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# Thermal physiology: A new dimension of the pace-of-life syndrome

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**Abstract**

1. Current syndrome research focuses primarily on behaviour with few incorporating components of physiology. One such syndrome is the pace-of-life syndrome (POLS) which describes covariation between behaviour, metabolism, immunity, hormonal response, and life-history traits. Despite the strong effect temperature has on behaviour, thermal physiology has yet to be considered within this syndrome framework.

2. We proposed the POLS to be extended to include a new dimension, the cold–hot axis. Under this premise, it is predicted that thermal physiology and behaviour would covary, whereby individual positioning along the thermal continuum would coincide with that of the behavioural continuum.

3. This hypothesis was tested by measuring thermal traits of delicate skinks (*Lampropholis delicata*) and linking it to their behaviour. Principal components analysis and structural equation modelling were used to determine if traits were structured within the POLS and to characterize the direction of their interactions.

4. Model results supported the inclusion of the cold–hot axis into the POLS and indicated that thermal physiology was the driver of this relationship, in that thermal traits either constrained or promoted activity, exploration, boldness and social behaviour.

5. This study highlights the need to integrate thermal physiology within a syndrome framework.

**KEYWORDS**

behaviour, *Lampropholis*, lizard, optimal performance temperature, selected body temperature, sprint speed, structural equation modelling, thermal physiology

## 1 | INTRODUCTION

The ecological, social and physiological conditions confronting a given individual are in constant flux, imposing a myriad of selective pressures that vary in both intensity and duration. Adaptive evolution should enable individuals to mitigate such pressures by having phenotypic traits which are highly plastic (Sih & Bell, 2008). Each extrinsic context would thus have its own distinct trait optima within which all individuals could adapt accordingly. However, counter to this optimality view, limited flexibility is apparently the rule rather than the exception (Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Individuals not only vary consistently in how they modulate their phenotypes within and across contexts but the consistent expression of one trait is also often linked with that of another (Dingemanse, Dochtermann, & Nakagawa, 2012; Sih, Bell, Johnson, & Ziemba, 2004). When traits are organized in this manner, they are referred to as a syndrome. Adaptive or not, an individual is often confined to this single manifestation of its phenotype.

Furthermore, the impacts arising from syndromes may even extend beyond one's current state into ensuing ontogenetic stages or generations as the constituent traits are unable to evolve independently (Reale et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004; Wolf & Weissing, 2012). Rather, they become coupled causing selection to work upon them as a single unit rather than independently (Sih, Bell, Johnson, & Ziemba, 2004).

Given both their prevalence and potential ecological and/or evolutionary consequences, there has been a surge of research interest on syndromes. Among the most extensively studied are the life history (Stearns, 1977), dispersal (Cote & Clobert, 2007), behavioural (Dingemanse et al., 2007; Sih, Kats, & Maurer, 2003) and invasion syndromes (Chapple, Simmonds, & Wong, 2012; Michelangeli, Wong, & Chapple, 2016). Each of these predicts that various aspects of behaviour or life history are linked. However, only recently have lower level processes, such as physiology, been integrated within this syndrome framework (Coppens, de Boer, & Koolhaas, 2010; Kluen, Siitari, & Brommer, 2014; Koolhaas, De Boer, Coppens, & Buwalda, 2010). At the forefront of this research is the pace-of-life syndrome (POLS) (Biro & Stamps, 2010; Reale et al., 2010). Stemming from the slow–fast concept (Lovegrove, 2003), the POLS hypothesis predicts that individual variation in behavioural traits will covary with physiological (e.g. hormonal, metabolic and immunity) and life-history traits with each trait profile falling along a slow–fast continuum; "Fast" individuals would thus have high metabolic rates (MR), high growth and fecundity, early reproduction, low immune response, low hypothalamus–pituitary–adrenal responsiveness, and exhibit elevated levels of activity, exploration, boldness, and aggressiveness, while the opposite suite of traits would characterize individuals that tend to be "slow."

A review (Biro & Stamps, 2010) investigating the link between energy metabolism and behaviour has revealed mounting evidence in support of these components of the POLS. It indicated that nearly 75% of the studies had demonstrated a positive relationship between some measure of MR (basal [BMR], resting [RMR] or standard [SMR]) and a behavioural trait (e.g. aggressiveness, boldness and activity) (Biro & Stamps, 2010). Several additional studies since the review's publication have reported similar findings (Krams et al., 2013; Mathot & Dingemanse, 2015). For example, interspecific variation in exploration thoroughness among muroid rodents has shown to be negatively correlated with BMR (Careau, Bininda-Emonds, Thomas, Réale, & Humphries, 2009; Lantova, Zub, Koskela, Sichova, & Borowski, 2011). In other words, individuals that exhibit slow exploratory behaviour have similarly low BMR measurements. Likewise, mass-specific MR was significantly higher in risk-taking than in risk-avoiding carp (*Cyprinus carpio*) (Huntingford et al., 2010). However, negative relationships or no relationship between metabolism and behaviour have also been observed, suggesting that the linkage may be more complex involving additional factors such as ontogeny, sex, reproductive status and environmental conditions (Careau et al., 2015; Gifford, Clay, & Careau, 2014; Houston, 2010; Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013; Le Galliard, Paquet, Cisel, Montes-Poloni, & Franklin, 2012).

