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Eastern Black Kingsnake *Lampropeltis nigra* dorsal scale colouration primarily adapted for thermoregulation

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The Eastern Black Kingsnake *Lampropeltis nigra* exhibits variation in colouration and pattern throughout its range. Drivers behind this colour variation remain largely unknown. To elucidate patterns in the percentage of light pigmentation in *L. nigra* dorsal scales (% light) we compared two primary hypotheses. Our first hypothesis posited that *L. nigra* colouration has been adapted for thermoregulation (thermoregulation). Alternatively, we hypothesised that *L. nigra* colouration has been adapted to avoid detection by predators and prey (crypsis). To test our hypotheses, we modeled *L. nigra* % light from 46 counties within Mississippi as a function of average temperature, average maximum temperature (thermoregulation) and soil value (darkness of soil colour; crypsis). We included percentage forest cover as a modifying variable in the thermoregulation hypothesis and an interacting variable in the crypsis hypothesis. The best competing model included average temperature and percent forest cover as explanatory variables (LOOIC = -291.3, weight = 0.84, Bayesian R^2 = 0.37 [fixed] and 0.55 [total]). There was a positive relationship between % light and average temperature (β = 0.23, 95% CIs = 0.13, 0.34) and average maximum temperature (β = 0.11, 95% CIs = -0.00, 0.21), and a negative relationship with percent forest cover (β = -0.14, 95% CIs = -0.23, -0.04). These results support the thermoregulation hypothesis. The climate in Mississippi, as in most of the world, is expected to experience shifts over the next century. If ambient temperatures experienced through these changes are outside of *L. nigra*'s thermal optima, as based on colour patterns and relationships observed in our study, then behavioural adaptations may result in some individuals experiencing thermal advantages that influence this species' distribution. The patterns observed in our study, and expected changes in *L. nigra* behaviour and distribution, are likely to occur among other ectothermic species with relatively static colouration.

Keywords: Colour adaptation, homeostasis, Mississippi

INTRODUCTION

An organism's colouration can afford multiple benefits through communication (e.g. aposematism), crypsis or camouflage (e.g. antipredator adaptation), and homeostasis (e.g. disease resistance, thermoregulation, and protection from ultraviolet radiation; Mappes et al., 2005). Colour can vary significantly among individuals within a population due to local abiotic and biotic conditions (Means & Krysko, 2001; Langkilde & Boronow, 2010; Westphal et al., 2011). For instance, individual colour may vary due to prey availability and competition, predator assemblage and climate and landscape characteristics (Merilaita et al., 1999; Means & Krysko, 2001; Langkilde & Boronow, 2010; Westphal et al., 2011; Cox & Davis Rabosky, 2013). Subsequently, colour variation can reflect individual and population benefits across ecosystems (Farallo & Forstner, 2012).

Colouration in reptiles is controlled by chromatophores (Huey, 1982; Cox & Davis Rabosky, 2013). Some squamates can alter pigments within chromatophores to quickly change their colouration in response to changes in conditions (e.g. predator presence; Stuart-Fox & Moussalli, 2009; Vroonen et al., 2012) – species of chameleons (Chamaeleonidae) and anoles (Dactyloidae) are prominent examples. Snakes, however, have relatively static and generally immutable colouration that cannot be changed rapidly but may provide benefits all the same (Cuthill et al., 2005). The deepest layers of chromatophores in snakes, melanophores, produce the dark pigment melanin that largely contribute to their colouration and pattern (Bechtel, 1978; Clusella-Trullas et al., 2007; Goiran et al., 2017). Melanin is synthesised from the amino acid tyrosine, and the resulting black, brown or reddish pigment that is stored in the melanosomes (Ullate-Agote & Tzika, 2021).

While environmental stimuli can affect colouration, there is a genetic basis regulating melanin production in snakes (Bechtel & Bechtel, 1962; 1978). For instance, albinism, or amelanistic colour variations result from mutations in genes that regulate the synthesis of melanin (Rosenblum et al., 2004). Melanism, on the other hand, can occur through an increase in the relative amount

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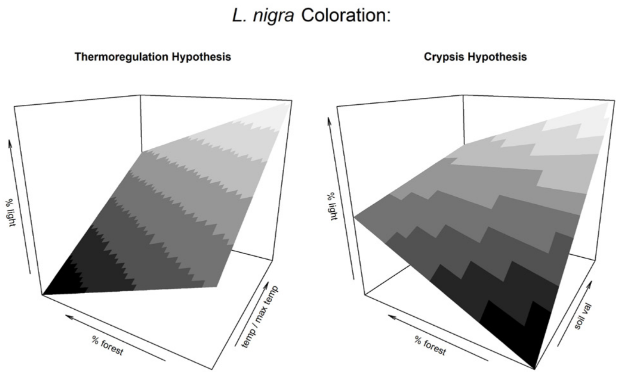

