

ELEVATION-DRIVEN VARIATION IN THERMAL TOLERANCE AND METABOLIC PERFORMANCE IN A HIGH-ALTITUDE LIZARD

Dr. Brooke L. Bodensteiner¹, Dr. Eric J. Gangloff², Prof. Martha M. Muñoz³

¹ Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA

² Department of Biological Sciences, Ohio Wesleyan University, Delaware, Ohio, USA

³ Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA

Corresponding Author: Dr. Brooke L. Bodensteiner

Email: brooke.bodensteiner@yale.edu

Abstract

*In ectothermic reptiles, there are distinct thermal environments due to elevational gradients, which clearly affect physiological performance. High-elevation lizards are very valuable for insights into the effects of environmental variability on traits of thermal tolerance, body temperature regulation, and energy expenditure. This study investigated elevation-driven variation in thermal tolerance and metabolic performance in a high-altitude lizard using a quantitative secondary data analysis approach. Ecological and physiological records of *Phrynocephalus vlangalii* were analyzed, including elevation, air temperature, surface temperature, body temperature, CTmin, CTmax, preferred temperature, body size, and metabolic rate. Descriptive statistics, Shapiro–Wilk normality testing, Spearman correlation analysis, Kruskal–Wallis testing, and multiple linear regression were applied to evaluate relationships among variables. Body temperature declined with increasing elevation and showed strong positive associations with both air temperature and surface temperature. Surface temperature emerged as the strongest predictor of body temperature. CTmin differed significantly among elevations and decreased at higher elevations, indicating enhanced cold tolerance, whereas CTmax remained relatively stable across populations. Preferred temperature also varied significantly, with the lowest values recorded at 4200 m. Total metabolic rate was highest at the highest elevation, suggesting greater energetic demand under colder environmental conditions. Overall, elevation influenced multiple physiological traits, demonstrating that high-altitude lizards may persist through a combination of thermal tolerance adjustment, microhabitat-dependent thermoregulation, and metabolic compensation under alpine conditions.*

Keywords: thermal tolerance, metabolic rate, elevation gradient, high-altitude lizard, thermoregulation

1. Introduction

Thermal regulation is an essential ecological factor that affects vital processes in reptiles, as well as their survival and habitat use, and physiological performance. Reptiles are ectotherms, and their metabolic activity, locomotion, digestion, and reproduction are highly affected by thermal environments in their surroundings. Thus, environmental temperature is an important factor in influencing lizard population ecologies and physiology (Unger et al., 2020). Body temperature, thermal tolerance and preferred temperature are closely related to thermal traits of the environment and can differ significantly between habitats of different thermal regimes. Thermal ecology is a key tool in the study of how reptiles respond adaptively when climatic conditions change, and how energetic balance and physiological function are related to temperature (Taylor et al., 2021). Thermal adaptation can be studied through elevational gradients, as they have natural systems where the temperature, oxygen content, and environmental variation vary with elevation. The high-altitude habitats tend to be colder and have less available thermal energy and fewer hours of daylight activity than low-elevation habitats. These conditions are extremely physiological stressors for ectotherms and can result in adaptive changes in thermal physiology and metabolic function. Reptiles have been found to have physiological responses that change with exposure to high elevation environments both during embryonic and post-embryonic development, indicating strong environmental influence on thermal adaptation (Li et al., 2020). Therefore, in an alpine setting, thermal regulation may be crucial to ensure ecological performance and physiological stability.

It is important to note that recent research has highlighted the importance of evolutionary history, environmental exposure and ecological specialization in determining thermal physiology in reptiles. While there are some thermal traits that are phylogenetically conserved, adaptive divergence has been found when populations are exposed to different thermal environments (Bodensteiner et al., 2021). Research on urban populations of reptiles has also shown that repeated exposure to high temperatures can create a rapid physiological response that leads to thermal trait divergence, suggesting that reptiles are highly ecologically plastic with regard to their physiological responses to temperature (Campbell-Staton et al., 2020). The results underscore the need to consider thermal physiological differences along environmental gradients for understanding ecological adaptations in reptiles.

