Temporal variation in thermal plasticity in a free-ranging subalpine lizard

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ARTICLE INFO

ABSTRACT

Thermally variable environments are particularly challenging for ectotherms as physiological functions are thermo-dependent. As a consequence, ectotherms in highly seasonal environments are predicted to have greater thermal plasticity. However, much of our understanding of thermal plasticity comes from controlled experiments in a laboratory setting. Relatively fewer studies investigate thermal plasticity in free-ranging animals living in their natural environment. We investigated the presence of thermal plasticity within a single activity season in adult males of a natural high elevation population of White's skink (*Liopholis whitii*) in south-eastern Australia. This species lives in a permanent home site (rock crevice and/or burrow), facilitating the repeated capture of the same individuals across the activity season. We monitored the thermal variation across the field site and over the activity season, and tested thermal tolerances and performance of male *L. whitii* on three occasions across their activity season. Maximum and average temperatures varied across the field site, and temperatures gradually increased across the study period. Evidence of temporal plasticity was identified in the critical thermal minimum and thermal tolerance breadth, but not in the critical thermal maximum. Thermal performance was also found to be plastic, but no temporal patterns were evident. Our temporal plasticity results are consistent which much of the previous literature, but this is one of the first studies to identify these patterns in a free-ranging population. In addition, our results indicate that performance may be more plastic than previous literature suggests. Overall, our study highlights the need to pair laboratory and field studies in order to understand thermal plasticity in an ecologically relevant context.

1. Introduction

Environments are inherently dynamic; variation occurs across a range of biotic and abiotic factors, and over vast temporal and spatial scales (Chesson, 1986). Thermal variation, in particular, has the capacity to influence fundamental aspects of a species' biology (Overgaard et al., 2011; Schulte et al., 2011; Gutierrez-Pesquera et al., 2016; Childress and Letcher, 2017). This is especially true for ectothermic organisms, as their physiological functions are dependent on the external thermo-environment (Huey and Stevenson, 1979; Huey and Berrigan, 2001; Angilletta, 2009). Studies commonly estimate thermo-physiological traits at a single point in time (Angilletta, 2009). These static measurements are frequently used to infer physiological differences between species or populations and across different habitats (Gutierrez-Pesquera et al., 2016); for instance, increasing thermal

tolerance with increasing elevation in scarab dung beetles in southern Africa (Gaston and Chown, 1999). Such a methodology assumes that any temporal differences in thermal tolerance are negligible and unlikely to affect overall patterns (Herrando-Pérez et al., 2018).

Plasticity (i.e. the ability of a single genotype to generate diverse phenotypes in response to environmental variation) of thermal tolerances, or thermal acclimation, is an important mechanism for organisms responding to thermal variation (Andrew et al., 2013; Seebacher et al., 2015). Such plasticity is thought to facilitate higher fitness across a greater diversity of environments and thus may be adaptive for ectotherms inhabiting highly seasonal or thermally variable environments (Ghalambor et al., 2007). Thermal tolerance plasticity is predicted to vary across taxa, and to be greater in generalist species with larger distributions (e.g. heat shock protein expression in *Bactrocera* fruit flies, Hu et al., 2014) and in species occupying seasonal environments (e.g.

Drosophilia species in eastern Australia, Overgaard et al., 2011; Ghalambor et al., 2006; Sheldon and Tewksbury, 2014). The future persistence of species affected by climate change will largely be mediated by an ability to acclimate in response to changing environmental temperatures and increased climatic variability (Kearney et al., 2009; Haines et al., 2017). Therefore, understanding how thermal tolerances change temporally in response to thermal variation is increasingly important given the predicted impacts of climate change on environmental temperatures (Schulte et al., 2011; Seebacher et al., 2015), and the increase in studies predicting range shifts and extinction using thermal tolerance data (Herrando-Pérez et al., 2018). One important form of plasticity in thermophysiolgy is plasticity within an animals' activity period. Plasticity within an activity season has been identified in a number of thermal traits including thermoregulatory behaviour, thermal preferences and basal metabolic rates (Diaz and Cabezas-Diaz, 2004; Basson and Clusella-Trullas, 2015; Ortega and Perez-Mellado, 2016). For example, meat ants (*Iridomyrmex purpureus*) in temperate Australia exhibit seasonal variation in several key aspects of their thermal biology, including thermal tolerances and locomotor performance (Andrew et al., 2013).

Within Australia, the alpine-montane areas south-east of the continent are some of the most sensitive ecosystems to global climatic changes (Hughes, 2003, 2011; Sinervo et al., 2010; Caldwell et al., 2015). These high elevation areas are also some of the most seasonal, experiencing fluctuations in temperature daily and throughout the year (Hughes, 2011). Worldwide, ectotherms inhabiting alpine environments already withstand extreme seasonal shifts in environmental temperature (e.g. insects, Dillon et al., 2006; lizards, Monasterio et al., 2009; Mendez-Galeano and Calderon-Espinosa, 2017), and therefore Australian alpine species likely exhibit some degree of plasticity in thermal tolerance in response to this temperature variation within the activity season (e.g. invertebrates, Hay and Ball, 1979; lizards, Senior et al., 2019). High elevation montane environments therefore provide valuable settings in which to study thermal plasticity (Ghalambor et al., 2006; Basson and Clusella-Trullas, 2015).

Empirical studies on thermal tolerance plasticity have mostly been undertaken on model species such as *Drosophila* sp.*,* and other invertebrates (Esperk et al., 2016; Chevin and Hoffmann, 2017). Field-based empirical studies using non-model organisms are logistically challenging but can provide valuable insights into thermal plasticity in an ecologically relevant context (Klok and Chown, 2003; Hoffmann et al., 2013). Here we examined temporal variation in thermal tolerance (critical thermal minimum and maximum) and locomotor performance in adult males in a high elevation, free-ranging, wild population of White's skink, *Liopholis whitii*. *Liopholis whitii* is a medium-sized viviparous species (75–100 mm adult snout-vent length; SVL), with a widespread distribution along the eastern coast of Australia (Chapple et al., 2005; Wilson and Swan, 2017). The species occurs along an elevational gradient: from sea level to approximately 1200 m (Chapple, 2005; Wilson and Swan, 2017). Due to its large geographical and altitudinal range, this species is considered a generalist compared to other members of the *Liopholis* genus (Chapple, 2003), and thus may have broader thermal tolerances and greater levels of plasticity than other members of the genus (e.g. Senior et al., 2019). The species is inactive over the austral winter, sheltering in burrow systems. During the active season *L. whitii* exhibits high burrow fidelity and occurs in small stable family groups, enabling the same individuals to be easily recaptured and thermal trait plasticity to be measured (Chapple and Keogh, 2005, 2006).

