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PHYSIOLOGICAL ECOLOGY OF THE GROUND SKINK, *SCINCELLA LATERALIS* IN SOUTH CAROLINA: THERMAL BIOLOGY, METABOLISM, WATER LOSS, AND SEASONAL PATTERNS

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Abstract.— Reptiles with small body size and high surface-to-volume ratios face challenges in thermoregulation and water balance because they rapidly exchange heat and lose moisture via evaporation to the environment. The purpose of this study is to determine the thermoregulatory mode of the skink *Scincella lateralis* in the field, as well as how temperature and season influence metabolism and water balance in this species. I measured field body temperatures (T_{bf}) and environmental temperatures during May to December 2012. I measured selected substrate temperatures in laboratory thermal gradients. For both summer and winter acclimatized skinks, I measured oxygen consumption at 24, 28, 32 and 36 °C. In the laboratory, I measured rates of heating and cooling in dry or humid air to determine the influence of evaporative cooling on heat exchange. I measured evaporative water loss at 28, 32 and 36 °C. In the field, skinks thermoregulated more effectively during autumn/winter (d_e - d_b = 9.0) than spring/summer (d_e - d_b =2.1), yet maintained similar average body temperatures between seasons (T_b autumn/winter: 28.0 °C vs. T_b spring/summer: 29.2 °C). Metabolic rates of summer and winter acclimatized skinks measured in the laboratory were temperature insensitive between 28–33 °C (Q_{10} ≈ 1), corresponding to the skink's preferred temperature range. Metabolic rates were approximately twice as high during summer than winter indicating no seasonal acclimatory increase in metabolic rate. Heating and cooling rates in dry versus humid air indicated that skinks heated more slowly than they cooled in dry air, whereas heating and cooling rates were similar in humid air. Results of the study suggests that distribution and activity of skinks may depend on availability of microenvironments with suitable temperature and moisture conditions, which permit skinks to maintain body temperature and water balance within preferred ranges.

Key Words.— Evaporation; heating rate; lizards; oxygen consumption; thermal acclimation; thermoregulation

INTRODUCTION

Understanding how environmental factors influence spatial distribution and seasonal activity patterns of organisms is one of the fundamental goals of ecological studies. Even in geographically widespread species, distribution across the landscape is often patchy, with local abundance determined by microhabitat characteristics of the landscape matrix (Brown 1984). Temperature and moisture are two primary abiotic factors that influence the spatial distribution and activity patterns of small ectothermic vertebrates such as lizards (Adolph 1990; Neilson 2002; Parker and Andrews 2007; Basundhara et al. 2010). Metabolic rate in ectotherms is also temperature-dependent, therefore activity is constrained both by thermal quality and temporal availability of temperatures that enhance essential processes such as foraging, digestion, and reproduction (Grant and Dunham 1988; Adolph 1990). Behavioral thermoregulation effectively increases daily activity time by allowing individuals to exploit thermally favorable microenvironments and thereby maintain body temperatures (T_b) within optimal ranges for enhanced physiological function (e.g. Adolph and Porter 1993; Quirt et al. 2006). Water balance is also intimately linked to the thermal environment because evaporative water loss increases with temperature (Mautz 1980, reviewed in Lillywhite 2006). As a consequence, temperature can influence activity and habitat use through its effect on water balance (Dawson et al. 1966; Neilson 2002; Kearney and Porter 2004).

