

Integrating thermal physiology within a syndrome: Locomotion, personality and habitat selection in an ectotherm

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Abstract

1. Physiology and temperature can both have a profound influence on behaviour and metabolism. Despite this, thermal physiology has rarely been considered within the animal personality framework, but could be an inherent mechanism maintaining consistent individual differences in behaviour, particularly in species that need to thermoregulate (i.e. ectotherms).
2. Here, we present evidence for a thermal-behavioural syndrome and detail how it is linked to variation in habitat selection in an Australian lizard, the delicate skink, *Lampropholis delicata*.
3. We predicted that individuals would occur along a cold-hot continuum—analogue to the slow-fast continuum proposed by the pace-of-life hypothesis—whereby an individual's placement along a thermal physiological axis will correspond with their placement along a personality axis. We first tested the thermal-behavioural syndrome by measuring the thermal preferences and optimal performance temperature of individual skinks and linking it to their activity, exploratory, social and boldness behaviours.
4. In line with our predictions, we found that individuals with a “hot” thermal type performed optimally at higher temperatures, had faster sprint speeds and were more active, explorative and bold relative to “cold” thermal types.
5. We then monitored each individual's habitat selection within an artificial environment containing three microhabitats differing in their thermal characteristics.
6. We found that an individual's thermal type mediated their use of habitat, in which “hot” individuals utilized a hotter microhabitat more regularly than both “cold” and “intermediate” thermal types, suggesting that the thermal-behavioural syndrome could drive ecological niche partitioning in this species.
7. We envisage that the thermal-behavioural syndrome concept is likely to extend to other study systems, particularly to ectothermic organisms that rely heavily on behavioural thermoregulation to maintain optimal body temperature.

KEYWORDS

behavioural syndrome, life history, metabolic rate, microhabitat use, niche specialization, pace-of-life, sprint speed

1 | INTRODUCTION

Within populations, individuals often consistently differ in an array of behaviours across time and context. Consistent individual differences in behaviour can also become correlated, whereby a shift in one behavioural trait corresponds with a shift in another (Sih, Bell, & Johnson, 2004). For example some three-spined sticklebacks (*Gasterosteus aculeatus*) are consistently more aggressive towards conspecifics (Huntingford, 1976), but these individuals also consistently take more risk in the presence of predators (Bell, 2005). Such consistent individual differences in behaviour are broadly termed animal personality, but can also be labelled temperament, coping styles or behavioural syndromes (Réale, Dingemanse, Kazem, & Wright, 2010). One of the key challenges within animal personality theory is understanding why and how consistent behaviour is maintained when optimality theory suggests that selection should favour behavioural flexibility over behavioural consistency (Sih et al., 2004). Several ideas have been proposed to support the prevalence of animal personalities including the life-history trade-off and productivity hypotheses (Biro & Stamps, 2008; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007), individual niche specialization (Bolnick et al., 2003; Dall, Bell, Bolnick, & Ratnieks, 2012) and the pace-of-life syndrome (POLS: Réale, Garant, et al., 2010). Whilst these concepts interrelate in many respects, they all suggest that consistent behavioural traits are likely to covary with other underlying functional traits related to physiology that might constrain an individual into a more predictable behavioural profile (Réale, Garant, et al., 2010).

The POLS hypothesis, in particular, has provided a foundation for the integration of physiology into animal personality research. Emerging from classic *r/K* selection theory (Pianka, 1970) and, more recently, the slow-fast concept (Lovegrove, 2003), the POLS predicts that consistent individual differences in behaviour will covary with physiological (e.g. metabolism, endocrine function) and life-history traits with each trait profile falling along a slow-fast gradient (Réale, Garant, et al., 2010). "Fast" individuals are categorized as having high metabolism, high growth and fecundity rates, early reproduction, and high levels of aggression, activity, exploration and boldness, whereas "slow" individuals have the opposite set of traits. Indeed, in support of POLS hypothesis, a wealth of studies have now demonstrated that metabolism is a repeatable physiological trait that often covaries with consistent individual differences in behaviour (e.g. Careau, Réale, Humphries, & Thomas, 2010; Le Galliard, Paquet, Cisel, & Montes-Poloni, 2013). Individuals with high metabolic rates (either resting [RMR], basal [BMR] or standard [SMR]) are often found to be consistently more active, aggressive and bold, as these behaviours are commonly associated with high foraging rates and, thus, high-energy assimilation that helps maintain a large "metabolic machinery" (Biro & Stamps, 2010). However, the relationship between metabolism and behaviour is not always predictable, as there are often other biotic and abiotic factors that can alter this relationship (Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013; Mathot & Dingemanse, 2015). For example it is well-known that temperature can both have a profound influence on behaviour (e.g. damselfish: Biro, Beckmann, & Stamps,

2010) and on metabolic rate (e.g. sand boas: Al-Johany & Al-Sadoon, 1996). Yet, despite a tight relationship between temperature, behaviour and metabolism, thermal physiology (i.e. optimal performance temperature, selected body temperature) is only recently being considered within the animal personality framework (Bestion, Clobert, & Cote, 2015; Cerqueira et al., 2016; Goulet, Ingley, Scarf, & Pruitt, 2016; Goulet, Thompson, Michelangeli, Wong, & Chapple, 2017; Rey, Digka, & MacKenzie, 2015). This has been a surprising oversight, as thermal physiology is potentially an inherent mechanism contributing to the maintenance of personality traits, particularly in species that need to behaviourally thermoregulate.

