RESEARCH ARTICLE

Ecophysiology of a small ectotherm tracks environmental variation along an elevational cline

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Funding information
Australian Research Council

Handling Editor: Daniel Chapman

Abstract

Aim: Physiological responses to climate can be used to quantify the environmental limits that a species can tolerate and are, therefore, key to biogeographical studies. Several ecophysiological responses to climatic factors may shape the distribution of species, but our knowledge is mostly centred in thermal ecophysiology. We applied an integrative approach to investigate how ecophysiological responses of a small ectotherm are modulated by climatic variation across an elevational gradient.

Location: Victoria, Australia.

Taxon: *Lampropholis guichenoti* (Scincidae, Squamata).

Methods: We examined metabolic rate, evaporative water loss, thermal physiology and locomotor performance, of four populations of the skink *Lampropholis guichenoti* across an elevational gradient in Australia (17–1546 m). We applied biophysical modelling to test how behaviour impacts the survival and activity of these skinks.

Results: Populations from the lowlands had lower metabolic rates and evaporative water loss, lower thermal preferences, higher optimal temperatures and increased locomotor performance compared populations from high elevations. Biophysical models revealed that behaviour allows skinks from high elevation to maintain their body temperatures above freezing and is key to determining activity patterns.

Main conclusions: Our holistic study shows that a combination of physiological and behavioural responses allows ectotherms to survive in different climatic environments. The interplay between physiology and behaviour can help to explain how climate sets limits for the geographical range of ectotherms.

KEYWORDS
behaviour, lizards, locomotion, metabolism, thermal preference, water balance

1 | INTRODUCTION

Climate is recognised as a key driver of species distribution since organisms must cope with climatic conditions to survive in their environments. The way organisms respond to climate is key for biogeographical studies because such responses may indicate how they are able to live where they occur (Gaston et al., 2009). Responses to climate usually involve physiology, which directly affects the performance of ecological activities and hence the survival of organisms in different environments (Kearney et al., 2013; Vázquez & Stevens, 2004). In particular for ectotherms, our knowledge about physiological responses to climate across geographical gradients have mostly centred on thermal physiology (Clusella-Trullas & Chown, 2014; Gvoždík, 2002; Ortega et al., 2016; Trochet et al., 2018). However,

other physiological (metabolism and water balance) and behavioural responses to climate may be involved in shaping species distributions (Muñoz & Boldensteiner, 2019; Rozen-Rechels et al., 2019). Integrating many physiological and behavioural responses to climate may provide insights into our understanding of the distributional limits of ectotherms (Kearney et al., 2013).

Elevational clines are geographical gradients characterised by changing climatic conditions across short distances (Sheldon et al., 2018). Hence, ectotherms living along an elevational gradient must cope with distinct environmental stressors. For example, ectotherms living at high elevations, where temperatures are cold, exhibit lower critical thermal minimum (Muñoz et al., 2014; Sheldon et al., 2018). However, wind speed, solar radiation, oxygen concentration and water availability vary along elevational gradients, and may also influence physiological responses (Clusella-Trullas et al., 2011; Gangloff & Telemeco, 2018; Porter & Gates, 1969; Rozen-Rechels et al., 2019). Across elevations, therefore, balancing water and energetic budgets is vital for maintaining homeostasis and consequently for the performance of ecological activities (Belasen et al., 2017; Kearney et al., 2013) and ultimately survival (Dominguez-Godoy et al., 2020). Indeed, water conservation has key implications for ectotherms performance, and for this reason in drier environments, mechanisms that retain water body content may be favoured by natural selection (Cox & Cox, 2015; Dupoué et al., 2017; Pintor et al., 2016; Rozen-Rechels et al., 2019). Moreover, metabolic rates can have important fitness implications for organisms (Arnold et al., 2021; Auer et al., 2017; Mathot et al., 2019). Through metabolic regulation, energy can be conserved and then allocated to vital functions, which can be beneficial in scenarios with changing temperatures (Žagar et al., 2018), limited energetic resources (Angilletta, 2001), and low water availability (Christian et al., 1999; Dupoué et al., 2016). Thus, across elevations, metabolism and water balance, in addition to thermal physiology, may be involved in buffering ectotherms against challenges imposed by climatic variability (Belasen et al., 2017; Kearney et al., 2013).

For many ectotherms, thermoregulatory behaviour is a buffer against climatic variability. For example shifts in microhabitats to regulate body temperature (T_b) can reduce exposure to detrimental conditions stemming from climatic variability (Kearney et al., 2009; Porter et al., 1973; Vickers et al., 2011). Hence, climatic differences across elevations may be accompanied by behavioural adjustments to compensate for stressful situations (e.g. cold temperatures) (Gvoždík, 2002; Muñoz et al., 2014). Ultimately, shifts in preferred body temperature can be beneficial to physiological functions and consequently to the performance of ecological activities (Blouin-Demers & Nadeau, 2005; Logan et al., 2019). Indeed, changes in the thermal preference might be accompanied by shifts in the thermal sensitivity of physiological traits (i.e. metabolism and water loss), and by shifts in the thermal optimum for the performance of ecological tasks, such as locomotion (Angilletta et al., 2002; Hertz & Huey, 1981; Hertz et al., 1983; Huey & Stevenson, 1979; Llewelyn et al., 2017). A comparative and integrative analysis of how behaviour and physiological responses vary across geographical gradients may highlight the strategies employed by ectotherms to survive in challenging environments.