There are also large energetic implications to thermal regulation. Energy expenditure and activity levels can be modified by cardiovascular and metabolic changes that are coordinated to physiological thermoregulation in ectothermic vertebrates (Parlin & Schaeffer, 2022). The metabolic requirements of cold-adapted species may be augmented by environmental factors related to cold environments, especially at high altitudes where organisms rely on their metabolic processes to keep their body temperature within a tolerable range. Metabolic adaptation is thus an important factor in the ecological resilience of reptiles. Comparative metabolic analyses of *Phrynocephalus vlangalii* have revealed biochemical and physiological signatures linked to adaptation to the high altitude, further highlighting the importance of thermal environments in influencing metabolic processes (Zhang et al., 2023).

Reptiles are not only physiologically adapted to the heat, but developmental and reproductive strategies may also be influenced by thermal adaptation. It has been suggested that environmental temperature can influence the adaptive responses at several stages of the life history, since there are differences in embryonic traits, in maternal investment, and in energy allocation patterns across climatic gradients (Schlindwein et al., 2022). Likewise, the use of embryo energy, a physiological investment strategy, has been found to vary between populations, also depending on climatic conditions in the cool part of the climate, explaining the selection pressure of such climatic factors (Pettersen et al., 2023). All these results show that thermal ecology can affect several biological processes and plays a significant role in the ecological specialization of reptiles.

Although there has been a growing interest in the thermal ecology of reptiles, there is still a lack of understanding of how multiple physiological traits interact across elevational gradients. Most of the previous studies have concentrated on individual responses of a given thermal parameter or on the distribution of a given species without considering the body temperature, thermal tolerance, preferred temperature and metabolic performance in a single ecological context. Whilst thermal ecology has helped increase our understanding of reptilian adaptation, there is little data available on how several physiological traits interact within alpine populations of lizards across the high altitudes. Moreover, the majority of studies focus on experimental methods carried out in a laboratory environment, and there are relatively few that examine the physiological variation occurring naturally under field conditions.

Thermal physiological response to elevational gradients has gained greater significance as it is thought that global climate change will influence the distributions and ecological function of reptiles worldwide. Alpine ectotherms are likely to be more vulnerable to physiological instability and changes in thermal landscapes due to future climate change (Moss & MacLeod, 2022). The diversity and distribution of reptiles have also been projected to change significantly at the global level, in part based on the sensitivity of this group to climate change, especially in sensitive areas (Biber et al., 2023). Therefore, assessing the degree of thermal adaptation in such heterogeneous habitats could yield valuable information on the ecological resilience and adaptation to future environmental change. The high ecological complexity and adaptive diversity found in lizards continue to support their use as model organisms for evolutionary and physiological adaptations to changing thermal environments (Zamora-Camacho & Comas, 2021).

This study was thus undertaken to examine the variation in thermal tolerance and metabolic performance with elevation in a high-altitude lizard. It was in particular the dependence of elevation, environmental temperature, body temperature, thermal tolerance, preferred temperature and metabolic rate with respect to the different elevational habitats that were of interest and were analyzed in this study. The study's objective was to gain a better understanding of thermal adaptation and environmental responses for alpine reptile populations by incorporating both ecological and physiological factors.

2. Methodology

2.1 Research Design

The present study used a quantitative secondary data analysis design to analyze the elevational variation in thermal physiology and ecological responses of *Phrynocephalus vlangalii*. The study aimed to assess relationships of elevation, environmental temperature, thermal tolerance, preferred temperature, and metabolic characteristics based on the existing ecological and physiological data. A cross-sectional analytical method was used because the data set comprised measurements from several populations from varying elevational habitats.

