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ORIGINAL PAPER

Evaluating cognition and thermal physiology as components of the pace-of-life syndrome

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Abstract

The pace-of-life syndrome (POLS) suggests that behavioral traits are correlated and integrate within a fast–slow physiological continuum. At the fast extreme, individuals having higher metabolic rates are more active, exploratory, and bold with the opposite suite of traits characterizing those at the slow physiological extreme. A recent framework suggests that behavioral types may also differ consistently in their cognitive style. Accordingly, we propose that cognition could be further incorporated into the POLS framework comprised of behavioral and thermal physiological traits. Under this premise, fast behavioral types having high thermal traits are predicted to acquire a novel task faster but at the cost of accuracy while slow behavioral types with low thermal traits would be more attentive, responding to cues at a slower rate leading to higher accuracy and flexibility. This was tested by measuring physiological and behavioral traits in delicate skinks (*Lampropholis delicata*) and testing their learning ability. Correlations were detected between cognition and behavior but not thermal physiology. Contrary to our predictions, individual positioning along these axes opposed our predicted directions along the fast–slow continuum. Fast lizards preferring lower body temperatures expressed higher activity, exploration, sociality, and boldness levels, and learned the discrimination learning task at a slower rate but made the most errors. Additionally, modelling results indicated that neither thermal physiology, behavior, or their interaction influenced cognitive performance. Although the small number of animals completing the final stages of the learning assays limits the strength of these findings. Thus, we propose that future research involving a greater sample size and number of trials be conducted so as to enhance our understanding into how the integration of cognitive style, behavior, and physiology may influence individual fitness within natural populations.

Keywords Behavior · Discrimination learning · Lizard · Thermal physiology

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Introduction

Evolutionary links between behavioral and physiological traits underlie several ecological phenomena (Killen et al. 2013). Mounting evidence across taxa has not only revealed that behavior and physiology differ systematically between individuals but that these traits have also coevolved (Careau et al. 2009, 2010; Šíchová et al. 2014; Sild et al. 2011) (see review Biro and Stamps 2010). This particular suite of correlated traits is referred to as the pace-of-life syndrome (POLS) (Reale et al. 2010). Stemming from the fast–slow concept (Lovegrove 2003), the POLS integrates behavioral variation along a physiological continuum (Le Galliard et al. 2012). It predicts that "fast" individuals having high metabolic rates (Modahl et al. 2018) will exhibit elevated levels of activity, exploration, boldness, and aggressiveness whilst the opposite suite of traits characterizes individuals that tend to be "slow" (Biro et al. 2010; Careau et al. 2012; Niemela et al. 2013a; Reale et al. 2010). Furthermore, together with MR, thermal traits are also another component of the physiological continuum upon which behavioral variation is mapped (Goulet et al. 2017a, b; Le Galliard et al. 2012). Just as is the case with MR, the "pace" of thermal traits ranges from slow to fast whereby activity, exploration, and boldness increase with optimal performance and preferred body temperatures.

This link between physiology and behavioral traits could be due to the fact that the expression of most behaviors has important energetic and thermal consequences (Careau et al. 2009; Goulet et al. 2017a, b). Higher MRs are thought to be supported by larger, more efficient, metabolic machineries (Biro and Stamps 2008; Reale et al. 2010). A greater aerobic capacity would, in turn, promote a more active lifestyle, particularly with respect to those behaviors that maximize food intake, such as locomotion, exploration, aggression, and boldness (Biro and Stamps 2010; Clarke and Fraser 2004; Stapley 2006). Thermal preferences would also be equally high in order to assimilate adequate energy to support energetically expensive organs and activities (Careau and Garland 2012). Slower individuals, on the other hand, would have lower energy and thermal requirements, reducing their need to engage in high levels of activity in pursuit and defense of resources (Le Galliard et al. 2012).

Differential investment patterns towards foraging and thermoregulations associated with the pace of an individual, however, varies in its adaptive advantage. A fast physiological-behavioral profile brings in greater short-term rewards yet has the potential to come at a high fitness cost in terms of increased predation exposure and oxidative stress (Arnold et al. 2015; Mathot et al. 2014). High MRs and thermal requirements impose a constraint upon individuals to meet their energy budget and optimal body temperatures. Frequent foraging and thermoregulation that is needed by those who are fast would have to be performed at all levels of predation risk, potentially lowering survival. And greater food consumption is also thought to place a heightened demand on the body by weakening the immune system (Arnold et al. 2015). Slow profiles would compensate for such costs but at the expense of fewer gains that could otherwise improve important biological functions such as growth and reproduction (Reale et al. 2010; Sih and Del Giudice 2012).

Another trait which is also thought to fall along the same fast–slow concept that serves as the basis of the POLS is cognition. This has recently been proposed in a review by Sih and Del Giudice (2012). Broadly, cognition is defined as all the processes (e.g., perception, attention, learning, and decision-making) by which animals acquire, retain, process, store, and use information (Shettleworth 2001). Cues range in importance and must be discriminated from one another within the context of variable and noisy environments (Niemela et al. 2013b). The ability to extract the pertinent information and employ an appropriate behavioral response can, therefore, have direct fitness consequences (Dukas 2004; Niemela et al. 2013b). For instance, parasitic wasps (*Biosteres arisanus*) that learned to successfully select a host substrate (egg-infested fruit) have higher reproductive output compared to those that are learning-deficient (Dukas and Duan 2000). Additionally, in an discrimination task for diet choice, the growth rate of grasshoppers (*Schistocerca Americana*) was shown to increase among individuals that are capable of differentiating between food types of high versus low nutritional value (Dukas and Bernays 2000).