Figure 1. Graphical representation of competing hypotheses. The left plot represents our thermoregulation hypothesis – *Lampropeltis nigra* colouration (percentage of light colouration on dorsal scales; % light) is mostly explained by average temperature (temp) and/or average maximum temperature (max temp) and moderated by forest cover (% forest). The right plot represents our crypsis hypothesis – *L. nigra* colouration (% light) is mostly explained by soil value (darkness to lightness; soil val) and has an interactive effect with forest cover (% forest).

of melanophore density, or a lack of pigment cells other than melanophores in the skin (Kuriyama et al., 2016). A review of some of the processes that influence the synthesis of melanin, the migration of chromatoblasts to the dermis, and the density of these cells, is provided in Kuriyama et al. (2020).

Melanin-based colouration has been associated with a variety of behaviours and traits and linkages between this colouration and these traits is thought to have an embryonic origin (San-Jose & Roulin, 2020). For colouration among snakes, it has been shown, through a theoretical approach, that cell-to-cell and cell-to-environment interactions can affect the motility of pigment cells to sites within the skin during embryonic development (Kuriyama et al., 2020). Colouration is therefore sensitive to internal and external drivers and the evolution of melanistic-based colour patterns can involve balance between lethal and non-lethal mutations in the development of novel colour patterns (Kuriyama et al., 2020). Subsequently, it is expected that the rate of mutation among the suite of physiological conditions that influence colouration can vary with selection pressure (Rosenblum et al., 2004; Wan et al., 2021).

Environment can influence colouration and affect ectotherms, including snakes' ability to thermoregulate (Bechtel, 1978; Geen & Johnston, 2014). Darker individuals can absorb more radiation over a shorter period and reach operative temperature faster than lighter-coloured individuals or those with greater contrast between elements of disruptive colouration (Lattanzio & Buontempo, 2021). However, as body colouration is not plastic within generations of most snakes, rapid changes in ambient temperatures without access to thermal refugia can result in increased mortality rates in populations that cannot adapt (Sears et al., 2011), influencing the demographics of these populations (Lelièvre et al., 2013). Such effects can induce changes to proximate and ultimate factors affecting the distributions of these organisms (Shine & Harlow, 1993; DeGregorio et al., 2015; Tully et al., 2020).

Lampropeltis nigra (Eastern Black Kingsnake; Serpentes: Colubridae; Pyron & Burbrink, 2009) is a large (maximum total length 208 cm) constrictor found in North America east of the Mississippi River, ranging from Illinois to Ohio following the Appalachian Mountains south-westerly to the Gulf of Mexico in Alabama to Louisiana (Conant & Collins, 1991). It inhabits a variety of ecosystems from upland forest, river floodplains, coastal marshes, prairieland and agricultural periphery. Colouration of *L. nigra* is characterised by black dorsal scales with a white to yellow dot in the centre – a pattern that appears weaker in higher latitudes where scales of adults may be almost completely black (Conant & Collins, 1991). The diet of *L. nigra* is diverse, including reptile eggs, snakes, mammals and birds (Ernst & Ernst, 2003). Predators of *L. nigra* are primarily raptors and meso-predators (e.g. raccoons, skunks and opossums; Ernst & Ernst, 2003). Colour and pattern variation in *L. nigra* has, presumably, been adapted to benefit individuals across biotic and abiotic conditions (Means & Krysko, 2001; Krysko & Smith, 2005).

Hypotheses

We hypothesised that *L. nigra* colouration has been adapted for thermoregulation (thermoregulation hypothesis). Alternatively, we hypothesised that *L. nigra* colouration has been adapted to avoid detection from predators and prey (crypsis hypothesis). To test which of our hypotheses is more likely, we related spatial patterns in *L. nigra* colouration (percentage of light area on dorsal scales) within Mississippi to average temperature, average maximum temperature, percentage forest cover and soil value (darkness to lightness of soil based on organic matter content). If these data supported the thermoregulation hypothesis, we expect colour variation in snakes to be explained mostly by average temperature and average maximum temperature, with darker specimens in counties with lower average temperatures and average maximum temperatures. If data supported the crypsis hypothesis, we expect colour variation in snakes to be explained mostly by soil value, with darker specimens in counties with lower soil values (darker soils). We expect percentage forest cover to moderate the effects of average temperature and average maximum temperature, influencing the efficiency of basking (Harvey & Weatherhead, 2010) and ultimately, the thermoregulation hypothesis. Here, given similar temperatures, darker snakes would be found in counties with higher forest cover. However, we would also expect percentage forest cover to have an interactive effect in the crypsis hypothesis where snakes would become less monochromatic (i.e. more speckled) with increased forest cover across soil values, pattern matching dappled sunlight and the litter mosaic of the forest floor. Generically, the thermoregulation and crypsis hypotheses can be visualised in Figure 1.