2.2 Data Source

For this study, we used data from Jiang et al. (2023) on range shifts and physiological responses of lizard populations along an elevational gradient in a changing climate. Ecological, environmental and physiological data were obtained from several lizard populations in low, mid and high elevation habitats. Records available were body temperature, surface temperature, air temperature, thermal tolerance indices, preferred temperature, morphometric measurements, and observations of metabolic rate.

2.3 Study Variables

The major dependent variables were body temperature, preferred temperature, critical thermal minimum (CT_{min}), critical thermal maximum (CT_{max}) and metabolic rate. Independent variables consisted of elevation, air temperature, surface temperature, body mass, and snout–vent length. Elevation was used as a continuous environmental variable as well as a grouping variable, representing 2600 m, 3400 m and 4200 m populations.

2.4 Data preparation and Processing.

All data were checked for the presence of duplication, formatting errors, and missing data before analysis. Character string elevations were converted to numeric variables in order to allow quantitative analysis. The names of variables were standardized between the datasets to ensure uniformity in statistical procedures and in visualization.

2.5 Statistical Analysis

All the environmental, physiological and morphological parameters were subjected to descriptive statistics such as mean, standard deviation, median, minimum and maximum values. The Shapiro–Wilk test was used to determine the normality of data distributions. Several of the variables failed to meet the assumptions for normal data, and non-parametric statistical methods were used for subsequent analysis. Spearman correlation analysis was used to measure the relationships between environmental and physiological variables. The Kruskal-Wallis test was used to compare the differences among the elevational groups. A p-value of < 0.05 was considered statistically significant.

3. Results

3.1 General patterns of body temperature and environmental conditions

The body temperature of the participants varied greatly, with temperatures ranging from 13.5 °C to 44.2 °C, while the average body temperature was 35.36±2.86°C. On the other hand, the surface temperature ranged from 10.6 °C to 66.4°C, while the temperature of the air ranged from 5.8 to 39.6°C. Mean elevation of sampled individuals was 3416.48 ± 521.12 m (Table 1).

Table 1. Descriptive statistics of environmental, morphological, and physiological variables measured across datasets.

Dataset	Variable	N	Mean	Standard Deviation	Median	Minimum	Maximum
Body Temperature	Body Temperature	971	35.36	2.86	35.60	13.50	44.20
Body Temperature	Surface Temperature	971	32.65	8.63	32.70	10.60	66.40
Body Temperature	Air Temperature	971	21.04	5.18	21.00	5.80	39.60
Body Temperature	Snout Vent Length	971	5.07	0.85	5.20	2.20	7.20
Body Temperature	Elevation	971	3416.48	521.12	3400.00	2600.00	4200.00
Thermal Tolerance	CT _{min}	64	4.49	1.23	4.30	1.70	7.70
Thermal Tolerance	CT _{max}	64	45.69	0.74	45.80	43.60	47.10
Thermal Tolerance	Snout Vent Length	64	5.11	0.72	5.00	3.80	6.60
Thermal Tolerance	Body Mass	64	4.97	2.12	4.52	2.25	11.33
Thermal Tolerance	Elevation	64	3350.00	666.67	3400.00	2600.00	4200.00
Preferred Temperature	Preferred Temperature	60	35.42	1.14	35.53	32.80	37.44
Preferred Temperature	Snout Vent Length	60	5.40	0.59	5.40	4.40	6.60
Preferred Temperature	Body Mass	60	6.38	2.42	6.25	2.70	13.71

Preferred Temperature	Elevation	60	3400.00	658.71	3400.00	2600.00	4200.00
Metabolic Rate	Body Temperature	210	25.00	10.02	25.00	10.00	40.00
Metabolic Rate	Body Mass	210	5.19	2.39	4.99	1.83	11.82
Metabolic Rate	Mass Specific Metabolic Rate	210	0.18	0.15	0.12	0.01	0.66
Metabolic Rate	Total Metabolic Rate	210	0.86	0.87	0.57	0.03	5.07
Metabolic Rate	Elevation	210	3400.00	654.76	3400.00	2600.00	4200.00

Body temperature tended to decrease gradually with increasing altitude, and people from the higher altitude group (at 4200 m) were found to have lower body temperatures compared with those at other altitudes. Figure 1 is the illustration of the body temperature distribution among the different altitude groups.