Clearly, no one individual exhibits the same level of perception, attentiveness, learning, or decision making (Dukas 2004). Nor do they typically excel across all of these processes (Moiron et al. 2016). Rather, Sih and Del Giudice (2012) suggested that individuals differ in the way they acquire and act upon information, known as their cognitive style, irrespective of their cognitive ability *per se*. The degree to which any of these mechanisms are expressed arises from the same risk-reward trade-offs. Cognitive ability can, therefore, vary according to an individual's behavioral type paralleling the same fast–slow physiological paradigm embodied by the POLS. Accordingly, an individual's propensity to be active, exploratory, and bold is also associated with an equally fast cognitive style where individuals sample less and make faster decisions based on routines (Sih and Del Giudice 2012). This translates into the rapid acquisition of novel learning tasks, but at a cost (Guillette et al. 2011). Superficial sampling and routine formation often results in a reduction in both decision-making accuracy and ability to flexibly respond to changes in environmental cues (Brust et al. 2013; Chittka et al. 2009; Guenther et al. 2013).

Slow cognitive styles, by contrast, are associated with neophobic and inactive behavioral types and are characterized by high attentiveness and learning accuracy (Mamuneas et al. 2014; Sih and Del Giudice 2012). By sampling more thoroughly, individuals with slow cognitive styles are capable of perceiving and storing more information into their long-term memories that can then be used for future decision-making (Sih and Del Giudice 2012). This covariation between cognition and behavior is well supported (Brust et al. 2013; Dugatkin and Alfieri 2003; Guenther et al. 2013; Guillette et al. 2009, 2011; Matzel et al. 2006; Titulaer et al. 2012). Overall findings indicate that individuals having fast behavioral profiles learn a novel task more rapidly but are less apt to perceive changes in the meaning of cues, whereas slow individuals take more time in sampling their environment, are more accurate, and, through greater attentiveness, are better at adapting to changes in an already-learned task.

Such evidence clearly demonstrates the links between cognitive and behavioral traits. Yet, what is still not well understood is if cognitive traits are in fact correlated with the other key component of the POLS, physiology, whereby individual cognitive styles are positioned along a fast–slow physiological continuum. Various measures of cognitive function (e.g., cognitive style, learning, brain size, neurogenesis) do increase with MR (Isler and van Schaik 2006). This positive association between cognition and MR lies in the fact that neural structures are energetically costly to develop, maintain, and utilize (Isler and van Schaik 2006; Maille and Schradin 2017). A larger brain size, therefore, relies upon a high MR to generate a sufficient amount of usable energy as a means of compensating for the high energetic demands it imposes (Niemela et al. 2013b). But unlike behavior, relatively few studies have directly investigated the relationship between cognition and physiology, with most focusing on MR as the physiological trait (Coomber et al. 1997; Mesquita et al. 2015a). For example, among common carp (*Cyprinus carpio*), individuals who have high MRs employ a stereotypical learning strategy whilst those having lower MRs are more flexible in learning an associative task (Mesquita et al. 2015a). Similar results were found in a study by Kotrschal et al. (2015) who found that guppies (*Poecilia reticulata*) that have been under selection for either small or large brains differed in terms of their physiology and cognition. Specifically, larger brained fish exhibit low learning flexibility, excrete low levels of cortisol [which is associated with high MRs; (Andersson et al. 2013)], and interestingly, are also highly active, exploratory, and bold, suggesting that a fast cognitive style is indeed correlated with both a high physiological, as well as behavioral, type.

Despite the lack of empirical evidence directly substantiating the link between cognition and physiology, particularly in regards of thermal traits, this relationship is nevertheless plausible based upon a thermic-metabolic-cognitive pathway. It is well established that positive relationships occur between: (1) MR and thermal physiology (Artacho et al. 2013; Biro et al. 2010; Careau et al. 2008; Merritt et al. 2013; Stapley 2006); (2) MR and environmental temperatures (Biro and Stamps 2010; Clarke and Fraser 2004; Pruitt et al. 2011); (3) thermal physiology and environmental temperatures (Angilletta et al. 2002, 2006); (4) MR and cognition (see above); and (5) environmental temperatures and cognitive function [brain development (Coomber et al. 1997); memory (Jones et al. 2005); learning (Amiel et al. 2013; Amiel and Shine 2012; Clark et al. 2014b)]. Thus, one can envisage that thermal physiology may, either directly or indirectly, influence cognition through its tight covariation with MR and environmental temperatures, each of which have been shown to be correlated with aspects of cognitive function.

Given these strong inter-relations between physiological, behavioral and cognitive traits, we propose to test the theories put forth by Reale et al. (2010) and Sih and Del Giudice (2012) and evaluate the inclusion of cognition and thermal physiology within the POLS framework. Under this premise, it is predicted that individuals would be positioned along the fast–slow physiological continuum integrating seven axes: hot–cold thermal traits, fast–slow performance, active–inactive, exploratory–neophobic, bold–shy, antisocial–social, fast–slow learning, and superficial–accurate sampling (Table 1). Natural selection should favor the functional integration and, ultimately, coevolution among these traits, with physiology as the common underlying mechanism. However, no study has formerly tested their interplay simultaneously. Thus, we tested the predictions put forth by the extended POLS hypothesis comprising physiological, behavioral, and cognitive traits in the delicate skink (*Lampropholis delicata*) in order to: (1) determine if individual variation in behavior and thermal physiology is correlated with differences in cognitive style and integrated into the extended POLS; and (2) identify if individual variation in behavioral and/or thermal physiology influences cognitive performance.