One of the fundamental ways the thermal environment impacts physiology of ectotherms is through its effect on metabolism (Andrews and Pough 1985; Angilletta 2001). Metabolic rate in reptiles is generally an exponential function of ambient temperature (Murrish and Vance 1968; Alesksiuk 1971). Departure from thermal dependence of metabolic processes, however, occurs in several species of reptiles and is indicated by a decreasing Q_{10} (i.e. decreased sensitivity of metabolism to temperature change) with increasing temperature near the preferred body temperature (e.g. Aleksiuk 1971; Dutton and Fitzpatrick 1975; Bennett and Dawson 1976; Cartland and Grimmond 1994; Wu et al. 2009). Q_{10} is the temperature coefficient describing the increase in reaction rate of chemical process over 10 °C (Bělehrádek 1930). Additionally, metabolic rate reflects acclimatory adjustments in physiological processes associated with seasonal changes in temperature (John-Alder 1984;

Beyer and Spotila 1994). Although there is considerable variation among species, winter-active lizard species often exhibit higher metabolic rates over a given temperature range during winter compared to summer (Dutton and Fitzpatrick 1975; Tsuji 1988). This pattern presumably reflects a compensatory acclimatory response to maintain function of physiological processes at cooler seasonal temperatures. In light of these observations, measuring metabolic responses to temperature is important for studies in physiological ecology because it provides information on fundamental to physiological processes such as energy allocation, growth, and reproduction, which ultimately affect individual fitness (Secor and Nagy 1994; Litzgus and Hopkins 2003; Zaiden 2003).

The Ground Skink (*Scincella lateralis*; Fig. 1) is a small (0.6–1.5 g) diurnal scincid lizard with a geographic distribution across the United States corresponding closely to that of the humid subtropical climate zone defined by the Köppen climate classification system (reviewed in Ackerman 1941). *Scincella lateralis* differs from the majority of North American lizard species in that it is generally considered a forest-dweller (Lewis 1951; Conant and Collins 1998) with a relatively low preferred T_b of approximately 29 °C (Hudson and Bertram 1966). Lizard species inhabiting forested environments are generally predicted to be thermconformers, and accordingly, exert relatively little active thermoregulatory behavior due to the high cost of thermoregulation in environments where sunlight patches are limited (Huey and Slatkin 1976). Smith (1997) concluded that thermal biology of *S. lateralis* is consistent with that of a thermoconformer, because T_b of skinks in the field is closely correlated with ground temperature. In contrast, body temperatures of captive *S. lateralis* measured in laboratory thermal gradients suggests that *S. lateralis* actively thermoregulates, avoiding ambient temperatures between 15–25 °C while actively selecting ambient temperatures between 25–36 °C (Hudson and Bertram 1966). In absence of comparative data on selected body temperatures relative to available environmental temperatures, however, the thermoregulatory mode of *S. lateralis* remains undefined for skinks in the field. If *S. lateralis* is a thermoconformer, individuals should exhibit little directed temperature selection and instead occupy thermal environments at random within their habitat (Huey et al. 1977; Adolph 1990**).** Alternatively, if *S. lateralis* engages in behavioral thermoregulation, individuals should select thermal environments non-randomly to maintain T_b within their preferred range. The latter alternative, of course, assumes that competitors or predators do not restrict the range of thermoregulatory options available.

In coastal South Carolina, *S. lateralis* is active year round over a wide range of seasonal temperatures (Hudson and Bertram 1966; pers. observ.). Daily maximum temperatures in July average 33 °C, with temperatures not uncommonly exceeding 36 °C (National Oceanic and Atmospheric Administration 2013. National Climatic Data Center. Monthly climatological summary for Conway, South Carolina. Available at http://www.ncdc.noaa.gov/cdo-web/ [Accessed 1 July 2013]). In contrast, daily maximum temperatures in January average 14 °C. Based on its relatively small size and high surface to volume ratio, *S. lateralis* should have limited capacity to resist changes in temperature and moisture compared to larger species of lizards (Dawson et al. 1966; Fraser and Grigg 1984; Stevenson 1985). Surprisingly, very few comprehensive studies have examined the thermoregulatory mode of *S. lateralis* in the field nor determined how environmental temperature influences thermoregulation, metabolism, and water balance in this common species of lizard. To meet these aims, I tested three hypotheses: (1) *S. lateralis* selects thermal environments randomly within its habitat (i.e., is a thermoconformer); (2) metabolic rate is elevated during winter to compensate for lower ambient temperatures during the winter season; and (3) *S. lateralis* heat more slowly than they cool due to high surface to volume ratio and corresponding elevated evaporative water loss.