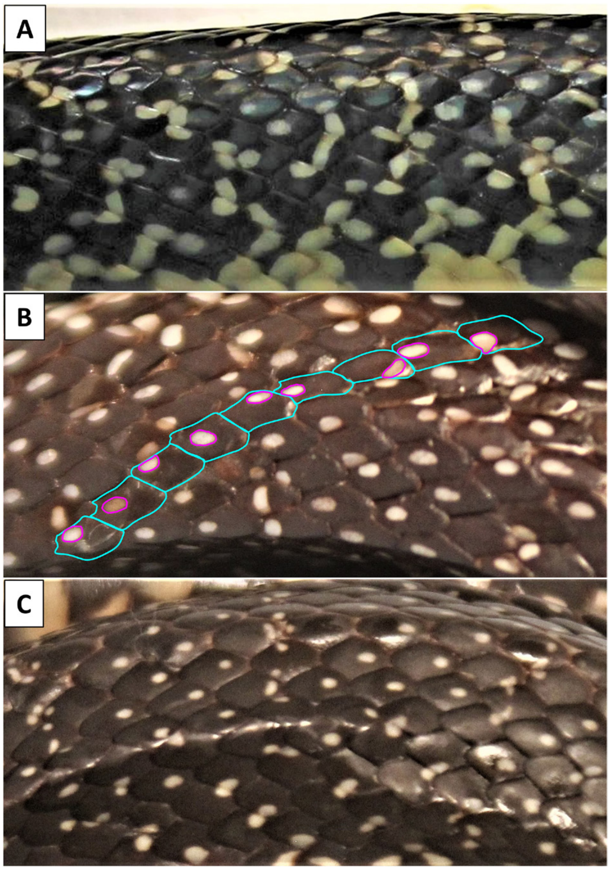

Figure 2. Example photos of an Eastern Black Kingsnake *Lampropeltis nigra* from which percentage area of colouration of nine dorsal scales was calculated (% light). Magenta lines encircle light pigmented areas while cyan lines encircle dark pigmented areas. Specimens are ordered from lightest (**(A)**; MMNS 9284) to darkest (**(B)** then **(C)**; MMNS 2392 and 9793) with % light values of 19.9%, 11.2% and 7.0%, for A, B, and C respectively. Specimens archived at the Mississippi Museum of Natural Science.

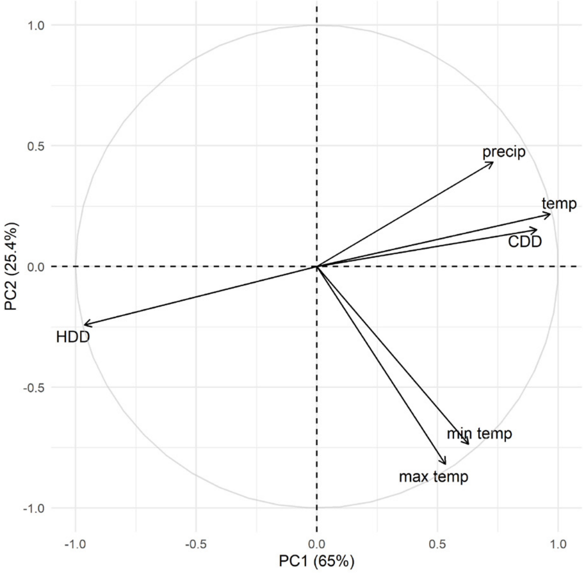

Figure 3. Variable loadings of six climate variables screened for inclusion in model building and comparisons. The x-axis represents the first principal component (PC1) which accounts for 65% of the variation among climate variables. The y-axis represents the second principal component (PC2) which accounts for an additional 25.4% of the variation among climate variables. Angle of arrows represents the association between climate variables and principal components (PC1 and PC2). The length of arrows represents loadings for climate variables which are also represented in the inset table. Data was retrieved from National Centers for Environmental Information county climate database (ncei.noaa.gov) for the 46 Mississippi counties where *Lampropeltis nigra* were collected. Note: temp = average temperature; max temp = average maximum temperature; min temp = average minimum temperature; CDD = cooling degree days; HDD = heating degree days; and precip = average precipitation.