The delicate skink, as an ectotherm, offers a promising system within which to test these predictions given the exceptionally strong influence thermal physiology has on behavior and cognitive function in this group (Amiel et al. 2013; Amiel and Shine 2012; Briffa et al. 2013; Clark et al. 2014b; Coomber et al. 1997; Pruitt et al. 2011; Stapley 2006). In particular, this species is capable of learning a color association task (Chung et al. 2017), and exhibits consistent inter-individual variation in metabolism, sprint speed, thermal preferences, activity, exploration, boldness, and sociability (Chapple et al. 2011b; Goulet et al. 2017b; Merritt et al. 2013; Michelangeli et al. 2016a, b; Moule et al. 2016). Furthermore, correlations among traits also indicate that they are structured into behavioral and physiological syndromes that map along a fast–slow continuum (Goulet et al. 2017a, b; Moule et al. 2016).

To quantify the interplay between physiology, behavior, and cognition we began by first measuring sprint speed and evaluating thermal physiological traits of lizards whose activity, exploratory behavior, boldness, and sociability had been previously scored (Michelangeli et al. 2016b). Thermal physiology as presented here includes optimal performance

Table 1 A summary of hypotheses contrasting physiological, behavioral, and cognitive traits for individuals at each extreme of the fast–slow continuum as predicted by the extended POLS

Trait	Slow profile	Fast profile
Physiology		
Preferred body temperature	Low	High
Preferred body temperature range	Broad	Narrow
Lower temperature range	Low	High
Upper temperature range	Low	High
Optimal performance temperature	Low	High
Performance breadth	Broad	Narrow
Lower performance breadth	Low	High
Upper performance breadth	Low	High
Behavior		
Sprint speed	Slow	Fast
Activity	Low	High
Exploration	Low	High
Boldness	Low	High
Sociability	High	Low
Cognition		
Learning accuracy	Accurate	Inaccurate
Learning speed	Slow	Fast

This table was modified from that presented in Sih and Del Giudice (2012)

temperature and thermal preference indices. Next, we exposed lizards to a discrimination learning task employing a standard Y-maze. A combination of principal component analyses and Bayesian Markov chain Monte Carlo (MCMC) general linear mixed models were used to assess the interrelationship between behavioral, thermal physiological, and cognitive traits.

Methods and materials

Study species and field collection

The delicate skink is a small [35–55 mm adult snout-vent length (SVL)] heliotherm that is locally abundant and geographically widespread in eastern Australia (Chapple et al. 2011a). This species' native distributional range spans 26° of latitude from north Queensland to southern Tasmania (Chapple et al. 2011a). In addition, this species has been introduced to Hawaii, New Zealand, and Lord Howe Island (Chapple et al. 2013a, b, 2014; Tingley et al. 2016). Within both its native and introduced range, delicate skinks occur in moist habitats, including rainforests, wet sclerophyll forests, woodlands, heaths, and is also able to inhabit urban settings (Chapple et al. 2014).

Thirty adult male lizards with complete tails were collected from the Sydney region (New South Wales, Australia: 27°38S 153°05E) in November 2013 and April 2014. Each was marked with a unique Visible Implant Elastomer (Northwest Marine Technology) color code and transported back to the animal housing facility at Monash University

(Clayton, Victoria, Australia). Lizards were maintained at 20 °C with a 14 h light: 10 h dark cycle (0600–2000 h) and fed crickets (*Acheta domesticus*). Physiological and behavioral tests were performed in 2014 while cognitive tests were conducted in 2015. Experimental trials were conducted when lizards were in a post-absorptive state (Shine 2003). All animal care and experimental procedures were approved by the Monash University Animal Ethics Committee (BSCI/2012/17, BSCI/2013/19, BSCI/2014/11, BSCI/2014/26).

Behavioral and thermal physiology measurements

Thermal preferences

Lizards ($n = 30$) were placed into a 400 × 1000 mm thigmo-thermal gradient constructed of aluminum and partitioned into four equal runways. A near linear gradient ranging from 15 to 36 °C was produced by hanging two 250-W infrared bulbs at one end of the chamber and placing a cold plate beneath the other end. Because the delicate skink is heliothermic, infrared bulbs were used to eliminate the effect of light as a potential confounding factor. At the onset of the test, lizards were placed individually into the midpoint of the test arena. After a 1 h acclimation period body temperatures were measured at 30 min intervals from 9:00 to 15:00 using a thermal imaging camera (FLIR E4, FLIR Systems, Inc.) (Luna and Font 2013). These data were used to calculate: mean selected body temperature, setpoint range (T_{set}) defined as the central 50% of recorded T_bs, and lower (LT_{set}) and upper (UT_{set}) set-point temperatures for each individual.

Locomotor performance

Lizards ($n = 30$) were run down a 1 m racetrack (100 mm width: as per Goulet et al. 2017b) at each of five temperatures (15, 20, 25, 30, and 35 °C) in a random order. Lizards were tested at a single temperature three times each test day with at least 30 min between successive runs. Prior to the first trial, and in between trials, lizards were placed into a thermal chamber set to the race temperature for at least 15 min. Sprint speed was determined by infrared sensors positioned at 250 mm intervals. Each race produced a velocity measurement for each of the four segments between the sensors, with the fastest 250 mm interval speed for each temperature being designated as an individual's V_{max}. A Gaussian function was used to estimate individual performance curves based on maximum speed data (Angilletta 2006) using OriginPro version 9.1 (Origin Inc. 2015). From these curves four performance measures were calculated: optimal performance temperature (T_{opt}) defined as the T_b that maximizes performance, performance breadth (B_{80}) defined as the range of T_bs over which lizards can perform ≥ 80% of their maximum speed, and the lower (LB_{80}) and upper (UB_{80}) bounds of the performance breadth. Critical thermal minima (4.7 °C) and maxima (40.8 °C) used in estimating the curves were based upon published data (Greer 1989).