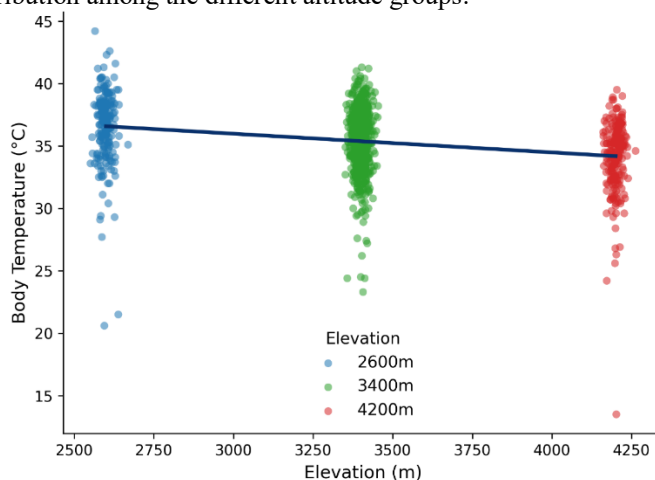


Figure 1. Body temperature across elevational gradients shows the relationship between elevation and body temperature.

3.2 Relationship between environmental temperature and body temperature

The body temperature had a positive correlation with the air temperature and surface temperature. The Spearman correlation test indicated that the body temperature correlated positively with the air temperature ($r = 0.584, p < 0.001$) but even more strongly with the surface temperature ($r = 0.671, p < 0.001$). On the other hand, elevation had a negative correlation with body temperature ($r = -0.300, p < 0.001$) (Table 2).

Table 2. Spearman correlation analysis among environmental, morphological, and physiological variables.

Dataset	Variable 1	Variable 2	Spearman Correlation	p Value	Interpretation
Body Temperature	Elevation	Body Temperature	-0.300	<0.001	Significant
Body Temperature	Air Temperature	Body Temperature	0.584	<0.001	Significant
Body Temperature	Surface Temperature	Body Temperature	0.671	<0.001	Significant
Body Temperature	Snout Vent Length	Body Temperature	0.084	0.009	Significant
Thermal Tolerance	Elevation	CTmin	-0.329	0.008	Significant
Thermal Tolerance	Elevation	CTmax	0.115	0.365	Not significant
Thermal Tolerance	Snout Vent Length	CTmax	0.335	0.007	Significant
Thermal Tolerance	Body Mass	CTmax	0.351	0.004	Significant
Preferred Temperature	Elevation	Preferred Temperature	-0.304	0.018	Significant
Preferred Temperature	Snout Vent Length	Preferred Temperature	-0.125	0.340	Not significant
Preferred Temperature	Body Mass	Preferred Temperature	-0.200	0.125	Not significant
Metabolic Rate	Body Temperature	Mass Specific Metabolic Rate	0.841	<0.001	Significant
Metabolic Rate	Body Temperature	Total Metabolic Rate	0.823	<0.001	Significant
Metabolic Rate	Body Mass	Total Metabolic Rate	0.263	<0.001	Significant
Metabolic Rate	Elevation	Total Metabolic Rate	0.166	0.016	Significant

Figure 2 demonstrates that body temperature rose steadily with rising air temperatures at all elevations; however, individuals inhabiting higher elevations were in cooler environments.

