Journal of Thermal Biology 83 (2019) 178–186

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Drop it like it's hot: Interpopulation variation in thermal phenotypes shows counter-gradient pattern*

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ARTICLE INFO

Keywords:
Acclimation
Local adaptation
Climate responses
Counter-gradient
Intraspecific variation

ABSTRACT

Ectotherms utilise a complex array of behavioural and physiological mechanisms to cope with variation in suboptimal thermal environments. However, these mechanisms may be insufficient for population persistence under contemporary climate change, resulting in a greater need to understand how local populations respond to geographic variation in climate. In this study, we explored the potential for local adaptation and acclimation in thermal traits and behaviours using wild and captive populations of a small agamid lizard (the jacky lizard, *Amphibolurus muricatus*). We predicted that wild lizards from a high elevation site would have cooler thermal preferences compared to those at low elevation sites to match the more restricted thermal resources at higher, cooler elevations. We additionally explored whether variation in thermal traits was due to recent acclimation or fixed population differences, such as due to developmental plasticity or local adaptation. In contrast to our predictions, we found high-elevation lizards began panting at higher temperatures and had higher thermal preferences relative to lower elevation lizards. When allowed to bask freely, there was no difference in the intensity of basking or daily duration of time spent basking between lizards from different elevations. Although the high-elevation lizards appeared to show stronger acclimation to recent air temperatures compared to low-elevation lizards, this difference was not significant. Similarly, captive lizards acclimated under long and short basking regimes showed no major differences in thermal traits or basking behaviour. Our results are consistent with the presence of counter-gradient variation in thermal phenotypes of lizards, and suggest that these are driven by local adaptive responses or developmental effects rather than recent acclimation.

1. Introduction

Anthropogenic climate change and the warming world are predicted to pose serious changes to the thermal niche of organisms. Altered species distributions (Walther et al., 2002; Perry et al., 2005; Walker et al., 2015), changed phenology (Parmesan et al., 2003) and local extinctions in lizards (Sinervo et al., 2010), frogs (Pounds et al., 2006) and invertebrates (Thomas, 2004) have already been attributed to contemporary climate change. With this growing body of evidence showing how vulnerable animals are to changing thermal environments, it is clear we need a better understanding of the ability of species to respond to altered thermal landscapes through both physiological and behavioural pathways (Logan et al., 2014). Physiological alterations include metabolic performance (Madeira et al., 2016), muscle function (Johnston and Temple, 2002), heat shock protein expression (Pörtner, 2001; Dutton and Hofmann, 2009; Li et al., 2015) and biochemical activity (Seebacher et al., 2003). Behavioural adjustments, which may pre-empt physiological stress, occur in response to spatial or temporal variation in temperature and include modifications to phenology (Parmesan et al., 2003; Parmesan, 2007), nesting preferences (Schwanz and Janzen, 2008) and basking behaviour (Hertz et al., 1981; Cadby et al., 2014; Caldwell et al., 2017). Understanding the behavioural and physiological mechanisms that facilitate population and species persistence across current spatial and temporal variation in climate will allow the construction and implementation of more accurate conservation frameworks (Ashley et al., 2003; Valladares et al., 2014).

An organism's response to thermally distinct environments is dictated by two primary processes - plasticity (such as physiological acclimation; Stillman, 2003) and local adaptation (Parmesan et al., 2003). Both processes influence traits key to individual performance – thermal performance curves and behaviours associated with thermoregulation.

* Author Contribution Statement MJH and LES conceived and designed experiments. MJH performed the fieldwork and experiments. MJH and LES analysed the data. MJH and LES wrote the manuscript.

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https://doi.org/10.1016/j.jtherbio.2019.05.016
Received 12 September 2018; Received in revised form 17 May 2019; Accepted 19 May 2019
Available online 21 May 2019
0306-4565/ © 2019 Published by Elsevier Ltd.

Plasticity is an organism-level response. For example, individual thermal sensitivities (e.g. in locomotor performance, enzyme functionality or metabolism) may change in response to altered thermal conditions through physiological acclimation (Brattstrom, 1968, 1970; Jacobson and Whitford, 1970; Seebacher et al., 2003; Glanville and Seebacher, 2006). Plasticity in thermal sensitivity is usually short term (though it can occur seasonally) and requires high energy investment to alter biochemical and cellular processes. One hypothesis posits that acclimation results in immediate fitness benefits in the new thermal environment (Beneficial Acclimation Hypothesis; Fernandez and Ibarguegoytia, 2012; Kingsolver and Huey, 1998; Pintor et al., 2016a; Rogers et al., 2007; Wilson and Franklin, 2002). Extensive work conducted in invertebrates and fish has indicated the widespread occurrence of thermal acclimation (Podrabsky and Somero, 2006; Sgrò et al., 2010; Calabria et al., 2012). In reptiles, acclimation plays a crucial ecological role by adjusting performance as a function of body temperatures in response to fluctuating environmental temperatures (Christian et al., 1999; Phillips et al., 2015; Pintor et al., 2016a). Behaviours associated with maintaining optimal body temperature are also highly plastic. Daily activity timing and microhabitat selection change across seasons with changing air temperatures (Huey and Pianka, 1977; Flesch et al., 2017; Grimm-Seyfarth et al., 2017; Falcón et al., 2018), and flexible thermoregulatory behaviours allow animals to maintain optimal body temperatures across variable environmental conditions (Cadena and Tattersall, 2009; Basson et al., 2017; Ma et al., 2018; Schwanz et al., 2018).

