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# Journal of Thermal Biology

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# The effect of skin reflectance on thermal traits in a small heliothermic ectotherm



ournal of THERMAL RIOLOGY

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### ARTICLE INFO

Article history: Received 2 March 2016 Received in revised form 16 June 2016 Accepted 20 June 2016 Available online 21 June 2016

Keywords: Cooling rate Heating rate Preferred body temperature Reflectance Spectrometry Sprint speed Thermal optimum Thermal physiology

# ABSTRACT

Variation in colour patterning is prevalent among and within species. A number of theories have been proposed in explaining its evolution. Because solar radiation interacts with the pigmentation of the integument causing light to either be reflected or absorbed into the body, thermoregulation has been considered to be a primary selective agent, particularly among ectotherms. Accordingly, the colour-mediated thermoregulatory hypothesis states that darker individuals will heat faster and reach higher thermal equilibria while paler individuals will have the opposite traits. It was further predicted that dark colouration would promote slower cooling rates and higher thermal performance temperatures. To test these hypotheses we quantified the reflectance, selected body temperatures, performance optima, as well as heating and cooling rates of an ectothermic vertebrate, *Lampropholis delicata*. Our results indicated that colour had no influence on thermal physiology, as all thermal traits were uncorrelated with reflectance. We suggest that crypsis may instead be the stronger selective agent as it may have a more direct impact on fitness. Our study has improved our knowledge of the functional differences among individuals with different colour patterns, and the evolutionary significance of morphological variation within species.

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# 1. Introduction

Variation in colour patterning is one of the most pervasive and conspicuous outcomes of the selective process. Such diversity is not only prevalent among species but within species as well. Understanding the mechanisms which underlie the emergence and maintenance of colour variants across levels of biological organization has, therefore, become a central topic in evolutionary biology (Galeotti et al., 2003; Mckinnon and Pierotti, 2010; Roulin, 2004). A number of theories have been proposed to explain the evolution of colour pattern variation, with crypsis (Endler, 1984; Stuart-Fox et al., 2004) and communication (Dufva and Allander, 1995; Geen and Johnston, 2014; Joron and Mallet, 1998; Wang and Shaffer, 2008) being the most common. For example, colour can provide critical information used in evaluating the fitness among potential mates (Andersson and Simmons, 2006), it can act as a signal of aggressiveness or toxicity towards competitors and predators (Da Silva et al., 2013; Wang and Shaffer, 2008), and it can serve as camouflage through background matching or disruptive patterning (Endler, 2006; Stuart-Fox et al., 2004).

Alternatively, variation in colour patterning may instead arise in response to physiological selective pressures whereby it serves a thermoregulatory function. Skin colouration influences thermal traits through its mechanistic link with solar radiation, pigmentation, and reflectance (Norris and Kunz, 2012). As incoming visible, ultraviolet, and infrared wavelengths interact with the pigmentation of the integument, the biophysical character of colour

producing cells referred to as chromatophores causes the light to either be reflected or absorbed in differing degrees (Bechtel, 1978; Harris et al., 2012). Dark colouration arising from the diffuse distribution of melanin, has low reflectance, allowing more solar radiation to penetrate into the body relative to pale colouration produced by iridophores (Bechtel, 1978). Thus, the type and distribution of colour pigments throughout an organism's skin is expected to directly impact the rate at which solar radiation is absorbed and converted into heat (Ahnesjö and Forsman, 2006; Schultz and Hadley, 1987; Watt, 1968).

This colour-mediated thermoregulatory strategy should be especially important among ectothermic species as they are reliant upon the acquisition of external radiant energy for optimal body temperature regulation. Accordingly, darker individuals are able to heat up faster, reach a higher equilibrium temperature, and cool slower than lighter individuals of the same body size, enabling them to maintain their body temperature within an optimal range for longer (Clusella-Trullas et al., 2008; De Keyser et al., 2015; Harris et al., 2012). Locomotory, digestive, and reproductive performance would then be maximized with minimal energetic or time investment (Zhang et al., 2008). This apparent thermal advantage conferred by dark colouration may, however, only be realized within particular environments such as low levels of solar radiation or cool climates. Pale colouration, on the other hand, may be more beneficial under extreme radiative conditions or hotter climates in that a higher reflectance would reduce the risk of overheating (Clusella-Trullas et al., 2007).