Paradoxically, one aspect of physiology that has yet to be considered within the POLS despite its tight relationship with both metabolism (Artacho, Jouanneau, & Le Galliard, 2013; Pruitt, Demes, & Dittrich-Reed, 2011; Stapley, 2006) and behaviour (insects [Pruitt & Riechert, 2012]; fish [Biro, Beckmann, & Stamps, 2010]; snakes [Brodie & Russell, 1999]; and lizards [Stapley, 2006]) is thermal physiology, specifically selected body temperature and optimal performance temperature. It is intuitive to consider that such correlations could arise due to the direct effect internal body temperature has on locomotor performance (Brodie & Russell, 1999), growth (Angilletta Jr, 2001), energy budgets (Angilletta Jr, 2001; Stapley, 2006) and endocrine function (Flores, Tousignant, & Crews, 1994), each of which dictates how an individual behaves. Overall, individuals with higher thermal preferences tend to be more aggressive (i.e. low sociability), bolder, active, perform better and have higher metabolic rates than those functioning at lower internal body temperatures (Angilletta, 2009; Biro et al., 2010; Briffa, Bridger, & Biro, 2013; Careau et al., 2015; Goulet, Thompson, & Chapple, 2017; Nakayama, Laskowski, Klefoth, & Arlinghaus, 2016; Pruitt et al., 2011).

The direction from which such patterns emerge is, however, still unresolved. From a thermal physiological perspective, physiology could dictate an individual's behaviour in that as thermal traits increase so would MR. Higher MRs would be supported by larger, more efficient metabolic machineries (Biro & Stamps, 2008; Reale et al., 2010). This greater aerobic capacity would, in turn, promote a more active lifestyle, particularly with respect to those behaviours that maximize food intake, such as locomotion, exploration, aggression and boldness (Biro & Stamps, 2010; Clarke & Fraser, 2004; Stapley, 2006). Thermal preferences would thus be equally high in order to assimilate adequate energy to support energetically expensive organs and activities (Careau & Garland, 2012). Conversely, behavioural tendencies may instead drive changes among thermal traits through the thermoregulatory and/or energetic demands they impose (Biro & Stamps, 2010). Elevated levels of activity, exploration and boldness would increase daily energy expenditure resulting in a greater food intake rate as a means of compensating for their energetic costs. Metabolic rates and thermal traits would then increase in order to maximize digestion efficiency.

We therefore propose the POLS be extended to include a new dimension, the cold–hot axis, characterized by a suite of inter-correlated thermal traits (e.g. selected body temperature, optimal performance temperature and critical thermal tolerances). Under this premise, it is predicted that thermal physiology and behaviour would covary, whereby individual positioning along the thermal continuum would coincide with that of the behavioural continuum. At one extreme would be the "hot" types whose profile is comprised of high thermal traits, fast locomotor performance, low tolerance for conspecifics, and high levels of activity, exploratory behaviour and boldness. Conversely, the "cold" type is associated with low thermal traits, slow sprint speed, high sociability, and low activity, exploratory behaviour and boldness levels.

Ectotherms offer a promising system within which to test the inclusion of the cold–hot axis within the POLS as the relationship between

their thermal physiologies and behaviour is especially tight (Briffa et al., 2013; Pruitt et al., 2011; Stapley, 2006). Unlike endotherms, ectothermic species must behavioural thermoregulation (e.g. basking, postural adjustments and seeking refuge) in order to achieve and maintain an internal body temperature that maximizes performance (e.g. locomotion, digestion and growth). Through this functional integration, the presence of inter-individual differences can have profound and measurable effects on a vast array of ecological phenomenon including foraging, competitive interactions, mate choice, predator–prey interactions, dispersal and habitat selection (Killen et al., 2013). Indeed, it has been well documented that individual variation in both thermal and behavioural traits is quite prevalent among ectotherms (Angilletta Jr, Niewiarowski, & Navas, 2002; Artacho et al., 2013; Garland, 1985; Pruitt, Riechert, & Jones, 2008; Stapley, 2006). One such species for which these traits are extremely well characterized is the delicate skink, *Lampropholis delicata* (De Vis 1888). This species is a small (35–55 mm adult snout-vent length [SVL]) heliothermic lizard (gains heat from the sun) that is locally abundant and geographically widespread across eastern Australia. Recent studies (Chapple, Simmonds, & Wong, 2011; Goulet, Thompson, & Chapple, 2017; Merritt, Matthews, & White, 2013; Michelangeli et al., 2016; Moule, Michelangeli, Thompson, & Chapple, 2016) have already reported that *L. delicata* exhibits consistent inter-individual variation in traits such as metabolism, sprint speed, thermal preferences, activity, exploration, boldness and sociability. But as of yet, neither their integration into the POLS nor the causal direction of their relationships have been evaluated.

Here we use *L. delicata* to test the predictions put forth by the extended POLS. Specifically, we aimed to determine: (i) if individual thermal physiology and behaviour covary along the cold–hot, slow–fast, inactive–active, neophobic–exploratory, shy–bold, and social–asocial axes; and (ii) the underlying structure of the syndrome. To do so, we first evaluated thermal traits of lizards whose activity, exploratory behaviour, boldness and sociability were previously scored. Thermal physiology as presented here includes thermal preference, sprint speed and optimal performance temperature indices (Hertz, Huey, & Nevo, 1983). Correlations among traits were then assessed to see whether thermal physiology and behaviour were integrated within the POLS concept. Finally, we evaluated the patterns in which the measured traits interacted in order to identify if physiology, behaviour or a combination of both were the drivers of this relationship.

## 2 | MATERIALS AND METHODS

### 2.1 | Field collection

The study used 54 adult male lizards whose behaviour had previously been scored (Michelangeli et al., 2016). They were collected from the Sydney region (New South Wales, Australia: 33°47S 151°08E) in November 2013. Each was individually marked with a unique visible implant elastomer colour code and transported back to the animal housing facility at Monash University (Clayton, Victoria, Australia). Lizards were held in groups of five and maintained at 20°C with a

14 hr light:10 hr dark cycle (0600-2000 h). Basking lamps created a thermal gradient of 20 to 35°C to promote natural thermoregulatory behaviour. Lizards were fed crickets (*Acheta domesticus*) three times weekly and provided water ad libitum.

All lizards were exposed to physiological experiments assessing locomotor performance and thermal preferences. Seventy-two hours separated test days to avoid interactions among experimental responses and to minimize carry-over effects. Tests were performed when lizards were in a post-absorptive state (2 days without food) (van Berkum, Huey, Tsuji, & Garland, 1989). Snout-vent length and mass were measured prior to each test to assess body size effects.