In contrast, local adaptation occurs at a population level over a generational scale in response to selection. For example, climate appears to have driven local adaptation in thermal traits across populations in *Drosophila* sp. flies (Hoffmann et al., 2003; Van Heerwaarden and Sgrò, 2011; Van Heerwaarden et al., 2012), reptiles (Labra et al., 2009; Pontes-da-Silva et al., 2018) and amphibians (Barria and Bacigalupe, 2017). Current evidence suggests that upper thermal limits are weakly heritable and as such selection can effectively lead to evolution in these traits (Llewelyn et al., 2016a; Belasen et al., 2017; Logan et al., 2018). Regardless, there is a limited *in situ* understanding of the potential for rapid evolution in response to accelerated climate change (Hendry et al., 2008; Hoffmann and Sgrò, 2011). Species distribution modelling predicts that the capacity for evolutionary response can increase population persistence, which in turn reduces the vulnerability of species to climate change (Urban et al., 2014; Catullo et al., 2015; Bush et al., 2016).

When populations have been shown to differ in thermal biology, there are two patterns that occur. The intuitive co-gradient response occurs when animals from cooler environments have lower thermal preferences and better performance at lower temperature relative to conspecifics in warmer regions (Brattstrom, 1965; Mitchell and Lampert, 2000). In contrast, many populations have been shown to display a counter-gradient pattern, where individuals from hotter environments having lower thermal preferences/optima relative to cooler conspecifics (Levins, 1969; Conover and Schultz, 1995; Wilson, 2001; Freidenburg and Skelly, 2004; Angilletta, 2009; Llewelyn et al., 2016a). Counter-gradient patterns were initially identified as patterns in which genotypic and phenotypic variation acted in opposite directions along an environmental gradient (with early definitions focusing exclusively on growth rate over altitudinal gradients; Levins, 1969; Berven et al., 1979). In more recent years the definition of counter-gradient variation has altered to encompass a wider breadth of terms and within thermal literature describes patterns in which thermal phenotypes respond in contrary directions along an environmental gradient. For the context of this study we adopt a definition presented by Llewelyn et al., (2016a) where counter-gradient variation is the process in which a thermal phenotype (behavioural or physiological) negatively correlates with an environmental gradient. Counter-gradient patterns are thought to arise due to several factors including individuals showing compensation for reduced thermal opportunities (e.g. in growth rates, locomotor performance or thermoregulatory behaviour; Conover and Schultz, 1995; Fangue et al., 2009; Llewelyn et al., 2016a; McElroy, 2014) or as a function of trade-offs with other fitness related traits (Conover and Schultz, 1995). In a similar compensatory way, plastic thermoregulatory behaviours, such as microhabitat selection, may buffer individuals against thermal variation, thereby reducing selection on thermal physiologies and limiting evolutionary responses to climate change (Bogert, 1949; Van Damme et al., 1989; Zuk et al., 1995; Gvoždík, 2002; Cadby et al., 2014; Gunderson et al., 2015).

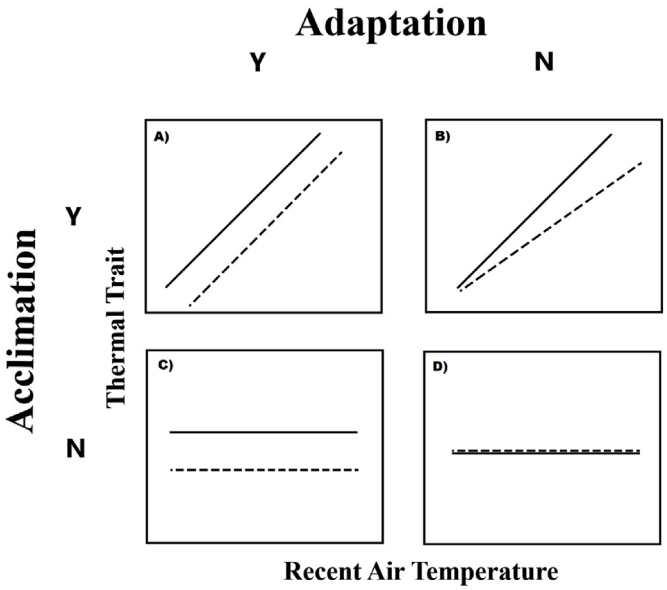

Fig. 1. Conceptual hypothesis figure showing predicted responses of a thermal trait under local adaptation (significant population difference) or acclimation (significant correlation with the environment) when plotted against air temperature. The solid line is representative of a theoretical high elevation population, whilst the dashed line is representative of a theoretical low elevation population. A positive trendline is shown for illustrative purposes. On the X axis, title Y is a scenario with the presence of adaptation and title N is representative of a scenario absent of adaptation. On the Y axis, title Y is a scenario with the presence of acclimation and title N is representative of a scenario absent of acclimation. A, acclimation and local adaptation; B, acclimation only; C, local adaptation only; D, no evidence for either local adaptation or acclimation.