Convincing support for the association between thermal traits and colour has been found in many invertebrate species (Davis et al., 2008; Forsman, 2000; Forsman et al., 2002; Harris et al., 2012; Jong et al., 1996; Kingsolver and Huey, 1998; Parkash et al., 2010; Telonis-Scott et al., 2011). For instance, in pygmy grasshoppers (*Tetrix subdulata*) darker phenotypes were shown to heat up faster and prefer higher body temperatures than paler phenotypes (Forsman, 2000). Similarly, common garden experiments involving six altitudinal populations of *Drosophila melanogaster* indicated that dark coloured flies exhibited positive correlations with cold resistance and negative correlations with heat resistance while pale coloured flies exhibited the opposite pattern (Parkash et al., 2010). These findings suggest that the thermal environment may impose selective pressures on both skin pigmentation and physiology causing the traits to coevolve.

In contrast, empirical evidence investigating the colour-mediated thermoregulation theory among vertebrates remains more equivocal. To date only a few studies have reported that dark colouration influences heating rates and equilibrium temperatures [*Thamnophis sirtalis*: Gibson and Falls (1979); *Vipera berus*: Forsman (1995) and Forsman et al. (2002); and *Tiliqua scincoides*: Geen and Johnston (2014)]. And even fewer have shown that dark colouration is able to confer a thermal advantage under cold conditions [*Rana temporaria*: Alho et al. (2010); *Cordylus niger and Cordylus oelofseni*: Clusella-Trullas et al. (2009)]. However, in other studies, even of the same species, colour patterning was not found to influence heating rates or body temperature preferences [*Liolaemus multiformis*: (Pearson, 1977); *Anolis carolinensis*: Claussen and Art (1981); *T. sirtalis*: Bittner et al. (2002)].

So why do studies of vertebrate taxa provide ambiguous results? One reason could be inconsistency in the methodology employed, particularly with respect to quantifying colour (Geen and Johnston, 2014). The use of standard techniques, such as spectrometry, or natural colour variants were not always utilized by previous authors, but instead, colour was described qualitatively or animals were painted as a means of comparing different phenotypes (Ahnesjö and Forsman, 2006; Alho et al., 2010; Bittner et al., 2002; Broennimann et al., 2014; Forsman, 1995; Forsman et al., 2002). Thus, in order to acquire greater insight into the generality of the colour-mediated thermoregulatory hypothesis we evaluated the relationship between reflectance (a proxy of colour) and four thermal traits, optimal performance temperature  $(T_{opt})$ , thermal preferences (Ernst et al., 2014), and heating and cooling rates of untreated (e.g., not painted) delicate skinks (Lampropholis delicata) using standard methods. This species was selected as it exhibits a high degree of inter- as well as intra-population variability in terms of its: 1) dorsal colouration and patterning, 2) thermal traits and 3) its microhabitat use (Chapple et al., 2014; Wilson and Swan, 2013). Moreover, this is the only study that we are aware of that has examined the physiological impact of colour on traits beyond temperature equilibria and heating rates. In considering the full suite of thermal traits of a polymorphic habitat generalist, the fitness-related effects of colour can therefore be fully evaluated.

# 2. Methods and materials

## 2.1. Study species and field collection

The delicate skink is a small [35–55 mm adult snout-vent length (SVL)], heliothermic, insectivore that is locally abundant and geographically widespread in eastern Australia (Chapple et al., 2011; Wilson and Swan, 2013). Its distributional range spans 26° of latitude from north Queensland to southern Tasmania (Chapple et al., 2011). Common habitat associations include moist habitats, including rainforests, wet sclerophyll forests, woodlands, and heaths. Adult male lizards with complete tails were collected from the Brisbane region (Queensland, Australia: 27° 38 S 153° 05 E) between October and December 2013. Each were 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 four and maintained at 20 °C with a 14 h light: 10 h dark cycle (06:00–20:00 h). Basking lamps created a thermal gradient of 20–35 °C to promote natural thermoregulatory behaviour. Lizards were fed crickets (*Acheta domesticus*) three times weekly and provided water *ad libitum*. All procedures were conducted in accordance with our Monash University Animal Ethics Committee approvals (BSCI/2012/17, BSCI/2013/03).

## 2.2. Physiological measurements

Lizards (n=22) were exposed to laboratory assays within three weeks of capture. Assays quantified physiological and morphological traits, including  $T_{opt}$ ,  $T_{sel}$ , heating and cooling rates, and skin reflectance. Seventy-two hours separated test days to avoid interactions among experimental responses. All tests were performed when lizards were in a post-absorptive state (two days without food) (van Berkum et al., 1989). Inter-limb length (ILL), SVL, and mass were measured prior to each test to assess body size effects.