Our overarching hypothesis was that since *L. whitii* lives in a seasonally variable environment, we would expect to see temporal variation in key aspects of its thermal biology. Specifically, as CTmin appears to be evolutionarily flexible in ectotherms (Clusella-Trullas and Chown, 2014), we predicted plastic increases in critical thermal minimum, and plastic decreases in thermal tolerance breadth driven by a decreasing tolerance to cold environmental temperatures as the active season progressed (Yuni et al., 2018). Similarly, we predict an increase in locomotor performance at higher temperatures across the active season as mean environmental temperatures increased, similarly to what can occur in lizards acclimated to higher temperatures over time in laboratory settings (Sun et al., 2014). In contrast, as CTmax appears to be evolutionarily constrained in ectotherms (Clusella-Trullas and Chown, 2014), we predicted critical thermal maximum would not change significantly throughout the active season, despite increases in mean environmental temperatures (e.g. Hoffmann et al., 2013; Clusella-Trullas and Chown, 2014; Senior et al., 2019). This information is valuable in order to model and better assess how *Liopholis* skinks, and alpine ectotherms more broadly, are likely to respond to anthropogenic climate change.

2. Methods

The peak activity period for *L. whitii* occurs from late October to April. Male skinks were used throughout the study, caught initially in October and then re-caught twice over the season; resulting in three separate experimental blocks between October 2017 and January 2018. Due to the constraints of the academic year for Australian honours students, we were unable to conduct fieldwork during the second half of the activity period for *L. whitii*. Male skinks were used as females were gravid during the study period, and changes in physiology during pregnancy may skew the results of thermal trials (Edwards and Jones, 2001).

2.1. Animal collection

All *L. whitii* were caught from a high elevation population adjacent to Lake Jindabyne, New South Wales (NSW), Australia (elevation 915 m; 36.346 °S, 148.598 °E). The first collection period commenced on the October 23, 2017 and involved exhaustively sampling the population. Adult skinks were caught using a noosing pole with mealworm (*Tenebrio molitor*) bait, or hand caught. Once caught, the sex of the skink was determined by eversion of the hemipenes in males. Females were immediately released. The GPS coordinates of the capture site were recorded to assist with future release and recapture (GARMIN GPSMAP® 64sc).

At the completion of the first collection period only, skinks were tagged with passive integrated transponder devices (PIT tags) (Trovan ID100 (1.25) FDX-A Nanotransponder). This involved injecting a PIT tag (7 mm long and 1.2 mm diameter) under the skin on the left ventral side with a 12-gauge needle, and served as a permanent coded maker. Skinks were then weighed (± 1 g) and their SVL and hind limb length (HLL) was measured (± 0.1 mm). Two subsequent collection periods occurred during the study, commencing on November 30, 2017, and January 9, 2018, respectively. In these collection periods, males that were captured in period one were targeted for recapture. Upon recapture, skinks were scanned for a PIT tag to confirm their identity. During all three capture periods, field body temperatures were measured immediately after capture using an infrared thermometer (DIGITECH QM-7218; sensor distance: spot ratio 1:1) (± 1.0 °C, Chukwuka et al., 2019). Skinks were then placed individually into calico bags and transported to a nearby field laboratory facility for thermal trials.

For the duration of thermal trials, skinks were held in the field laboratory (ambient temperature 22–26 °C) in individual plastic enclosures (60 × 40 × 35 cm) lined with paper towel. Flat granite rocks were provided for basking and a plastic hide was provided for shelter. Skinks were provided with a heat source in the form of a 40 W incandescent light bulb suspended from the roof of the enclosure at one end, providing a thermal gradient of 22–40 °C for a 12 h period (07:00–19:00 h), that allowed for thermoregulation. Skinks were fed every second day on a diet of mealworms dusted in calcium and vitamin supplements (Vetafarm, Multical dust), water was available *ad libitum*. Skinks were held in the laboratory for up to 10 days per testing period. Following thermal

trials, skinks were released at the site of capture.

2.2. Thermal trials

Three separate thermal trials were undertaken to measure the critical thermal minimum (CTmin), critical thermal maximum (CTmax), thermal tolerance breadth, and thermal performance, within each of the three testing periods (here called 'experimental blocks'). Capture and transport can be stressful (Cartledge et al., 2005), therefore skinks were given 24 h to acclimate to captivity before beginning thermal trials and only underwent one type of thermal trial per day, with a rest day in between trials. Testing of CTmin was always performed before CTmax to control for any potential crossover effects, as CTmax is more stressful for the skinks (Qu et al., 2011). In each experimental block, at the completion of laboratory thermal trials, all skinks were released back into the field at the location of capture.

For CTmin and CTmax measurements, each skink was first placed in an incubator set to 15 °C for 1 h to acclimate. Once at temperature, a thermocouple probe (1 mm diameter; Eutech Instruments; EcoScan JKT; accuracy ± 0.5 °C) was inserted into the cloaca and taped into place with Leukopor tape, and the skink placed into a clear plastic container (25 × 13 × 23 cm) which was placed into an ice bath for CTmin measurements. The body temperature of the skink was recorded at 30 s intervals for the duration of the trial. Once the body temperature of the skink dropped below 8 °C the skink was turned onto its back at 30 s intervals to check for righting reflex. The CTmin was reached once the skink was no longer able to right itself. Once the CTmin was reached the skink was removed from the ice bath and placed into another container in a 20 °C water bath until its body temperature rose to 15 °C. The skink was then monitored, and once activity levels returned to normal the skink was returned to its enclosure. Critical thermal maximum was measured following a similar procedure as CTmin; however, the skinks were gradually warmed to 38–42 °C, using a 50 °C hot water bath. Once the skinks body temperature rose above 37 °C skinks were turned onto their back every 30 s. The CTmax was reached when the skink could no longer right itself. As soon as CTmax was reached, the skink was removed from the 50 °C degree bath and placed into a 20 °C water bath until the body temperature dropped to 25 °C. The skink was then monitored, and once activity levels returned to normal the skink was returned to its enclosure. To calculate the thermal tolerance breadth of skinks, the CTmin was subtracted from the CTmax for each skink (Sheldon and Tewksbury, 2014). It should be noted that one skink did not complete CTmax because during the trial its body temperature would not rise above 41 °C after and it was deemed dangerous to continue the trial for a prolonged period. CTmax was reattempted but we encountered the same issue and thus this skink was removed from the CTmax trial.

For thermal sensitivity of locomotor performance, maximal sprint speed was characterised at three body temperatures (15 °C, 25 °C and 30 °C). These temperatures were chosen as they reflect the range of temperatures that the species is active over (Senior et al., 2019). Prior to each trial, skinks were acclimated to the desired body temperature in an incubator, and then chased down a 1 m race track lined with sandpaper to assist with grip. Each skink was run three times at each temperature, with the time recorded using a stopwatch. The fastest time for each temperature treatment was recorded as the sprint speed variable. Sprint speed was calculated by dividing distance over time.