Our study explored local adaptation and acclimation in thermal physiology and behaviour in a temperate Australian lizard, the jacky lizard (*Amphibolurus muricatus*), using two wild populations from different elevations and a captive population subjected to an acclimation experiment. We examined three aspects of the jacky dragons thermal biology: (1) temperature preferences; (2) thermal limit (panting threshold); (3) basking behaviour. Our first aim was to assess the potential roles of local adaptation versus acclimation in the wild populations by testing for population differences that might reflect local adaptation (Fig. 1A,C) and for correlation with recent air temperature that would support acclimation (Fig. 1A and B). Our second aim was to test for acclimatory ability using an experimental manipulation where captive lizards were held for several months under treatments of long or short daily basking opportunity.

2. Materials and methods

2.1. Study species, study sites and captive population

Jacky lizards (*Amphibolurus muricatus*) are a heliothermic lizard that inhabits areas of coastal heathland and dry sclerophyll forest along the South-Eastern coast of Australia (Cogger, 2015). Two groups of lizards were used in this study: wild caught lizards from the Sydney Region

(New South Wales, Australia) were used to explore natural, inter- and intra-population variation in thermal traits (Aim 1) and lizards from a long-term captive colony used to examine acclimation to lab thermal manipulations (Aim 2). All lizards were measured for three thermal traits (see below). Up to four wild lizards were captured each sampling trip; the first two lizards captured on each trip had thermal preferences and panting threshold measured the day succeeding capture, while the latter two were placed into the basking behaviour assay. Lizards were then rotated into the alternate assay on the consecutive day. All lizards used in the study were non-gravid adults (> 70 mm snout-vent length; Harlow and Taylor, 2000).

Wild caught lizards were collected via noosing in the austral summer between 11-Dec-2015 and the 08-Mar-2016 at two sites in the Greater Sydney Region: Richmond (6 males, 9 females; −33.658610, 150.752802 ; elevation ~20 m; mean August–April temperature 25.7 °C) and Woodford (7 males, 7 females; −33.707543, 150.492847; elevation ~630 m ; mean August–April temperature 24.3 °C). Hereafter, Richmond is referred to as low elevation and Woodford is referred to as high elevation for reader clarity. Lizards were brought back to the University of New South Wales animal facility and were housed individually in opaque plastic cages ('holding cages': 430 mm × 300 mm × 250 mm) with a sand substrate and a single elevated tile (300 mm × 100 mm × 5 mm) as a basking object. They were provided a 10% UVB light tube, with the photoperiod being determined by sunrise and sunset times in Sydney, NSW over the duration of thermal assays. A basking lamp (40 Watt incandescent bulb) was provided for 7 h a day to replicate access to basking resources that would likely be experienced at field sites. Lizards were provided *ad libitum* water throughout the captive period and were not supplied any food items. After assays (see below) and prior to release, mass (nearest 1 g) and Snout-Vent-Length (SVL, nearest 1 mm) were recorded. After release, cage furnishings were washed with deodorising agents and the sand substrate was mixed within the cage to remove scent marking effects.

Captive colony lizards were originally caught from a cool-climate population in Bywong, NSW, Australia in 2012 and 2013 (−35.190442, 149.315562; elevation ~800 m) or were the 2-year-old captive-born offspring of those individuals. Colony lizards had been housed under one of two thermal treatments since August 2015: 11hrs of basking opportunity each day (Long Bask) and 7hrs of basking opportunity (Short Bask). As part of the colony breeding program, lizards were housed in groups of four (1 male, 3 females) in opaque cages (500 mm × 300 mm × 300 mm) with sand substrate and multiple basking objects. Water was provided *ad libitum*, and each lizard was fed 4–6 crickets 3 times per week, dusted with vitamins. Captive lizards were moved from their regular cages to holding cages a day prior to the assays to allow for environmental acclimation.

2.2. Measurement of thermal preferences

Thermal preferences of lizards were measured using a 1.2 m-long thermal gradient with an aluminium floor and a temperature range of 10 °C–45 °C (heated and cooled at each end by peltier plates). The thermal gradient was divided lengthways into two lanes (1200 mm × 57.5 mm), separated by an opaque divider (see Schwanz et al., 2018). Four water bowls were evenly spaced along the length in each lane to give lizards ad lib access to water during the assay. Immediately prior to being placed in the thermal gradient, thermocouple probes (type T welded tip PFA thermocouple, 0.2 mm diameter; TC Direct, Oakleigh, Vic., Australia) were inserted into the cloaca of each lizard and secured with medical tape at the base of the tail. Lizards were then placed into the centre of the gradient and assays ran from 9:00 to 15:00 h. Thermocouple temperatures were recorded every 30 s via a temperature logger (YC-727U hand-held thermocouple logger; TC Direct, Oakleigh, Vic., Australia) and lizards were provided with ambient room light only. Visual barriers were constructed to prevent visual disturbances in the animal facility impacting lizard position in the thermal gradient.

Several temperature preference metrics were calculated using records between 11:00 and 15:00 (discarding the first hour of data as apparatus acclimation time): preferred temperatures (T_{pref}), selected temperature range (T_{sel}), voluntary maximum temperature (VT_{max}) and voluntary minimum (VT_{min}) were measured. Preferred temperature (T_{pref}) was calculated as the median of all temperature records, select temperature range (T_{sel}) was calculated as the difference in °C between the 1st and 3rd quartile of recordings, voluntary maximum temperature (VT_{max}) and voluntary minimum (VT_{min}) were measured as the single highest and lowest recordings respectively.