### 2.2 | Behavioural measurements

The behavioural assay methodology is described in detail in Michelangeli et al. (2016). Briefly, behaviour was evaluated in four contexts: activity, exploration, boldness and sociability in a temperature controlled room (20°C). Each assay was run twice for either 45 min (activity, exploration and sociability) or 25 min (boldness) with a 10-min acclimation period. Activity was measured by placing lizards individually into an opaque-walled experimental arena (550 × 320 × 240 mm) marked with 20 equal grid squares. The level of activity was scored based on the number (ACT1) and rate (ACT2) of transitions between squares. Exploration was measured by presenting skinks with two types of obstacles, a tube (EXP1) and trapezium barrier (EXP2), which divided an arena into two compartments. Time to reach the goal compartment was used as a measure of exploratory behaviour. Boldness was measured by exposing lizards to a simulated predatory attack. The level of boldness was based on the time spent active (BOLD1) and basking (BOLD2) 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 no choice zone. The social zone was comprised of a basking site that was divided in half by a clear Perspex™ partition that ran the length of the test arena. Three stimulus lizards were placed behind the partition. The asocial zone located at the opposite end of the arena was identical however it contained no stimulus lizards. The amount of time spent basking with conspecifics (SOC1) and within the asocial zone (SOC2) was used as measures of sociability.

### 2.3 | Thermal physiology and performance measurements

#### 2.3.1 | Sprint speed and locomotor performance

Lizards were raced down a 1-m racetrack (10 cm width: as per Cromie & Chapple, 2012) 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 25-cm intervals. Each race produced a velocity measurement for each of the four segments between the sensors with the fastest 25-cm 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). From these curves, four performance measures were calculated: optimal performance temperature ($T_{opt}$) defined as the $T_b$ which maximizes performance, performance breadth ($B_{80}$) defined as the range of $T_b$'s 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).

### 2.3.2 | Thermal preferences

Lizards were placed into a 40 × 100 cm thigmo-thermal gradient constructed of aluminium 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. The thermal preference experiments were conducted in a temperature-controlled room to ensure the temperatures within the gradient remained stable throughout the trial. At the onset of the test, lizards were placed individually into the mid-point of the test arena. After a 1-hr acclimation period, body temperatures were measured at 30-min intervals from 0900 to 1500 h. using a thermal imaging camera (FLIR E4; FLIR Systems, Inc., Notting Hill, Australia) (Luna & Font, 2013). Images were processed using FLIR ThermaCam SC500 Infrared Camera Inframetrics & Researcher Software. These data were used to calculate the following thermal preference measures for each individual: mean selected body temperature ($T_s$) defined as the average body temperature measured at each time-point within the thermal gradient, set-point range ($T_{set}$) defined as the central 50% of recorded $T_b$s within the thermal gradient, and lower ($LT_{set}$) and upper ($UT_{set}$) set-point temperatures.

### 2.4 | Statistical analyses

Analyses were conducted using the statistical programs SPSS version 20.0 (SPSS Inc., 2011; SPSS, Chicago, IL, USA), OriginPro version 9.1 (Origin Inc., 2015; San Clemente, CA, USA) and AMOS 22.0 (SPSS). All data were checked for normality and homogeneity of variance using Kolmogorov–Smirnov and Levene's tests. Data not meeting these assumptions ($V_{max}$, $T_{opt}$, $LB_{80}$, $B80$, $T_{sel}$, $LT_{set}$, $UT_{set}$, ACT2, EXPLOR1, EXPLOR2. SOC1, SOC2, BOLD2 and BOLD3) were log-transformed. Nonparametric tests were employed when transformation was not possible. Neither SVL nor mass were associated with any of the traits (linear regression: $p > .01$), therefore they were not included in further analyses. Sprint speed values are presented in cm/s and the variables $B_{80}$ and $T_{set}$ are in number of degrees (°C). Statistical significance was assigned at $\alpha = 0.05$.

To determine if the physiological and behavioural traits were associated within the POLS, bivariate correlations of all variables were assessed using Spearman rank correlation. As significant correlations were found, a principal component analysis (PCA) with varimax rotation was then performed (Tabachnick, Fidell, & Osterlind, 2001). Estimation of relevant components to be extracted was based on the Kaiser–Guttman criterion (eigenvalues >1) (Niemela, Dingemanse, Alioravainen, Vainikka, & Kortet, 2013). A contribution to each component >0.50 was considered significant (Tabachnick et al., 2001). Individual scoring on the extracted components was estimated by the Anderson–Rubin method.

Structural equation modelling (Gouveia et al., 2014) was used to identify an interaction model that best described the underlying structure of the extended POLS. This is a more powerful approach than most traditional multi-variate methods as it combines within a single analysis the statistical strength of regression models, factor analysis, robust estimation (e.g. maximum-likelihood and Bayesian approaches), and model validation to simultaneously assesses the weight and directionality of relationships between observed and latent variables as well as error terms (Santos & Cannatella, 2011). It also has the added benefit of allowing for the statistical comparison of competing models.

To begin, we constructed a priori a series of models (Figure 2a–c; Figure S1a–o) which captured various combinations of direct and indirect effects between thermal physiology and behaviour. Each model was comprised of four latent variables (performance, thermal preferences, boldness and activity), 14 indicator variables that are measured directly ($T_{sel}$, $LT_{set}$, $UT_{set}$, $T_{opt}$, $V_{max}$, $LB_{80}$, BOLD1, BOLD2, EXP1, EXP2, SOC1, SOC2, ACT1 and ACT2) and their associated error terms representing unexplained variances such as measurement error or effects of unaccounted latent variables (Santos & Cannatella, 2011). To ensure that the number of model parameters to be estimated was less than the number of observations (e.g. model identification), three physiological variables ($T_{set}$, $B_{80}$ and $UB_{80}$) were excluded from these analyses due to their relatively lower predictive power indicated by the PCA analyses (Table S2). The models are depicted by path diagrams which are comprised of the following components: circles or ellipses represent unobserved or latent variables including error terms, squares represent measured variables also called indicators, single-headed arrows represent direct effects of one variable on another and double-headed arrows represent unanalysed correlations. Compound paths represent by-product associations, which are otherwise not evident from bivariate correlation analyses, and involve one or more intervening variables presumed to transmit some of the causal effects of prior variables onto subsequent variables. The connecting paths characterize the relationships between the variables with their strength being indicated by their path coefficient. For a more comprehensive discussion of the SEM modelling approach used here refer to Byrne (2013).