2.3. Microclimate conditions

Microclimate conditions at the field site were recorded using temperature data loggers (thermometer iButtons DS1921G, Maxim Integrated, USA) placed at the entrances of five occupied burrows. These burrows were chosen at random, but were spread across different aspects at the site. At each of the five burrows, four data loggers were placed around the burrow entrances to capture the thermal variation in habitats utilised by the skinks. The data loggers were placed into

balloons to increase water resistance, and then positioned under rocks (~10 cm in diameter) to reduce capacity for movement. The temperature was recorded every hour from the October 24, 2017 to January 10, 2018 (excluding a period from 1–8 December 2017 when loggers were removed from the site for data download). Hourly temperatures were averaged at each burrow across the four data loggers for the entire experimental period. The average daily temperature and the minimum and maximum temperature per day were calculated for each burrow.

2.4. Statistical analysis

All analyses were conducted in R (R Development Core Team 2017). One-way repeated measures ANOVAs were used to examine how the daily minimum, daily average and daily maximum temperatures changed over time. One-way ANOVAs and post-hoc Tukey's honest significant difference tests were used to compare the average, minimum and maximum daily temperatures across each of the five monitored burrow entrances. A one-way ANOVA and a post-hoc Tukey's honest significant difference test examined whether field body temperatures changed across the experimental blocks.

Linear mixed effects models were produced using the 'lme4' package (Bates et al., 2014) to investigate overall variation in CTmin, CTmax, thermal tolerance breadth and sprint speed across the active season. The models included experimental block as the fixed effect and skink ID as the random effect to account for variation between skinks. To normalise the residuals, a rank normal transformation was applied to thermal tolerance breadth, sprint speed at 15 °C was square root transformed, and sprint speed at 25 °C underwent a rank normal transformation.

Paired *t*-tests were undertaken to investigate changes in CTmin, CTmax and thermal tolerance breadth within individual skinks across the active season. Wilcoxon signed rank tests were undertaken to investigate changes in sprint speed within individual skinks for each temperature treatment across the active season. Wilcoxon singed rank tests were used as data transformations were unsuccessful. For both tests each experimental block was compared to one another (1 vs 2, 2 vs 3, 1 vs 3). As skink re-capture was not consistent across all catching periods, skinks were grouped according to whether they were caught in all three blocks (block 3a), or in two blocks (block 3b). These groups were then analysed separately for all pairwise comparisons.

The Bonferroni p-value adjustment was applied to account for multiple comparisons in these tests, where the p-value was multiplied by the number of comparisons made, thus reducing the risk of type I errors (Crowley, 1985; Crawley, 2012).

3. Results

In total, 24 skinks were repeatedly captured and subsequently underwent thermal trials during the study. Catching rate was not consistent across all experimental blocks, with 12 skinks caught and tested in all three blocks, and 12 caught and tested in two of the experimental blocks.

3.1. Microhabitat conditions and field body temperatures

The temperatures at the study site ranged from 5 °C to 48.5 °C during out study period (Table 1). The average daily temperature increased steadily as the active season progressed, $F_{(4, 70)} = 27.56$, $p < 0.001$ (Fig. 1). The daily minimum temperature increased across the active season $F_{(4, 70)} = 19.97$, $p < 0.001$ as did the daily maximum temperature $F_{(4, 70)} = 9.52$, $p < 0.001$. The microhabitat temperatures varied across the site, with differences across monitored burrow entrances in the average daily temperature ($p < 0.001$; Table 2) and the maximum daily temperatures ($p < 0.001$; Table 1). The average minimum temperature did not differ across monitored burrow entrances ($p = 0.25$; Table 2). Post-hoc Tukey's test showed that average daily temperature differed significantly between 2 burrows by 1.8 °C and

Table 1

Descriptive statistics looking at the daily average temperature, daily minimum and daily maximum temperature across five monitored burrow entrances at the study site.

Temperature variable	Minimum	Maximum	Mean	Standard deviation	Range
Minimum daily temperature °C	5	13.13	13.5	2.95	5–20.63
Maximum daily temperature °C	20.63	48.5	31.71	4.05	13.13–48.5
Average daily temperature °C	9.625	31.32	20.21	7.58	9.62–31.32

2.86 °C ($p = 0.049$, $p = < 0.001$, Table S1, Fig. 1). Significant differences were identified in 6 out of 10 pairwise comparisons for maximum daily temperature (Table S1). Field body temperatures varied across the active season ($p = 0.037$; Table 3; Fig. S1). Post-hoc Tukey's tests showed that field body temperatures increased by 2.02 °C between block 1 and 2 ($p = 0.03$; Fig. S1).

3.2. Critical thermal minimum, critical thermal maximum, and thermal tolerance breadth

The CTmin of skinks increased across the active season ($p < 0.001$; Fig. 2, Table 4), by 0.96 °C between block 1 and block 2, and by 1.45 °C between block 1 and block 3 ($p < 0.001$). Pairwise comparisons of within skink variation identified increases in CTmin between block 1 and 2 ($p = 0.005$; Table 5), and block 1 and 3a and 3b ($p = 0.02$; $p = 0.034$; Table 5).

The CTmax of skinks did not change across the active season as there was no changes across experimental blocks ($p < 0.05$; Fig. 2, Table 4). The linear mixed effect model showed that a skink ID explained a high percentage of the variance within CTmax (Table 4). Pairwise comparisons looking at within skink variations showed similar results with no significant differences between blocks (Table 5).

As expected, given the above results, the thermal tolerance breadth of skinks also decreased across the active season ($p < 0.001$; Fig. 2, Table 4). The thermal tolerance breadth of skinks decreased by 0.5 °C between experimental blocks (Table 4). The linear mixed effect model showed that a skink ID explained a high percentage of the variance within thermal tolerance breadth (Table 4). Pairwise comparisons looking at within skink variation identified significant decreases in thermal tolerance breadth between block 1 and 2 ($p = 0.018$; Table 5), and block 1 and 3a and 3b ($p = 0.007$; $p = 0.029$; Table 5).

3.3. Thermal sensitivity of sprint speed

Sprint speed was variable across the active season (Fig. 3, Table S2). The linear mixed effects models identified differences in sprint speed in experimental block 2 when compared to block 1 and block 3, which was evident across all temperature treatments (15 °C, 25 °C, 30 °C). In the 15 °C treatment, the sprint speed of skinks decreased by 0.09 m/s between block 1 and block 2 ($p < 0.001$; Fig. 3, Table S2). Similarly, in the 30 °C treatments sprint speed decreased by 0.02 m/s between block 1 and block 2 ($p < 0.001$; Fig. 3, Table S2). Conversely, sprint speed increased by 1.68 m/s in the 25 °C treatment between block 1 and block

Table 2

The results of three ANOVAs, looking at daily average temperature, daily minimum and daily maximum temperature across five monitored burrow entrances at the study site. * indicates statistical significance.

| Temperature variable	Predictor	*df*	SS	MS	F	*P*
Daily average	Burrow	3	307	76.76	4.8	<0.001*
	Residual	363	5803	15.99		
Daily minimum	Burrow	4	58	15.50	1.35	0.25
	Residual	363	3888	10.71		
Daily maximum	Burrow	4	3620	905	18.91	<0.001*
	Residual	363	17371	47.9		

Table 3

The results of the ANOVA looking at the field body temperatures of *L. whitii* across three capture periods over the active season. * indicates statistical significance.