Thermal physiology may influence animal personality via its direct effects on biological processes associated with behaviour, including locomotion, growth, endocrine function and energy budgets (Brodie & Russell, 1999; Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, et al., 2017). For example when operating at higher body temperatures imposed by increases in environmental temperatures, individuals have been shown to become more aggressive (Biro et al., 2010), active and explorative (Cerqueira et al., 2016), risk-averse (Herrel, James, & Van Damme, 2007) and asocial (Pruitt, Demes, & Dittrich-Reed, 2011). These behavioural patterns likely exist because increases in body temperature are associated with increases in energy metabolism. Thus, individuals that select and perform optimally at higher body temperatures likely have a greater aerobic capacity and adopt a proactive behavioural profile that maximizes energy assimilation for enhanced metabolic function (Biro & Stamps, 2010; Careau & Garland, 2012). From this perspective, Goulet, Thompson, and Chapple (2017) recently proposed that the POLS be extended to include inter-correlated traits related to thermal physiology (e.g. selected body temperature, optimal performance temperature). Specifically, the authors predicted that thermal physiology would covary with behaviour (i.e. a thermal-behavioural syndrome) and that individuals could be categorized within a "thermal type", which was related to their positioning along a cold-hot continuum, analogous to the proactive-reactive or fast-slow continuum posited by the POLS (Goulet, Thompson, & Chapple, 2017; Réale, Garant, et al., 2010). At one end of the continuum, "hot" thermal types would select and perform optimally at higher body temperatures, have faster locomotor capabilities, low sociability and high levels of activity, exploration and boldness. In contrast, "cold" thermal types, would select and perform optimally at lower body temperatures, have slower locomotor capabilities, would be more social and have low activity, exploration and boldness levels (Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, et al., 2017).

Thermal physiology may also serve to maintain consistent individual differences in behaviour by mediating how individuals within a population select and use habitats. The habitat-dependent hypothesis suggests that different personalities may have a greater advantage in certain habitats, leading to a non-random distribution of individuals throughout an environment (i.e. ecological niche partitioning: Dall et al., 2012). Indeed, different habitats are usually heterogeneous in their thermal characteristics and may accommodate a particular subset of individuals that are more thermally suited to that microclimate (Huey, 1991). This may be particularly true for animals that need to

behaviourally thermoregulate, as microhabitat selection is often an important fitness decision. First, whether an individual wants to bask or avoid overheating, microhabitat selection can dictate the heat load an individual receives, and thus mediates how fast they are able to reach their optimal body temperature for ecological performance. Second, as basking is considered a risky activity, microhabitat selection can also have important implications for predation risk (Martín & López, 1999). For instance more “open” habitats may receive more sunlight and heat than shaded habitats, but these habitats may be more exposed to predators (Vanhooydonck & Van Damme, 2003). Thus, it seems intuitive to expect that “hot” and “cold” thermal types would utilize a different subset of the species overall ecological niche to reflect the trade-offs associated with different habitats. Alternatively, if thermal traits and behaviour were more labile, then we would likely see a more generalist approach to habitat selection.

Accordingly, we used a lizard species as our model to examine whether an individual's thermal physiology correlates with their personality, and then asked whether or not this predicted their use of simulated microhabitats. The delicate skink (*Lampropholis delicata*) is a small heliothermic (34–55 mm snout–vent length [SVL]), group-living lizard that has a large, native geographical distribution across eastern Australia. Previous studies have shown that the delicate skink exhibits consistent variation in metabolism (Merritt, Matthews, & White, 2013), sprint speed and thermal preferences (Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, et al., 2017) and microhabitat use (Chapple, Reardon, & Peace, 2016; Howard, Williamson, & Mather, 2003; Peace, 2004). A behavioural syndrome between activity, exploratory behaviour and sociability has been found within the species (Michelangeli, Wong, & Chapple, 2016) and it occurs in both sexes (Michelangeli, Chapple, & Wong, 2016). Interestingly, we have also found a consistent activity–exploratory syndrome and a boldness syndrome across four geographically distinct populations of the species (M. Michelangeli, D. G. Chapple, B. B. M. Wong, unpublished data), suggesting that these syndromes may be maintained by some intrinsic mechanism (e.g. pleiotropic genes or physiology) that is not easily modified by local environmental conditions.

In this study, we first aimed to assess whether personality and thermal physiology would form a syndrome by scoring a lizard's activity, exploratory, boldness and social behaviours, and characterizing their thermal physiology (i.e. optimal performance temperature and selected body temperature). We looked for correlations between these traits to determine whether we could categorize individuals along the cold–hot continuum (i.e. “thermal typing”: Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, et al., 2017). Our second aim was to determine whether or not an individual's thermal type was related to their microhabitat use within an artificial environment setup. We hypothesized that thermal physiology would covary with animal personality and that lizards would exhibit a consistent thermal type. We also predicted that individuals categorized as “hot” thermal types would select artificial microhabitats with higher environmental temperatures more regularly than individuals categorized as “cold” thermal types.

2 | MATERIALS AND METHODS

2.1 | Animal collection and husbandry

We collected 54 adult (SVL > 34 mm), full-tailed (SVL > tail length) male skinks from Sydney (New South Wales, Australia: 33°47'S 151°08'E) in October 2014. We selected full-tailed adult males in order to avoid the potential confounding influence of tail loss (Cromie & Chapple, 2012) and gravidity (Shine, 2003) on behaviour. Lizards were caught using trapping methods that have previously been shown not to retain bias towards particular personality types (i.e. mealworm fishing and hand capture: Michelangeli, Wong, et al., 2016).

Skinks were transported back to animal housing facilities at Monash University. Upon arrival, individuals were given a unique permanent identification code using different colour combinations of Visual Implant Elastomer (Northwest Marine Technology, WA, USA). Skinks were housed in groups of five in plastic containers (300 mm × 230 mm × 370 mm). On one end of each housing container, a basking area was created using a heat lamp over a terracotta basking tile. This provided a thermal gradient in the housing container (22–32°C), that allowed thermoregulation from 08.00 to 17.00 hr. Small plastic pots were added to provide shelter. UV lighting was placed above the containers, and was activated from 08.00 to 18.00 hr. All housing containers were in a temperature-controlled room with an ambient temperature of c. 22 °C and room lighting from 07.00 to 21.00 hr daily. Skinks were fed a diet of crickets (*Acheta domesticus*), dusted in a vitamin supplement (Reptivite™), three times a week, and water was provided *ad libitum*. Lizards had been held in captivity for 1 month prior to any experiments.