To evaluate how ecophysiology varies across elevational gradients, we studied a small lizard, the garden skink *Lampropholis guichenoti*. These skinks are heliothermic and oviparous animals that inhabit open woodlands and dry forests in south-eastern Australia, but are also commonly found in disturbed areas. They have a widespread distribution, including the alpine region of Victoria (Wilson & Swan, 2017), where they can be found in elevations from the sea level to up to 1550 m (Figure S1 and Table S1). Across this elevational gradient, climate shifts drastically, from warm and dry lowlands to cold and wet highlands (Table 1; Chubb et al., 2011). Given that *L. guichenoti* populations are exposed to distinct climatic conditions, their physiology may respond differently depending on their local environment. We hypothesised that compared to mid and high elevations, low-elevation populations may exhibit reduced evaporative water loss (EWL) in response to drier conditions. Moreover, due to the cold temperatures, mid and highland populations may exhibit increased standard metabolic rate (SMR) and lower critical temperatures (CT_{min}), as well as lower thermal preference (T_{pref}). Consequently, changes in thermal sensitivity of physiological traits and ecological performance (e.g. locomotion) can also be expected. Thermal performance curves are expected to be broader at high elevations, and optimum temperatures to be lower owing to cold conditions (Hertz et al., 1983). Lastly, behavioural thermoregulation allows ectotherms to maintain their body temperatures within limits that are beneficial for their performance (thermal window for activity) and for their survival (within critical limits). Hence, to evaluate how behaviour may impact the survival and activity of *L. guichenoti*, we applied mechanistic niche modelling (Kearney & Porter, 2020). We compared models without behaviour (i.e. null model in which the predicted physiological traits are direct effects of climate) to models with behaviour (which account for behaviour such as burrowing, thermoregulation and

TABLE 1 Bioclimatic variables (BioClim, Fick et al., 2017) extracted from the sites where the lizards were collected. Temp. indicates temperature (°C) and Precip. indicates precipitation (mm)

Site	Mean Annual Temp.	Mean Annual Precip.	Mean Temp. Range	Max. Temp. Warmest Month	Min. Temp. Coldest Month	Precip. Wettest Month	Precip. Driest Month
Alpine	7.8	133.6	10.8	21.4	−2.4	14.6	6.0
Dargo	11.2	95.2	11.9	24.5	5.0	9.5	5.3
Calulu	13.8	78.6	11.5	25.1	3.4	9.0	4.2
Forge Creek	14.1	69.9	11.1	24.9	4.0	8.0	3.4

activity). This may indicate the extent that behavioural adjustments can affect performance and survival under natural conditions. We anticipated that our models would predict that behaviour can maintain the physiology of skinks within suitable limits (e.g. body temperatures above lower thermal limits).

2 | MATERIALS AND METHODS

2.1 | Fieldwork

Fieldwork was conducted along an elevational gradient in the mountain ranges of north-eastern Victoria, Australia, between 4th and 8th April 2019. We selected four field-sites ranging from the lowlands near the shore up to the highlands in the mountains: Forge Creek (17 m a.s.l), Calulu (228 m a.s.l), Dargo (772 m a.s.l) and Alpine National Park (1546 m a.s.l.) (for more details see Figure S1, S2 and Table S1). In the field, we actively searched for the skinks during their active time. Once spotted, we collected the skinks by hand or by mealworm fishing. We collected only adult males in order to avoid ontogenetic and reproductive state effects that may affect physiology and behaviour.

2.2 | Housing

After collection, the animals were transported to Monash University (Clayton, Victoria, Australia). Upon arrival, the skinks were individually marked with a unique identification using non-toxic paint on their backs. The skinks were housed in groups of four to six, in plastic tubs (25 × 20 × 18 cm). Each tub provided skinks with multiple shelters, and a lamp suspended over the tub allowed lizards to bask/thermoregulate. The temperature inside the room was maintained at 22°C with a 12 h light:12 h dark photoperiod. We fed the skinks with crickets (*Acheta domesticus*) dusted in calcium and vitamins three times weekly, water was *ad libitum*. Importantly, to ensure the skinks were post-absorptive when tested, they were not fed for at least 48 h. Between the experiments, the lizards recovered in their respective cages for at least 24 h. Body mass of the lizards was monitored daily, and none of the lizards exhibited decreases in body condition.

We transported the skinks to the laboratory 1 day after the fieldwork was finished, and the experiments started 3 days after their arrival in the laboratory. We first conducted the experiments to measure metabolism and evaporative water loss over a period of 10 days. Two days after finishing these experiments, we conducted the T_{pref} measurements which lasted another 5 days. Next, we measured sprint speed over 7 days. Finally, we quantified the lower critical thermal limits followed by the upper thermal limits.