MATERIALS AND METHODS

Collection and animal maintenance.—I collected adult *Scincella lateralis* (n = 64) in Conway, Horry County, South Carolina, USA (33°47'8.72"N, 79°2'0.04"W) from May, 2012 to December, 2012. The research area consisted of an approximately 2 ha area of mixed pine and hardwood forest including large areas of dry open clearings covered by patchy short perennial grasses and small shrubs (< 1.5 m; Fig. 1). Immediately after capture I measured surface body temperatures (see methods below). From these captured individuals, I obtained measurements of selected substrate temperature, metabolic rate, water loss and heating and cooling rates (described below).

I transported lizards captured in the field soon after capture to Coastal Carolina University and housed them in plastic terraria (290 × 220 × 220 mm, three to four individuals per container). Terraria were provided with a substrate of shredded coconut fibers (Zoo Med Eco-Earth, Zoo Med, San Luis Obispo, California, USA) for lizards to bury in and a layer of clean dry oak leaves as a matrix for both cover as well as for basking. I fed lizards small banded crickets (*Gryllodes sigillatus*) every other day and provided them with water by misting daily. To ensure lizards remained acclimated to seasonal environmental conditions, I maintained terraria outdoors under a covered open air shelter. The outdoor housing arrangement allowed lizards to be acclimated to ambient

FIGURE 1. (A) Adult *Scincella lateralis* from Conway, Horry County, South Carolina, USA. (B) Representative image of *S. lateralis* habitat in research area.

seasonal temperature and photoperiod. During spring and summer, lizards received morning sun (0700–1000) but were otherwise shaded for the majority of the day. During fall and winter, lizards received direct sunlight in their enclosures for approximately 5 h (0800–1300) per day. These periods of sun are likely reasonable approximations of the seasonal amounts of direct sunlight that skinks would experience in their environment. During late spring and summer, for example, high environmental temperature largely limits activity of skinks to morning and evening hours (see results section). Conversely, in winter, skinks have greater access to sunlight on the surface of the ground due to loss of leaves from deciduous trees.

Thermoregulation: field and selected substrate temperatures.—I measured surface body temperatures of adult male and female *S. lateralis* (n = 64) in the field within 1 min of capture (nearest 0.01 °C) using a handheld infrared (IR) thermometer (VWR, model number 36934-182, VWR International, Radnor, Pennsylvania, USA). The IR thermometer was calibrated against a National Institute of Standards and Technology (NIST)-certified thermometer. I used the measurement of surface body temperature with the IR thermometer to estimate core body temperature because measurements can be obtained more quickly with less handling than required for cloacal temperatures. Calibration trials indicated that surface body temperatures did not differ significantly from cloacal temperatures (t = 0.14, df = 8, P = 0.89); surface body temperatures were within ± 0.5 °C of cloacal temperatures measured using a thermocouple thermometer calibrated using a National Institute of Standards and Technology (NIST)-certified thermometer. Accordingly, surface body temperature is hereafter referred to as field body temperature (T_{bf}). After initial capture, lizards were quickly grasped by the hind leg, suspended in the air within 5 cm of the surface of the ground so that I could measure T_{bf}. I judged that the measurement of T_{bf} in this manner reduced convective heat loss by wind, while also reducing potential conductive exchange that could result by maintaining skinks in contact with the ground. I obtained field body temperatures by holding the IR thermometer approximately 10 cm above the dorsal body surface of the skink. Given an IR beam field of view ratio of 50:1, the area of temperature being measured at 10 cm above the body surface is approximately 1 mm in diameter. There was no significant difference in T_{bf} among male (28.6 ± 0.680 °C, n = 23), gravid female (30.4 ± 0.90 °C, n = 17), and non-gravid female (28.8 ± 0.67 °C, n = 24) skinks ($F_{2,60}$ = 1.50, P = 0.223), thus sexes were pooled in all analyses of T_{bf}. I conducted surveys for skinks throughout August, however, I did not find any adult *S. lateralis* in this month. Consequently, I did not record field body temperatures of skinks during this time.