The structural relationship among the traits for each model was derived from empirical data as well as the physiology-performance-behaviour-fitness paradigm put forth by Careau and Garland (2012). Together, these sources suggested that the functional links were either driven by physiology or by behaviour. Thus, our developed models were

of two general classes, physiologically driven and behaviourally driven. Physiologically driven models asserted that thermal physiology would determine an individual's performance capacity and behaviour by establishing its thermoregulatory and energetic requirements. High thermal traits, and assumingly MR, would increase both thermoregulatory and food intake needs promoting a lizard to be more active, exploratory and bolder as they would be forced to bask and forage at a greater frequency across all levels of predation risk. High sprint speed would thus increase predator evasion and prey capture. Low thermal traits would instead reduce an individual's demands to thermoregulate and forage, resulting in a slower, less active and less bold lizard. In contrast, the behaviourally driven models suggested that an individual's underlying behavioural type would establish its thermal profile where those that tend to be more active, exploratory and bold would incur larger energetic and thermoregulatory costs and result in high thermal traits.

The initial model that we proposed was of the physiologically driven class (Figure 2a). Specifically, it predicted that: (i) thermal preferences would directly influence performance; (ii) the joint effects of thermal preferences and performance would directly affect boldness; and (iii) activity would be directly related to boldness and indirectly related to thermal physiology through the mediating effects of boldness. The 17 alternative models (Figure 2b,c; Figure S1a-o) varied according to the direction of the relationships as well as in how many parameters were fixed (i.e. parameterization). Their overall fit was evaluated using several indices generated by the maximum-likelihood estimator, including the $\chi^2$; Steiger–Lind root-mean-square error of approximation (RMSEA), which is a measure of how close the implied matrix is to the observed variance–covariance matrix; RMSEA 90% confidence interval; Rucker–Lewis index (TLI), which is a measure of the discrepancy between the chi-squared value of the hypothesized model and the chi-squared value of the null model; and the goodness-of-fit index (Wikelski, Lynn, Breuner, Wingfield, & Kenagy, 1999), which is an absolute fit index that estimates the proportion of variability in the sample covariance matrix explained by the model (Kline, 2006). The best supported models would have a nonsignificant $\chi^2$, RMSEA ≤ 0.60, RMSEA lower CI ≤ 0.05, RMSEA upper CI ≤ 0.10, TLI > 0.95, CFI > 0.90 and GFI > 0.80 (Byrne, 2013). Final model selection for all supported models was then assessed using the Akaike's information criterion (AIC), the Bayesian information criterion and overall parsimony (i.e. models having the least number of parameters to estimate) (Santos & Cannatella, 2011; Tebbich, Stankewitz, & Teschke, 2012).

# 3 | RESULTS

## 3.1 | Principal component analysis

The principal component analysis based on the eight thermal and eight behavioural traits resulted in four components accounting for 64.92% of the total variation with cross-loadings occurring among some of the measurements (Table S2). PC1 explained 25.29% of the variation and related to thermal preferences and boldness. This component can be interpreted as lizards that select higher body temperatures (Ernst, Creque, Orr, Hartsell, & Laemmerzahl, 2014) are more social

(SOC1 and SOC2) and more active after a predatory attack (BOLD1). PC2 explained 19.81% of the variation with performance measures ($V_{max}$, $T_{opt}$, $LB_{80}$, $UB_{80}$ and $B_{80}$) and exploration (EXP2) loading most strongly. It indicated that highly exploratory lizards ran faster and did so at higher temperatures and within a narrower range (Figure 1). PC3 explained 10.83% of the variation and was associated with activity, exploratory and boldness behaviour. According to this component, lizards that moved further (ACT1) and more frequently (ACT2) passed through the tube at a faster rate (EXP1), and spent more time basking following a perceived predatory attack (BOLD2). Finally, PC4 explained 9.00% of the variation and described performance ($UB_{80}$ and $B_{80}$) and thermal preference range ($T_{set}$), whereby lizards with wide performance breadths also had wide thermal preferences.

## 3.2 | Structural equation modelling

A physiologically driven model (Figure 2b) describing thermal preferences as the primary factor driving behaviour was strongly supported
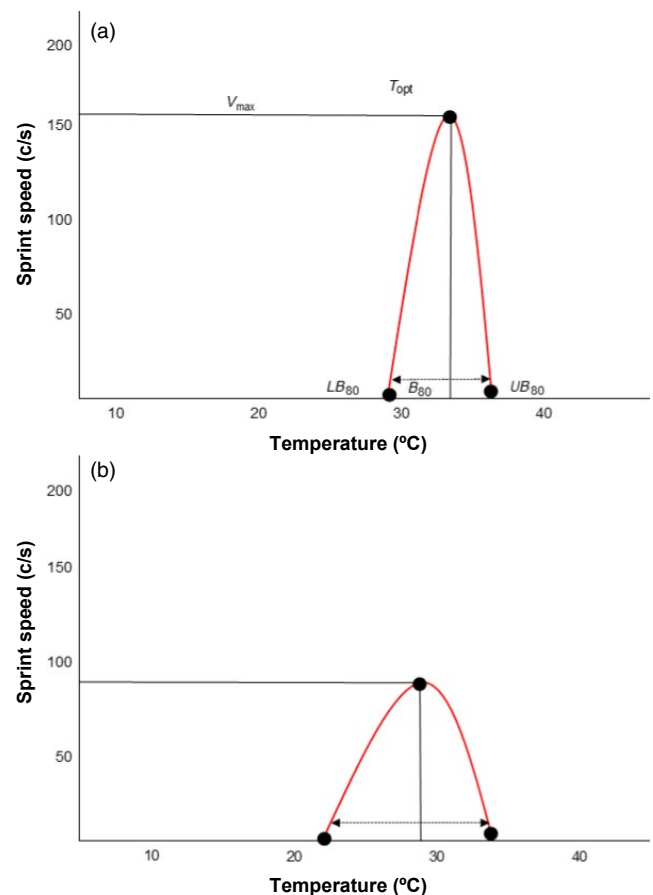