2.3 | Metabolism and water loss

Rates of carbon dioxide production and water loss were measured using positive pressure open-flow respirometry according to standard techniques (Lighton, 2008). We first weighed the skinks (Scientech ZSA210, ±0.0001 g) and then placed them in a small-insulated glass chambers (25 ml) and subsequently in a controlled-temperature chamber (Dometic Cool Ice 22 L) that maintained temperature within ±1.5°C. Measurements were conducted at five ecologically relevant temperatures: 15, 20, 25, 30 and 35°C. The respirometry system was supplied with room air that was pushed through a column of soda lime (Labchem, Ajax Finechem Pty Ltd) and Drierite (W. A. Hammond Drierite Company Ltd) to remove CO_2 and water vapour respectively. The flow rate of air through each of the eight channels of the system was regulated nominally to 60 ml min^{-1} by a mass flow controller (Aalborg, Model GFC17), as is appropriate for this species (Merrit et al., 2013). The animals were allowed a 15-min settling-in period at the beginning of measurements, and mean rates of CO_2 production and H_2O loss were calculated for a minimum period of at least 60 min following the settling-in period. Following standard procedures for respirometry (Lighton, 2008) and methods utilised for a congeneric species (see Merrit et al., 2013), we calculated the CO_2 and H_2O production of a 5-min period over which the rates of CO_2 production and H_2O loss were stable and constant. Each skink from each population was tested at one temperature per day. The experiments were conducted in a random order, randomising population, individual skinks and test-temperature.

2.4 | Sprint speed and thermal performance curve

For the determination of the thermal performance curves, we focused on locomotor performance because foraging, reproduction, escape from predators and many other ecologically relevant activities are inextricably associated with locomotion in reptiles (Huey & Stevenson, 1979). We measured skinks sprint speed at eight test temperatures (15, 20, 23, 25, 27, 30, 33 and 35°C) in a random order, testing each skink at one temperature each day.

In order to quantify sprint speed, we ran the skinks down a racetrack (1 m long × 10 cm wide), and calculated their speed using a high-speed camera (Casio EX-ZR50, 30 frames per second). Skinks were stimulated to run by touching them gently on the back with a paintbrush. They were run on the racetrack twice at each temperature, with 30 min between each run. Prior to the run, the skinks were placed for 20 min into a chamber set to the test temperature. Given the small body sizes, the skinks' T_b quickly equilibrated with the test temperature (Fraser & Grigg, 1984). Before each trial, the skinks' cloacal temperature was measured (Eutech EcoScan Temp, ±0.1°C) to ensure the animal was at the desired body temperature. The sprint speed was calculated as the time the skink took to cover the distance in the racetrack (Friard & Gamba, 2016). Finally, for each skink at each temperature, we calculated sprint speed as the average speed of the two runs. However, if the skinks tried to escape from the racetrack, if they stopped running, or if they did not complete a run, we discarded that observation.

Thermal performance curves were estimated using the package *rTPC* (Padfield et al., 2021) in R environment, and following Angilletta

(2006). For each individual, we bounded the curves with the critical temperatures (minimum and maximum) and we fitted the data using a Gaussian distribution, which is recommended for locomotor data (Taylor et al., 2021). Optimal performance temperatures (the temperature at which an individual performs its maximum speed), the maximum speed (speed attained at the optimum temperature, i.e. peak) and the thermal performance breadth (the range at which an individual performs at 80% of its maximum) were extracted from each individual curve.

2.5 | Thermal preference

To estimate T_{pref}, we used a thigmo-thermal gradient constructed of aluminium and portioned in four equal runways. A near-linear thermal gradient ranging from 14 to 36°C was produced by hanging two 250 W infrared bulbs at one end of the chamber and placing a cold plate cooled down by freezing water underneath. Since *L. guichenoti* is a heliothermic skink, infrared bulbs were used to avoid the effect of light as a potential confounding factor. A row of iButtons dataloggers (DS1995L-F5+, Maxim Integrated) spanned the length of each lane to measure the surface temperature. The dataloggers were calibrated against a subset of skinks to ensure they accurately reflect the skinks' body temperature. Individual skinks were placed in the thermal gradient at each iButton position for 2 min. Skinks T_b was recorded with a T-type thermocouple taped (Leucopore^{TM}) above their pelvic girdle for two minutes. The directly measured skinks T_b was regressed onto iButton temperature to produce a regression equation from which skinks T_b was calculated (skink $T_b = 1.0185*iButton - 0.6125, R^2 = 0.979$).

At the onset of the experiment, the skinks were placed individually into the middle of the gradient and allowed 30 min for acclimation period. We then monitored the location of each skink using video cameras positioned over the gradient for 4 h. The experiments were conducted from 8:00 until 18:00 h. Given the short time constant of small skinks' heating and cooling rates (1.30 min; Fraser & Grigg, 1984), estimations of T_b were inferred from the selected positions along the gradient. Over these data, we calculated the mean selected body temperature (mean T_{pref}). We also calculated the lower and upper set-points as the 25th and 75th quartiles, respectively, which were used to parametrise the biophysical modelling (see below).

2.6 | Critical temperatures

We determined the critical thermal minimum (CT_{min}) and maximum (CT_{max}) by placing the skinks individually inside Falcon tubes submerged in a water bath (Labec DCW-1015). Temperature either increased or decreased at a rate of 1°C/min. The CT endpoints were established as the temperature the skinks lost their ability to right themselves, within 15 s, when manually turned upside down. Immediately after the loss of the righting reflex, we measured the body temperature of the skinks using an infrared thermometer and

then we put them in water at ambient temperature for recovery. Additionally, we calculated the thermal tolerance range of each individual as the difference between the CT_{max} and CT_{min}.