Predictor	*df*	SS	MS	F	*P*
Block	2	40.7	20.36	3.45	0.037*
Residual	63	368.9	05.86		
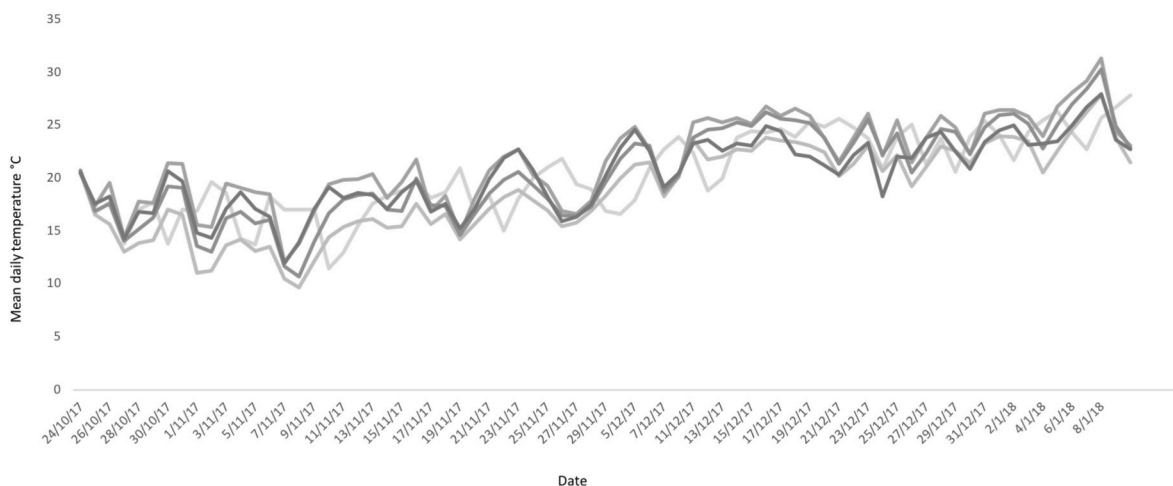
Fig. 1. The mean daily temperature °C across the five monitored burrow entrances at the field site from October 2017 to January 2019. Each line represents a separate burrow system.
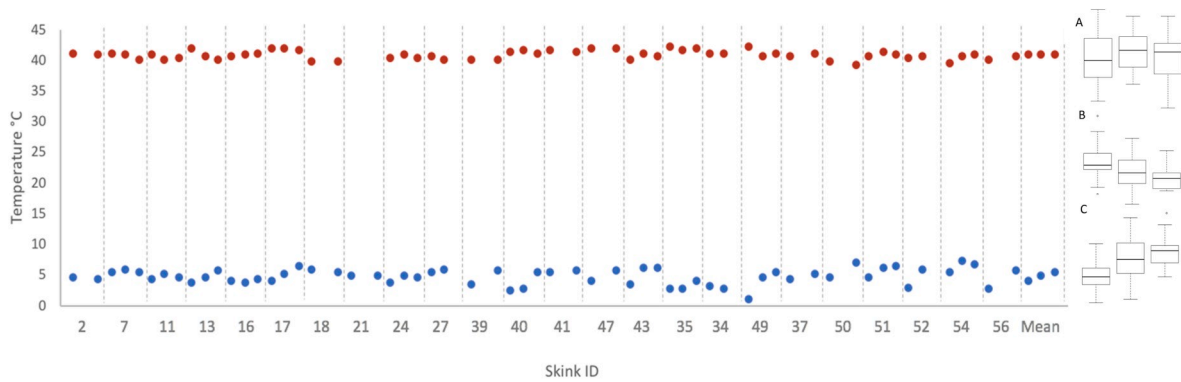
Fig. 2. Plot showing the critical thermal minimum (blue circles) and the critical thermal maximum (red circles) temperature for each *L. whitii* skink across three experimental blocks. The difference between the critical thermal minimum and maximum is the thermal tolerance breadth. Three experimental blocks were undertaken shown by the three circle for each skink, however catching rate was not consistent for all skinks. Gaps indicate where skinks were not captured in a block and thus did not undergo trials. Boxplots show the median and upper and lower quartiles looking at the overall variation in (A) Critical thermal maximum, (B) Thermal tolerance breadth, (C) Critical thermal minimum, across the three experimental blocks.

Table 4
The results of the linear mixed effect model showing the relationship between the critical thermal minimum, critical thermal maximum and thermal tolerance breadth of *L. whitii* and the experimental block. Skink ID was controlled for as a random effect. * indicates statistical significance.

Thermal variable	Significant block	Effect size	+/− SE	df	t value	P
Critical thermal minimum	Block 2	1.45	0.24	43.75	6.17	<0.001 *
	Block 3	0.96	0.27	45.54	3.60	<0.001 *
	Random effects	Percentage of variation explained				
	Skink ID	44.8%				
	Residual	55.2%				
Critical thermal maximum	Block 3	−0.09	0.15	37.2	−0.58	0.566
	Block 2	0.01	0.17	38.11	0.08	0.940
	Random effects	Percentage of variation explained				
	Skink ID	52.6%				
	Residual	47.4%				
Thermal tolerance breadth	Block	−0.50	0.09	34	−5.76	<0.001 *
	Random effects	Percentage of variation explained				
	Skink ID	58%				
	Residual	41.9%				

Table 5
The results of the paired *t*-tests looking at within skink variation in critical thermal minimum, critical thermal maximum and thermal tolerance breadth of *L. whitii* across experimental blocks. For statistical analysis, block 3 is divided into two groups; a) skinks caught in all experimental blocks, b) skinks caught only in block 1 and 3. * indicates statistical significance.

| Thermal variable	Blocks compared	Mean of the differences	df	t	Confidence interval	P
Critical thermal minimum	Block 1-2	−1.11	14	−3.83	(-1.72, −0.49)	0.005 *
	Block 2-3a	−0.53	11	−1.78	(-1.19, 0.12)	0.306
	Block 1-3a	−1.67	11	−4.68	(-2.49 ,-0.90)	0.002 *
	Block 1–3b	−1.1	8	−2.55	(-2.09-0.12)	0.034 *
Critical thermal maximum	Block 1-2	0.08	14	0.36	(-0.40, 0.56)	2.169
	Block 2-3a	0.14	11	1.00	(-0.17, 0.45)	1.011
	Block 1-3a	0.2	11	0.77	(-0.37, 0.77)	1.362
	Block 1–3b	−1.1	8	−2.55	(-2.09-0.12)	0.034 *
Thermal tolerance breadth	Block 1-2	1.19	14	3.23	(0.40, 1.97)	0.018 *
	Block 2-3a	0.68	11	1.98	(-0.07, 1.42)	0.218
	Block 1-3a	1.89	11	3.92	(0.83 ,2.95)	0.007 *
	Block 1–3b	1.22	7	2.75	(0.17, 2.27)	0.029 *

2 (*p* < 0.001; Fig. 3, Table S2).