**FIGURE 1** Comparison of thermal performance curves of a "hot" lizard (a) with high thermal traits, sprint performance, activity, boldness, exploratory and social behaviour, and a "cold" lizard (b) derived from the data. The hot lizard has a faster sprint speed ($V_{max}$), narrower performance breadth ($B_{80}$) and higher optimal temperature ($T_{opt}$) indicating that it runs best at a high temperature within a narrow range of temperatures, whereas the cold lizard has a wider $B_{80}$ but lower sprint speed and $T_{opt}$ relative to the cold individual [Colour figure can be viewed at wileyonlinelibrary.com]
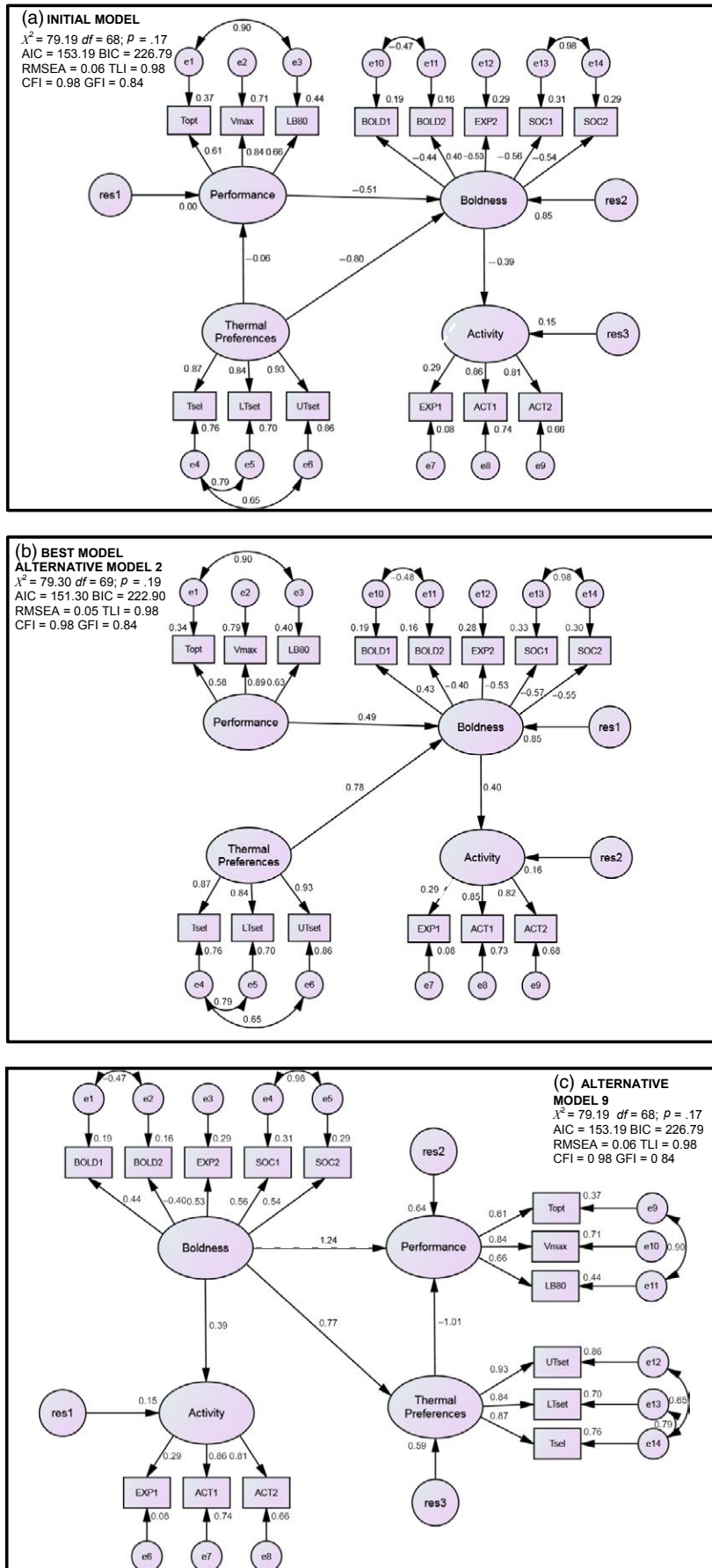
**FIGURE 2** Path diagrams and associated fit statistics of the best SEM model (alternative model 2 depicting physiological traits as driving bold behaviours and indirectly influencing activity through the joint effect of performance and thermal preferences) and two supported models (initial model depicting thermal preferences as the driver, directly influencing both performance and bold behaviour and indirectly activity through the joint effect of both performance and thermal preferences; alternative model 9 depicting bold behaviour as the driving force directly influencing activity and thermal preferences while indirectly influencing performance through its effect on thermal preferences; ΔAIC < 2). Model components are as follows: ellipses are latent variables (Thermal Preferences, Performance, Boldness and Activity), circles are error (e) and residual terms (r), and boxes are measured variables (indicators). Values near the single-headed arrows represent standardized path coefficients (single-headed arrows) and correlations (double-headed arrows). Hatched lines are nonsignificant paths. Values above the indicators represent the $R^2$. Fit statistics include the Akaike information criterion (AIC), Bayesian information criterion, goodness-of-fit ($\chi^2$) and associated $p$-value ($p > .05$), degrees of freedom (*df*), AIC, differential AIC (ΔAIC), Bayesian information criterion (Tebbich, Stankewitz & Teschke), Steiger–Lind root-mean-square error of approximation (RMSEA ≤ 0.60 = good fit), Rucker–Lewis index (TLI > 0.95 = good fit) and the goodness-of-fit index (GFI > 0.80 = good fit) [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 1** Comparison of SEM models describing the relationships between physiological and behavioural traits. For each model, we present the number of parameters ($k$), $\chi^2$ goodness-of-fit ($\chi^2$) and associated $p$-value ($p$), degrees of freedom ($df$), Akaike information criterion (AIC), differential AIC ($\Delta$AIC), Bayesian information criterion (Tebbich et al., 2012), Steiger–Lind root-mean-square error of approximation (RMSEA), RMSEA 90% confidence interval, Rucker–Lewis index (TLI) and the goodness-of-fit index (Wikelski et al., 1999). Model fit was based on a nonsignificant $\chi^2$, RMSEA < 0.60, RMSEA lower CI < 0.05, RMSEA upper CI < 0.10, TLI > 0.95, CFI > 0.90 and GFI > 0.80. Final model selection for all supported models was determined by the lowest AIC and BIC indices and a $\Delta$AIC < 2 from the best model