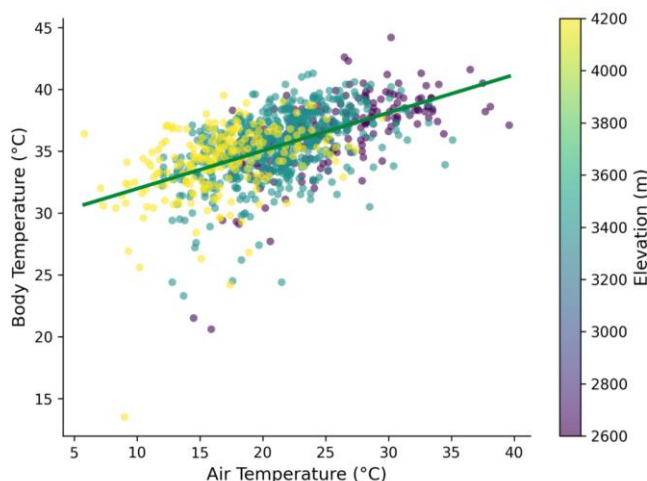


Figure 2. Relationship between air temperature and body temperature across elevational gradients.

There is a very high positive correlation between surface temperature and body temperature, as shown in Figure 3, indicating that substrate thermal conditions strongly influence body temperature regulation.

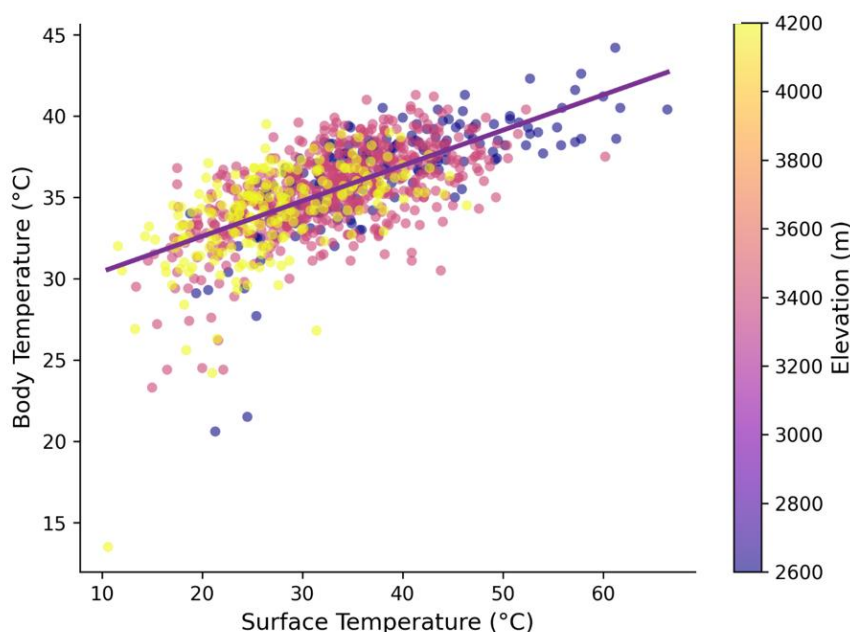


Figure 3. Relationship between surface temperature and body temperature across elevational gradients.

3.3 Elevational variation in thermal physiology

Significant variation was found among elevational groups for a number of physiological attributes (Table 3). The body temperature significantly varied among elevations ($H = 87.232, p < 0.001$), with the highest values recorded at elevation 2600 m and the lowest values found at elevation 4200 m. The surface temperature and air temperature also significantly varied according to elevation (both $p < 0.001$).

The CTmin value significantly varied among elevations ($H = 8.076, p = 0.018$), with lower average values at higher elevations, while CTmax did not significantly differ among elevations ($H = 4.923, p = 0.085$). The preferred temperature significantly differed among elevations ($H = 18.465, p < 0.001$), with higher preferred temperatures at elevation 3400 m. The mass-specific metabolic rate and total metabolic rate also significantly varied among elevational groups.

Table 3. Elevational group comparison using Kruskal-Wallis analysis.