2.7 | Climatic and biophysical modelling

The package *NicheMapR* (Kearney & Porter, 2020), for the R programming environment, includes a suite of programs for computing energy and mass exchange between organisms as a function of microclimate. The package includes a microclimate model (function *micro_ncep*) that integrates historical 6-hourly macro climatic data sets from the National Centers for Environmental Predictions and terrain/shade adjustments. The function *micro_ncep* is connected to the package *microclima* (Maclean et al., 2019), which generates time series of microclimatic variables in air temperature, humidity, wind speed, soil temperature and soil moisture, as well as radiation conditions. We used the *micro_ncep* to downscale the macroclimate data from NCEP and we modelled microclimates under unshaded conditions. We used all default settings, simulating unshaded conditions on flat ground, with the soil moisture routine (Kearney & Maino, 2018) turned on. The model was set to run daily for 3 years (from 2015 to 2017) to allow soil moisture calculations to reach steady state. Next, we computed the heat and water budget of a dry-skinned ectotherm using the microclimatic predictions as input.

For each population, we inputted the coordinates and elevation of the collection site (Table S2). We then modelled a lizard at steady-state body temperature and without thermoregulatory behaviour, and a lizard with thermoregulatory behaviour, using the function *ectotherm*. This function runs based on the information provided in the *micro_ncep* function. For the model without thermoregulation, we only provided the body mass and we set activity as diurnal. Without thermoregulation, the modelled lizard was unable to seek for shade, shelter and burrows. We also set the parameter *live* on (i.e. simulating an alive animal). For the model with thermoregulation, we set the thermal physiological parameters and body mass for each population as shown in Table S2, and allowed the lizard to seek shade and burrows. We then computed the daily number of hours with body temperatures above CT_{min}, and also the daily number of hours the lizards are active (this is calculated as the time window the simulated lizards are active according to the parameters listed in Table S2).

2.8 | Data analyses

As our aim was to test differences between four elevational sites, we treated elevation as a factor. To evaluate the effects of elevation and temperature variation on EWL and MR, we performed a linear mixed-effects model (LME) using the package *lmer4* (Bates et al., 2015). We set elevation as fixed factor, and body mass and test temperature as continuous covariables. To account for random variation (i.e. as random effects), we set individual identification, channel (i.e. in which chamber the skink was placed in for the measurement) and block of experiments (i.e. the day they were performed). Moreover, significant

effects of the interaction between elevation and test temperature can reveal differences in thermal sensitivity. However, since we did not find the effects of the interaction between test temperature and elevation (SMR: $F_{3, 292} = 2.025$, $p = 0.110$; EWL: $F_{3, 292} = 2.258$, $p = 0.082$), we excluded the interaction from the models.

We also tested the effects of elevation and test temperature on sprint speed by performing a LME. We set elevation as fixed factor, and body mass and test temperature as continuous covariables. As random factors, we set individual identification and block of experiment. We also included the interaction between test temperature and elevation. However, as we did not find the effects of body mass on sprint speed ($F_{1, 473} = 0.079$, $p = 0.778$), we excluded this variable from the model.

To evaluate how elevation affects CT_{min}, CT_{max}, tolerance range, thermal optimum, thermal performance breadth and maximum speed, we performed one-way ANOVAs setting elevation as a factor. We tested if these traits were correlated with body mass; however, we did not find any significant relationship ($p > 0.2$ for all these traits). These traits were also normally distributed with homogeneity of variance.

For T_{pref}, we first ran a general linear model including time in captivity (i.e. block of experiments) and elevation as the predictors. We found no effect of time in captivity ($p = 0.5835$). Hence, as T_{pref} was not normally distributed, we performed a Kruskal–Wallis test with elevation as single factor.

To compare the biophysical modelling outputs, we applied a two-way ANOVA. We set either the daily number of hours with temperatures above CT_{min} or the daily activity time as dependent variables, and elevational site and modelling input (i.e. with or without behaviour) as factors. The interaction term between elevation and modelling input was also included in the model.

3 | RESULTS

3.1 | Metabolism and evaporative water loss

Metabolic rate was positively affected by temperature (LME coefficient ± SD: 0.115 ± 0.011; $F_{1, 309} = 103.25$, $p < 0.001$) and body mass (LME: 0.466 ± 0.147; $F_{1, 309} = 10.06$, $p = 0.001$). Metabolic rate differed among elevations (LME: Forge Creek = -0.249 ± 0.092; Calulu = -0.280 ± 0.090, Dargo = -0.195 ± 0.098, Alpine: -4.363 ± 0.335; $F_{3, 307} = 3.935$, $p = 0.008$; Figure 1A; Tables S3 and S4).

Evaporative water loss (EWL) was positively affected by (LME: 0.07 ± 0.008; $F_{1, 309} = 78.96$, $p = 0.001$), but not by body mass (LME: 0.202 ± 0.177; $F_{1, 309} = 0.683$, $p = 0.252$). EWL differed among elevations (LME: Forge Creek = -0.273 ± 0.079, Calulu = -0.221 ± 0.111, Dargo = -0.379 ± 0.119, Alpine = -0.557 ± 0.240; $F_{3, 307} = 3.841$, $p = 0.010$; Figure 1B; Tables S5 and S6).