2.2 | Behavioural measurements

We conducted a series of behavioural assays to examine individual variation in four personality traits related to the POLS hypothesis: activity, exploration, sociability and boldness (Réale, Garant, et al., 2010). Individuals were placed through each behavioural assay twice (each re-test was 1 week apart) to evaluate behavioural repeatability (Bell, Hankison, & Laskowski, 2009). Behavioural repeatability is a standardized measure of individual differences (i.e. individuality) in a given behavioural trait (e.g. voraciousness), and is an informative estimate of how consistent a behavioural trait is through time (Roche, Careau, & Binning, 2016). All behavioural assays were conducted in opaque-walled experimental arenas (550 mm × 320 mm × 240 mm) in temperature-controlled rooms that matched the lizard housing temperature (22–23°C). Skinks were allowed to acclimate under transparent containers for 10 min prior to the start of each trial. All trials were recorded using JVC Everio GZ-E100 video cameras (at 30 fps) for later playback. All equipment was thoroughly washed between trials with hot water and scentless dishwashing detergent to prevent scent contamination amongst trials.

2.2.1 | Non-directed activity (NDA)

To measure individual activity, skinks were allowed to roam freely in a test arena marked with 20 equal grid squares. The level of activity of skinks was scored based on the number of transitions between grid squares the skink made over 20 min (sensu Michelangeli, Wong, et al., 2016; Michelangeli, Chapple, et al., 2016; Goulet, Thompson, & Chapple, 2017).

2.2.2 | Novel environment test (NET)

To measure an individual's propensity to explore and/or hide in a novel environment, skinks were placed into a test arena containing a shelter site and an obstacle. The obstacle was in the form of a trapezium-shaped barrier, which divided the arena into two compartments. Lizards started in compartment 1 which contained the shelter site. The only way lizards could reach compartment 2 was by exploring the barrier and squeezing themselves through small gaps situated at either end of the barrier. Over a 30 min observation period, we measured the time lizards spent exploring the barrier, how much time they spent active (i.e. not stationary, not hiding, not exploring the barrier), how much time they spent hiding in the shelter site and how many occasions they passed the barrier to reach compartment 2. Time spent hiding in a novel situation is often considered an accurate estimate of boldness within the animal personality literature (e.g. Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011), thus we also used this metric as our measure of boldness. Skinks that explored the barrier more often and were able to pass the barrier to explore compartment 2 were considered to have a higher exploration tendency (sensu Goulet, Thompson, Michelangeli, et al., 2017; Michelangeli, Chapple, et al., 2016; Michelangeli, Wong, et al., 2016).

2.2.3 | Social odour test (SOT)

Delicate skinks are often observed either basking in small groups (c. 2–10 individuals, single or mixed sex) or alone in the wild. Thus, we conducted a dichotomous choice experiment to measure the social behaviour of skinks. Delicate skinks were given a choice between basking on a tile covered in the odour of male conspecifics or a basking tile with no odour (sensu Cote & Clobert, 2007). This species is known to respond to the olfactory cues of conspecifics (Paull, 2011). To obtain olfactory cues, we placed pieces of absorbent paper on the floor of six tubs housing groups of five non-focal male lizards. We also set up six control tubs that had absorbent paper on the floor, but housed no lizards. This was done to ensure lizards were responding to the olfactory cues, rather than the absorbent paper itself. We left the absorbent paper in the tubs for 2 weeks to allow sufficient time for olfactory cues to be obtained. This timeframe was staggered so that all pieces of absorbent paper used in the trials were exactly 2 weeks old.

Test arenas were partitioned into three 15 cm zones: a social zone, asocial zone and an intermediate zone. Both the social and asocial zones were comprised of a basking tile positioned under a 40-W heat lamp. In the social zone, the basking tile was covered in the absorbent

paper containing the odour of male conspecifics, whereas in the asocial zone, the basking tile was covered in the control, odourless absorbent paper. The intermediate zone was left bare. We recorded that amount of time lizards spent basking in the social zone over 30 min of trial.

2.3 | Thermal physiological measurements

2.3.1 | Sprint speed and locomotor performance

Sprint speed is often used as an index for the individual's optimal performance capacity, and is a thermally sensitive trait (Bauwens, Garland, Castilla, & Van Damme, 1995). Therefore, we tested each lizard's sprint speed across five different temperatures (15, 20, 25, 30 and 35°C) in a random order to assess individual traits related to locomotor and optimal temperature performance. This was achieved by first either cooling or warming lizards to the desired test temperature in a thermal chamber for 30 min. Lizards were then raced down a 1 m racetrack (10 cm width: as per Cromie & Chapple, 2012; Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017) set at the desired test temperature. Sprint speeds were determined by photodiode sensors positioned at 25 cm intervals along the racetrack. A velocity measurement was produced for each of the segments between the four sensors. Following their first run, lizards were returned to the thermal chamber and were allowed to rest for 30 min before being run down the racetrack again. In total, we recorded eight sprint speed measurements (i.e. across two trials) for each lizard at each temperature, with the fastest 25 cm interval speed for each temperature being designated as an individual's V_{\max} .

We estimated individual performance curves using the maximum sprint speed data in Origins Pro version 9.1 (OriginLab, Northampton, MA, USA). Curves were modelled using a recommended exponential Gaussian function (Angilletta, 2006). From these curves, we generated four performance measures (sensu Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017): optimal performance temperature (T_{opt}), performance breadth (B_{80}), which is defined as the range of body temperatures over which lizards can perform $\geq 80\%$ of their maximum speed, and the lower (LB_{80}) and upper (UB_{80}) bounds of the performance breadth. Critical thermal minima and maxima used in estimating the curves was based upon previously published data (Greer, 1989).