Dataset	Variable	Group Summary	Kruskal Wallis H	p Value
Body Temperature	Body Temperature	2600m: 36.50 ± 3.01 ; 3400m: 35.44 ± 2.60 ; 4200m: 34.27 ± 2.66	87.232	<0.001
Body Temperature	Surface Temperature	2600m: 37.71 ± 9.23 ; 3400m: 32.90 ± 7.80 ; 4200m: 27.34 ± 6.26	134.338	<0.001

Body Temperature	Air Temperature	2600m: 25.68 ± 4.86; 3400m: 21.07 ± 4.10; 4200m: 16.43 ± 3.06	288.089	<0.001
Thermal Tolerance	CTmin	2600m: 4.79 ± 1.04; 3400m: 4.72 ± 1.55; 4200m: 3.91 ± 0.86	8.076	0.018
Thermal Tolerance	CTmax	2600m: 45.72 ± 0.55; 3400m: 45.43 ± 0.85; 4200m: 45.92 ± 0.61	4.923	0.085
Preferred Temperature	Preferred Temperature	2600m: 35.53 ± 0.97; 3400m: 36.16 ± 0.73; 4200m: 34.56 ± 1.23	18.465	<0.001
Metabolic Rate	Mass Specific Metabolic Rate	2600m: 0.16 ± 0.15; 3400m: 0.15 ± 0.15; 4200m: 0.23 ± 0.16	11.475	0.003
Metabolic Rate	Total Metabolic Rate	2600m: 0.83 ± 0.89; 3400m: 0.63 ± 0.69; 4200m: 1.12 ± 0.98	15.730	<0.001

Elevational gradients of CTmin, preferred temperature, and total metabolism are illustrated in Figure 4. As shown in Figure 4A, CTmin exhibited slight decreases with increased elevation, reflecting an increase in cold resistance at higher elevations. As shown in Figure 4B, the preferred temperature reached its maximum value at intermediate elevations (3400 m) and showed a decrease at 4200 m. As indicated by Figure 4C, total metabolism was the highest at 4200 m, suggesting elevated energetic demands under high-elevation conditions.