MATERIALS & METHODS

We characterised *L. nigra* colouration as the percentage of area with light pigmentation in nine dorsal scales (% light) of specimens (n = 78) collected from 46 Mississippi counties. These nine dorsal scales were from a scale row along the dorsum of each specimen (Fig. 2B). While location of this row was approximately the mid-point between the snout and vent of each snake, variation among individuals may have occurred.

Snake specimens were part of archived collection housed at the Mississippi Museum of Natural Science (Jackson, Mississippi), a collection that spanned 70 years (1936–2006). We photographed scales mid-dorsum of each specimen using a single-lens reflex camera (Canon EOS 60 D) outfitted with a macro lens (Canon EFS 60 mm f/2.8) within a 61 × 61 × 91 cm (24 × 24 × 36 in) light shed (Impact Digital). Photos were taken at a distance of approximately 500 cm from each specimen, with the camera mounted on a tripod and positioned above the specimen. Photographs were imported into ImageJ v. 1.44 (Schneider et al., 2012). For each specimen we: 1) drew polygons around light and dark pigmented areas of scales (Fig. 2), 2) calculated the total area surveyed (light and dark pigmented areas), and 3) calculated the total area of light pigmentation and divided by the total area surveyed, multiplied by 100. We repeated this process for a subset of snakes considered as means to ensure consistency in measurement among specimens.

We conducted preliminary analysis to test if colouration of snakes differed with year of collection faded, as older specimens could have faded or become damaged. We used a logit linear model with a beta error distribution to test for an association between % light and year. The model indicated no relationship between % light and year ($\beta = 0.00$, 95% CIs = -0.01, 0.00) so we proceeded without including year as a covariate (Supplementary material Fig. 1).

Also, as a preliminary analysis, we screened climate variables shown to be associated with colouration and thermoregulation (Blouin-Demers & Weatherhead, 2001; Rozen-Rechels et al., 2019; Mack & Beaty, 2021).