Behavioral measurements

The behavioral assay methodology is described in detail in Michelangeli et al. (2016b). Briefly, behavior was evaluated in four contexts: activity, exploration, boldness, and sociability in a temperature-controlled room (20 °C). All assays were conducted within an opaque 550 × 320 × 240 mm experimental arena. Activity was measured by placing lizards individually into an experimental arena marked with 20 equal grid squares. The level of activity was scored based on the number and rate of transitions between squares. Exploration was measured by presenting skinks with two types of obstacles, a tube and trapezium barrier, which divided an arena into two zones, the start and finish zone. Time to maneuver the obstacle and reach the finish zone was used as a measure of exploratory behavior. Boldness was measured by exposing lizards to a simulated predatory attack using a mechanical bird model. The level of boldness was based on the number of grid square transitions and time spent basking after the attack. Finally, given that this species is often observed basking in groups naturally, sociability was measured in this same context by placing lizards in a test arena divided into three zones: social, asocial zone, and an intermediate neutral zone. The social zone was comprised of a basking site divided in half by a clear Perspex™ partition that ran the length of the test arena. Three stimulus lizards of the same size and gender were placed behind the partition. The asocial zone located at the opposite end of the arena was identical however it contained no stimulus lizards. Because selection of the neutral zone could either indicate asocial tendencies or the lack of need to thermoregulate, the amount of time spent basking with conspecifics and within the asocial zone were used as measures of sociability.

Discrimination learning

Apparatus and general design

To investigate discrimination learning ability, we used a standard Y-maze (Orchid Scientific & Innovative India Pty Ltd) that has been used for testing learning in a range of taxa, including the delicate skink (Fig. 1) (Amiel et al. 2013; Bezzina et al. 2014; Burger et al. 1991; Waldman 1985). Mazes were constructed from opaque white plastic with each arm (L: 375 × W: 65 × H: 130 mm) connecting to a central decision point (CDP). The start arm was fitted with a guillotine door and the two remaining arms were designated as decision arms. Both decision arms were painted with either blue or yellow horizontal stripes. These colors were selected because a lizard's visual system is capable of distinguishing between them (Clark et al. 2014a; Fleishman et al. 2011). A shelter (D: 57 mm × H: 43 mm) was placed at the end of each decision arm with the shelter

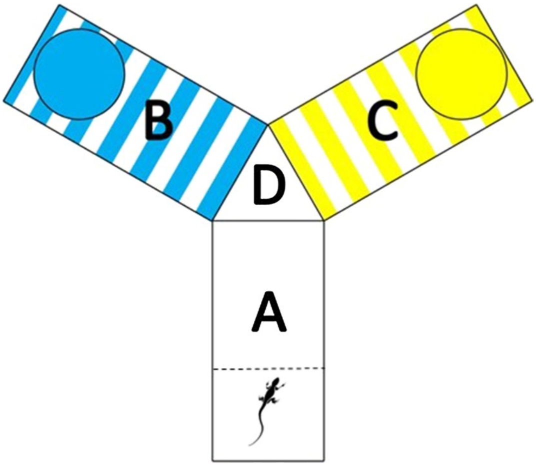

Fig. 1 The Y-maze used to test discrimination learning ability in delicate skinks. Each maze had three equally sized arms. The first arm (A) served as the start arm where the lizard was placed behind a guillotine door (dotted line) at the start of each trial. The other two arms were decision arms (B and C) that were painted with a striped pattern of contrasting colors (yellow and blue) and had similarly colored shelters at the ends. All color combinations were replicated and reversed. The central decision point (D) was used to score turning errors. (Color figure online)

matching the color of the arm. Lizards movements were recorded using a Panasonic HC-V130 video camera. All equipment was cleaned between trials with soap and water to remove olfactory cues (Cisterne et al. 2014).

Discrimination learning involves visual differentiation between two alternative stimuli presented simultaneously. The stimuli used in the present study were a "safe" and an "unsafe" shelter. The safe shelter was that in which lizards were permitted to remain inside without being disturbed while lizards were removed from the unsafe shelter (Carazo et al. 2014). A visual cue (color) was provided to enable lizards to discriminate between the two stimuli, and to reinforce the association between cue and stimuli (positive or negative).

Lizards ($n = 28$) were exposed to a two-phase learning paradigm. Each phase differed in cue relevance to assess the lizard's ability to associate a color with a goal, in this case the safe shelter. The first phase (training phase) used both shelter location and color as cues and served to train lizards to discriminate between the two stimuli. While the second phase (learning) used only color cues to ascertain if the color association learnt in the training phase was employed to locate the safe shelter.

Phase 1: training

Prior to the onset of the training phase, lizards were randomly assigned a color that represented the safe shelter, which was held constant for the entire experiment. The spatial location (i.e. left or right) of the safe shelter remained constant for all trials thereby enabling lizards to use position and/or color cues to navigate to the goal. Lizards were subjected to up to two trials per day for a total of 15 trials, or until the training criterion of five correct trials within six consecutive trials was met (Clark et al. 2014b; Noble et al. 2014). Lizards not reaching criterion were considered untrained and removed from the experiment whereas all trained lizards continued onto the learning phase. This criterion was selected based on previous work on this species which showed that, over the course of 15 trials, delicate skinks learned a similar Y-maze task as indicated by a reduction in both their latency to reach the goal as well as the number of errors made during each trial (Bezzina et al. 2014). All cognition assays were scored in real time with the observer present behind a black screen.