3.2 | Sprint speed and thermal performance curve

Sprint speed was affected by test temperature (LME: 0.112 ± 0.022; $F_{1, 489} = 238.485$, $p < 0.001$) and by
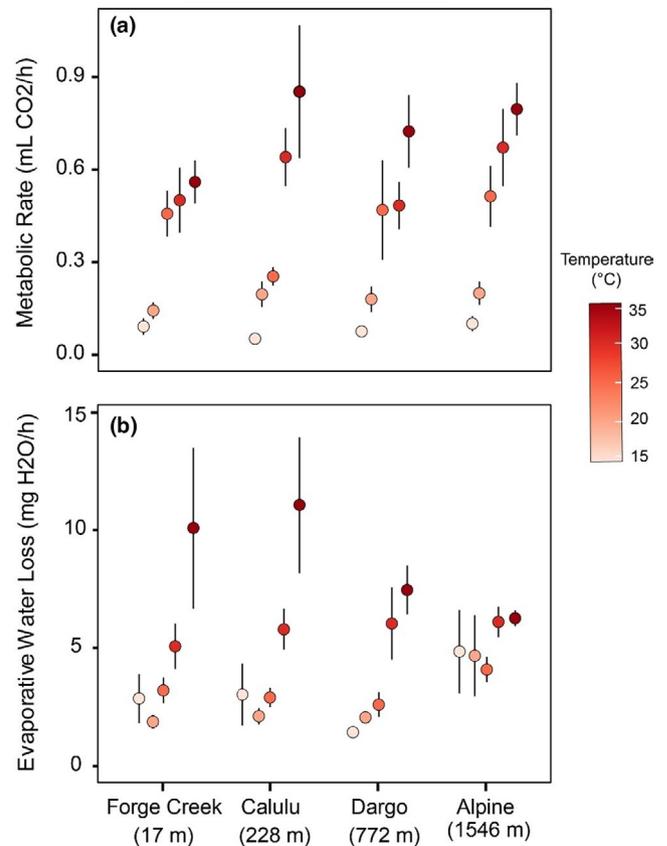

FIGURE 1 Mean (points) and standard error (whiskers) of the metabolic rate (a) and evaporative water loss (b) measured at different temperatures for four populations of the small skinks *Lampropholis guichenoti* living at different elevations

elevation (LME: Calulu = -2.781 ± 0.880, Dargo = -2.783 ± 0.895, Forge Creek = -2.556 ± 0.921; $F_{3, 489} = 4.801$, $p = 0.002$). The interaction of elevation and test temperature was positively with all elevational sites (LME: Forge Creek = 0.071 ± 0.034, $p = 0.037$; Calulu × Temperature = 0.139 ± 0.032, $p < 0.001$; Dargo × Temperature: 0.111 ± 0.033, $p < 0.001$; $F_{3, 489} = 6.75$, $p = 0.001$; Table S7), indicating that thermal sensitivity of sprint speed varies among elevations.

For the thermal performance curves, the maximum speed attained by the skinks differed among sites ($F_{3, 59} = 7.83$, $p < 0.001$; Figure 2). The thermal optimum ($F_{3, 59} = 4.947$, $p = 0.003$) and thermal performance breadth ($F_{3, 59} = 3.67$, $p = 0.017$) also differed among elevational sites, such that skinks from the highest elevation showed reduced optimum temperatures and increased B80 (Figure 2). Overall, thermal performance curves of all populations showed a typical shape for ectotherms (Figure S3).

3.3 | Thermal preference and critical temperatures

The thermal preference (T_{pref}) differed among elevations (Kruskall–Wallis $X^2 = 13$, d.f. = 3, $p = 0.004$) as did CT_{min} ($F_{3, 56} = 16.78$, $p < 0.001$) and thermal tolerance range ($F_{3, 56} = 10.78$, $p < 0.001$). Skinks from the high elevations showed higher T_{pref} and lower CT_{min}
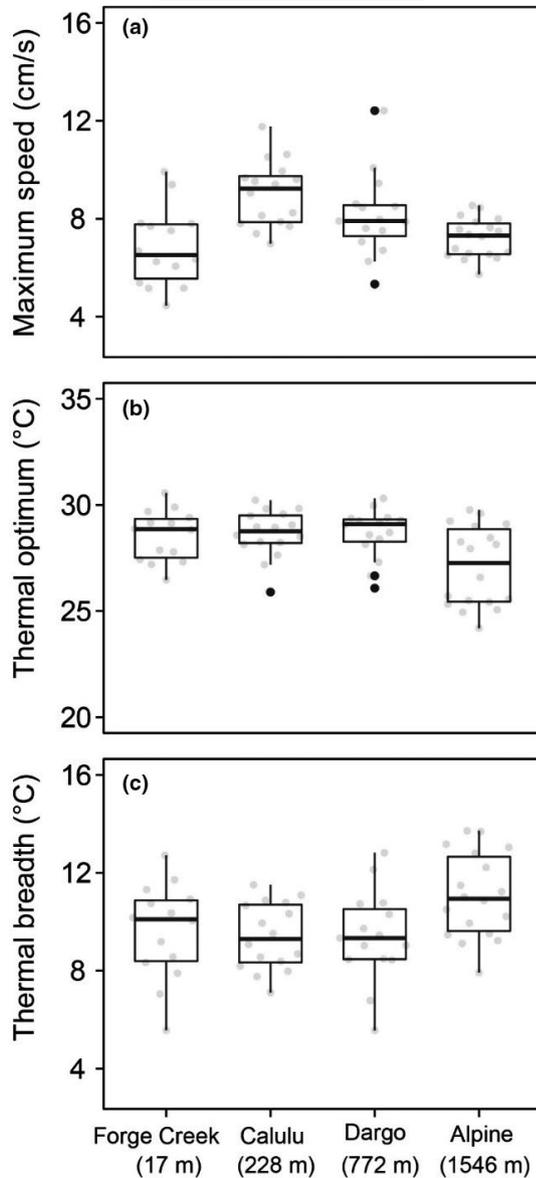
FIGURE 2 Parameters estimated from thermal performance curves of the small skinks *Lampropholis guichenoti* living at different elevations. (a) Maximum speed attained as predicted by the thermal performance curve; (b) thermal optimum for sprint speed and (c) thermal performance breadth, estimated as the range of temperature skinks reached 80% of maximum performance