2.3.2 | Thermal preferences

To determine an individual's preferred body temperature, we constructed a 40 × 100 cm thigmo-thermal arena made from aluminium that was partitioned into four equal runways. A thermal gradient ranging from 15–36°C was produced by hanging two 250-W infrared bulbs at one end of the arena and a temperature-controlled cold plate beneath the other end. We used infrared bulbs to eliminate the effect of light as a potential confounding factor. To begin the test, lizards were placed individually into the midpoint of a runway. After a 1 hr acclimation period, body temperatures were measured every 30 min

for 4 hr using a thermal imaging camera (FLIR E4, FLIR Systems Inc.) (Luna & Font, 2013). These images were used to calculate the following thermal preference measures for each individual (sensu Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017): mean selected body temperature (T_{set}), set point range (T_{set}) defined as the central 50% of recorded body temperatures, and the lower (LT_{set}) and upper (UT_{set}) set-point temperatures.

2.4 | Microhabitat selection

To determine an individual's habitat use, we observed lizards within an artificial environment created in large polyethylene terrariums (110 cm × 55 cm; see Figure S1 in Supporting Information) containing three distinct microhabitats, comprising (1) a vegetated microhabitat (V_p) that consisted of two stands of plastic grass tussocks (22 cm height), (2) a rocky microhabitat (R_p) that consisted of rocks and hollow cement paving tiles aimed at replicating a rocky outcrop refuge site and (3) a log/open microhabitat (L_p) consisting of a single log (c. 6 cm × 13 cm). All microhabitats were surrounded by mulch. Parts of the terrarium that did not contain a habitat patch had a sand substrate (Figure S1). Habitat patches were designed to replicate the variation in microhabitats that delicate skinks are observed to use in the wild (Chapple et al., 2016; Howard et al., 2003; Peace, 2004). A 40-W heating lamp was placed above each microhabitat. Each lamp was positioned at approximately the same height, so that each habitat would receive the same heat load. An iButton™ (Maxim Integrated Inc.) was placed in each microhabitat that recorded the temperature of the patch every 30 min. We also placed two iButtons in areas that were not provided with any heat (O_p). We found that the rocky microhabitat was the warmest of the three patches, with the vegetated and non-heated patches being the coolest ($M \pm SE$ [°C], R_p : 30.13 ± 0.62 , L_p : 29.13 ± 0.40 , V_p : 27.75 ± 0.49 , O_p : 26.82 ± 0.41 ; one-way ANOVA: $F_{4,33} = 2.66$, $p < .001$). These temperatures are within the range of recorded microclimate temperatures experienced by *Lampropholis* lizards in the wild (Torr & Shine, 1996). Water was also present in all three microhabitat patches. Lizards were fed the day before the trial, but were not fed during the observational period.

After an initial hour acclimation period, we recorded the microhabitat occupied by the skink every hour between 08.00 and 17.00 hr over 3 days. Observations were filmed (using JVC Everio GZ-E100 video cameras), to avoid observer disturbance and so that we could

accurately determine the habitat patch that was occupied by the skink for the majority of each 1 hr interval. At the end of each trial, we calculated the proportion of time each individual spent in each microhabitat as the total number of observations in each habitat patch divided by the total number of observations (i.e. 24).

2.5 | Statistical analysis

Data analysis was conducted in the statistical program R (R Development Core team, 2014). Several behavioural variables were transformed prior to analysis (Table 1). Thermal measurements that did not approximate a Gaussian error distribution were log transformed (V_{max} , T_{opt} , UB_{80} , T_{set}). Using linear regression, we found that SVL was not associated with any of the measured traits ($p > .1$), we therefore excluded the factor from the rest of our analysis.

Whilst our previous studies have found that activity, exploratory behaviour, sociability and boldness are repeatable behaviours in the delicate skink (Michelangeli, Wong, et al., 2016; Michelangeli, Chapple, et al., 2016; Moule, Michelangeli, Thompson, & Chapple, 2016), the behavioural assays used in this study were slightly modified from those reported in earlier studies. Thus, to account for the possibility that repeatability estimates in this study may differ from our earlier work, we calculated the repeatability of behavioural traits using the variance components obtained from univariate linear-mixed effects models (lmer function; "lme" package: Bates, Maechler, Bolker, & Walker, 2014) containing Individual ID as a random factor (Dingemans & Docter, 2012). Repeatability is calculated as the ratio of between-individual variation to total phenotypic variation (between-individual variation + within-individual variation). Ninety-five percent confidence intervals were calculated using parametric bootstrapping following methods described by Nakagawa and Schielzeth (2010). Note that we did not calculate the repeatability of thermal traits because we used the same methods to measure thermal physiology as previous studies, which found consistency in these thermal traits within the same population of lizards (i.e. Sydney: Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017).

We ran principal component analyses (PCA) with varimax rotation to reduce our data into related principal component scores. We ran separate PCAs for behavioural (no. of grid square transitions, time spent exploring barrier, time spent active, time spent hidden

TABLE 1 Repeatability with confidence intervals (CIs) of behavioural measurements from three behavioural assays (NDA, non-directed activity; NET, novel environment test; SOT, social odour test), including associated variance components (Var_A , among-individual variance; Var_W , within-individual variance). Some behavioural measurements were transformed (Trans) before analysis to approximate a Gaussian error distribution