At the start of each trial, lizards were individually placed behind the guillotine door for 5 min of acclimation. The gate was then lifted allowing them to move freely throughout the maze. Each lizard was given up to 10 min to enter half of its body into the safe shelter. Lizards remaining motionless for 15 continuous seconds were gently tapped on their pelvic girdle with a small paint brush to instigate movement. If the lizard entered the incorrect (unsafe) shelter, it was immediately tipped back out into the maze. If the goal was not reached within 10 min the lizard was chased into the safe shelter as reinforcement. Lizards were left in the safe shelter until they exited on their own. Trials were only scored as correct if the lizard initially turned into the goal arm and entered half of its body into the safe shelter without leaving that arm. All other choices were scored as incorrect. The trial at which the criterion was achieved was designated as the training trial and served as a measure of learning speed. Additional metrics recorded during each trial were the number of incorrect turns (into non-goal arms from the CDP) as a measure of learning accuracy (Mamuneas et al. 2014) as well as latency to the safe shelter. Lizards not entering the goal by the end of the trial were assigned 10 min as their latency.

Phase 2: learning

In phase 2, the general methods, learning criterion, and metrics remained the same as that of the training phase described above except for the location of the safe shelter and number of trials. The location of the safe shelter alternated between trials which acted in greater level of difficulty. By changing the position of the goal, the use of spatial cues was eliminated leaving only color as the relevant cue. To account for the additional level of complexity of the task the number of trials was increased to 20. Lizards were considered as having learnt the discrimination task if they correctly met the criterion (five correct trials within six consecutive trials), while those that did not meet the criterion were considered non-learners.

Statistical analyses

All data were checked for normality and homogeneity of variance using Kolmogorov–Smirnov and Levene's tests. Statistical significance was assigned at $\alpha = 0.05$.

Pearson correlation was performed to assess the relationships among the raw data. Correlations between variables were detected, thus a principal component analysis (PCA) was performed to summarize the behavioral, thermal physiology, and cognitive measures into related principal component scores using SPSS version 20.0 (SPSS Inc. 2011). Each major axis was analyzed separately. And given the low number of learners, a separate PCA was also conducted for each of the cognitive phases (training and learning) to improve accuracy. A contribution to each component > 0.30 was considered significant (Tabachnick and Fidell 2001). Individual scoring on the extracted principle components (PC1) was estimated by the Anderson-Rubin method. Spearman rank correlation tests were used to reveal links between the principal component loading scores from the separate PCAs and determine the presence of a syndrome. The thermal and behavioural principal components (PC1s) were used in later statistical analyses.

Markov chain Monte Carlo linear and generalized linear models (MCMCglmm R package: Hadfield 2010), some of which included a mixed effect framework, were then used to assess learning curves and to determine how behavior and thermal physiology influenced cognitive performance. Training and learning phases were analyzed separately using the following models.

(1) The influence of thermal and behavioral traits on the probability of becoming trained or a learner was examined using a binomial distribution with a 'logit' link function. Thermal physiology PC1 and behavioral PC1 were included as fixed effects. For the training phase data, we also included the interaction between the thermal physiology and behavioral PC1 in this model. We were unable to include this interaction in models that assessed the learning phase because of our sample size (applies to models 1–5).
(2) The influence of thermal and behavioral traits on the number of trials taken to achieve the training and learning criterion was examined using a Poisson distribution with a 'log' link function. Thermal physiology PC1, behavioral PC1, and their interaction were included as fixed effects.
(3) The influence of thermal and behavioral traits on the probability of trial success was examined using a binomial distribution with a 'logit' link function. Trial number, thermal physiology PC1, behavioral PC1, and the interaction between PC1s were included

as fixed effects, and skink identity was included as both a random intercept and slope over trial number.

(4) The influence of thermal and behavioral traits on the number of incorrect turns during each trial was examined using a Poisson distribution with a ‘log’ link function. Trial number, thermal physiology PC1, behavioral PC1, and the interaction between PC1s were included as fixed effects, and skink identity was included as both a random intercept and slope over trial number.

(5) The influence of thermal and behavioral traits on the latency to reach the safe shelter during each trial was examined using a Gaussian distribution. Trial number, thermal physiology PC1, behavioral PC1, and the interaction between thermal and behavioral PC1s were included as fixed effects, and skink identity was included as a was a both a random intercept and slope over trial number.

Before running the models, we explored variation in Markov chain lengths, prior specification, thinning intervals, and burn-in lengths to obtain models that had adequate sampling of the posterior distribution and showed limited autocorrelation among samples. For the final models, we used default diffuse uniform priors for fixed effects and a random effect variance–covariance matrix prior specification $V = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$ and $nu = 0.002$ for models including random effects (Hadfield 2010). Models were run for 10 million iterations with the first 200,000 discarded (burn-in) that were sampled every 5000 iterations (thinning interval), which results in an effective sample size of < 1000. Trace plots were visually inspected to ensure chains had good mixing. Autocorrelation among samples was assessed to ensure levels were low (lag < 0.1) using the *autocorr* function in the R package *coda* (Plummer et al. 2015). Parameter estimates were considered significant when the credible intervals did not include zero and if P_{MCMC} values were less than 0.05 (Hadfield 2010). When the fitted values from the models were predicted for visualization of training and learning over progressive trials, thermal physiology PC1 and behavior PC1 were set to the intercept-level value, and we did not include variance from random effects in our estimation.

Results

Thermal physiology

Thermal preferences ranged from 19.9 to 36.7 °C (mean ± SE: 27.6 ± 0.92) and selected body temperature breadth (T_{set}) ranged 1.8–16.5 °C. Lizards ran at a rate of 46.99–168.92 cm/s (mean ± SE: 89.02 ± 5.50) with their performance being highest at temperatures (T_{opt}) ranging from 24.76 to 31.92 °C (mean ± SE: 27.54 ± 0.36).