I obtained all body temperature measurements from 0900–2000 in spring/summer and 0900–1800 in autumn/winter. I measured field body temperatures 3–5 days per week throughout the sampling period and searches were conducted with equal frequency during morning (0900–1159), afternoon (1200–1459), late afternoon (1500–1759), and evening (1800–2000). The only exception was that surveys for measurement of T_{bf} ended at 1800 during autumn/winter due to the shortened photoperiod and resultant cessation of skink activity. Although the interval over which I measured temperatures was unequal between seasons (9 h fall/winter versus 11 h spring/summer), this approach better captured daily thermoregulatory patterns of skinks than would have been possible by restricting seasonal measurements to the same time frame (0900–1800) during both summer and winter. To test whether unequal sampling interval biased comparisons of monthly T_{bf}s, I analyzed mean monthly T_{bf} using a

single-factor ANOVA, but with spring/summer T_{bf} data from 1800–2000 removed from the analysis. Exclusion of the 1800–2000 T_{bf} data did not change results of the initial analysis of T_{bf} as function of month ($F_{6,55}$ = 1.20, P = 0.34); in either case, T_{bf} did not vary significantly among months (see Results section) regardless of whether I made statistical contrasts using the unequal or equal time frames for temperature measurement. I estimated skink activity based on the frequency of temperature measurements obtained during the daily activity period.

I measured selected substrate temperatures (T_{sel}, n = 57) of adult male and female *S. lateralis* July-November (nearest 0.01 °C) in laboratory thermal gradients using a thermocouple thermometer (Model 800024C, Sper Scientific, Scottsdale, Arizona, USA). I covered the bottoms of the gradients with 5–10 mm of shredded coconut husk and housed the gradients in a room maintained at a constant temperature of 23 °C. I suspended heat lamps at graded heights along each runway to produce a linear temperature gradient ranging from 24 to 45 °C. The gradients were surrounded with foam insulation to minimize temperature fluctuations in the gradient. I fasted lizards for 48 h before placing them in the gradients to ensure that they were post-absorptive (Robert and Thompson 2000). At 1600 on the day after fasting, I removed lizards from group enclosures and placed them into runways (one lizard per runway) and allowed them to equilibrate overnight (Daut and Andrews 1993). I turned on heat lamps at 0800 and I measured selected substrate temperature of each lizard approximately every 2 h beginning at 0900 until 2000. I turned off heat lamps after the final measurement was made at 2000. I measured selected substrate temperatures by placing the thermocouple probe on the surface of the substrate at the midpoint of the lizard's body. Because of their small size, I deemed direct measurement of cloacal temperatures impractical because repeated measurements of T_{sel} would have likely resulted in excessive stress to individuals. Substrate temperatures at mid-body are a common and reliable method to estimate T_{sel} in small lizard species with high surface to volume ratios (Andrews 1994; Wu et al. 2009). To verify this assumption, I placed a *S. lateralis* carcass (0.851 g) at five locations spanning the length of the thermal gradient and allowed it to equilibrate for 20 min at each location followed by measurement of substrate and cloacal temperatures using the Sper Scientific thermocouple probe. Substrate and cloacal temperatures did not differ significantly (t = 0.14, df = 8, P = 0.89). On average, the two sets of measurements differed by less than ± 0.2 °C. Preliminary analysis indicated that there was no significant difference in T_{sel} among male (28.5 ± 0.32 °C, n = 23), gravid female (28.3 ± 0.69 °C n = 9), and non-gravid female (28.6 ± 0.67 °C, n = 24) skinks ($F_{2,53}$ = 0.80, P=0.922), thus I pooled sexes in all analyses of T_{sel}. I used the central 50% of selected substrate temperatures to calculate the set point temperature range (T_{set}).