Test	Behaviour	Trans	Var_A	Var_W	Repeatability (CIs)	p
NDA	No. of grid squares crossed	-	3.45	0.91	0.79 (0.67, 0.87)	<.001
NET	Time exploring barrier	sqrt (x)	22.79	29.02	0.45 (0.21, 0.64)	<.001
	Time active	sqrt (x)	45.76	21.91	0.68 (0.50, 0.80)	<.001
	Time in shelter	Ranks	0.35	0.63	0.36 (0.10, 0.57)	.018
SOT	Time in social zone	-	4.32	8.26	0.34 (0.08, 0.56)	.006

in shelter, number of times passed the barrier and time spent in the social zone) and thermal physiology (V_{\max} , T_{opt} , B_{80} , LB_{80} , UB_{80} , T_{set} , LT_{set} , UT_{set} , T_{set}) measurements. Both PCAs were implemented using a correlation matrix standardizing all variables (Tabachnick & Fidell, 2013). Bartlett tests were significant, indicating that the correlation matrices were significantly different from the identity matrices. Principal component analyses components were retained based on the Kaiser–Guttman criterion (eigenvalues $c. 1$; Jackson, 1993). Variables with a loading of at least 0.4 were considered to contribute to a component based on recommendations from Tabachnick and Fidell (2013). The degree of association between each behaviour on each PCA component was also checked via spearman rank correlation tests. For each individual and each trial, we calculated principal component scores from both PCA's which we used for the subsequent analysis.

We used spearman rank correlation tests to uncover any links between the principal component loading scores from the separate PCAs (i.e. behavioural PCA: B1, B2; and thermal physiology PCA: TP1, TP2, TP3) and determine the presence of a thermal-behavioural syndrome. Spearman rank correlation tests found a positive association between the principal component scores that explained the majority of the variance in the behavioural PCA (B1: 52% variance explained) and in the thermal physiology PCA (TP1: 32% variance explained). From these components, we used *K*-means clustering to separate individuals into three groups along the behavioural-thermal physiology paradigm (sensu Cerqueira et al., 2016). We used one-way ANOVA, followed by post hoc Tukey's test, to certify that group means (i.e. three groups in total) significantly differed.

Finally, we assessed differences in the proportion of time spent in each habitat between the three groups using generalized linear models with a binomial error distribution (glm function, "LME package": Bates et al., 2014). We also used logistic regression to assess associations between habitat use and thermal preference (i.e. data which were not considered in the cluster analysis).

3 | RESULTS

3.1 | Principal component analysis

We found repeatability (i.e. consistent individual differences) across all measured behavioural traits (Table 1).

Spearman rank correlation tests revealed strong associations between several variables, both within the behavioural dataset and thermal physiology dataset (see Table S1). Indeed, Kaiser–Guttman analysis of the PCA containing all behavioural variables revealed two factors that explained 70% of the total variance (Table 2). B1 explained 52% of the variance and loaded strongly towards number of grid squares crossed, time spent exploring the barrier, number of times passed the barrier, time spent active and time spent inside the shelter. Thus, B1 suggests that more active lizards in the NDA assay, were more active in the NET assay, were more willing explorers, more likely to pass an obstacle and were less likely to hide in the shelter site (i.e. were more bold). B2 explained 18% of the variance but only loaded

TABLE 2 Component loadings of behavioural traits observed on two orthogonally rotated principal components (B1, B2). Behaviours with a factor loading of at least 0.4 were considered to contribute to a component (highlighted in bold)

	B1	B2
	Reactive–proactive	Sociability
No. of grid squares crossed	0.70	0.03
Time exploring barrier	0.89	0.02
Time spent active	0.93	–0.08
Time in shelter	–0.75	–0.01
Passed the barrier	0.65	–0.26
Time spent in social zone	0.01	0.98
% of variance explained	0.52	0.18
Total variance explained	0.70	

strongly towards time spent in the social zone, suggesting that social behaviour was independent from any behavioural syndrome.

Kaiser–Guttman analysis of the PCA containing all thermal physiological traits revealed three factors that explained 82% of total variance (Table 3). TP1 explained 34% of variance and loaded strongly towards V_{\max} , T_{opt} , B_{80} and LB_{80} . The variables V_{\max} , T_{opt} , LB_{80} were positively associated with each other, but were negatively associated with B_{80} . These variables are related to locomotor performance and suggest that lizards that have higher maximal sprint speeds, require high body temperatures for optimal performance, but perform optimally within a narrower temperature range. TP2 explained 30% of variance and loaded most strongly towards T_{set} , LT_{set} , T_{set} . The variables T_{set} and LT_{set} were positively associated with each other, but were negatively associated with T_{set} . These variables are related to thermal preferences, and indicate that lizards that selected higher body temperatures on average, also utilized a narrower set of temperatures. Finally, TP3 explained 19% of the variance and loaded strongly towards T_{opt} , UB_{80} and UT_{set} . The variables T_{opt} , UB_{80} and UT_{set} were positively associated with each other. This suggests that lizards that had higher optimal performance body temperatures also selected higher body temperatures.

3.2 | Assessing thermal physiology within a syndrome

We found a strong positive correlation between B1 (reactive–proactive syndrome) and TP1 (locomotor performance), suggesting that more active, exploratory and bold lizards (i.e. proactive lizards) run faster at higher optimal body temperatures and within a narrower temperature range ($\rho = 0.32$, $p < .001$, Figure 1). There was also a positive correlation between B1 and TP3 (thermal tolerance), which suggests that proactive lizards also prefer higher body temperatures ($\rho = 0.20$, $p = .04$). Together, these results suggest that thermal physiology covaries with behaviour, as predicted by the extended POLS hypothesis.

There was no correlation between B1 and TP2 (thermal preference) ($\rho = 0.02$, $p = .80$), B2 (sociability) and TP1 ($\rho = 0.01$, $p = .92$), B2 and TP2 ($\rho = -0.02$, $p = .83$) and B2 and TP3 ($\rho = 0.12$, $p = .20$).