Sprint speed was measured by racing lizards down a 1 L m  $\times$  10 W cm racetrack at each of five temperatures (15, 20, 25, 30, and 35 °C) in a randomized order (Cromie and Chapple, 2012). 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 segment being considered its V<sub>max</sub>. Maximum speed data at each temperature were then used to generate individual performance curves from which  $T_{opt}$ , defined as the  $T_b$  which maximizes performance, was calculated using OriginPro version 9.1 (Origin Lab, Northampton MA, USA). Critical thermal minima and maxima needed to construct the curves were based upon published data (Greer, 1989).

Lizards were placed into a  $40 \times 100$  cm thigmo-thermal gradient constructed of aluminium and partitioned into four equal runways. A row of iButton dataloggers spanned the length of each lane to measure surface temperature. Dataloggers were calibrated against a subset of lizards. 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 cool end. After a 1 h acclimation period the locations of each lizard was monitored from 10:00-16:00 with video cameras positioned over the chamber. In having a short time-constant  $(1.30 \pm 0.338 \text{ min}; (\text{Fraser and Grigg, 1984})), T_{b}$ 's were inferred from the selected positions along the gradient. These data were used to calculate individual  $T_{sel}$ , defined as the mean selected body temperature.

Heating rates were measured using radiant energy as a heat source. Prior to each trial, lizards were placed into a thermal chamber set to 20 °C for 15 min  $T_b$ 's were measured with a T-type thermocouple attached to a quick-read digital thermometer (Eutech Instruments model PT100). Thermocouples were inserted  $\leq 5$  mm into the cloaca of the lizard and secured to the base of the tail using surgical tape (Leucopore<sup>©</sup>). Lizards were then transferred to a 9 cm<sup>3</sup> aluminium chamber fitted with two 28 W bulbs

#### Table 1

Summary statistics (range, mean), Pearson correlations (r), and ordinary linear regression ( $r^2$ ) analyses of thermal traits (dependent variables) and average reflectance ( $R_{av}$ ; independent variables) for each of the spectral ranges (UV-vis=ultraviolet-visible range; nIR=near infrared range).

				R <sub>av</sub> UV-vis				R <sub>av</sub> nIR			
	N	Range	Mean ( $\pm$ SD)	r	Р	r <sup>2</sup>	Р	r	Р	r <sup>2</sup>	Р
T <sub>opt</sub>	22	26.07-34.15	30.55 (±2.11)	0.25	0.14	0.06	0.27	0.03	0.45	0.00	0.89
T <sub>sel</sub>	22	22.72-27.80	26.58 (±1.41)	-0.08	0.36	0.01	0.71	-0.25	0.13	0.06	0.26
Cooling rate	22	1.71-3.12	$2.42(\pm 0.47)$	-0.23	0.15	0.01	0.29	-0.22	0.16	0.05	0.32
Heating rate	22	1.4-2.16	1.43 (±0.39)	0.11	0.32	0.01	0.63	0.14	0.27	0.02	0.54
$R_{av}$ UV–vis	22	11.20-33.30	19.87 (± 5.82)								
R <sub>av</sub> nIR	22	15.56-46.79	33.73 (±8.19)								

 $T_{opt}$ , optimal performance temperature;  $T_{sel}$ , preferred body temperature; SD=standard deviation.

suspended 15 cm above the centre. The size of the chamber was small enough to prevent lizards from using postural adjustments thus individual variation in rates of heating and cooling therefore reflected physiological rather than behavioural differences. Once  $T_{\rm b}$ 's reached 35 °C lizards were immediately placed into another thermal chamber set to 20° C to determine cooling rates. Rates were calculated as follows: rate =  $\Delta T/t$ , where  $\Delta T$  is the difference in  $T_{\rm b}$  from  $t_0$  (onset of test) to  $t_1$  (end of test) and t is the time to reach target  $T_{\rm b}$ .

#### 2.3. Spectrometry

Skin reflectance from upper and lower dorsal regions of lizards was measured in the  $260 \le 700$  nm (UV-vis) and 700-900 nm (nIR) spectral ranges using an AvaSpec 2048 spectrometer and an AvaLight DHS halogen light source (Avantes, The Netherlands) connected through a bifurcated fiber-optic probe (Fig. 1). UV-vis and nIR were assessed separately as these two components are known to be converted to heat at varying degrees among squamates (Clusella-Trullas et al., 2007). The probe was fitted at the end with a plastic cylinder to standardise measuring distance and shield out ambient light. Lizards were placed in a thermal chamber set at 20 °C to insure that each individual's body temperature was the same. Upon reaching test temperature, individuals were removed from the chamber and two measurements of each position were taken with the probe being held perpendicular to the surface of the lizard's body. Reflectance (R) of each dorsal position was calculated relative to a WS-2 white standard. Raw spectra were imported into the programme AvantesSoft 8, smoothed using a running average computed over a 20 nm interval, and the average reflectance  $(R_{av})$  of all four measurements was then calculated for UV-vis and nIR.