2.3. Measurement of the thermal limit

Panting threshold (T_{pant}) was measured as an ecologically-relevant upper thermal limit. Panting is a behavioural measure to prevent overheating at the cost of water loss; thus it reflects underlying physiological tolerances as well as behavioural and physiological trade-offs. As animals are unlikely to bask to extreme temperatures that result in loss of muscle control (i.e. the Critical Thermal Maximum), thermal thresholds influenced by behavioural decisions are more relevant for understanding links between animals and their thermal ecology. Assays were conducted at 15:00hrs directly after the conclusion of the thermal gradient assay. Lizards were confined to the region of the thermal gradient where the surface temperature was ~35c (average preferred temperature for the species is 34.8c;Firth and Webb, 1973; Schwanz et al., 2018) using insertable dividers (~15 cm long chamber). A 40 W incandescent light bulb was suspended above the chamber at 30 cm and lowered in increments of 10 cm every 2 min until contact with the lid of the chamber was made, at which point it was left at this height until panting occurred. Panting was defined as the point at which lizards opened their mouth and began sustained gular movements. Body temperature was continuously monitored with the cloacal probe and temperature logger, so that temperature at which panting first occurred could be recorded. At panting, lizards were immediately moved to a cold-water bath and held there until internal temperatures dropped below 25 °C. All research equipment was disinfected between lizards.

2.4. Measurement of basking behaviour

Behavioural differences in thermal resource use in captive and wild animals were quantified by examining the basking of individuals. Basking behaviour was recorded within the holding cages described above. As with the temperature preference assay, a thermocouple probe was inserted into each individual's cloaca and secured with medical tape. Holding cages had a single 40-W heat source available from 9:00–16:00 h, during which time body temperature was recorded every 30 s. For details on how records were used to quantify basking behaviour refer to Data Analysis.

2.5. Local climate of field sites

To determine whether thermal traits of wild-caught lizards was related to recent air temperatures at their capture site, local climate data was accessed through the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/- Accessed June 2016). Minimum and Maximum air temperature measurements were used from the Richmond RAAF (33.6000S;150.7800E; elevation 19 m) and Springwood Bowling Club (33.7100S; 150.5800E; elevation 320 m) weather stations for comparison to low elevation and high elevation populations of lizards respectively. Each station was approx.10 km away from the field sites. Although the Springwood weather station was at a lower elevation than the high elevation capture site, comparison of Springwood records to a weather station at higher elevation than Woodford (Katoomba, 33.7100S; 150.3100E; elevation 1015 m)

indicated little variation in mean daily temperatures between the two (results not presented), thus Springwood provides reasonable weather data for the high elevation population during our sampling time of year.

2.6. Data Analysis

To reduce the number of thermal preference traits and avoid correlated variables, we conducted PCAs of T_{pref}, T_{sel}, VT_{max} and VT_{min} data from wild populations combined and from the captive population. One low elevation lizard had more than 30% of its thermal preference records lost due to a probe malfunction. PCAs both with and without this individual yielded similar results, so we present results including the low elevation lizard. One long bask treatment captive lizard was not included in the final analysis as the lizard ejected the probe from its cloaca at an undetermined point making the values unreliable.

To examine population and environmental effects on thermal traits in wild-caught lizards, linear models were created using PC1, PC2 and T_{pant} values as response variables with fixed effects of population ID, recent air temperature, and their interaction. Two recent air temperature averages were calculated (mean of daily mean temperature and mean of daily maximum temperature) for each of four time intervals (2, 7, 14 and 28 days prior to the capture of a lizard). Akaike Information Criterion (AIC) model comparison was used to select the time interval that provided the best model for each response variable and air temperature mean; models with a ΔAIC of < 2 were considered equivalent. To test for acclimation in the colony experiment, Welch two sample t-tests were conducted on PC1, PC2 and T_{pant} with basking treatment (Long vs. Short) as the predictor variable.

Basking data were used to investigate the potential of behavioural compensation for different thermal conditions between wild populations and between captive treatments. We focused on body temperature records above the species' preferred temperature of 34.8 °C (Schwanz et al., 2018) and above an extreme threshold of 40 °C. This extreme threshold was chosen as it was an intermediate panting threshold in our wild populations (see results). Two methods were used to investigate potential differences: 1) Counting the number of records that exceeded 34.8 °C or 40 °C for each individual; and 2) calculating the cumulative sum of degrees C spent above these temperature values for each individual. These basking response variables were examined in separate t-tests for the wild and captive lizards to test for effects of group (population or lab treatment). Differences in preferred basking time of day were also examined between populations using a mixed effects model with the mean hourly temperature as a response variable and hour of day as a fixed effect and lizard ID as a random effect. One lizard from the high elevation site had to be excluded from analysis due to the fracturing the enclosure and escaping during the assay. Another high elevation lizard tangled the probe and pulled it out towards the end of the assay, 1 h of data was discarded as a result. All statistical analysis occurred in R Studio Version 0.99.903 with base R version 3.3.1.