TABLE 3 Component loadings of thermal traits observed on three orthogonally rotated principal components (TP1, TP2, TP3). Only behaviours with a loading of at least 0.4 were considered to contribute to a component (highlighted in bold)

	TP1	TP2	TP3
	Locomotor performance	Thermal preferences	Thermal tolerance
V_{\max}	0.83	0.01	-0.09
T_{opt}	0.71	0.09	0.65
B_{80}	-0.95	-0.09	0.22
LB_{80}	0.94	0.05	0.28
UB_{80}	-0.22	0.10	0.91
T_{sel}	0.08	0.92	0.23
LT_{set}	0.04	0.96	-0.01
UT_{set}	0.09	0.20	0.48
T_{set}	0.04	-0.91	-0.01
% of variance explained	0.34	0.30	0.19
Total variance explained	0.82		

V_{\max} , maximum sprint speed; T_{opt} , optimal performance temperature; B_{80} , optimal performance breadth; LB_{80} , lower bounds of performance breadth; UB_{80} , upper bounds of performance breadth; T_{sel} , mean selected body temperature; LT_{set} , lower set point range; UT_{set} , upper set point range; T_{set} , set point range.

As B1 explained the majority of the variance within the behavioural PCA, and TP2 explained the majority of the variance within the thermal physiological PCA, and there was a strong correlation between the two components, we used these component loadings to categorize our lizards into a thermal type. *K*-means clustering generated two groups: cold ($n = 23$), and hot ($n = 24$) thermal types. Lizards that were not allocated to either group (i.e. cold or hot) were designated to a separate group—intermediate thermal type ($n = 7$). Thus, in total, we established three thermal type groups. These groups were based on an individual's activity, exploratory behaviour, boldness, maximal sprint speeds, optimal performance temperature and performance breadth (Figure 1). Hot thermal types were more active, exploratory and bold (i.e. B1) than cold (one-way ANOVA, Tukey's post hoc: $t = 7.62$, $p < .001$) and intermediate thermal types ($t = 3.30$, $p = .003$), whereas cold and intermediate thermal types did not significantly differ from each other ($t = 1.86$, $p = .15$). Hot thermal types also had significantly faster sprint speeds, higher optimal performance temperatures and narrower performance breadths than cold ($t = 10.15$, $p < .001$) and intermediate ($t = 2.66$, $p = .02$) thermal types.

3.3 | Thermal types and habitat use

We found that, regardless of thermal type, lizards spent, on average, the highest proportion of time in the vegetated microhabitat (proportion of time, $M \pm SE$, cold: 0.74 ± 0.03 , intermediate: 0.72 ± 0.08 ,

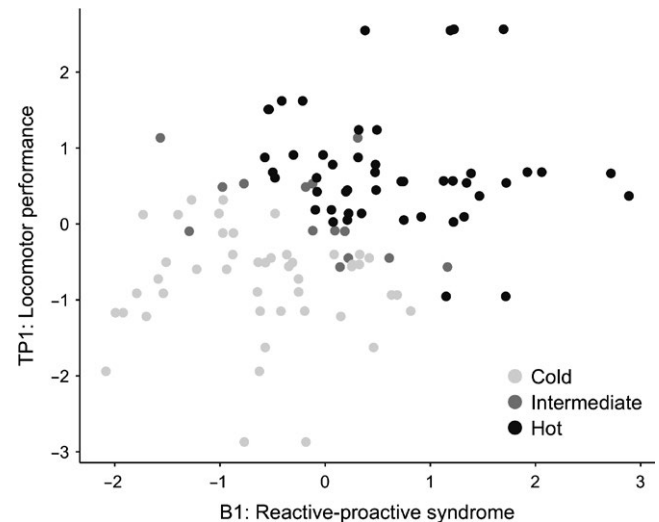


FIGURE 1 Correlation between components generated from separate principal component analysis on behavioural (B1, 52% variance explained) and thermal (TP1, 34% variance explained) measurements. Distinct clustered groups (i.e. Thermal types: cold [$n = 23$], intermediate [$n = 7$], hot [$n = 24$]) were determined from *k*-means cluster analysis. “Hot” thermal types that were more active, exploratory and spent less time hiding, also had higher sprint speeds, performed better at higher temperatures and had narrower temperature performance breadths than “cold” thermal types. “Intermediate” individuals were not allocated to a single cluster and thus were grouped on their own

hot: 0.55 ± 0.04 , Figure 2). However, lizards with a hot thermal type spent significantly less time in the vegetated microhabitat than cold ($z = -6.31$, $p < .001$) and intermediate thermal types ($z = -3.95$, $p < .001$). Instead, “hot” thermal types spent more time in the rocky microhabitat compared to cold ($z = 8.56$, $p < .001$) and intermediate ($z = 4.82$, $p < .001$, Figure 2) thermal types. There was no difference in time spent in the open/log microhabitat between the different thermal types ($\chi^2 = 2.03$, $df = 2$, $p = .363$).

We also found a relationship between principal component TP2 (thermal preference) and habitat use. Lizards that preferred higher body temperatures, but selected temperatures within a narrow range, were more likely to use the rocky microhabitat than lizards that preferred lower body temperatures but selected temperatures within a broader range ($\chi^2 = 22.13$, $df = 1$, $p < .001$, Figure 3).

4 | DISCUSSION

We predicted that individuals would differ in traits associated with thermal physiology and that this variation would correspond with an individual's position along a behavioural continuum. Consistent with our prediction, we found evidence of a thermal-behavioural syndrome in the delicate skink. Individuals were classified along a cold-hot continuum, whereby “hot” thermal type lizards that were more active, explorative and bold (i.e. more proactive), also had higher maximal sprint speeds, performed better at higher optimal