# 2.4. Statistical analyses

Analyses were conducted using the statistical programme SPSS version 20.0 (SPSS IBM, Sydney, Australia). All data were checked for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene's tests. SVL (33.18–42.40 mm;  $\mu$ =33.18 ± 2.49), ILL (17.34–24.55 mm;  $\mu$ =21.38 ± 1.99) and mass  $(0.78-1.85 \text{ g}; \mu = 1.31 \pm 0.24)$  were not associated with any of the thermal traits (linear regression: P > 0.05), therefore they were not included in further analyses.  $T_{opt}$  and  $T_{sel}$  values are presented in number of degrees (°C), heating and cooling rates are in °C/min, and reflectance in % transmission. Statistical significance was assigned at  $\alpha = 0.05$ .

To assess the relationship between the thermal traits and reflectance, we first conducted pairwise correlations using Spearman rank correlation. Ordinary least-squares (OLS) regressions were then performed with  $T_{opt}$ ,  $T_{sel}$ , and heating and cooling rates as dependent variables and  $R_{av}$  for UV–vis and nIR as predictors.

# 3. Results

Summary statistics of thermal traits and reflectance measures are presented in Table 1.  $T_{opt}$  was higher than  $T_{pref}$  (30.55 versus 26.58 °C, respectively) and also had a wider range (26.07–34.15 versus 22.72–28.14 °C, respectively). Lizards cooled at a faster rate than they heated (2.42 versus 1.43 °C/min, respectively). Overall reflectance differed between the two ranges (t= –151.95, P < 0.001, SE=0.09), with mean  $R_{av}$  being higher within the nIR spectral range than the UV–vis range (Appendix A). Both UV–vis and nIR reflectance measures showed no significant relationship with any of the thermal traits considered (Table 1).

## 4. Discussion

In examining the relationship between reflectance and physiology among adult male *L. delicata* individuals, our results countered the predictions advanced by the colour-mediated thermoregulatory hypothesis. We found that variation in colouration did not have a significant effect on thermal traits for this population. Not only were heating rates and thermal preferences uncorrelated with reflectance at the UV–vis and nIR wavelengths, but optimal performance temperature and cooling rate also exhibited no relationship.

# 4.1. Colour-mediated thermoregulatory hypothesis

Ectotherms may vary in their thermoregulatory efficiency and capacity due to individual differences in dorsal colouration (Forsman, 1995). Such physiological variation arises because colours differ in their reflectance levels, which in turn, has a direct effect on the quantity and rate of solar radiation that is absorbed by the body. Accordingly, the colour-mediated thermoregulatory hypothesis states that colour and thermal physiology should co-evolve resulting in thermal equilibria and heating rates to be modulated by dorsal pigmentation (Clusella-Trullas et al., 2008). The adaptive significance of colouration among these taxa should, therefore, translate into a thermoregulatory advantage where darker, less reflective, individuals will heat faster, select higher body temperatures, and ultimately have the capacity to exploit low solar and ambient temperature environments while paler, more reflective individuals will heat slower, have lower thermal equilibria, and optimize their fitness under hotter, sunnier conditions (Angilletta, 2009; Clusella-Trullas et al., 2009; Forsman et al., 2002; Harris et al., 2012).

The absence of correlation between skin reflectance and thermal traits ( $T_{sel}$ ,  $T_{opt}$ , heating rate, and cooling rate) demonstrated here were similar to the results of a large-scale, phylogenetic review on 68 species of heliothermic lizards (Clusella-Trullas et al., 2008). These authors found that neither critical thermal tolerances (e.g.,  $CT_{min}$  and  $CT_{max}$ ) nor  $T_{sel}$  were positively associated with dorsal reflectance. Likewise, the rate of thermal exchange and thermal budgets in other ectothermic vertebrates, including *A. carolinensis, Podarcis dugesii*, and *V. berus* did not differ between colour morphs (Claussen and Art, 1981; Crisp et al., 1979; Forsman, 1995).

Several explanations can be put forth as to why our study, as well as the aforementioned studies, did not support the colourmediated hypothesis. Firstly, the rates of evolution of thermal physiology and morphology may differ resulting in an apparent dis-association between the two (Clusella-Trullas et al., 2008). Similarly, behavioural thermoregulation may act to dampen physiology's selective strength, thereby preventing these traits from undergoing correlated evolution (Clusella-Trullas et al., 2008; Huey et al., 2003). In other words, strategies such as micro-habitat choice, basking, shuttling, or postural adjustment may reduce the influence that colouration has on the maintenance of optimal body temperatures, resulting in behaviour acting as an inertial factor. Both these suppositions are seemingly plausible, nevertheless no studies as of yet have linked the evolutionary rates of physiological variables with those of integument reflectance in lizards.