| Model | $k$ | $\chi^2$ | $p$ | $df$ | AIC | $\Delta$AIC | BIC | RMSEA | Low RMSEA 90% CI | Up RMSEA 90% CI | TLI | CFI | GFI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Null model** | | | | | | | | | | | | | |
| A1 | 38 | 113.83 | .00 | 70 | 189.83 | 38.53 | 265.41 | 0.11 | 0.07 | 0.14 | 0.91 | 0.93 | 0.79 |
| **Physiology as driver** | | | | | | | | | | | | | |
| A2[a] | 36 | 79.30 | .19 | 69 | 151.30 | 0.00 | 222.90 | 0.05 | 0.00 | 0.10 | 0.98 | 0.98 | 0.84 |
| Initial[b] | 37 | 79.19 | .17 | 68 | 153.19 | 1.89 | 226.79 | 0.06 | 0.00 | 0.10 | 0.98 | 0.98 | 0.84 |
| A3 | 38 | 81.67 | .12 | 68 | 157.67 | 6.37 | 233.25 | 0.06 | 0.06 | 0.11 | 0.98 | 0.97 | 0.83 |
| A4 | 36 | 102.92 | .01 | 69 | 174.92 | 2362 | 246.53 | 0.10 | 0.05 | 0.13 | 0.93 | 0.95 | 0.81 |
| A5 | 35 | 88.16 | .07 | 70 | 158.16 | 6.86 | 227.77 | 0.07 | 0.00 | 0.11 | 0.97 | 0.97 | 0.82 |
| A6 | 39 | 85.26 | .07 | 67 | 163.26 | 11.96 | 240.83 | 0.07 | 0.00 | 0.01 | 0.96 | 0.97 | 0.83 |
| A7 | 37 | 82.20 | .12 | 68 | 156.20 | 4.90 | 229.79 | 0.06 | 0.00 | 0.11 | 0.97 | 0.98 | 0.83 |
| A8 | 37 | 108.99 | .00 | 69 | 182.99 | 31.69 | 256.58 | 0.10 | 0.07 | 0.14 | 0.92 | 0.94 | 0.79 |
| **Behaviour as driver** | | | | | | | | | | | | | |
| A9[a] | 37 | 79.19 | .17 | 68 | 153.19 | 1.89 | 226.79 | 0.06 | 0.00 | 0.10 | 0.98 | 0.98 | 0.84 |
| A10 | 38 | 79.19 | .15 | 67 | 155.19 | 3.89 | 230.78 | 0.06 | 0.00 | 0.10 | 0.98 | 0.98 | 0.84 |
| A11 | 36 | 86.20 | .09 | 70 | 158.20 | 6.90 | 229.81 | 0.07 | 0.00 | 0.11 | 0.97 | 0.98 | 0.82 |
| A12 | 37 | 86.56 | .06 | 68 | 160.56 | 9.26 | 234.15 | 0.07 | 0.00 | 0.11 | 0.96 | 0.97 | 0.82 |
| A13 | 37 | 93.96 | .02 | 69 | 167.96 | 16.66 | 241.55 | 0.08 | 0.03 | 0.12 | 0.95 | 0.96 | 0.82 |
| A14 | 37 | 98.04 | .01 | 69 | 172.04 | 20.74 | 245.63 | 0.09 | 0.04 | 0.13 | 0.94 | 0.96 | 0.81 |
| A15 | 38 | 93.86 | .02 | 68 | 169.86 | 18.56 | 245.45 | 0.08 | 0.03 | 0.12 | 0.95 | 0.96 | 0.82 |
| A16 | 36 | 103.96 | .00 | 69 | 175.96 | 24.66 | 283.57 | 0.10 | 0.06 | 0.13 | 0.93 | 0.95 | 0.82 |
| **Physiology-behaviour** | | | | | | | | | | | | | |
| A17 | 33 | 167.51 | .00 | 72 | 233.51 | 82.21 | 299.15 | 0.16 | 0.13 | 0.19 | 0.82 | 0.86 | 0.71 |

[a]Best model.
[b]Supported models based on $\Delta$AIC <2.