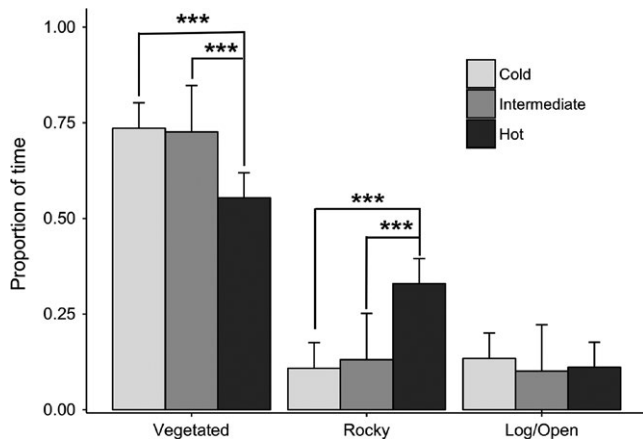


FIGURE 2 $M \pm SE$ proportion of time thermal types (i.e. “cold”, “intermediate”, “hot”) spent in three different microhabitats (vegetated, rocky, and log/open). ***Denotes significant differences between group means at $\alpha = 0.001$

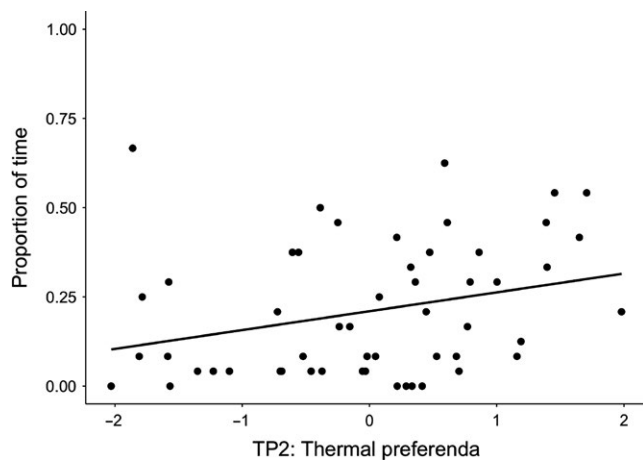


FIGURE 3 Observed relationship between a principal component describing an individual's thermal preference (i.e. mean preferred body temperature [T_{sel}] and preferred body temperature range [T_{set}]) and the proportion of time an individual spent in the rocky microhabitat over a 3 day trial period. Smoother line was fitted using a linear model with binomial error distribution

body temperatures, and within a narrower performance temperature range, when compared to “cold” thermal type lizards. This result corroborates with previous research on the delicate skink, which has also demonstrated the existence of thermal types (Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017). We also hypothesized that individual's thermal preferences would be a component of the syndrome, although, unexpectedly, we did not find this direct relationship. However, thermal preference indices have been linked to the thermal-behavioural syndrome previously (Goulet, Thompson, Michelangeli, et al., 2017) and there is some evidence from this study that selected body temperature is related to behaviour. We also show that an individual's thermal type influenced their use of microhabitat within an artificial environment. While all thermal types spent the majority of their time in the vegetated microhabitat, hot thermal types spent less time using the

cooler vegetated microhabitat and more time in the warmer rocky microhabitat than cold thermal types. Broadly, our results suggest that thermal physiology may be a stable intrinsic mechanism maintaining animal personality (at least in our study species) and could be an important factor promoting ecological niche partitioning.

The results from this research add to the growing number of studies linking behavioural and physiological syndromes, and provide support for the POLS to be extended to include traits related to thermal physiology. We envisage that the thermal type concept could extend to other study systems, particularly to ectothermic organisms that rely heavily on behavioural thermoregulation (e.g. postural changes, basking, refuge seeking) to maintain optimal body temperature. Temperature has often been found to affect the behaviour of animals, and although this is true for both ectotherms (e.g. Pruitt et al., 2011) and endotherms (e.g. Careau et al., 2010), links between thermal physiology and animal personality have only been found in the former (Biro et al., 2010; Cerqueira et al., 2016; Goulet, Thompson, Michelangeli, et al., 2017; Rey et al., 2015; Stapley, 2006). For example Nile Tilapia (*Oreochromis niloticus*) that had proactive personalities (i.e. more active, explorative and bold) selected higher water temperatures when compared to reactive conspecifics (Cerqueira et al., 2016). Similarly, consistently aggressive and active mountain log skinks (*Pseudemoia entrecasteauxii*) were found to select higher body temperatures than passive and less active counterparts (Stapley, 2006). Our results, together with these earlier studies, suggest that there is an intrinsic relationship between personality and thermal physiology that is potentially widespread in ectotherms. Such a relationship could also provide a mechanism that maintains stable behavioural syndromes across even geographically distinct populations (Pruitt et al., 2010). This is because thermal physiology likely constrains individuals along a predictable behavioural continuum (e.g. “hot” and “cold”) due to the dependence of behaviour on inherently stable physiological and biomechanical processes (e.g. locomotion) that are regulated by body temperature (Careau & Garland, 2012; Goulet, Thompson, Michelangeli, et al., 2017). Thus, even when traits related to thermal physiology are plastic or vary between populations, due to the tight relationship between temperature, physiology and behaviour, we would also expect a predictable concomitant shift in personality (e.g. a shift towards a lower selected body temperature, results in a shift towards a behavioural profile that is less active and explorative: Gilbert & Miles, 2016). Future research that examines the thermal type concept across species, populations and environmental contexts would provide valuable insight into the practicality of these hypotheses.