Correlations between cognition, behavior, and thermal physiology

The behavioral PC explained 35.95% of the variation with exploration, sociality, boldness, and performance loading loaded significantly onto this component (Table 2). The behavioral PC shows that lizards with higher mean and maximal sprint speeds also made a greater number of transitions at a faster rate during undirected activity assays, were faster at maneuvering over an obstacle, spent greater time basking with other lizards, and were more active after a predatory attack. Although, faster, more active and

Table 2 Results of principal components analyses

Trait	PC1
Behaviour	
# Transitions during non-directed activity	**0.31**
Time between transitions	**– 0.45**
Latency through tube	**0.53**
Latency over obstacle	**– 0.65**
Total social time	**0.91**
Total asocial time	**– 0.92**
# Transitions after predatory attack	**0.57**
Time basking after predatory attack	**0.52**
V_{MAX}	**0.40**
Mean V_{MAX}	**0.41**
% Variation	35.95
Thermal physiology	
T_{opt}	**– 0.76**
LB_{80}	**– 0.76**
UB_{80}	**– 0.56**
B_{80}	**0.42**
T_{sel}	**0.64**
LT_{set}	**0.64**
UT_{set}	**0.86**
T_{set}	– 0.06
% Variation	35.31
Cognition-training phase	
Number of errors	**0.96**
Mean latency to goal (phase 1)	**0.85**
Number of trials to criterion	**0.63**
% Variation	67.60
Cognition-learning phase	
Number of errors	**0.95**
Mean latency to goal (phase 2)	**0.79**
Number of trials to criterion	**0.58**
% Variation	62.10

Percent variation and eigenvalue scores indicate the relative contributions of the three PC axes to explaining variation. Factor-loading scores above 0.30 are in bold

exploratory lizards also took longer to move through a tube and spent less time basking after being exposed to the simulated attack. For the thermal physiology PC1, the component explained 35.31% of the variation and was associated with the metrics of performance temperature and thermal preferences. According to this component, lizards that performed best at higher temperatures did so within a narrow range and preferred lower body temperatures. Finally, for the cognitive PC1s, our analyses revealed the principal component for the training and learning phase loaded strongly towards latency to the safe shelter, mean number of incorrect turns, and training or learning speed with 67.60% and 62.10% of the variation, respectively, explained. Specifically, lizards that were slower at reaching the safe shelter also made the greatest number of errors and required more trials to reach criterion during both phases.

Evidence for the presence of the broader definition of the POLS involving cognition, thermal physiology, and behavior was not detected. Significant correlations were found between behavioral and thermal physiology PC1s ($r = -0.38$, $P = 0.02$), as well as between behavioral PC1 and the cognition PC1 for the training phase ($r = 0.56$, $P = 0.01$). The negative relationship between behavior and thermal physiology indicates that fast lizards who exhibited high levels of activity, exploration, sociality, and boldness performed best at high temperatures but selected lower body temperatures. Additionally, the positive relationship between behavior and cognitive performance during the training phase shows that fast lizards also made the most errors and required more time to reach the safe shelter as well as reaching training criterion.

Influence of behavior and thermal physiology on cognitive performance

Seventeen of the 30 lizards (57%) passed the training phase, and eight of the 17 trained lizards (47%) went on to become learners. Lizards took between 6 and 15 trials (mean ± SE: 11.07 ± 0.76; median = 11) to reach training criterion (phase 1) and trained lizards took 6 to 17 trials (mean ± SE: 12.57 ± 1.76; median = 15) to discrimination reach learning criterion (phase 2).

Learning of the discrimination task was evidenced by an increase in the probability of task success during the learning phase (95% CIs = 0.003–0.149, $P_{MCMC} = 0.038$; Table 3; Fig. 2f) and a reduction in the number of errors in the training phase (95% CIs = −0.135–0.007, $P_{MCMC} = 0.048$; Table 3; Fig. 2a) across successive trials. Additionally, the number of incorrect turns during the learning phase, latency to the safe shelter during both phases and the number of incorrect turns during the learning phase both decreased while the probability of completing a successful trial increase (Fig. 2b–e, respectively), however, the effect of trial number was not significant on any of these metrics (Table 3). Yet, despite a significant decrease in the number of errors over time, which is a common metric in assessing learning (Amiel et al. 2013; Carazo et al. 2014; Day 1999; McQuillan et al. 2018; Papp et al. 2014; Pasquier and Grüter 2016), in visually assessing the learning curves, lizards did not appear to reach a plateau. This suggests that that the training and learning criteria or number of trials may have been inadequate to fully evaluate if lizards had actually learnt the task.

In terms of the effect of thermal physiology, behavior, or their interaction on cognitive performance, none influenced the probability of task success, the number of trials to reach criterion, the probability of trial success, the number of errors made during a trial, or the latency to reach the goal within a given trial (Table 3).

Discussion

Overall, this study provides partial support for the inclusion of cognition within the POLS framework. Only correlations occurring between cognitive performance and behavior as well as between physiology and behavior were found, but none between cognition and physiology. It was expected that, through shared risk-reward trade-offs, individual cognitive, behavioral, and physiological profiles would fall along a fast–slow gradient (Sih and Del Giudice 2012). Fast types, in being active, bold, and requiring

Table 3 Pooled posterior modes and highest posterior density intervals from Bayesian Markov chain Monte Carlo linear and mixed effect models evaluating the effect of a lizard's thermal physiological traits, behavioural traits, and their interaction (derived from the first principal component of PCAs) on cognitive performance