3. Results

3.1. Variation in thermal preferences

Across all thermal traits (T_{pref}, T_{sel}, VT_{max}, VT_{min}, T_{pant}) calculated, lizards from the low elevation site had lower means than the lizards found at the higher elevation site, although among-individual variation was high. Conversely, in our captive population, the lizards housed under short bask conditions had slightly lower mean thermal traits compared to those housed under long bask conditions (Table 1). Correlations between variables in wild populations showed that T_{pref} is strongly positively correlated with VT_{min} ($r^2 = 0.70$, n = 29), as well as VT_{max} ($r^2 = 0.688$, n = 29). Captive lizards had a strong positive correlation between VT_{min} and T_{pref} ($r^2 = 0.747$, n = 23) and a strong negative correlation between VT_{min} and T_{sel} ($r^2 = -0.819$, n = 23).

In the wild populations, PC1 explained 68.6% and PC2 explained 21.0% of total variance (Table S1). PC1 had negative eigenvectors for VT_{max} (−0.603), T_{pref} (−0.672) and VT_{min} (−0.430), indicating lizards with higher PC1 scores prefer lower body temperatures relative to those with lower scores. Increased PC2 scores reflected a reduced range of selected temperature associated with having a high minimum temperature but low maximum temperature (Eigenvectors; VT_{max},-0.-0.557; T_{pref}, 0.124; VT_{min}, 0.628 and T_{sel}, −0.529).

For the captive colony, PC1 and PC2 similarly explained 73.7% and 19.7% of total variance (Table S1). While PC1 eigenvectors for captive lizards were similar to wild populations in having negative loadings (higher PC1 indicate lower overall temperatures), they differed in that T_{sel} has a positive loading (wider range of temperatures). Higher PC2 values in captive lizards indicated lower VT_{max} and T_{pref}.

3.2. Population comparisons in thermal preferences, behaviours and limits

The panting threshold and temperature preferences (PC1) differed significantly between the two wild populations when accounting for 2, 7 and 28-day recent air temperature averages (Table 2 and Fig. 2a), with the higher elevation population having a higher thermal phenotypes. Recent climate itself was not a significant predictor of T_{pant}, either as a main effect or in an interaction with population. PC2 scores of thermal preferences in wild populations were not predicted by location, recent mean air temperature over any time frame, or the interaction term of the two (Table 2).

Models run substituting maximum daily air temperature instead of mean showed a similar effect of population location on T_{pant} and PC1 and no significant effects of any predictor on PC2 (Table 3). Recent (mean) maximum air temperature was not a significant predictor of any response variable.

Population differences in basking behaviour were not found between low elevation and high elevation lizards when examining number of records or the cumulative sum above 34.8 °C and 40 °C (Table 4). Lizards from the two populations did not differ when examining basking at hourly intervals (Table 5).

3.3. Captive treatment group comparisons in thermal preferences, behaviours and limits

Captive basking treatment did not impact PC1 ($t = -0.21$, $df = 17.85$, $p = 0.83$), PC2 (t = -1.69, df = 17.61, p = 0.11) or panting threshold ($t = 0.70$, $df = 18.45$, $p = 0.49$). Similarly, captive basking treatment had no impact on basking above the 34.8 °C threshold (Table 4). No captive lizards exceeded 40 °C in the basking assay. Mean body temperature was significantly impacted by hour of day (Table 5), with post hoc analysis indicating differences were driven by lower selected temperatures between 1400 and 1500 h compared to earlier in the day ($t = -2.24$, $df = 105$, $p = 0.02$). Treatment and the interaction variable of Time and treatment did not significantly impact temperature (Table 5).

4. Discussion

Local environment is a significant driver of phenotypic variation within species (Valladares et al., 2014). In particular, local thermal environments can influence the thermal preferences, thermal limits and thermoregulatory behaviour of organisms through plastic and evolutionary mechanisms (Huey et al., 2012). Understanding these local responses to thermal conditions and the pathways causing them (acclimation and adaptation) is crucial in predicting species persistence in novel thermal environments (Huey et al., 2009a; Valladares et al., 2014). Our study found that the upper thermal limits and thermal preferences of an Australian lizard (*A. muricatus)* differed between two populations at different elevations. Because we found no substantial evidence of acclimation to recent temperatures in the wild populations or in our captive experiment, these results suggest fixed population

Table 1
Summary statistics of the thermal preferences of the four functional populations. All values except T_{pant} were calculated from body temperature records from 11-Dec-2015 and the 08-Mar-2016 in a thermal gradient. Values are mean ± SD.

	Wild Populations		Captive Population	
	Richmond (20 m) (n = 15)	Woodford (630 m) (n = 14)	Long Bask (n = 10)	Short Bask (n = 12)
VT_{min}	22.51 ± 3.53	25.99 ± 5.08	28.42 ± 5.45	28.03 ± 4.50
VT_{max}	35.88 ± 6.71	38.88 ± 3.95	40.62 ± 2.00	38.86 ± 3.53
1st quartile	24.91 ± 4.82	30.33 ± 4.96	33.57 ± 4.55	31.81 ± 5.52
3rd quartile	29.67 ± 5.51	35.38 ± 3.37	38.13 ± 1.12	35.58 ± 4.08
T_{pref}	27.43 ± 5.81	33.44 ± 3.83	35.25 ± 3.86	33.63 ± 4.79
Mean	27.71 ± 5.06	32.87 ± 3.68	35.50 ± 2.01	33.67 ± 4.26
T_{sel}	04.76 ± 2.14	05.05 ± 3.62	04.56 ± 4.28	03.77 ± 3.04
T_{pant}	39.83 ± 1.36	40.70 ± 0.93	41.57 ± 1.34	41.26 ± 0.95

VT_{min}, voluntary minimum temperature; VT_{max}, voluntary maximum temperature; 1st quartile, the first quartile of records; 3rd, the third quartile of records; T_{pref}, preferred temperature; T_{sel}, select temperature range; T_{pant}, panting threshold.