over all others (AIC = 151.30, $k$ = 36; Table 1). It is comprised of four latent variables: thermal preferences, performance, boldness and activity. Thermal preferences as a latent variable was comprised of selected body temperature indices ($T_{sel}$, $T_{set}$, $LT_{set}$ and $UT_{set}$), performance by sprint speed measures ($V_{max}$, $T_{opt}$ and $LB_{80}$), boldness integrated exploratory, boldness and social measures, and activity integrated exploratory and activity measures. Latent variables were connected by the following paths: thermal preferences → boldness, performance → boldness, and boldness → activity. The strengths of these paths were all significant (solid lines). Two compound paths were also evident: thermal preferences → boldness → activity, and performance → boldness → activity. The strength of these paths is measured by the mathematical product of all path coefficients along the flow of the path (i.e. 0.49 × 0.40 = 0.20). Other compound paths corresponded to the association between the indicators of the same latent variable (i.e. $T_{sel}$ → Thermal Preferences → $LT_{set}$). Overall, path coefficients were for the most part consistent with the hypotheses that high thermal traits would promote a greater performance capacity as well as high measures of boldness, exploration and activity. Counter to our predictions, however, sociability also exhibited a positive relationship with thermal physiology. The reliability of each indicator on its latent variable is identified by the square of the path coefficient, where values greater than 0.30 provide moderate support and those greater than 0.7 provide high support. Thus, thermal preferences were predicted with the greatest level of reliability by $T_{sel}$ (0.87), $LT_{set}$ (0.84) and $UT_{set}$ (0.93), whereas boldness was measured with the lowest overall reliability as all of its indicators had low (BOLD1 = 0.19 and BOLD2 = 0.16) to moderate (EXP2 = 0.28, SOC1 = 0.33 and SOC2 = 0.30) predictive ability.

Two additional models also require additional consideration as their ΔAIC values were less than two (initial model AIC = 153.19, alternative model 9 AIC = 153.19; Table 1) (Dingemanse, Dochtermann, & Wright, 2010; Dochtermann & Jenkins, 2007). They included the initial model (Figure 2a) as previously described and a behaviourally driven model (Figure 2c). This alternative model is comprised of the significant direct paths between boldness → activity, boldness → thermal preferences, and thermal preferences → performance and a compound path boldness → thermal preferences → performance. The path boldness → performance was not significant (C.R. = 1.57, $p$ = .12).

# 4 | DISCUSSION

Here we modelled the extended POLS as a phenotypic network integrating thermal physiology and behaviour within a population of *L. delicata*. With the inclusion of the cold–hot dimension, it was predicted that lizards would be similarly positioned along thermal and behavioural continuums. Overall results were in support of the inclusion of the cold–hot axis within the POLS framework in that individual rankings along the thermal, performance, activity, exploratory and boldness axes were in alignment with the posited predictions. "Hot" lizards (i.e. high thermal preference indices) ran faster at higher

temperatures and exhibited greater levels of activity, exploration and boldness relative to "cold" lizards (i.e. low thermal preference indices). However, counter to our expectations, individuals with the "hot" profile were also more social. It was initially thought that these lizards, despite being tested at a constant temperature (20°C), would be intolerant of conspecifics because high body temperatures are shown to be associated with asocial behaviour in other species (Pruitt et al., 2011; Stapley, 2006). In this respect, the positive relationship demonstrated here could be driven by a hot lizard's strong physiological need to bask. Frequent basking would increase the number of interactions with conspecifics as high-quality sites would likely be limited and therefore need to be shared. Consequently, having a greater level of tolerance would serve to minimize the negative impacts arising from high vigilance and competitive contests.

The structure underlying the extended POLS was found to follow one of two possible patterns of causation: (1) shifts in thermal traits precede changes in behaviour or (2) behaviour acts as the mediator of physiology. Based on the best supported models (initial model and model 2), the former better characterizes the direction of influence, with thermal preferences being the initial driver. Specifically, individual variation in selected body temperatures directly influences performance through its strong effect on maximum sprint speed, optimal temperature and lower performance range. The joint effect of these physiological traits, in turn, has both a direct and indirect influence on behaviour. Boldness is immediately influenced by both thermal preferences and performance, whereas the combined influence on activity is instead mediated by "risky" behaviours, primarily exploration and social interactions. In other words, hot lizards who select and run faster at high body temperatures are then able to engage in greater levels of activity even under elevated levels of threat. By having greater sprinting capacities, such individuals would be better able to avoid predators and out-compete conspecifics resulting in higher availability to key resources such as food, high-quality basking sites and mates. Cold types on the other hand, with their lower thermal preferences and slower sprint speeds could be forced to have reduced activity periods to avoid overheating or falling victim to predation. Studies focusing on components of the models (e.g. the relationship between thermal traits, between behaviours, or between a single thermal trait and behaviour) have found similar patterns. For example, both activity and aggressiveness increased with thermal preferences in male mountain log skinks (*Pseudemoia entrecasteauxii*) (Stapley, 2006). Individuals who selected higher body temperatures tended to exhibit a greater level of dominance displays towards conspecifics and more actively courted females. Similarly, juvenile common lizards (*Zootoca vivipara*) who had high locomotory abilities were also more exploratory when tested in a neutral test arena (Le Galliard et al., 2012).

## 4.1 | Thermal–metabolic pathway

Mechanistic linkages between thermal traits and metabolism and metabolism and behaviour provide a plausible pathway of causality between thermal physiology and behaviour. This linkage could arise through the tight covariation of metabolism with temperature,

particularly among ectotherms, and its regulatory effect over energy budgets (Artacho et al., 2013; Briffa et al., 2013; Clarke & Fraser, 2004). High body temperatures promote cellular activity, causing the metabolic rate to become elevated (Chappell, Garland, Robertson, & Saltzman, 2007; Clarke & Fraser, 2004). Livers, kidneys, hearts and intestines respond to this sustained elevation in metabolic rate by increasing their size (Biro & Stamps, 2010). In being larger, these metabolic systems are then capable of processing a greater amount of food more rapidly and more efficiently which, in turn, acts to bolster energy stores (Clarke & Fraser, 2004). Greater energy availability ultimately equates to a greater capacity to engage in energetically demanding behaviours (Mathot et al., 2014).