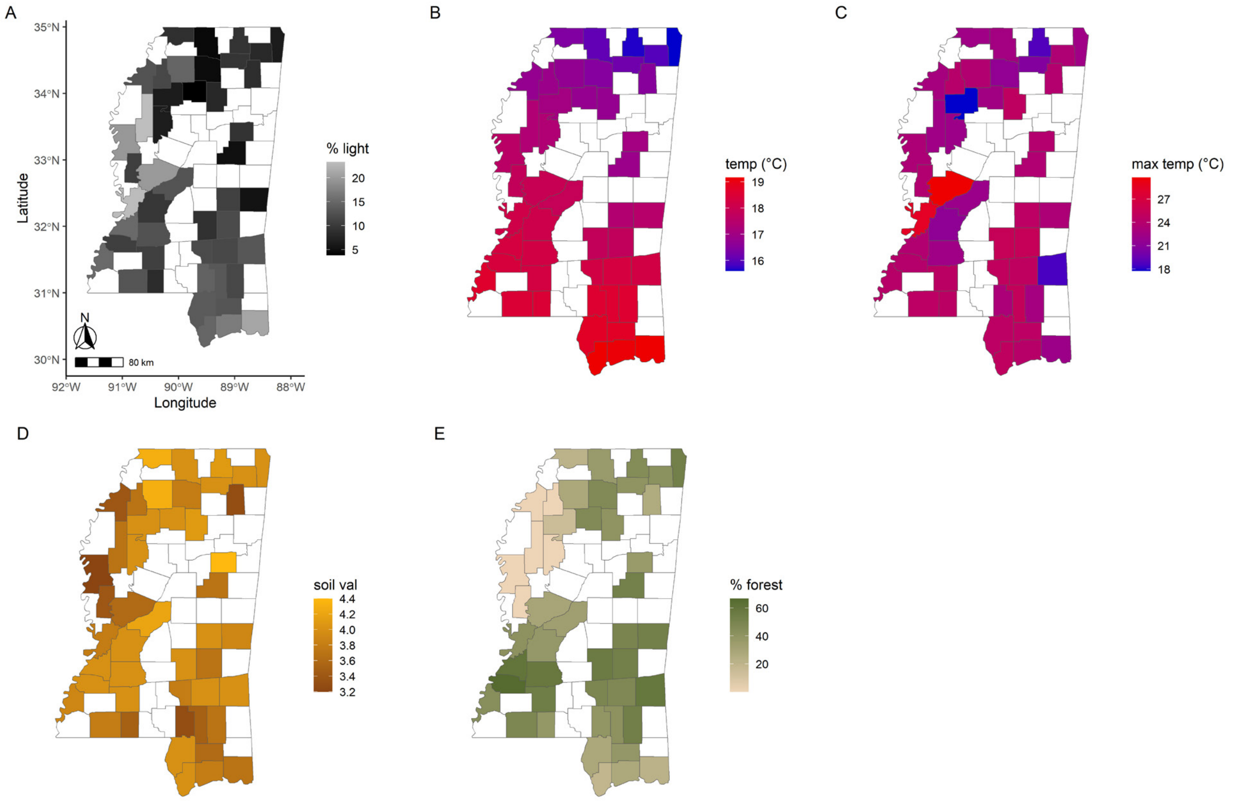

Figure 4. Distribution of *Lampropeltis nigra* percentage of light colouration on dorsal scales (% light; **A**), average temperature (temp [°C]; **B**), average maximum temperature (max temp [°C]; **C**), soil value (lightness to darkness; soil val; **D**), and percentage forest (% forest; **E**) in the 46 Mississippi counties where specimens were collected.

We retrieved average temperature, average minimum temperature, average maximum temperature, heating degree days, cooling degree days and precipitation for counties from which specimens were collected from the National Centers for Environmental Information county climate database (ncei.noaa.gov), which reports averages using data from 1901 to 2000. Using principal components analysis, we selected orthogonal variables with the highest principal components loadings (James et al., 2013). Average temperature (temp) had the highest loading (0.49) on the first principal component (Fig. 3; Supplementary material Table 1) and had high correlations with heating degree days (ρ = -0.99), cooling degree days (ρ = 0.95), and precipitation (ρ = 0.73; Supplementary material Fig. 2). Average maximum temperature (max temp) had the highest loading (-0.66) on the second principal component and had a high correlation with average minimum temperature (ρ = 0.90). Additionally, max temp was chosen over average minimum temperature because our study organism retreats to hibernaculum during winter months, avoiding selection pressures of cold temperatures (Wund et al., 2007). The first two principal components explained 90.4% of the variation in climate variables. We considered average temperature and average maximum temperature together in models representing thermoregulation.

We determined the average soil value (dark to light, lower to higher values respectively) for the three dominant soil classes of each county from which specimens had been collected (soil val). These data were extracted from the United States Department of Agriculture's Soil Survey (websoilsurvey.sc.egov.usda.gov). Soil colour has been shown to influence the distribution of some herpetofauna as a process of crypsis (Heinen, 1993; Isaac & Gregory, 2013). We applied similar logic in our expectation that *L. nigra* would distribute to areas of soil value most akin to their colouration.

The percentage of forested area in each county was derived from 2011 land use/land cover data retrieved from the Mississippi Automated Resource Information System (maris.mississippi.edu; % forest). We assumed that the percentage of forested area in counties has changed little between the time when specimens were collected and when data were collected for 2011 land use/land cover dataset. We acknowledge that some of our samples are before and after this assessment but also recognise that there has been limited change in land cover identified within much of Mississippi during the last 70 years (Karstensen & Sayler, 2009; English, 2011). Though there is a theoretical basis for including elevation and geology in studies of thermoregulation (radiative, convective and conductive heating) and crypsis (pattern matching), we did not consider them here as Mississippi has little variation in elevation (elevation range approx. 245 m) and most of its surface geology is unconsolidated sediments (Blouin-Demers & Weatherhead, 2001; Mappes et al., 2005; Dockery & Thompson, 2016). The spatial distribution of *L. nigra* % light, temp, max temp, soil val, and % forest are displayed in Figure 4.