Table 2
Model comparison of prior time frame (in days) over which mean of daily mean air temperature at the wild population site were calculated and included as a covariate. Lowest AIC for each response variable are bolded to show best model. Models with a ΔAIC of < 2 were considered equivalent. P-values ≤ 0.05 are bolded.

Response Variable	AIC	Time Frame (days)	Temperature Average	Location	Location*Temperature Interaction
T_{pant} (n = 29)	**95.450**	2	f = 0.80	f = 4.64	f = 2.35
			p = 0.38	p = **0.04**	p = 0.14
	95.928	7	f = 0.05	f = 5.79	f = 1.42
			p = 0.83	p = **0.02**	p = 0.24
	99.204	14	f = 1.94	f = 1.83	f = 0.01
			p = 0.18	p = 0.19	p = 0.91
	98.334	28	f = 1.7	f = 4.51	f = 0.01
			p = 0.68	p = **0.04**	p = 0.94
PC1 (n = 29)	**204.037**	2	f = 0.28	f = 7.46	f = 0.59
			p = 0.60	p = **0.01**	p = 0.45
	205.365	7	f = 2.65	f = 4.20	f = 0.00
			p = 0.11	p = **0.05**	p = 0.95
	204.408	14	f = 4.62	f = 2.73	f = 0.55
			p = **0.04**	p = 0.11	p = 0.46
	203.989	28	f = 1.25	f = 6.20	f = 0.93
			p = 0.27	p = **0.02**	p = 0.35
PC2 (n = 29)	177.535	2	f = 0.07	f = 0.37	f = 0.01
			p = 0.80	p = 0.55	p = 0.93
	175.480	7	f = 0.15	f = 0.27	f = 1.89
			p = 0.70	p = 0.60	p = 0.18
	174.972	14	f = 0.00	f = 0.67	f = 2.13
			p = 0.94	p = 0.42	p = 0.16
	175.518	28	f = 0.02	f = 0.51	f = 1.76
			p = 0.90	p = 0.48	p = 0.20

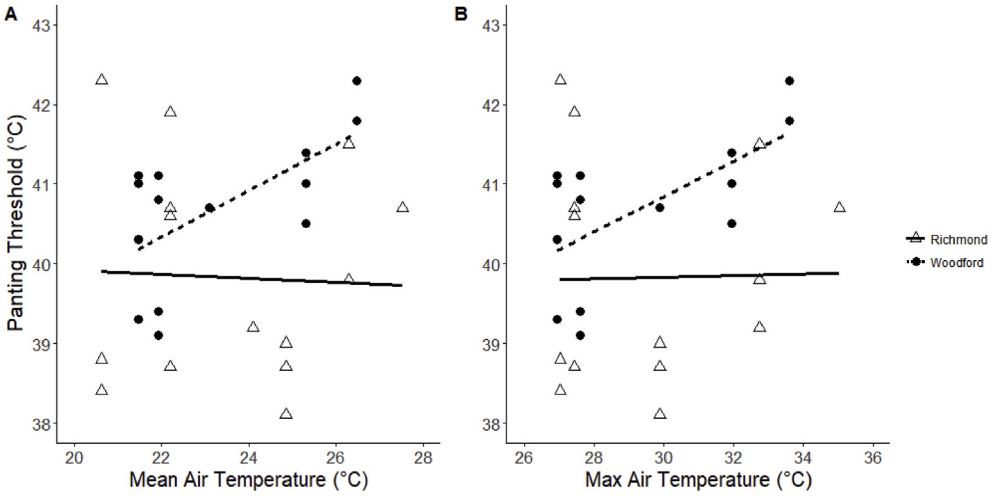

Fig. 2. Scatterplots of panting threshold compared to two-day prior recent mean and maximum air temperature. Unfilled triangles and solid line are the Richmond population (low elevation), filled circles and broken line are the Woodford population (high elevation). Panel A are averages calculated from mean daily air temperature across two most recent days. Panel B are averages calculated from maximum daily air temperature across two most recent days.

Table 3
Model comparison of prior time frame (in days) over which mean of daily maximum air temperature at the wild population site were calculated and included as a covariate. Lowest AIC for each response variable are bolded to show best model. Models with a ΔAIC of < 2 were considered equivalent. P-values ≤ 0.05 are bolded.