Pairwise comparisons of within skink variation in the 15 °C treatment, identified decreases in sprint speed between block 1 and 2 (*p* = 0.002; Table S3). Pairwise comparisons of within skink variation at the 25 °C identified increases in speed between block 1 and 2 (*p* = 0.006; Table S3), with decreases in sprint speed between block 2 and 3a (*p* = 0.0016; Table S3). Pairwise comparison of the 30 °C treatments,

identified decreases in sprint speed between block 1 and 2 (*p* = 0.05; Table S3), with increases in sprint speed block 2 and 3a (*p* = 0.03; Table S3).

4. Discussion

This study builds upon recent studies (Llewelyn et al., 2016; 2018;
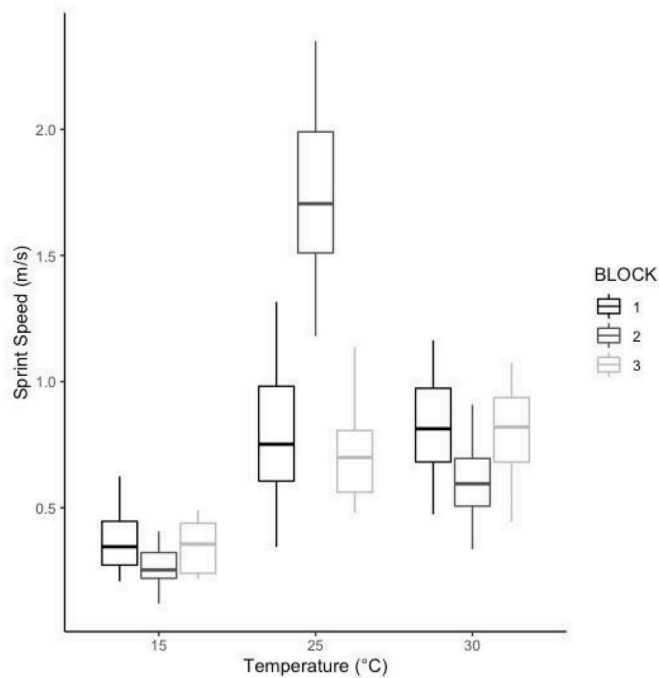
Fig. 3. Boxplots showing the sprint speed of *L. whitii* at the three body temperatures (15 °C, 25 °C and 30 °C), measured across three experimental blocks over the active season. The boxplots show the median (bold), the upper and lower quartiles. At 15 °C, sprint speed decreased between block 1 and 2. At 25 °C, sprint speed increased between blocks 1 and 2, and decreased between blocks 2 and 3a. At 30 °C, speed decreased between blocks 1 and 2, and increased between blocks 2 and 3a.

Abayarathna et al., 2019) that have demonstrated thermal plasticity across the active season using free-ranging animals, exposed to seasonal fluctuations in environmental temperatures. Increases in environmental temperature were apparent across the study period, and significant thermal variation was evident across the field site. Our results were consistent with the majority of our predictions, with plasticity identified in CTmin, thermal tolerance breadth and sprint speed, but not CTmax. Our results suggest that increases in environmental temperatures during the first half of the active season (Fig. 1) may drive plasticity of cold tolerance, but that heat tolerance is constrained throughout the active season. Thermal sensitivity of sprint speed was plastic but fluctuated across the season rather than increasing at the higher temperature treatments with environmental temperatures as predicted.

4.1. Thermal variation across microhabitats

Burrow entrance temperatures increased over the first half of the active season (October–January; Fig. 1). *Liopholis whitii* exhibits high fidelity to its burrow system, seldom venturing more than a couple of metres from it during the activity season (Chapple and Keogh, 2005, 2006). Thus, changes in temperature across the active season are likely to be one of the most important factors shaping the plasticity observed in the thermal tolerances of *L. whitii*. An increase in environmental temperature minimums and mean daily temperatures were evident across the field site (Fig. 1). Steady increases in the environmental temperatures likely reduce the selective pressures that maintain a low critical thermal minimum in *L. whitii* during the colder seasons. Average and maximum daily temperatures, but not minimum daily temperatures, significantly differed between the monitored burrow entrances. The monitored burrows were located at different aspects, with varying levels of vegetation cover and shade. These results suggest that there is significant thermal variation between the burrow entrances, which likely extends to the microhabitats across the entire site. Thermal

heterogeneity of the environment is critical for behavioural thermoregulation in ectotherms (Kearney et al., 2009). Ectotherms thermoregulate via a number of behaviours including shuttling between different microclimates, varying posture and altering daily activity times (Huey, 1974; Dillon et al., 2006; Kingsolver et al., 2013). The thermal variability across the site suggest that *L. whitii* may be able to behaviourally avoid high temperatures, and travel between microhabitats to achieve preferred body temperatures (e.g. Huey and Pianka, 1977; Dillon et al., 2006). The consistency of minimum temperatures across the site suggests that skinks may be less able to behaviourally buffer low temperatures (Kearney et al., 2009). It has been proposed that ectotherms should respond to thermal variation through a combination of behavioural and physiological alterations (Dillon et al., 2006), in proportions that are energetically efficient for the organism (Seebacher, 2005). Thus, taking into account the potential for behavioural thermoregulation is important when considering thermal biology and seasonal plasticity of thermal tolerances.

4.2. Temporal plasticity in critical thermal minimum but not critical thermal maximum

The CTmin of high elevation *L. whitii* follows the trend of increasing environmental temperatures across the active season, as lizards became less able to tolerate cold temperatures. Variability of minimum tolerances has previously been identifed within the *Liopholis* genus (Senior et al., 2019), as well as decreases in minimum tolerances in response to acclimation treatments (Spellerberg, 1972). Additionally, seasonal plasticity has been documented in a number of Australian lizards that do not enter winter dormancy, with minimum tolerances higher in summer than winter (Spellerberg, 1972). Minimum tolerance plasticity has been identified in *Drosophila* (Hoffmann et al., 2003; Overgaard and Sorensen, 2008; Clemson et al., 2016), as well as non-model species including meat ants (*Iridomyrmex purpureus*; Andrew et al., 2013), mealworms (*Tenebrio molitor*; Allen et al., 2012) and scincid lizards (*Sphenomorphus taiwanensis*, *Sphenomorphus incognitus*, Huang et al., 2006; *Lampropholis similis*, Llewelyn et al., 2016, 2018). As critical thermal minima in ectotherms appears to be related to environmental temperatures (Clusella-Trullas et al., 2011), plastically shifting minimum thermal tolerances in line with environmental trends may be energetically beneficial for *L. whitii*, as high elevation skinks are less able to behaviourally avoid lower temperatures (e.g. Yuni et al. 2018).