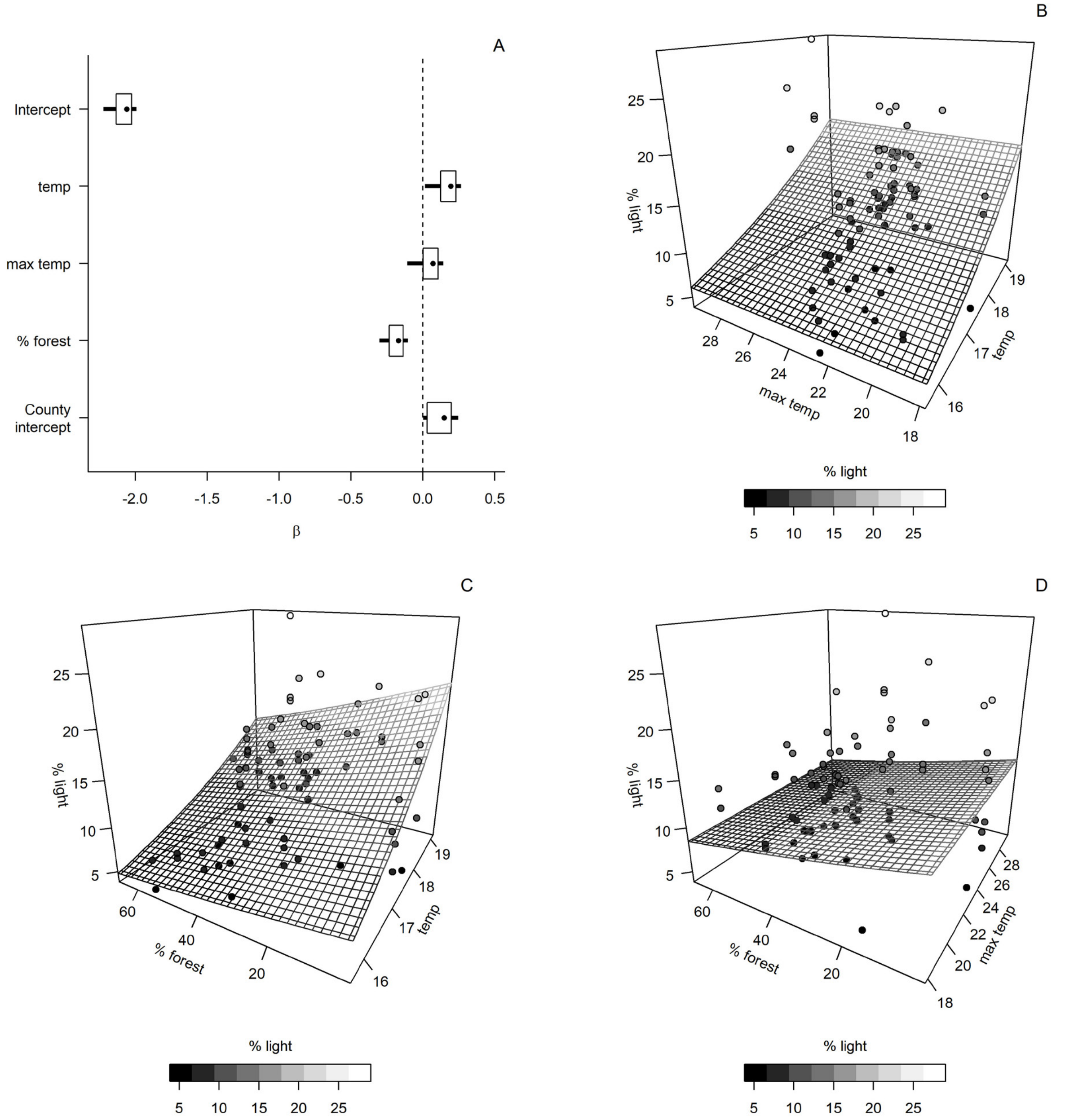

Figure 5. Relationship between proportion of light area on dorsal scales of *Lampropeltis nigra* (% light), average temperature (temp), average maximum temperature (max temp) and forest cover (% forest). Plot **A** displays coefficient estimates with central tendency (median) indicated by the filled circle, the 50% CIs represented by the box and the whiskers represent the 95% CIs. Plots **B**–**D** display model fit (grid plane)with observed data between combinations of explanatory variables. The grid plane and points are shaded in relation to their % light values.

We used logit linear mixed models with a beta distribution to relate *L. nigra* scale % light to temp, max temp, soil val, and % forest (fixed variables) with county as a categorical random variable to account for repeated sampling (multiple snakes) from within the same county (Supplementary material Table 2). For modeling, we transformed % light to its proportional form to meet assumptions of beta distribution (back-transformed for plotting). We developed six apriori models for comparison (Table 1). Model 1 included only the intercept as an ecological baseline to which hypothesised models could be compared. If model 1 received the most support, we considered our results to be inconclusive. Models 2 and 3 related % light to temp and max temp (model 2) and % light to temp and max temp and % forest (model 3). If models 2 or/and 3 received the most support, we considered colouration in *L. nigra* to be adapted for thermoregulation. Models 4 and 5 related % light to soil val (model 4) and % light to soil val, % forest, and the interaction of soil val and % forest (model 5). If models 4 or/and 5 received the most support, we considered colouration in *L. nigra* to be adapted for crypsis. Model 6 included % forest only for comparison. If model 6 received the most support, we considered our results inconclusive.