Response Variable	AIC	Time Frame (days)	Temperature Average	Location	Location*Temperature Interaction
T_{pant} (n = 29)	**95.476**	2	f = 1.62	f = 4.51	f = 1.64
			p = 0.21	p = **0.04**	p = 0.21
	94.399	7	f = 0.27	f = 8.05	f = 0.69
			p = 0.61	p = **< 0.01**	p = 0.41
	98.702	14	f = 1.27	f = 2.61	f = 0.44
			p = 0.27	p = 0.12	p = 0.51
	94.679	28	f = 0.00	f = 5.30	f = 0.06
			p = 0.96	p = **0.03**	p = 0.81
PC1 (n = 29)	203.947	2	f = 0.33	f = 7.32	f = 0.79
			p = 0.57	p = **0.01**	p = 0.38
	204.769	7	f = 1.48	f = 5.56	f = 0.46
			p = 0.23	p = **0.03**	p = 0.50
	205.172	14	f = 3.80	f = 3.15	f = 0.10
			p = 0.06	p = 0.08	p = 0.75
	198.026	28	f = 0.50	f = 6.79	f = 0.05
			p = 0.49	p = **0.02**	p = 0.82
PC2 (n = 29)	177.552	2	f = 0.01	f = 0.40	f = 0.03
			p = 0.94	p = 0.53	p = 0.86
	177.118	7	f = 0.04	f = 0.39	f = 0.39
			p = 0.83	p = 0.54	p = 0.54
	176.378	14	f = 0.05	f = 0.43	f = 1.00
			p = 0.81	p = 0.52	p = 0.33
	170.499	28	f = 0.37	f = 0.28	f = 1.32
			p = 0.55	p = 0.60	p = 0.26

Table 4
Impact of group (wild population or lab treatment) on basking preferences. No captive animals had records that exceeded the 40 °C threshold in the basking assay.

Model Type	Threshold Temperature (°Celcius)	Wild (n = 29)			Captive (n = 23)		
		t	df	p	t	df	p
Counts	34.8	0.45	25.50	0.66	0.37	19.28	0.71
	40	0.25	21.65	0.80	–	–	–
Sum	34.8	0.49	26.83	0.63	0.49	14.37	0.63
	40	−0.39	21.24	0.70	–	–	–

Table 5
Basking behaviour across the day, examined the mixed effect models. Body temperature is the response variable, with hour of day, site of capture (or lab treatment) and an interaction variable of the two.

Population	Predictor	df	f	p
Wild	Time	5	1.07	0.38
(n = 29)	Site	1	0.02	0.90
	Time x Site	5	0.32	0.90
Captive	Time	5	2.46	**0.04**
(n = 23)	Treatment	1	0.21	0.65
	Time x Treatment	5	0.84	0.52

differences possibly reflecting local adaptation in thermal limits and preferences.

Panting threshold temperatures and thermal preferences (PC1 scores) differed consistently between wild populations across the models considered. Higher elevation lizards had higher thermal phenotypes compared to their lower elevation conspecifics. Given the cooler mean annual temperatures of the high elevation population compared to the low elevation population, this pattern is contrary to our initial hypothesis of a co-gradient response to environment and more supportive of counter-gradient responses. Previous research examining species thermal limits over elevational and latitudinal gradients suggest counter-gradient responses are common in extreme temperature limits of organisms (Van Damme et al., 1989; Laugen et al., 2003; Huey et al., 2009b; Llewelyn et al., 2016a). Similarly, thermal preferences are known to vary intraspecifically in both amphibians (Freidenburg and Skelly, 2004) and fish (Fangue et al., 2009). Our findings of thermal preferences varying geographically within a reptile suggests that further investigations are warranted to determine if this is widespread throughout ectothermic taxa. Contrary findings in other reptile taxa have led to suggestions that physiological plasticity and complex behavioural decisions associated with microhabitat choice and basking behaviour limit variation in thermal preferences between populations (Hertz et al., 1981; Gvoždík, 2002).

Several factors may explain counter gradient responses in upper thermal limits and thermal preferences (McElroy, 2014). Reptiles from environments with shorter seasons and/or cooler days may need to bask to greater extremes to compensate for limited thermal resources; this drives behavioural and physiological changes for higher thermal preferences and thermal limits in cool-climate reptiles compared to their warm-climate conspecifics (Hertz et al., 1981; Seebacher et al., 1999; Freidenburg and Skelly, 2004; Cadby et al., 2014; Halstead and Schwanz, 2015). In cooler environments where size is correlated with first winter mortality, selection for fast growth rates during the active season may be associated with higher temperature preferences to enhance metabolic activity relative to warmer conspecifics (Conover, 1992; Angilletta, 2009). Alternatively, animals from hotter environments often are exposed to greater temperature extremes and so may benefit from selecting cooler microenvironments when thermoregulating to prevent overheating (Wilhoft and Anderson, 1959; Conover and Schultz, 1995). Ultimately, it poses questions of whether counter gradient patterns in thermal traits result from correlation with alternative targets of selection and whether selection on these traits will be maladaptive in changing climates.

While some studies have found that acclimation plays a large role in driving variation of thermal limits due to the plastic nature of the trait (Brattstrom, 1968, 1970; Jacobson and Whitford, 1970; Llewelyn et al., 2016b), our findings suggest that the differences between our two wild populations reflect fixed population differences, such as due to local adaptation. We found no compelling evidence of acclimation to recent temperature in our study. While one model had a p-value < 0.05 associated with recent temperature influencing thermal preferences (PC1;