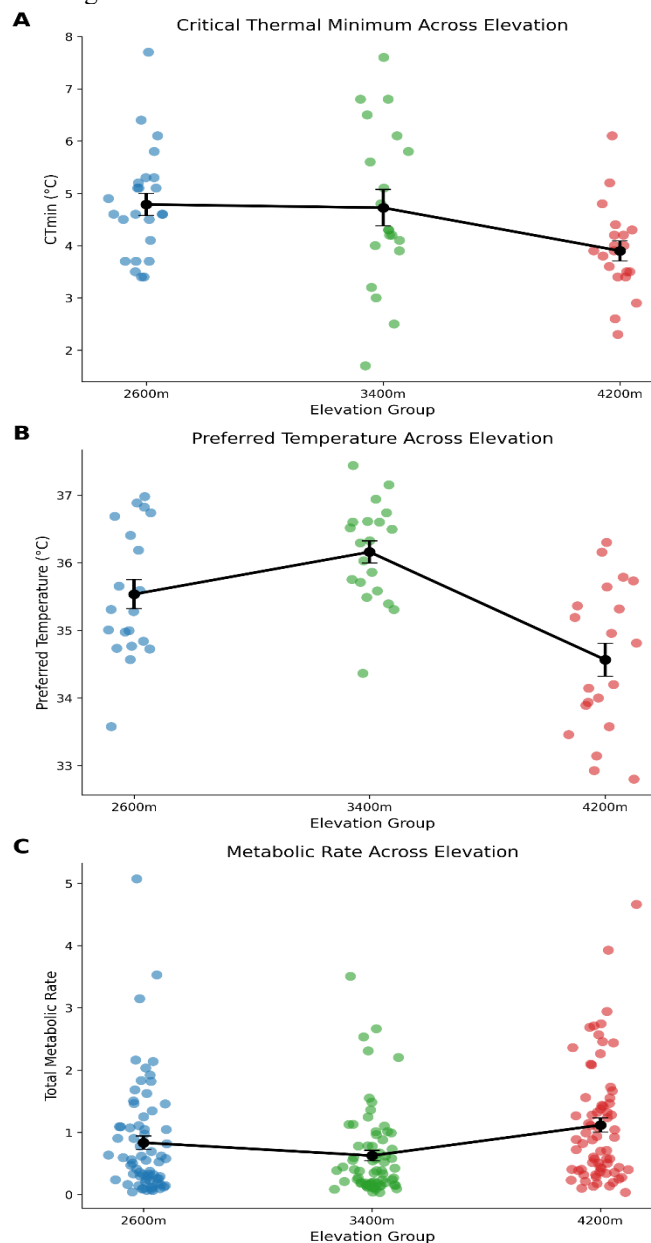


Figure 4. Elevational variation in (A) critical thermal minimum (CTmin), (B) preferred temperature, and (C) total metabolic rate across elevational groups.

4. Discussion

A clear thermal signal, as revealed by the physiological profile, was obtained in the high-altitude lizard population used in the present study. Body temperatures decreased by a continuous gradient between 2600 m and 4200 m, and air and surface temperatures decreased over the same gradient too. The pattern shows that the body temperature was closely related to the thermal environment, and people at high elevations had a lower operative temperature. There is a negative correlation between altitude and body temperature, and this provides an indication that there was a measurable impact on heat acquisition as elevation increased, although there was also a positive correlation, suggesting some level of thermoregulatory compensation. The temperature of the environment was one of the most important factors affecting body temperature. Surface temperature correlated more strongly with body temperature than did air temperature, indicating that heat exchange with the substrate is perhaps particularly significant for these terrestrial lizards. This is biologically feasible, since lizards often acquire heat through direct contact with sun-heated surfaces during basking and/or activity. This trend was confirmed by a regression model, which showed that surface temperature (after controlling for elevation, air temperature and body size) was the best predictor of body temperature. Thus, field body temperature seems to be more strongly influenced by the microhabitat temperature than by the general elevational location.

Thermal tolerance also was different along the elevational gradient. The more people live at a higher elevation, the lower their CT_{min} is, supporting the idea that people from colder regions are more tolerant of cold. The finding indicates that high elevation populations may have physiological adaptations that enable them to be active and survive at lower temperatures. In contrast, CT_{max} was not significantly different between elevations, suggesting that upper thermal limits were relatively uniform between populations. A decrease in CT_{min} and a change with no significant trend in CT_{max} indicate that the expression of this gradient of adaptation was primarily in the form of increased cold tolerance without a general change in the full thermal tolerance range. Evidence of elevational physiological differentiation was provided by preferred temp and metabolic rate. The highest preferred temperature occurred at 3400 m, but this decreased at 4200 m, suggesting that the relationship between thermal preference and altitude is not linear. The lower preferred temperature for the highest elevation may be due to acclimatization to cooler environmental conditions, where high body temperatures may occur less often. The total metabolic rate was highest at 4200 m, indicating a higher need for energy at high elevation. The pattern could be a compensatory metabolic response to colder habitats, but the difference between individuals suggests that metabolic responses were not consistent throughout the population. Together, these findings support the primary finding, the effect of elevation on various aspects of thermal physiology and energetic performance.

The elevational gradient in thermal traits observed is consistent with the evidence that lizards can exhibit functional differences along steep altitudinal gradients, especially when they experience a strong contrast in temperature and habitat conditions (Serén et al., 2023). Altitude may also influence physiological performance in reptiles – similar patterns of variation among closely related lizard species across elevation have been reported (Senior et al., 2019). The correlation between thermal physiology and elevational distribution is congruent with previous studies that have demonstrated that physiological thermal limits can be used to account for the elevational distribution of lizards (Huang et al., 2020). The present results also support the general pattern of climate-induced diversification of environmental temperature responses in lizards and the potential for environmental temperature to influence diversification across climate zones (García-Porta et al., 2019). The lack of change in CT_{max} reported here may not be as responsive to the cold high elevation conditions as CT_{min}.