than skinks from low elevations (Figure 3). However, we did not find differences in the CT_{max} ($F_{3, 56} = 0.386$, $p = 0.764$).

3.4 | Biophysical modelling

Simulated skinks with behaviour exhibited more hours with temperatures above the CT_{min} than simulated skinks without behaviour ($F_{1, 2912} = 1091.31$, $p < 0.001$). Daily hours of temperatures above the CT_{min} also varied among elevations ($F_{3, 2912} = 70.53$, $p < 0.001$), and the interaction between elevation and behaviour was significant ($F_{3, 2912} = 70.53$, $p < 0.001$). With behavioural capacity, the
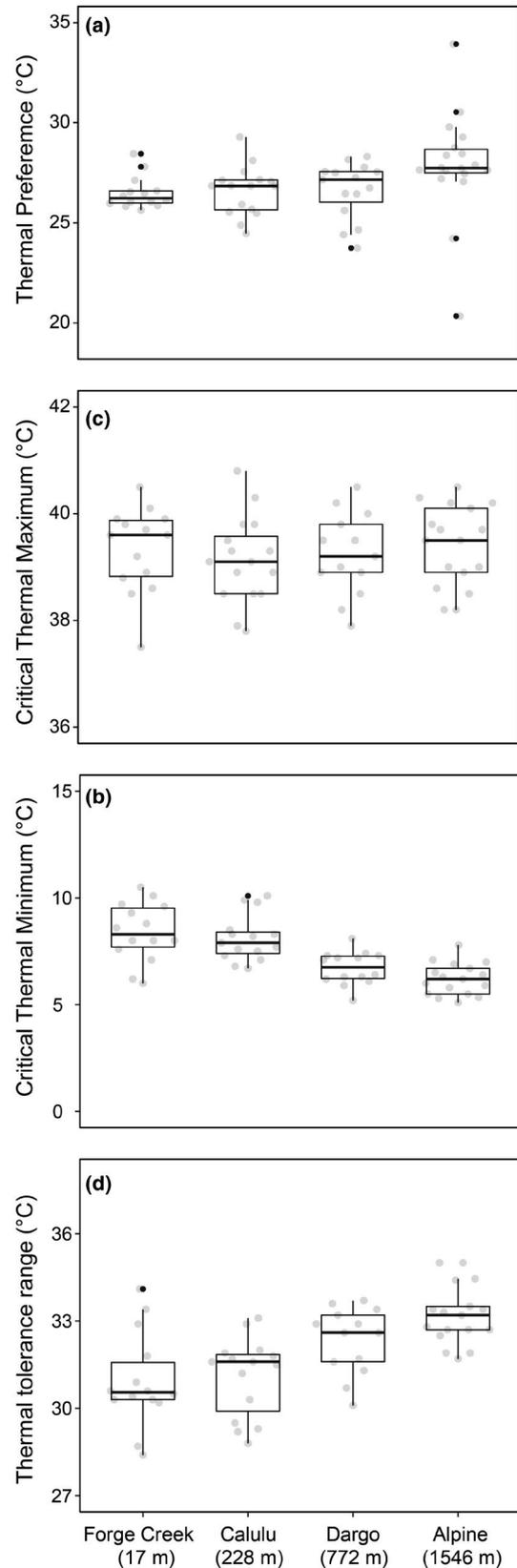

FIGURE 3 Thermal physiological parameters of four populations of the small skink *Lampropholis guichenoti* living at different elevations. (a) Thermal preference. (b) The thermal tolerance range calculated as the deviation between the thermal critical maximum and minimum. (c) Critical thermal minimum. (d) Critical thermal maximum

simulated skinks from all populations can stay most of the time with body temperature above CT_{min}, but without behaviour skinks from Alpine population spend long periods with body temperatures below CT_{min} (Figure 4a).

Models including behaviour also exhibited higher activity time (daily hours of activity) than models that did not include behaviour ($F_{1, 2915} = 48.98$, $p < 0.001$). Activity time also varied among elevations ($F_{3, 1805} = 11.23$, $p < 0.001$), and the interaction between elevation and behaviour was significant ($F_{3, 1805} = 20.58$, $p < 0.001$; Figure 4b).