Response	N		Thermal type			Behavioural type			Thermal type × behavioural type			Trial number		
	Obs	Ind	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper
Training phase														
Probability of task success	28	28	−0.07	−1.20	1.12	−0.52	−1.82	0.42	−0.20	−1.26	1.04	–	–	–
# of trials taken to complete task	15	15	−0.02	−0.19	0.22	0.17	−0.07	0.28	0.02	−0.17	0.14	–	–	–
Probability of trial success	348	28	0.05	−0.41	0.50	0.15	−0.34	0.41	−0.21	−0.64	0.25	0.03	−0.06	0.16
# of incorrect turns	348	28	0.08	−0.23	0.30	0.19	−0.05	0.38	0.16	−0.17	0.34	**−0.06**	**−0.14**	**−0.01**
Latency to safe shelter	348	28	−4.34	−26.98	15.07	6.41	−13.02	22.31	17.26	−8.51	38.19	−5.17	−8.28	0.88
Learning phase														
Probability of task success	15	15	0.26	−1.29	1.81	−0.18	−2.49	1.01	–	–	–	–	–	–
# of trials taken to complete task	9	9	0.38	−0.10	0.94	0.14	−0.28	0.58	–	–	–	–	–	–
Probability of trial success	248	15	−0.31	−0.85	0.27	−0.18	−0.69	0.21	–	–	–	**0.07**	**0.00**	**0.15**
# of incorrect turns	248	15	0.15	−0.17	0.45	0.28	−0.01	0.57	–	–	–	−0.04	−0.09	0.00
Latency to safe shelter	248	15	−4.72	−56.43	37.05	34.02	−3.37	73.29	–	–	–	−0.47	−6.52	2.41

Models also included the additional fixed factor of trial number as well as the random effect of skink identity when appropriate. Interactions were not included in the learning phase analyses due to small sample size. Bolded estimates are significant (95% credible intervals not including 0)

Obs, total observations; Ind, number of individuals

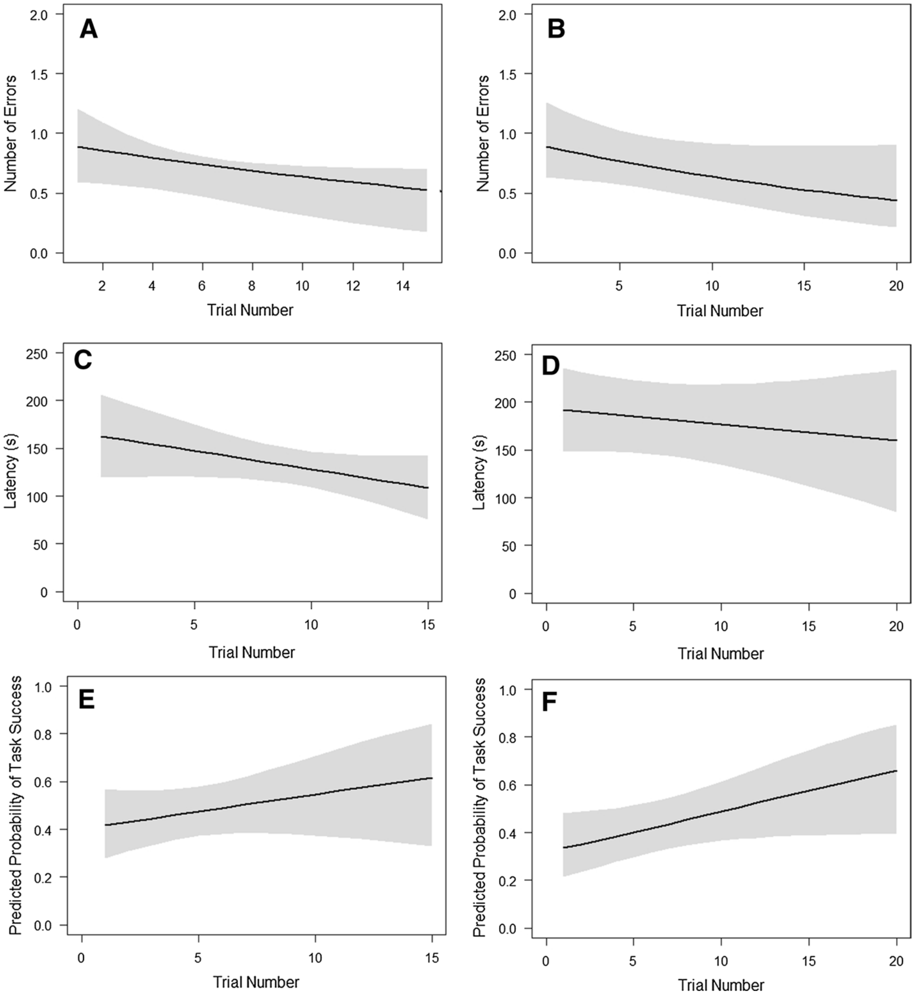

Fig. 2 Predicted learning curves for delicate skinks during the training (left) and learning (right) phases of a discrimination task. Latency to safe shelter (**a**, **b**), accuracy as measured by the number of errors made across trials (**c**, **d**), and probability of trial success (**e**, **f**) are depicted across trials. Gray areas represent 95% confidence intervals with fitted lines

high body temperatures, would need to employ a fast cognitive style based on speed over accuracy to mitigate the costs of higher energetic and thermal demands. Rapid sampling and the establishment of set routines would act to facilitate the monopolization of food resources and quality basking sites within stable environmental conditions (Guenther et al. 2013; Reale et al. 2010; Sih et al. 2004). Slow types, on the other hand, would have reduced access to resources due to their neophobic and inactive behavioral strategy. But, because their cognitive style would tend to emphasize accuracy over speed and rely upon external cues, slow types would be better able to respond to changes in cue information (Sih and Bell 2008). Under this premise, we predicted that fast lizards, having hotter thermal profiles would employ an equally fast cognitive style enabling them to reach the goal and learn the discrimination task more rapidly but make a greater number of errors due to stereotypical responses.