Fixed variables were scaled and centred before model fitting. We estimated model coefficients using the No-U-Turn Markov chain Monte Carlo algorithm

Table 1. Model number, model variables and pertinent hypothesis used to explain the percentage area of light colouration in dorsal scales (% light) of *Lampropeltis nigra*

Model No.	Variables*	Hypothesis
1	Intercept only	Inconclusive
2	temp + max temp	Thermoregulation
3	temp + max temp + % forest	Thermoregulation
4	soil val	Crypsis
5	soil val × % forest	Crypsis
6	% forest	Inconclusive

*All models included county as a random variable

with non-informative ("flat") priors in the brms R package (Bürkner, 2017; 2018). Posterior sampling was set to 2,000 warmup samples and 8,000 post-warmup samples thinned to 4,000. All models converged and we inspected model fit using posterior predictive checks - there was no indication of a violation of model assumptions (Supplementary material Figs. 3–8), so we continued with model comparisons. We used the leave-one-out cross validation information criterion (LOOIC) and corresponding model weights to compare models (Vehtari et al., 2017; Yao et al., 2018). The LOOIC is a Bayesian analogue to the more familiar Akaike information criterion (AIC) in that it provides an assessment of the quality of model fit relative to other candidate models, with the best competing model having the lowest LOOIC score (Arnold, 2010; Vehtari et al., 2017). Model weights based on LOOIC represent the relative likelihood of a given model base on the expected log predictive density (elpd; Yao et al., 2018). We also calculated total (fixed and random variables) and fixed Bayesian R^2 values to further characterise and compare models (Gelman et al., 2019). For the model with the lowest LOOIC and highest model weight, we plotted parameter estimates and their 50% and 95% credible intervals. All analyses and plots were produced in program R (R Core Team, 2021).

RESULTS

The % light of *L. nigra* dorsal scales averaged 12.24 (SD = 5.05), with a minimum value of 3.81 and a maximum value of 29.04 (Supplementary material Table 2). The temp from within counties in Mississippi where these snakes were collected was 17.71 ˚C (SD = 0.99 ˚C), with a minimum value of 15.56 ˚C and a maximum value of 19.17 ˚C. The max temp from within counties in Mississippi where these snakes were collected was 23.75 ˚C (SD = 2.16 ˚C), with a minimum value of 17.78 ˚C and a maximum value of 29.78 ˚C. The soil val measured for counties where snakes were collected averaged 3.82 (SD = 0.28), with a minimum value of 3.20 and a maximum value of 4.40. The % forest from within counties in Mississippi where these snakes were collected averaged 36.65 (SD = 17.81), with a minimum value of 0.09 and a maximum value of 66.84.

Table 2. Model number and fit metrics in relation to the percentage area of light colouration in dorsal scales (% light) of *Lampropeltis nigra*. Note: LOOIC = leave-one-out cross validation information criterion; elpd = expected log predictive density; Δ elpd = change in elpd in relation to best fit model; weight = weight of support for a model among candidate models; Bayesian R^2: fixed and total = relative fit of model to data for fixed variables and total (fixed and random variables).

Model	LOOIC	elpd	Δ elpd	weight	Bayesian R^2: fixed (total)
1	-278.0	139.0	-6.6	0.00	0.00 (0.55)
2	-286.7	143.3	-2.3	0.16	0.28 (0.53)
3	**-291.3**	**145.6**	**0.0**	**0.84**	**0.37 (0.55)**
4	-279.1	139.6	-6.1	0.00	0.08 (0.56)
5	-277.6	138.8	-6.9	0.00	0.14 (0.56)
6	-279.1	139.5	-6.1	0.00	0.07 (0.55)

The best competing model included temp and max temp and % forest (model 3) as fixed variables and county as a random variable (Table 2). There was a positive relationship between % light and temp (β = 0.23, 95% CIs = 0.13, 0.34) and % light and max temp (β = 0.11, 95% CIs = -0.00, 0.21), and a negative relationship between % light and % forest (β = -0.14, 95% CIs = -0.23, -0.04; Fig. 5). The total Bayesian R^2 value for the model was 0.55 while the fixed Bayesian R^2 value was 0.37. The second-best competing model included temp (β = 0.22, 95% CIs = 0.10, 0.33) and max temp (β = 0.10, 95% CIs = -0.01, 0.22), and had total and fixed Bayesian R^2 of 0.53 and 0.28 respectively.