4 | DISCUSSION

We applied an integrative approach to evaluate how physiological responses of a small ectotherm are modulated across an elevational gradient. We found that EWL, SMR, locomotor performance, thermal performance curves, thermal preference and critical thermal minimum varied across elevations. That is, at the highest elevation
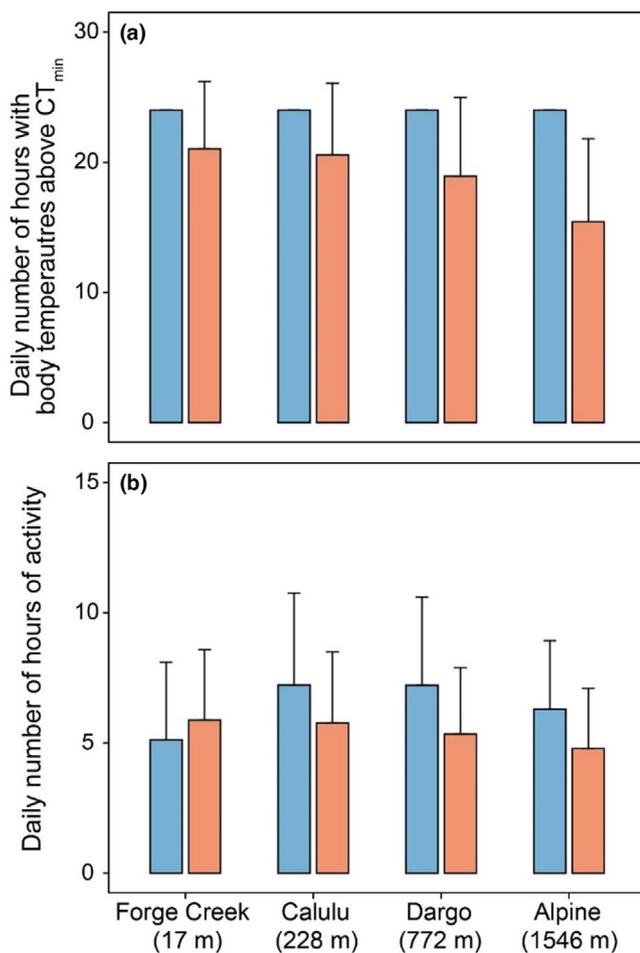

FIGURE 4 Skinks were simulated with behaviour (blue) and without behaviour (red) at each elevational site. (a) Daily hours with body temperatures above the critical thermal minimum (CT_{min}). (b) daily number of hours of activity. The bars indicate the average daily number of hours and the whiskers the standard deviation

behavioural thermoregulation and physiology might compensate for adverse climatic conditions. Furthermore, ectotherm models simulating the skinks in their respective environments showed that behaviour may keep the skinks' body temperature above their lower thermal limits and also increase the activity time to compensate for cold temperatures at the high elevations. These results highlight that physiology and behaviour can ultimately buffer ectotherms against environmental variation, allowing these animals to survive in different environments.

We observed that skinks from the highest elevational site exhibited higher EWL then skinks from other elevations. As ectotherms must keep homeostatic balance within suitable limits to avoid dehydration (Rozen-Rochels et al., 2019), environmental pressures for water conservation are likely reduced in high and wet elevations when compared to the drier lowlands (see also Caldwell et al., 2015). The reductions in EWL in dry regions is a widespread phenomenon observed in reptiles and it is linked to the conservation of water body content (Cox & Cox, 2015; Thompson & Withers, 1997; Withers et al., 2000). Conserving water is key for reptiles to inhabit and colonise dry environments, hence environmental pressures linked to water availability (via precipitation, relative humidity) may naturally select higher resistance to EWL in drier environments (Thompson & Withers, 1997; Withers et al., 2000). Indeed, recent work has shown that water balance traits are heritable (Llewelyn et al., 2018; Martins et al., 2019), suggesting that EWL is targeted by natural selection. Hence, the variation of EWL observed for *L. guichenoti* might be a heritable trait that limit the distribution of these animals (Martins et al., 2019).

Metabolic rates of ectotherms are known to be affected by environmental temperatures (Gaston et al., 2009). When compared to warm environments, ectotherms from cold environments tend to have higher metabolic rates (White et al., 2012; Žagar et al., 2018). This is known as the metabolic cold adaptation hypothesis (Gaston et al., 2009), and it has been reported for lizards (Angilletta, 2001; Hare et al., 2010; Plasman et al., 2020; but see Tsuji, 1988). In agreement with this hypothesis, our results showed that skinks living at higher, colder elevations tend to have increased SMR. This observation suggests that skinks may adjust their metabolic rates in responses to climate, but the mechanisms behind this response are hard to interpret. We suggest that high metabolic rates may allow skinks to perform well in their ecological activities at cold temperatures (Hare et al., 2007; Lourdais et al., 2013). Additionally, high metabolic rates may be associated with thermoregulation and energetic efficiency. As skinks might spend more time and energy thermoregulating at cold environments (Blouin-Demers & Nadeau, 2005; Lourdais et al., 2013), high metabolic rates may enhance energetic use when they reach optimum temperatures. Combined adjustments of metabolism and thermoregulation may contribute to a more efficient energetic use in cold environments, yet this topic deserves further investigation.