In the present study, however, the behavioral, physiological, and cognitive axes were related in seemingly opposing directions. Rather than fast behavioral types exhibiting an equally fast cognitive style and high thermal traits, delicate skinks expressing high maximal sprint speed, activity, exploration, sociality, and boldness levels selected lower body temperatures and learned the discrimination task at a slower rate as well as making the most errors. Perhaps though, the greater number of errors among fast lizards could indeed be an indication of a fast cognitive style in that lower accuracy could be due to superficial sampling and/or the establishment of set routines. Lizards may have made less accurate decisions by relying more on stereotypical responses rather than acquiring a greater amount of information about the experimental environment. Although, it would have been expected that such superficial sampling would have also resulted in reduced latencies in reaching the safe shelter through an increase in encounter rates of stimuli, which was not the case. Thus, speed over accuracy was not exhibited by fast behavioral types, which suggests that cognitive, physiological, and behavioral traits may not be linked as a result of such trade-offs in the delicate skink.

Our findings are in contrast to much previous research (Dugatkin and Alfieri 2003; Guenther et al. 2013; Guillette et al. 2009, 2011; Mathot and Dall 2013; Mesquita et al. 2015b; Boogert et al. 2006), which shows that active, bolder, more explorative individuals learnt novel tasks more rapidly but were less accurate than slow behavioral types. Furthermore, unlike other studies indicating a positive relationship between physiological profiles and cognition (Kotrschal et al. 2014; Mesquita et al. 2015b; Øverli et al. 2007), thermal physiology among delicate skinks was not correlated with cognitive performance. It should be noted however, that the physiological traits examined among these aforementioned studies were not thermal traits, but rather cortisol levels and metabolic rates, therefore not reflecting a direct comparison. Nevertheless, our results were still surprising as temperature and cognition have been linked in other ectotherms. For instance, the thermal environment under which development occurs has been shown to influence both thermoregulatory behavior (Blouin-Demers et al. 2000; Buckley et al. 2007) as well as cognitive performance (Amiel et al. 2013; Amiel and Shine 2012; Clark et al. 2014a; Jones et al. 2005), suggesting that these traits may indeed be interrelated, at least in other species.

So why did we find either a seemingly opposite or non-existent relationship between behavior, physiology, and cognition? One reason could be that behavior and thermal physiology may influence cognitive traits in a more complex, sex-specific way. Similar to our findings, Titulaer et al. (2012) showed that highly explorative male great tits (*Parus major*) were slower at learning a reversal task, whereas females that were less exploratory required fewer trials to learn. Variation in learning and behavior as a function of sex has been previously observed (Bettis and Jacobs 2009; Carazo et al. 2014; Pruitt and Riechert 2009; Range et al. 2006). Thus, males and females may process information differently, with different behavioral profiles influencing cognitive traits in opposing directions (Titulaer et al. 2012). Given that we only tested males and sexual dimorphism in behavior does occur in this species (Michelangeli et al. 2016a), it is possible that sex-related differences in behavior and cognition may be causing the observed patterns in our study.

Another, albeit not mutually exclusive, explanation may be one of experimental design and/or small sample size rather than of biological mechanism. For instance, inappropriate cue choice may have caused relationships to go undetected. Color may not be an ecologically relevant cue in delicate skinks, as it may not be as reliable as other cues like spatial positioning. Indeed, other investigations examining cognition among reptiles have also shown a higher level of learning when the cue was spatial rather than visual (Burghardt 1977; Day et al. 2003; Williams 1967). Finding and recognizing key resources in the wild may, therefore, be related more to their location relative to other objects rather than visual information for delicate skinks. With little to no contribution towards individual fitness, selection would likely not favour the correlation between cognition, physiology, and behavior within this discrimination learning paradigm. Or perhaps, lizards may in fact utilize visual information but not in the context of refuge selection, as used here. Instead, it may be where lizards rely upon features, such as color or brightness, when discriminating between prey items (Day et al. 2003). In either instance, it may only be when cues are biologically meaningful within a particular context that the correlation between behavioral, physiological, and cognitive traits, as well as their correspondence along the fast–slow gradient, becomes apparent (Titulaer et al. 2012).

Additionally, in having little value under natural conditions, the use of a colored shelter as the cue could have resulted in poor overall discrimination ability and ultimately low sample size in our study. This was clearly demonstrated by the fact that a greater number of lizards reached criterion during the training phase when positional cues were available compared to the learning phase when only color could be relied upon to find the safe shelter. A reduction in sample size across phases could also have served to mask any possible relationships between physiology, behavior, and cognitive style within our study.

Yet despite finding some correlations between behavior and cognition, our models indicated that the ability of a lizard to learn a discrimination task was not influenced by either their behavioral or physiological traits, or their interactive effects. These findings again counter those of previous empirical and theoretical studies (Carazo et al. 2008; Carere and Locurto 2011; Sih and Del Giudice 2012). As previously mentioned, our contrasting results could be because different components of cognition are driven by behavioral and thermal traits to varying degrees. But our results should be considered with caution given the incremental reduction in sample size across experimental phases. Therefore, modification of the study design, including increased sample size, greater number of trials to ensure training and learning criteria are adequately robust, the inclusion of both males and females, as well as cue choice, are recommended for future work in order to increase confidence in subsequent results and gain a more comprehensive understanding of the interrelationships between thermal physiology, behavior, and cognition in this species.

Conclusions

We have provided evidence suggesting that cognition and behavior, as well as thermal physiology and behavior, are correlated and structured into a syndrome. However, individual positioning along each of these axes does not correspond to the fast–slow continuum embodying the POLS. Few studies have empirically tested the inclusion of cognition and thermal physiology within the POLS. Accordingly, to fully evaluate whether the predictions put forth by this extended POLS concept holds for a species, cognition must also be assessed across time as well as over a variety of cognitive traits such as memory, discrimination, navigation, or problem-solving. Future studies should thus employ a robust study design and determine the stability of individual cognitive styles and their correlation with other phenotypic traits.

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