Thermal tolerance is not the only response to elevation. Blood traits and other internal physiological parameters can change with elevation in lizards, but this can differ among different mountain systems and populations (Gonzalez-Morales et al., 2023). These findings also align with studies that found metabolic plasticity can help increase the resilience of some lizard lineages to climate change (Sun et al., 2022). Climate, thermal history and species-specific physiological capacity, however, can influence the direction and magnitude of metabolic responses. In long-term thermobiological studies, lizards have been shown to be sensitive to abnormal seasonal temperatures, which means that thermal biology is not only spatially, but also temporally variable (Vicente Liz et al., 2019). The present results are relevant to the context of future warming, as there is substantial inter-taxa variation in climate change vulnerability, driven by exposure to climate change within the local environment, physiological tolerance, and adaptive capacity (Jarvie et al., 2022). There is also evidence of physiological mechanisms that allow reptiles to cope with short-term temperature stress (mechanistic studies of acute temperature adaptation), which may not compensate for long-term environmental change (Chang et al. 2022).

The results indicate that lizards living at high elevations use both behavioral and physiological mechanisms to allow them to perform at colder temperatures. Increased cold tolerance at 4200m could promote persistence in alpine environments, whereas a higher metabolic rate could be a reflection of the energetic cost of life in colder environments. Microhabitat structure is also emphasized, as surface temperature seems to exert a greater influence. These lizards need to have a certain degree of vegetation cover, soil exposure, rock availability and solar access, which, if altered, could directly affect the thermal opportunities these lizards need. The results show that from a conservation point of view, climate change assessments should not only be based on distribution but also on physiological traits. Different populations at different elevation levels may not react in the same way to warming due to differences in their thermal tolerances, preferences and metabolic requirements. In some contexts, populations at high elevation levels could benefit from warmer conditions, but in others, they could suffer if the habitat changes at a higher rate than behavioral and/or physiological responses.

There are some restrictions to be noted. As secondary data were used in the analysis, sampling design, field timing and measurement conditions could not be changed. There were also differences in the number of samples in each data set, with the body temperature data sets being larger than the thermal tolerance and preferred temperature data sets.

Furthermore, environmental variables were restricted to air temperature and surface temperature with no effect from solar radiation, humidity, wind exposure or habitat structure included.

Future research efforts should involve field measurements and controlled experiments to determine if measured patterns are due to local adaptation, acclimatization, or short-term plasticity. Multiple years of seasonal sampling would also be useful to assess the inter-year stability of thermal traits. The incorporation of microhabitat data, behavioral observations and physiological assays would improve the understanding of the responsiveness of high-elevation lizards to changing thermal environments in a mechanistic sense.

5. Conclusion

The high-altitude lizard studied showed significant differences in thermal physiology and energetic performance as a function of elevation. Body temperature decreased with elevation, and air and surface temperature were well correlated with body temperature, indicating the importance of local thermal conditions on shaping the field thermoregulation. Lower CT_{min} with increasing elevation was indicative of greater cold tolerance, while CT_{max} was relatively constant, indicating greater cold tolerance adjustment than for upper thermal tolerance. The preferred temperature also changed with elevation, being lowest at 4200 m, and the total metabolic rate was highest at that elevation, suggesting that energy demands are higher at high elevation under colder conditions. Results indicate that elevation affects a variety of physiological parameters, not just one response to a thermal parameter. The patterns suggest that high elevation lizards may be able to survive via cold tolerance, thermal preference adjustment, and metabolic compensation, but that these abilities may be more dependent on the thermal characteristics of microhabitat and future climate change.

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