The effect of elevation on the thermal preference of lizards has received mixed or sometimes little support (Clusella-Trullas & Chown, 2014). In some cases, T_{pref} is negatively related to elevation

(Trochet et al., 2018; Gvoždík, 2002). However, in *L. guichenoti*, we found that animals from the highest elevation showed a higher T_{pref} (see also Trochet et al., 2018). This suggests that altering T_{pref} plays an important role in the responses of *L. guichenoti* to climatic variation, likely affecting energetic budgets (as discussed above) and ecological performance (Cluesella-Trullas et al., 2011; van Damme et al., 1989; Vickers et al., 2011). In addition, the variation observed for thermal performance curves and for the thermal sensitivity of sprint speed across elevations suggest responses to climate. As high elevations skinks are exposed to greater thermal variations, broader thermal performance breadths may allow nearly optimum performance even at cold temperatures (Sheldon et al., 2018). While decreases of optimum temperatures suggest shifts on thermal performance curve to compensate potential low performance at cold conditions, or even to match thermal optimum with preferred ranges (Blouin-Demers & Nadeau, 2005; Caldwell et al., 2017). Indeed, matching body temperature with optimum temperatures may result in maximised performance in challenging environments, such as at high elevations (Caldwell et al., 2017; Dominguez-Godoy et al., 2020; Huey & Bennet, 1987). In contrast, lowland skinks exhibited narrow thermal performance breadths and high optimum temperatures to likely maximise their performance at warm conditions (Angilletta et al., 2002; Caldwell et al., 2017). In general, our results indicate that the thermal performance curves of the highland and lowland skink may have shifted to adjust to local climatic conditions.

We observed that the CT_{min}, but not the CT_{max}, of garden skinks varied across elevations. Skinks from the highlands are exposed to colder temperatures throughout the year, and they might experience nearly lethal low temperatures, especially when aestivating during cold months. This highlights the limited role of behavioural thermoregulation in buffering ectotherms against cold temperatures (Huey et al., 2003; Bodensteiner et al., 2020). As the inactive animals are not able to select warmer temperatures, cold tolerance might be the only alternative to endure the low temperatures. This can explain the increased evolutionary lability of CT_{min} in comparison to CT_{max} (Hoffmann et al., 2013; Munoz et al., 2014). In turn, the fact that the CT_{max} of garden skink did not show any variation is consistent with the limited lability of upper thermal limits (Hoffmann et al., 2013; Sandbloom et al., 2016). In reptiles, CT_{max} is strongly related to basking behaviour, rather than to environmental temperatures (Huey & Kingsolver, 1993; Muñoz et al., 2016; Spellerberg, 1972). This is because thermoregulatory behaviour buffers these animals against high temperatures, hence relaxing selection on CT_{max} (Boggert, 1949; Huey et al., 2003; Muñoz & Bodensteiner, 2019; Muñoz & Losos, 2018). It is unlikely that high elevation skinks reach their upper thermal limits, due to the low temperatures of their habitat and to their thermoregulatory behaviour. Likewise, although lowland skinks might face high temperatures, they can avoid overheating through thermoregulation. Overall, these results indicate that the distribution of ectotherms is likely limited by cold temperatures rather than by hot temperatures (Bodensteiner et al., 2020; Strangas et al., 2019).

Our biophysical modelling highlights the importance of behaviour to ectotherm survival. Especially for the high-elevation sites, models that did not incorporate behaviour exhibited more time at temperatures below CT_{min}. However, with behaviour, the risk of experiencing body temperatures below CT_{min} was largely reduced and equal to that observed for the lowland sites. Furthermore, levels of activity of the highland models were even higher than the observed for the lowest elevation site. This shows that selecting distinct microhabitats, seeking for shade, or burrowing, ectotherms can reduce the stresses of detrimental environmental conditions (Kearney et al., 2018). Also, by selecting body temperatures that match their optimum temperatures (i.e. body temperatures during activity), skinks can improve their level of performance in disadvantageous climatic conditions (e.g. cold temperatures). These physiological and behaviour adjustments have key implications for species distributions since behaviour and physiology determine where a species can live.

5 | CONCLUSIONS

We demonstrated that physiological responses differ between populations of the skink *L. guichenoti* across an elevational gradient. However, we cannot determine whether plasticity or adaptive variation influence our results (Llewelyn et al., 2016). Common garden experiments combined with genomics could disentangle genetic and environmental effects on the physiological traits (Llewelyn et al., 2018; de Villemereui et al., 2016).

Our integrative approach highlights that physiological and behavioural responses are key for the survival of skinks in challenging environments. Physiological and behavioural responses might work in tandem and establish the limits for the survival and hence distribution of ectotherms (i.e. fundamental niche). Water conservation might be strongly affected by selection and it can be seen as a potential factor limiting geographical ranges. While combined, adjustments in metabolic rates and thermoregulation might enhance the ecological performance of ectotherms, allowing them to survive in harsh environments (e.g. high elevation). Physiology and behaviour act as a modulator between organismal maintenance and ecological performance, allowing ectotherms to live in different environments. Incorporating different ecophysiological, environmental and behavioural aspects into a single common framework has the potential to provide valuable insights into the mechanisms underlying the distribution of ectotherms.

procedures involving animals described in this study were approved by the School of Biological Sciences Animal Ethics Committee—Monash University (Project ID: 2018—16711). Funding was provided by the Australian Research Council (DP170100684 and FT200100108 to DGC).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The physiological data empirically collected for *Lampropholis guichenoti*, and the R scripts used to conduct the statistical analyses and the biophysical modelling, are available in Bridges data repository (https://doi.org/10.26180/16834756).

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BIOSKETCH

Rodolfo O. Anderson is broadly interested in ecophysiology of ectotherms, and this work represents one of his chapters for his PhD thesis at Monash University, Australia. For more details see: https://www.chapplelab.com.

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