In contrast, there were no measurable trends in the CTmax of high elevation *L. whitii*, suggesting that maximum tolerances do not plastically respond as environmental temperatures increased over the course of four months. Seasonal plasticity of maximum tolerances has been identified in a meta-analysis on lizards, with maximum tolerances slightly higher in summer than winter (Clusella-Trullas and Chown, 2014). This plasticity is highly variable between species, and increases in maximum tolerances are consistently small ecotherms (Huang et al., 2006; Clusella-Trullas and Chown, 2014; Kellermann and Sgró, 2018). Significant increases in CTmax are often associated with strong acclimation treatments in laboratory experiments (Hoffmann et al., 2003; Terblanche and Chown, 2006; Allen et al., 2012; Esperk et al., 2016; van Heerwaarden et al., 2016). In *L. whitii*, CTmax was found to differ significantly between the population used in this study and another from 300 m higher in elevation (Senior et al., 2019). This suggests some capacity for CTmax plasticity in this species but not in response to temperature fluctuations across the active season. Whilst more significant differences may occur in *L. whitii* CTmax between summer and winter, we found no evidence of variability across the active season, implying little to no temporal plasticity in maximum thermal tolerances for this population. This may increase the susceptibility of *L. whitii* to warmer summer temperatures due to climate change (e.g. Sinervo et al., 2010).

As a result of the rise in CTmin and stability of CTmax, the thermal tolerance breadth of high elevation *L. whitii* also decreased across the active season. This suggests that high elevation population of *L. whitii*

are tolerant to the widest range of temperatures at the beginning of the active season when colder conditions are more likely. Seasonal plasticity in thermal tolerance breadth has rarely been directly investigated (Angilletta, 2009), but Sheldon and Tewksbury (2014) found that thermal tolernace increased with seasonality in beetles. Thermal tolerance breadth, however, can be inferred from the results of previous studies reporting both the CTmin and CTmax. Greater plasticity in CTmin, than CTmax, is common throughout the literature, and indicates plasticity within thermal tolerance breadth may be common across ectotherms (Klok and Chown, 2003; Hoffmann et al., 2005; Terblanche and Chown, 2006). A decrease in thermal tolerance breadth across the active season may be important for high elevation *L. whitii* as it reduces the thermal scope for performance (Huey and Hertz, 1984). However, during the warmer months, there may be less need for cold tolerance. Changes to an organisms' thermal tolerance breadth, facilitated by plasticity in thermal tolerances, has been proposed to be important when predicting species responses to climate change (Chevin et al., 2010). This may be particularly relevant for high elevation skinks, with increased thermal variability and temperature extremes predicted in high elevation environments (Hughes, 2003, 2011). Our results show that thermal tolerance breadth becomes narrower in summer, suggesting that high elevation *L. whitii* become more thermally specialised in response to seasonal increases in temperature.

Plasticity in such traits always impose a cost to the individual (Seebacher, 2005). These costs may include the energetic cost of the acclimation, the time required to acclimate, genetic costs, the maintenance of sensory and response pathways, and any potential trade-offs that occur (Seebacher, 2005; Angilletta, 2009). The maintenance of thermal plasticity must therefore reflect a balance between the costs and benefits of plasticity (Ghalambor et al., 2007). The lack of temporal plasticity in maximum tolerances of high elevation *L. whitii* may reflect an imbalance between the costs and benefits. Additionally, a combination of physiological and behavioural factors may limit plasticity in maximum tolerances. Plasticity in maximum tolerances may be limited by behavioural thermoregulation (Marais and Chown, 2008). Behavioural thermoregulation allows ectotherms to regulate their body temperature using the inherent variability in microclimates (Seebacher, 2005). By buffering organisms from thermal extremes, behaviour may reduce the selection for plasticity in maximum tolerances, as per the 'Bogert effect' (Huey et al., 2003; Marais and Chown, 2008). This may be particularly important within our study, as microhabitat data identified significant differences in the maximum temperatures across the site. If high elevation *L. whitii* are behaviourally avoiding temperature extremes across the active season, it may be an important factor explaining the lack of plasticity in CTmax.

4.3. Thermal performance is plastic, but not in response to season

Our study identified plasticity in the thermal performances of *L. whitii*; however, contrary to our predictions, there was no evidence that this followed temperature trends across the active season. Indeed, there was no clear pattern in sprint speed, either in response to temperature or testing period. This is in contrast to the observed seasonal acclimation of locomotion in Chinese blue-tailed skinks (*Plestiodon chinesis*, Sun et al., 2014). Importantly, a similar pattern was not detected when field populations of *P. chinesis* were sampled, suggesting that the combined influence of environmental variables may influence plasticity of thermal sensitivity of sprint spreed (Sun et al., 2014). Historically, sprint speed has been viewed as a highly conserved trait due to its direct impact on fitness (Crowley, 1985; Kaufmann and Bennett, 1989; Angilletta et al., 2002a). Our results suggest that sprint speed is plastic in high elevation *L. whitii;* however, as differences were only observed in experimental block two, plasticity in sprint speed sensitivity does not appear to follow an overall trend in environmental temperature increases. Plasticity within thermal performance may be influenced by smaller scale temperature fluctuations in the environment, rather than

trends within the active period (Andrew et al., 2013). The study site experienced a steep drop in temperature in the week preceding capture period two. Additionally, field body temperatures were significantly higher in capture period two. This may reflect changes in the basking behaviour of skinks induced by temperature variation. Although not monitored in this study, access to water, solar radiation, as well as food availability and predation history have also been proposed to influence sprint speed of skinks (Shu et al., 2010; Sun et al., 2014). We hypothesise that small-scale environmental changes, in combination with biotic factors may have contributed to the variation observed in the sprint speed of high elevation *L. whitii.*

5. Conclusions

This study investigated the plasticity of thermal tolerance and thermal performance across the active season in males in a high elevation population of *L. whitii.* We found support for our hypotheses, with temporal plasticity of CTmin and thermal tolerance breadth, and no plasticity in CTmax. We found mixed support for our hypothesis predicting temporal plasticity in thermal sensitivity of sprint speed, with some plasticity observed between experimental blocks. Our results highlight the importance of pairing field and laboratory studies, to place results into an ecologically relevant context. Furthermore, they provide evidence of complex environmental influences on thermal biology. Finally, our study has added to the overall understanding of seasonal thermal plasticity in field conditions using a non-model organism. Further field-based studies investigating the complex interactions between organisms and their changing environment may be particularly important in light of current climate change implications especially in light of our evidence of a lack of plasticity in CTmax.