As thermal physiology acts in conjunction with metabolism and metabolism can mediate behaviour (or vice versa: Biro & Stamps, 2010; Mathot & Dingemanse, 2015), consistent individual differences in metabolic rate could also be incorporated within the thermal-behavioural syndrome (or thermal physiology within the POLS: Réale, Garant et al., 2010). Covariation between thermal physiology, metabolism and behaviour could be maintained by a positive feedback mechanism, in which individuals with high body temperatures have an increased metabolic rate, which, in turn, can

have an influence on behaviours associated with energy assimilation (Biro & Stamps, 2010; Goulet, Thompson, Michelangeli, et al., 2017; Sih et al., 2015). For example in bank voles (*Myodes glareolus*) consistently proactive males also had consistently higher energy metabolism (Šíchová, Koskela, Mappes, Lantová, & Boratyński, 2014). Furthermore, increased metabolism can increase the size of metabolic organs (e.g. kidney, intestines) that aid in the processing of more energy (Burton, Killen, Armstrong, & Metcalfe, 2011) and this has also been suggested to maintain variation in animal personality (Biro & Stamps, 2010; but also see Bijleveld et al., 2014). Indeed, it has been shown across several squamate lineages that metabolic rate and body temperature are linked to traits associated with energy assimilation, including digestion, prey capture and diet breadth (Angilletta, 2001; Dorcas, Peterson, & Flint, 1997; Van Damme, Bauwens, & Verheyen, 1991). In this study, “hot” thermal types may have had a more proactive personality as a result of greater energy availability provided by a higher metabolism. Thus, in order to compensate for increased energy and thermoregulatory demands, “hot” thermal types adopt behaviours that generate more basking opportunities and higher food intake rates. For example being more active and exploratory can lead to more prey encounters and feeding attempts (Short & Petren, 2008), whilst higher body temperatures and increased metabolism aid in maximal digestion and energy production (Angilletta, 2001). We suggest that future studies investigating the links between metabolism and behaviour (i.e. POLS hypothesis: Réale, Garant et al., 2010) should consider thermal physiology in order to provide a more complete picture of this physiological-behavioural paradigm (Goulet, Thompson, Michelangeli, et al., 2017; Goulet, Thompson, & Chapple, 2017).

As we hypothesized, an individual's placement along the cold-hot continuum and their thermal preferences influenced their use of microhabitats in an artificial environment. Specifically, individuals that had a hot thermal type and higher preferred body temperature indices spent more time in the warmer rocky microhabitat and less time in the vegetated microhabitat. However, regardless of thermal type, lizards, on average, preferred to spend more time in the vegetated microhabitat. As vegetation often provides shade and cover from predators, individuals likely preferred the vegetated microhabitat because it constituted a safer environment (e.g. Michelangeli, Tuomainen, Candolin, & Wong, 2015). In contrast, rocky and open habitats are commonly more conspicuous to visually-oriented predators and thus individuals using those microhabitats may feel more vulnerable to predation (Martín & López, 1999). Rock substrates often represent stable, high quality heat sources for thermoregulation (Law & Bradley, 1990), and this was the case in our artificial environment. Consequently, a trade-off occurs whereby individuals that require higher body temperatures for ecological performance must weigh up the benefits of basking in a more thermally suitable location against the risk of being predated upon (Carter, Goldizen, & Tromp, 2010). For example male rock agamas (*Agama planiceps*) that spent more time basking, had shorter flight initiation distances, were bolder in the presence of predators and suffered higher levels of tail loss likely due to more frequent interactions with predators

(Carter et al., 2010). Hot thermal types could deal with this possible trade-off by having faster maximal sprint speeds. Studies across a range of taxa have demonstrated that individuals often use maximal sprinting capacities to effectively escape predators, allowing them to occupy more predator-exposed habitats (e.g. reptiles: Husak, 2006; insects: Hawlena, Kress, Dufresne, & Schmitz, 2011; Pruitt & Husak, 2010; amphibians: Landberg & Azizi, 2010). For instance funnel-web spiders (*Agelenopsis aperta*) from predator-high riparian habitats use their maximal sprint speeds when fleeing predators, whereas funnel-web spiders from predator-low arid habitats do not (Pruitt & Husak, 2010). Moreover, in lacertid lizard species, faster sprinters are more likely to use open habitats, whereas species that are slower sprinters are more likely to use shaded habitats (Vanhooydonck & Van Damme, 2003).

How different personalities and/or thermal types utilize space and habitats within an environment can affect important ecological processes, such as interaction rates with conspecifics, heterospecifics and varied resources (Spiegel, Leu, Sih, Godfrey, & Bull, 2015). In this regard, individual habitat preferences can influence the spread of parasites and diseases within populations (Spiegel et al., 2015), the transfer of information between individuals (Aplin et al., 2015), and dispersal decisions (Michelangeli, Smith, Wong & Chapple, 2017). Our study suggests that the thermal-behavioural syndrome could be a mechanism that drives ecological niche partitioning in the delicate skink, as skinks may specialize on a subset of the overall ecological niche that matches their habitat preferences, thermal requirements and energetic demands (Dall et al., 2012). For example lizards with a hot thermal type that spend more time in warmer microhabitats may be exposed to different individuals and prey that also utilize those habitats, compared to cold thermal types that spend more time in cooler microhabitats. Indeed, other limiting environmental pressures such as competition and fluctuating habitat availability may influence how individuals select and use habitats in the wild (Whitham, 1978), and only studies on populations within natural settings will reveal the complex interplay between these variables. Nevertheless, our study is one of the first to show thermal type dependent habitat use, and supports our previous research showing the existence of a thermal-behavioural syndrome in the delicate skink (Goulet, Thompson, Michelangeli, et al., 2017). Further empirical research is needed that integrates inherently stable variables, such as thermal physiology, and animal personality variation and determine the ecological consequences of this covariation, such as how it affects the distribution of individuals throughout an environment.

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CONFLICT OF INTERESTS

We have no competing interests.

AUTHORS' CONTRIBUTIONS

M.M. carried out fieldwork, laboratory experiments and data analysis, contributed to the design of the study and drafting of the manuscript. C.T.G. carried out laboratory experiments and contributed towards drafting the manuscript. H.S.K. carried out laboratory experiments. B.B.M.W. and D.G.C. contributed to the design of the study and drafting of the manuscript. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.r3g5s> (Michelangeli, Goulet, Kang, Wong, & Chapple, 2017).

ETHICAL STATEMENT

Research was conducted in accordance with appropriate collection and research permits (New South Wales: SL101203, Victoria: 1006866) and was approved by the Monash University animal welfare committee (BSCI/2014/02).

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