how precipitation shapes metabolic adaptations independently of ecosystem productivity. Notably, while water constraints strongly affect species

persistence [60], precipitation is usually not included in predictive models on climatic changes. General trends predict that annual rainfall should decrease in subtropical regions while it should increase in temperate areas [61]. Water requirements are, therefore, critical to integrate in order to understand and predict species responses to climate change.

Our study focuses on large-scale climatic gradients and their influence on physiological trends [43]. Yet, it would be important to account for variation in thermoregulation strategies. For instance, sympatric species can display contrasted thermal preference, microhabitat selection [62]. Such differences can directly contribute to energy and water budget and sensitivity to climatic factors [62]. Similarly, average temperatures at the locality do not provide information on thermal heterogeneity of the habitat which can strongly influence achieved body temperature [63]. While detailed information on species trait and thermal variation are often lacking they should contribute to refine the general trend observed in our model.

Overall, previous studies focusing on the determinants of MR at rest may have overlooked the additive effects of environmental temperature, precipitation and foraging modes. Our study provides, to our knowledge, for the first time clear evidence that MR at rest is better explained by the combined effects of lifestyle and climate. Previous studies suggest that tropical squamates are vulnerable to climate change owing to narrower thermal limits [64]. Yet maintenance requirements are also crucial to consider and will be profoundly affected by temperature increase. We posit that active foraging and/or cold adapted species will be particularly sensitive to climate change owing to their elevated MR at rest. Our results support lower MRs in arid environments as an energy and water saving mechanism. Projected changes in rainfall patterns may influence water loss and compromise water balance notably in tropical species with elevated MRs. Behavioural thermoregulation also has strong potential for buffering the physiological constraints induced by climate change [65]. Therefore, further work is required to better understand the short- (plastic) and long-term (evolutionary) physiological and behavioural responses to complex environmental changes.

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