CRediT authorship contribution statement

Emily M. Drummond: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft. **Anna F. Senior:** Conceptualization, Methodology, Data curation, Formal analysis. **Katelyn Hamilton:** Data curation. **Michael G. Gardner:** Conceptualization, Methodology. **Geoffrey M. While:** Conceptualization, Methodology. **David G. Chapple:** Conceptualization, Methodology, Writing - original draft.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102623.

Ethical statement

Research was conducted in accordance with appropriate collection and research permits (NSW Scientific Licence SL101932), and was approved by the Monash University animal ethics committee (BSCI/2017/17).

Data accessibility

All data is available on Figshare (https://doi.org/10.26180/5ec4 707b76b95).

References

Abayarathna, T., Murray, B.R., Webb, J.K., 2019. Higher incubation temperatures produce long-lasting upward shifts in cold tolerance, but not heat tolerance, of hatchling geckos. Biology Open 8, bio042564.

Allen, J.L., Clusella-Trullas, S., Chown, S.L., 2012. The effects of acclimation and rates of temperature change on critical thermal limits in *Tenebrio molitor* (Tenebrionidae) and *Cyrtobagous salviniae* (Curculionidae). J. Insect Physiol. 58, 669–678.

Andrew, N.R., Hart, R.A., Jung, M.-P., Hemmings, Z., Terblanche, J.S., 2013. Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. J. Insect Physiol. 59, 870–880.

Angilletta, M.J., 2009. Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University press, New York.

Angilletta, M.J., Hill, T., Robson, M.A., 2002a. Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. J. Therm. Biol. 27, 199–204.

Basson, C.H., Clusella-Trullas, S., 2015. The Behavior-Physiology Nexus: behavioral and physiological compensation are relied on to different extents between seasons. Physiol. Biochem. Zool. 88, 384–394.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1, 1–23.

Caldwell, A.J., While, G.M., Beeton, N.J., Wapstra, E., 2015. Potential for thermal tolerance to mediate climate change effects on three members of a cool temperate lizard genus, *Niveoscincus*. J. Therm. Biol. 52, 14–23.

Cartledge, V.A., Gartrell, B., Jones, S.M., 2005. Adrenal and white cell count responses to chronic stress in gestating and postpartum females of the viviparous skink *Egernia whitii* (Scincidae). Comp. Biochem. Physiol., A 141, 100–107.

Chapple, D.G., 2003. Ecology, life-history, and behavior in the Australian Scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. Herpetol. Monogr. 17, 145–180.

Chapple, D.G., 2005. Life history and reproductive ecology of White's skink, *Egernia whitii*. Aust. J. Zool. 53, 353–360.

Chapple, D.G., Keogh, J.S., 2005. Complex mating systema and dispersal patterns in a social lizard, *Egernia whitii*. Mol. Ecol. 14, 1215–1227.

Chapple, D.G., Keogh, J.S., 2006. Group structure and stability in social aggregations of White's skink, *Egernia whitii*. Ethology 112, 247–257.

Chapple, D.G., Keogh, J.S., Hutchinson, M.N., 2005. Substantial genetic structuring in southeastern and alpine Australia revealed by molecular phylogeography of the *Egernia whitii* (Lacertilia: Scincidae) species group. Mol. Ecol. 14, 1279–1292.

Chesson, P.L., 1986. Environmental variation and the coexistence of species. Community Ecol. 240, 54.

Chevin, L.M., Hoffmann, A.A., 2017. Evolution of phenotypic plasticity in extreme environments, 372. Philosophical Transactions of the Royal Society B-Biological Sciences, p. 20160138.

Chevin, L.M., Lande, R., Mace, G.M., 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol. 8, e1000357.

Chukwuka, C.O., Virens, J., Cree, A., 2019. Accuracy of an inexpensive, compact infrared thermometer for measuring skin surface temperature of small lizards. J. Therm. Biol. 84, 285–291.

Childress, E.S., Letcher, B.H., 2017. Estimating thermal performance curves from repeated field observations. Ecology 98, 1377–1387.

Clemson, A.S., Sgro, C.M., Telonis-Scott, M., 2016. Thermal plasticity in *Drosophila melanogaster* populations from eastern Australia: quantitative traits to transcripts. J. Evol. Biol. 29, 2447–2463.

Clusella-Trullas, S., Blackburn, T.M., Chown, S.L., 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am. Nat. 177, 738–751.

Clusella-Trullas, S., Chown, S.L., 2014. Lizard thermal trait variation at multiple scales: a review. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 184, 5–21.

Crawley, M.J., 2012. The R Book. John Wiley & Sons, Victoria.

Crowley, S.R., 1985. Thermal sensitivity of sprint-running in the lizard *sceloporus-undulatus* - support for a conservative view of thermal physiology. Oecologia 66, 219–225.

Diaz, J.A., Cabezas-Diaz, S., 2004. Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. Funct. Ecol. 18, 867–875.

Dillon, M.E., Frazier, M.R., Dudley, R., 2006. Into thin air: physiology and evolution of alpine insects. Integr. Comp. Biol. 46, 49–61.

Edwards, A., Jones, S.M., 2001. Changes in plasma progesterone, estrogen, and testosterone concentrations throughout the reproductive cycle in female viviparous blue-tongued skinks, *Tiliqua nigrolutea* (Scincidae), in Tasmania. Gen. Comp. Endocrinol. 122, 260–269.

Esperk, T., Kjaersgaard, A., Walters, R.J., Berger, D., Blanckenhorn, W.U., 2016. Plastic and evolutionary responses to heat stress in a temperate dung fly: negative correlation between basal and induced heat tolerance? J. Evol. Biol. 29, 900–915.

Gaston, K.J., Chown, S.L., 1999. Elevation and climate tolerance: a test using dung beetles. Oikos 86, 584–590.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G., 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr. Comp. Biol. 46, 5–17.

Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct. Ecol. 21, 394–407.

Gutierrez-Pesquera, L.M., Tejedo, M., Olalla-Tarraga, M.A., Duarte, H., Nicieza, A., Sole, M., 2016. Testing the climate variability hypothesis in thermal tolerance limits of tropical and temperate tadpoles. J. Biogeogr. 43, 1166–1178.

Haines, M.L., Stuart-Fox, D., Sumner, J., Clemann, N., Chapple, D.G., Melville, J., 2017. A complex history of introgression and vicariance in a threatened montane skink (*Pseudemoia cryodroma*) across an Australian sky island system. Conserv. Genet. 18, 939–950.

Hay, D.A., Ball, I.R., 1979. Contributions to the biology of freshwater planarians (Turbellaria) from the Victorian Alps, Australia. Hydrobiologia 62, 137–164.

Herrando-Pérez, S., Ferri-Yáñez, F., Monasterio, C., Beukema, W., Gomes, V., Belliure, J., Chown, S.L., Vieites, D.R., Araújo, M.B., 2018. Intraspecific variation in lizard heat tolerance alters estimates of climate impact. J. Anim. Ecol. 88, 247–257.

Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S., 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? Funct. Ecol. 27, 934–949.

Hoffmann, A.A., Shirriffs, J., Scott, M., 2005. Relative importance of plastic vs genetic factors in adaptive differentiation: geographical variation for stress resistance in *Drosophila melanogaster* from eastern Australia. Funct. Ecol. 19, 222–227.

Hoffmann, A.A., Sorensen, J.G., Loeschcke, V., 2003. Adaptation of *Drosophila* to temperature extremes: Bringing together quantitative and molecular approaches. J. Therm. Biol. 28, 175–216.

Hu, J.T., Chen, B., Li, Z.H., 2014. Thermal plasticity is related to the hardening response of heat shock protein expression in two *Bactrocera* fruit flies. J. Insect Physiol. 67, 105–113.

Huang, S.P., Hsu, Y., Tu, M.C., 2006. Thermal tolerance and altitudinal distribution of two *Sphenomorphus* lizards in Taiwan. J. Therm. Biol. 31, 378–385.

Huey, R.B., 1974. Behavioral thermoregulation in lizards: importance of associated costs. Science 184, 1001–1003.

Huey, R.B., Berrigan, D., 2001. Temperature, demography, and ectotherm fitness. Am. Nat. 158, 204–210.

Huey, R.B., Hertz, P.E., 1984. Is a jack-of-all-temperatures a master of none? Evolution 38, 441–444.

Huey, R.B., Hertz, P.E., Sinervo, B., 2003. Behavioural drive versus behavioural inertia in evolution: a null model approach. Am. Nat. 161, 357–366.

Huey, R.B., Pianka, E.R., 1977. Seasonal variation in thermoregulatory behaviour and body temperature of diurnal Kalahari lizards. Ecology 58, 1066–1075.

Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoology 19, 357–366.

Hughes, L., 2003. Climate change and Australia: trends, projections and imapcts *Austral*. Ecology 28, 423–443.

Hughes, L., 2011. Climate change and Australia: key vulnerable regions. Reg. Environ. Change 11, S189–S195.

Kaufmann, J.S., Bennett, A.F., 1989. The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. Physiol. Zool. 62, 1047–1058.

Kearney, M., Shine, R., Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc. Natl. Acad. Sci. Unit. States Am. 106, 3835–3840.

Kellermann, V., Sgró, C.M., 2018. Evdience for lower plasticity in CTmax at warmer developmental temperatures. J. Evol. Biol. 31, 1300–1312.

Kingsolver, J.G., Diamond, S.E., Buckley, L.B., 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. Funct. Ecol. 27, 1415–1423.

Klok, C.J., Chown, S.L., 2003. Resistance to temperature extremes in sub-Antarctic weevils: Interspecific variation, population differentiation and acclimation. Biol. J. Linn. Soc. 78, 401–414.

Llewelyn, J., Macdonald, S.L., Hatcher, A., Moritz, C., Phillips, B.L., 2016. Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. Divers. Distrib. 22, 1000–1012.

Llewelyn, J., Macdonald, S.L., Moritz, C., Martins, F., Hatcher, A., Phillips, B.L., 2018. Adjusting to climate: acclimation, adaptation and developmental plasticity in physiological traits of a tropical rainforest lizard. Integr. Zool. 13, 411–427.

Marais, E., Chown, S.L., 2008. Beneficial acclimation and the Bogert effect. Ecol. Lett. 11, 1027–1036.

Mendez-Galeano, M.A., Calderon-Espinosa, M.L., 2017. Thermoregulation in the Andean lizard *Anolis heterodermus* (Squamata: Dactyloidae) at high elevation in the eastern Cordillera of Colombia. Iheringia Ser. Zool. 107, e2017018.

Monasterio, C., Salvador, A., Iraeta, P., Díaz, J.A., 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. J. Biogeogr. 36, 1673–1684.

Ortega, Z., Perez-Mellado, V., 2016. Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. Acta Oecol. 77, 201–206.

Overgaard, J., Kristensen, T.N., Mitchell, K.A., Hoffmann, A.A., 2011. Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? Am. Nat. 178, S80–S96.

Overgaard, J., Sorensen, J.G., 2008. Rapid thermal adaptation during field temperature variations in *Drosophila melanogaster*. Cryobiology 56, 159–162.

Qu, Y.F., Li, H., Gao, J.F., Xu, X.F., Ji, X., 2011. Thermal preference, thermal tolerance and the thermal dependence of digestive performance in two *Phrynocephalus* lizards (Agamidae), with a review of species studied. Current Zoology 57, 684–700.

R Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for statistical computing, Vienna, Austria.

Schulte, P.M., Healy, T.M., Fangue, N.A., 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integr. Comp. Biol. 51, 691–702.

Seebacher, F., 2005. A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? J. Comp. Physiol. B 175, 453–461.

Seebacher, F., White, C.R., Franklin, C.E., 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. Nat. Clim. Change 5, 61–66.

Senior, A.F., Atkins, Z.S., Clemann, N., Gardner, M.G., Schroder, M., While, G.M., Wong, B.B.M., Chapple, D.G., 2019. Variation in thermal biology of three closely related lizard species along an elevation gradient. Biol. J. Linn. Soc. 127, 278–291.

Sheldon, K.S., Tewksbury, J.J., 2014. The impact of seasonality in temperature on thermal tolerance and elevational range size. Ecology 95, 2134–2143.

Shu, L., Sun, B.-J., Du, W.-G., 2010. Effects of temperature and food availability on selected body temperature and locomotor performance of *Plestiodon (Eumeces) chinensis* (Scincidae). Anim. Biol. Leiden 60, 337–347.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Cruz, M.V.S., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M.L., Meza-Lazaro, R. N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C. F.D., Ibarguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites, J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328, 894–899.

Spellerberg, I.F., 1972. Temperature tolerances of southeast Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. Oecologia 9, 23–46.

Sun, B.J., Tang, W.Q., Zeng, Z.G., Du, W.G., 2014. The Seasonal acclimatisation of locomotion in a terrestrial reptile, *Plestiodon chinensis* (Scincidae). Asian Herpetol. Res. 5, 197–203.

Terblanche, J.S., Chown, S.L., 2006. The relative contributions of developmental plasticity and adult acclimation to physiological variation in the tsetse fly, *Glossina pallidipes* (Diptera, Glossinidae). J. Exp. Biol. 209, 1064–1073.

van Heerwaarden, B., Kellermann, V., Sgro, C.M., 2016. Limited scope for plasticity to increase upper thermal limits. Funct. Ecol. 30, 1947–1956.

Wilson, S.K., Swan, G., 2017. A Complete Guide to Reptiles of Australia. New Holland Publishers, New South Wales.

Yuni, L.P., Jones, S.M., Wapstra, E., 2018. Thermal biology of the spotted snow skink, *Niveoscincus ocellatus*, along an altitudinal gradient. Aust. J. Zool. 66, 235–246.