DISCUSSION

Characteristics of ectotherms, like colouration, are highly influential on body temperature leading to selection of individuals which most efficiently thermoregulate in the local environment (i.e. the thermoregulation hypothesis; Huey & Kingsolver, 1989; Gross et al., 2004). Previous studies of snake colouration support these claims, with darker colouration (i.e. melanistic individuals) being more common in lower average temperature environments (Gibson & Falls, 1979; Andrén & Nilson, 1981; Seigel & Ford, 1987). Here we provide even greater support to this claim by showing a clear relationship between *L. nigra* colouration and temperature and how this relationship is modified by, or with respect to, forest cover. Conversely, we did not find support among our candidate models that colouration was related to soil value (i.e. the crypsis hypothesis).

The thermoregulation hypothesis posits that populations adapt to local thermal conditions but also predicts general large-scale patterns due to variation in thermal conditions. This has been observed repeatedly in other taxa including butterflies, flies, amphibians and other reptiles, most notably darker individuals are more common in higher latitudes (Clusella-Trullas et al., 2007;

Alho et al., 2010). In our study, average temperature (temp) was strongly correlated with latitude (r = -0.96, 95% CIs = -0.94, -0.98), supporting prior observations. Particularly, that lighter coloured *L. nigra* are expected to be found at lower latitudes, in more southerly Mississippi.

Temperature patterns in Mississippi are expected to continue to change, as is the case in most parts of the world (Fill et al., 2019; Sharma et al., 2022). As climates change, species that have adapted to localised conditions through adaptive colouration related to thermoregulation may experience detriments to physiology, depending on their ability to adjust to short and long-term changes. If, as shown in the present study, *L. nigra* and other squamates exhibit colouration linked to thermal conditions, they may experience thermally induced behavioural modifications, as squamates cannot readily adapt to rapidly changing ambient conditions (Bennett, 1990). If the ambient temperatures experienced are outside that of a species' thermal optima then behavioural adaptations may result wherein some individuals with specific colouration experience thermal advantages (Tanaka, 2007). Some of these advantages may be more pronounced during various times when thermal benefits or constraints are more pronounced (Tanaka, 2007). These changes could also induce proximate and ultimate pressures on these species affecting their distribution and other population metrics as well as the elements of the communities they inhabit (Shine & Harlow, 1993; DeGregorio et al., 2015; Tully et al., 2020).

It is expected that changes in land cover have occurred within our study area during the period in which specimens used in our analysis were collected. However, during the time frame of this study it is unlikely that these changes in land cover occurred uniformly over large geographic areas, allowing process of drift and dispersal to occur whereas organisms adapted to local conditions could still access similar conditions through dispersal. However, the coupling of climate change and anthropogenic land use may push species such as *L. nigra* into situations where drivers that affect these ectotherms are supplanted by other factors that affect the adaptability of these organisms over much shorter time frames. The capacity for species like *L. nigra* to adapt to changing environmental conditions will also depend on future land use and community changes, including those conditioned on historical land use.

Understanding how climate can influence the distribution of species is key to understanding current and expected ecosystem change (Montoya & Raffaelli, 2010). Soil is a major storage reservoir for heat within an ecosystem, absorbing energy during the day and releasing heat to the surface at night (Onwuka & Mang, 2018). Energy discharged by soil can vary daily as well as seasonally and changes in soil temperature can affect plant and invertebrate diversity within systems where warming occurs (Robinson et al., 2018). How organisms adapt to the landscape or spatial synchrony and cross-correlations between organisms and the environment is growing in interest as climate change has promulgated in a variety of phenological and other mismatches, typically at large spatial scales (Koenig, 1999). Conversely, neutral drift and dispersal limitations among organisms typically occur at intermediate to fine scales (Hubbell, 2001).

Further research on thermoregulation via colouration in *L. nigra* could help the conservation community better understand if physiology and behaviour of *L. nigra* have coadapted with colouration (Clusella-Trullas at al., 2007). Such studies could include measures of temperatures internal to each snake, relative to ambient conditions. Additional application of multigenomics can also help shed light on the processes of colouration in this and other ectotherms as well as their genetic adaptability. Knowledge gained through these studies can better inform our understanding of colouration in ectotherms and perhaps provide insight to the conservation of species through anticipated climate change, and help biologists brainstorm creative solutions in protecting this and similar species.

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DATA ACCESSIBILITY

Data and R scripts used in the analysis of this study are available in the online supplemental material at the journal website.

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