Based on this thermal–metabolic pathway, it can be inferred that a high metabolic rate, through its opposing effects on the energy budget, would promote an active lifestyle among "hot" lizards. The high degree of associated energetic and thermoregulatory requirements would be simultaneously compensated by enhanced foraging and basking capacities. For instance, the quantity of feeding attempts, rate of contacting prey, ability to successfully capture and handle prey (Van Damme, Bauwens, & Verheyen, 1991), as well as diet breadth (e.g. inclusion of prey items ranging in size and escape strategies) would all increase as a result of a heightened endurance and aerobic scope (Angilletta Jr, 2001). Once ingested, high internal body temperatures and large metabolic systems would act in maximizing digestion rate and energy assimilation (Angilletta Jr, 2001; Dorcas, Peterson, & Flint, 1997). Similarly, fast sprint speeds would also work to increase thermoregulatory opportunities by reducing predation risk through enhanced escape capacities (Garland Jr & Losos, 1994; Husak, 2006), thus broadening the range of basking conditions in which a "hot" lizard could exploit (Bauwens, Garland, Castilla, & Van Damme, 1995). Basking site selection would not be limited to those which provide cover from sight-orientated predators, but instead, more open sites which tend to be higher in thermal quality could be utilized (Blouin-Demers & Weatherhead, 2008). Moreover, high escape speeds would lessen both flight initiation distances and time spent hiding following a predatory attack (Cooper, 2009; Husak, 2006). Increased thermoregulatory opportunities, both spatially and temporally, would ultimately result in "hot" lizards attaining their high body temperatures more readily.

The general assumptions comprising the thermal–metabolic pathway is similar to the performance model put forth by Careau, Thomas, Humphries, and Reale (2008) and have been well supported throughout the literature in a variety of taxa (Biro & Stamps, 2010; Mathot & Dingemanse, 2015). For example, variation in RMR among laboratory mice is causally linked to variation in organ size and food intake, where high BMRs are shown to promote increases in organ size, namely intestines, kidneys and hearts, as well as food intake rates relative to low RMR (Książek, Konarzewski, & Łapo, 2004; Speakman, Król, & Johnson, 2004). Similarly, among reptile species (*Lacerata vivipara*: Van Damme et al., 1991; *Charina bottae*: Dorcas et al., 1997; *Sceloporus undulates*: Angilletta Jr, 2001; and *Glyptemys insculpta*: Dubois, Blouin-Demers, & Thomas, 2008), numerous aspects of energy assimilation,

including prey capture, food passage rates and digestion efficiency, all increase with body temperature as well as metabolic rate. With respect to behaviour, daily energy expenditure in field voles (*Microtus agrestis*) is positively correlated with RMR (Speakman et al., 2003). In other words, the amount of activity an individual is engaged in is dictated by its RMR; high RMRs promote high levels of activity, while low RMRs constrain activity. Yet some studies have instead yielded results countering the predictions put forth by both the performance model and thermal–metabolic pathway suggesting that other factors (e.g. food availability) may also be at play (Vaanholt, De Jong, Garland, Daan, & Visser, 2007; Wiersma & Verhulst, 2005).

Despite the two best-supported models indicating that the extended POLS is driven by physiology, the SEM analyses also revealed a third model which requires additional consideration. According to this competing model, behaviour was the primary driver in that boldness directly influences activity and thermal preferences and indirectly influences performance through its effect on thermal preferences. In other words, high levels of boldness, embodied by a willingness to: maintain activity even under threatening conditions, engage in superficial exploration, and interact with conspecifics; promotes both high activity and the selection of high body temperatures. High body temperatures, in turn, enabled locomotor performance to be maximized. Similar to the aforementioned mechanistic pathway, metabolism may once again be the link between behaviour and thermal physiology, but with the sequence of causality progressing in the opposite direction. Under this scenario, individuals engaging in frequent bouts of energetically expensive behaviours, such as territory defence, competitive contests or foraging, would be forced to process more food in order to compensate for their high daily energy expenditures (Biro & Stamps, 2010; Chappell et al., 2007). Greater net food intake rates would spur the growth of organs that function in converting ingested food into usable energy (Norin & Malte, 2012). MR and thermal traits would, in turn, be elevated in order to both support the high level of activity of these organ systems (Brzęk, Bielawska, Książek, & Konarzewski, 2007) as well as to maximize digestion efficiency and passage rate (Burton, Killen, Armstrong, & Metcalfe, 2011; Naya & Božinović, 2006). Considering that both patterns are plausible and are well supported, the relationship may instead be a bidirectional relationship where both physiology and behaviour can act as the driver. Determining whether the extended POLS is driven by behaviour or physiology, as suggested by the greater level of model support (e.g. more parsimonious), or both will require additional studies. We suggest that these future works consider other variables not measured here, such as foraging rate, digestion rate and/or metabolic measures, in order to disentangle the direction of causation.

In summary, this study provides new empirical evidence supporting the integration of cognitive traits into the POLS. Through this physiological approach, we were able to identify thermal traits, namely thermal preferences, as the potential driver underlying this relationship. It is, therefore, critical to incorporate the thermal biology of an organism within investigations of behavioural syndromes as their interaction underlie a vast array of ecological phenomenon, including

but not limited to foraging, competitive interactions, mate choice, predator–prey interactions and habitat selection (Killen et al., 2013). In doing so, can the evolution of complex suites of traits, such as those comprising the POLS, be revealed, enabling us to more effectively predict how populations will respond to shifts in ecological conditions by way of climate change or species invasions.

## AUTHORS' CONTRIBUTIONS

C.G. participated in the conception and design of the study, carried out the laboratory work, provided new methods, conducted data analysis and wrote the first draft of the manuscript; M.M. carried out the field and assisted in the laboratory work; M.T. participated in the design of the study and contributed substantially to manuscript revisions; D.C. participated in the conception and design of the study and contributed substantially to manuscript revisions; B.W. contributed substantially to manuscript revisions. All authors have given final approval for publication.

## DATA ACCESSIBILITY

All data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.1fk2s (Goulet, Thompson, Michelangeli, & Chapple, 2017).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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