Table 2), all other models had $p > 0.05$, suggesting it was likely a statistical artefact. During our study, the recent mean and max air temperatures were similar in each population, allowing us to compare thermal traits over the same range of acclimatory temperatures. We found no significant effect of recent air temperature, at any time scale, on panting threshold. However, the possibility of population variation in acclimation ability should not be ruled out. Although we found no significant interaction between location and recent temperature, consideration of the data (Fig. 2a and b) suggests that panting thresholds from the high elevation site are more responsive to recent air temperatures than those from the low elevation population. It is possible that due to our use of air temperature data from a lower elevation weather station (320 m) as a proxy for our high elevation site (630 m) that we have failed to statistically detect this effect. Certainly, the population difference detected in panting threshold is driven by lizards captured during warm periods. It is an intriguing possibility that lizards at the higher elevation site have a higher acclimation ability compared to lower elevation conspecifics. Such differences could reflect selection in high elevation populations to respond quickly to short-term increases in air temperature in order to take advantage of limited windows of thermal opportunity. Alternatively, it is possible that temperatures or variation in temperatures at the lower elevation site are not extreme enough to elicit a stress response for animals in the low elevation population as they may have a previously evolved tolerance, and as such low elevation populations have not evolved a plastic response unlike their high elevation counterparts. Such a possibility warrants future investigations to not only confirm if a response is present, but also characterise the environmental and climatic factors that drive such responses between populations.

Additional support for the differences in panting threshold and thermal preferences between populations being evolutionary and not acclimatory comes from our experiments using captive lizards sourced from a cool-climate population. In previous studies, it has been shown that captive jacky dragons bask as long as a basking lamp is available, such that individuals housed under long-bask conditions have a mean daily body temperature approximately 2 °C higher than those in short-bask housing (Schwanz, 2016). In the present study, however, acclimation to the basking lamp treatments did not influence the panting threshold or thermal preferences.

The experimental results should be considered carefully in comparison to the wild populations. Our experimental design altered the duration of access to optimal body temperatures, not the occurrence of thermal extremes. In studies of other taxa, there is evidence to suggest thermal phenotypes are more strongly influenced by the intensity of extremes, not the availability of thermal resources (Glanville and Seebacher, 2006; Angilletta, 2009; Phillips et al., 2015; Llewelyn et al., 2016a). In the field, recent air temperatures may influence the distribution of extreme-temperature microhabitats, leading to increased exposure to extremes and restrictions on activity (Huey et al., 2009b, 2012; Sinervo et al., 2010; Vickers et al., 2011). Similarly, we recorded negligible differences in basking behaviour between lizards from the two wild populations, suggesting either that behavioural differences in basking do not occur in our populations, or that differences are not detectable by the methods we used. Daily patterns in basking behaviours in the captive population may indicate that acclimation to predictable thermal opportunities produces behavioural strategies of meeting most thermal needs in the morning. Field and lab data from other species of lizards have shown that basking frequency and daily activity restriction can be related to altitudinal variation of source populations (Hertz, 1981; Cadby et al., 2014; Caldwell et al., 2017). Behavioural compensation in basking may be occurring in wild jacky dragons, but is most likely a complex plastic behaviour that is dictated by immediate microclimatic variation, thus difficult to measure within simplified captive situations. Further studies to examine behavioural compensation for climate would require field studies on basking behaviour across a climatic gradient or a lab based experiment with a more complex thermal landscape.

While the fixed population differences we recorded in thermal phenotypes may reflect non-plastic, local adaptation to thermal conditions, they are also consistent with alternative hypotheses. First, non-reversible developmental plasticity could lead to fixed population differences if the developmental environment or parental environment (i.e. parental effects; Mousseau and Fox, 1998) influences the thermal preferences of offspring. In captive jacky dragons, warmer parental thermal environments indirectly raise offspring preferred temperatures, and being reared post-hatch in cages with greater thermal opportunity tends to increase panting thresholds (So and Schwanz, 2018). Parental and developmental temperatures are known to influence offspring thermal traits in other reptiles, fish and invertebrates (Crill et al., 1996; O'Steen, 1998; Reiber et al., 1999; Blumberg et al., 2002; Donelson et al., 2011; Zizzari and Ellers, 2014; Le Roy et al., 2017). Second, while habitat was similar between our two sites, thermal microhabitats may vary and contribute to observed differences in thermal traits. In recent years, microhabitat availability and use have been shown to significantly impact reptile and amphibian thermal preferences (Belasen et al., 2017; Seebacher and Alford, 2018). Regardless, thermal physiology has been demonstrated across reptiles and amphibians to underpin response to habitat variation (Nowakowski et al., 2018). Third, population differences could reflect long-term acclimation across the season, which was not captured in our timespan of analysis. Recent data highlights that some species require 17 weeks for full physiological acclimation of certain thermal traits, meaning that a number of acclimation assays fail to fully investigate desired responses (Pintor et al., 2016b). Finally, the differences could be due to genetic drift or be side-effects of local adaptation to non-temperature-related selection. To confirm the hypothesis of local adaptation in thermal traits due to climate, further research should be done investigating thermal traits across a greater number and diversity of thermally-distinct populations that allow testing the importance of long-term and short-term climatic drivers.

Conflicts of interest

The authors declare they have no conflict of interest.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Acknowledgements

Field work was funded by the UNSW School of BEES, and the captive colony and equipment were funded by an ARC DECRA awarded to Lisa Schwanz (DE120101446). We would like to thank volunteers who helped with field collection: Naomi Hyunh, Coen Romalis, Kirby Duff, Ashley Brennan, Guy Taseski, Jordann Crawford-Ash and Lara Parata. In addition, many volunteers helped maintain the captive colony: Naomi Huynh, Emily Rayner, Claudia Crowther, Jordann Crawford-Ash and Claire Nelson. Alistair Poore and Daniel Noble provided comments to improve a draft manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.05.016.

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