An alternative explanation for the lack of support may be due to multiple selection pressures acting simultaneously on colour rather than it being exclusively shaped by thermoregulatory requirements (Clusella-Trullas et al., 2007; Sanabria et al., 2014). The resulting colour pattern may then represent a compromise between thermal balance and other functions. For small diurnal reptiles, like L. delicata, which are important prey resources for several visual predators, crypsis may be one such selective agent (Rosenblum and Beaupre, 2005). In having dorsal pigmentation that varies with substrate colour, conspicuousness would likely be reduced, and in turn, predation risk as well (Stuart-Fox et al., 2004). For example, Forsman and Shine (1995) found that the relationship between colour morph and survival differed according to sex and reproductive condition in L. delicata, where gravid females with a lateral stripe were less susceptible to predation than striped males. By holding eggs, the stripe's location on a gravid female shifts from its normal lateral position to a more dorsal position which may either increase her resemblance to the background or act as a disruptive pattern. The assertion that crypsis is the primary selective force for this species is further supported by the fact that microhabitat selection is also shown to vary according to colour morph (Forsman and Shine, 1995). This suggests that background matching as an anti-predator strategy may be the mechanism driving the evolution of colour variation in this species rather than thermal balance. In a similar study on collared lizards (Crotaphytus collaris), populations who experienced the strongest predation pressure were the most conspicuous (Macedonia et al., 2004).

Further investigations are needed before discounting the colour-mediated thermoregulatory hypothesis in L. delicata considering that some observations hint at a thermoregulatory function. For instance, the presence of a strong latitudinal cline in morph frequency, where the relative frequency of striped versus unstriped individuals decreases from north (e.g., tropical climate) to south (e.g., temperate climate), suggests that climate may play a role in the evolution of colour variation (Forsman and Shine, 1995). Similar latitudinal and altitudinal patterns have been exhibited in other ectothermic vertebrates such as the White's skink (Liopholis whittii) as well as montane populations of adders (V. berus) and asp viper (V. aspis) (Broennimann et al., 2014; Chapple et al., 2008). Likewise, further research is warranted given that we did not assess thermal traits under varying solar conditions. Because the thermal advantages of colour variation may not be detected under a single radiative intensity, it is imperative that this assumption be tested prior to making any conclusions as to the applicability of the colour-mediated hypothesis in L. delicata.

#### 5. Conclusions

In conclusion, the present study found no evidence to support the colour-mediated thermoregulatory hypothesis in this population of *L. delicata*, even when considering additional ecologicallyrelevant thermal traits such as optimal thermal performance and cooling rate. Instead we suggest that crypsis may be a possible selective agent responsible for maintaining colour variation in a heterogeneous environment. Cryptic functions of colouration, therefore, should be further explored through standard, quantifiable methodology as it might reveal other mechanisms that are critical for understanding colour pattern variation. Identifying the functional differences among colour variants seems central to understand the ecological and/or evolutionary significance of the maintenance of such morphological variation in this species.

# **Declaration of authorship**

GM participated in the conception and design of the study, carried out the laboratory work, conducted data analysis, and drafted the manuscript; CG participated in the design of the study, carried out the field and laboratory work, and assisted in drafting the manuscript; DC participated in the conception and design of the study and assisted in drafting the manuscript. KD was involved in the study design and data analysis as well as provided technical assistance. All authors gave final approval for publication.

# Data accessibility

All data will be deposited to Dryad.

## **Competing interests**

We have no competing interests.

# Acknowledgements

We thank L. Plenderleith for assistance during fieldwork and N. Deal, M. Michelangeli, and H. Kang for help with lizard captive husbandry. R. San Martin, I. Stewart, and P. Arnold provided access to the animal housing facility and construction of experimental equipment. The project was conducted in accordance with our Monash University Animal Ethics Committee approvals (BSCI/2012/17 and BSCI/2013/03), Associated Scientific Research Permits (Queensland: WISP12877513, WISP12160412; Victoria: 10006697, import permits 14330665, 14312742), and under special permission from the Brisbane City Council and Karawatha Forest Protection Society. Financial support was provided by the ANZ Trustees Foundation – Holsworth Wildlife Research Endowment.

#### Appendix A

Mean reflectance spectra for 22 *Lampropholis delicata* lizards from Brisbane, Queensland. Curves were derived from the average of the four measurements (two upper and two dorsal positions) taken on each individual.























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