Thermoregulation: environmental temperatures.—I measured environmental temperatures (T_e) at the study site during the skink daily activity period (nearest 0.1 °C) from 0900–2000 May-September (August omitted) and 0900–1800 October-December 2012 using Thermochron temperature data loggers (Model #, Maxim Integrated, San Jose, California). I sealed data loggers inside waterproof metal jackets (painted with brown "sandable" primer) and partially buried so that the surface of the jacket of data loggers were flush with the surface of the ground. *Scincella lateralis* are almost exclusively ground dwelling lizards (Conant and Collins 1998), therefore, substrate temperatures are likely representative of temperatures that skinks encounter in their environment. Reflective/absorbance values have not been determined for *S. lateralis*, consequently, the brown sandable primer used to paint waterproof jackets for data loggers may not match the actual reflectance/absorbance characteristics of this species. However, given the small size of *S. lateralis* and the relatively long period of time over which daily environmental temperature data were obtained (8 months), I judged that the contribution of reflectance to overall thermal profiles would be relatively minor (Shine and Kearney 2001). The results of my study comparing data logger temperatures to models/carcass support this conclusion (see below). I placed two to three data loggers randomly within each of the following habitat categories: forest clearing (no canopy cover), open forest (20–50% canopy cover), dense forest (> 60% canopy cover). I determined habitat categories by sampling canopy cover at three locations within each habitat using a spherical densiometer.

Environmental temperatures are herein considered operative temperatures (Bakken et al. 1985; Bakken and Angilletta 2014) based on the assumption that data loggers provide comparable estimates of operative temperature that skinks experience in the field (Vitt and Sartorious 1999; Robert et al. 2006; Vickers et al. 2011). To verify this assumption, I recorded environmental temperatures using ibutton data loggers sealed inside metal jackets (n = 2, described above), and thermocouple thermometers inserted inside a copper *S. lateralis* model and a *S. lateralis* carcass. The model consisted of a 20 × 5 mm section of copper tubing painted with brown sandable primer and sealed on each end with aquarium cement. I inserted a copper constantan thermocouple thermometer approximately 10 mm inside the center of the model. Care was taken to ensure that the thermocouple was not in contact with the sides of the model. I measured carcass temperatures by inserting a

thermocouple probe approximately 10 mm into the center of a previously frozen *S. lateralis* (0.880 g). I placed the models on the surface of the ground (data loggers buried flush with ground surface) in an open sunny location and temperatures recorded every 30 min from 1300–1800. During the experimental trial, overall environmental temperatures ranged from approximately 13 °C to 28 °C. Temperatures among ibutton data loggers, model, and carcass did not differ significantly ($F_{2,14}$ = 0.215, P = 0.81), and on average, sets of temperature measurements among the three categories differed by less than 1 °C. The approach used to calculate T_e admittedly does not provide a high resolution representation of the range of thermal heterogeneity within habitats. The measurements nonetheless quantify general thermal characteristics of the major habitats used by skinks during the year.

Indices of thermoregulation and thermal quality of environment.—I measured the accuracy of thermoregulation (d_b) and thermal quality of habitat (d_e) following Hertz et al. (1993). Accuracy of thermoregulation (d_b) was assessed as the mean of the absolute value of deviations of T_{bf} from the mean set point temperature (T_{set}). I assessed the thermal quality (d_e) of the three habitats within the study area as the mean of the absolute value of deviations of T_e from T_{set}. If $d_b < d_e$, then lizards are selecting thermal microhabitats non-randomly. I assessed the effectiveness of thermoregulation as d_e - d_b following Blouin-Demers and Weatherhead (2001). A value of d_e - d_b < 0 indicates that animals avoid thermally favorable habitats. A value of d_e - d_b = 0 indicates perfect thermoconformity, whereas d_e - d_b > 1 indicates thermoregulation. To facilitate comparisons of effectiveness of thermoregulation between seasons, I grouped data from May-September as the spring/summer season and October-December as the autumn/winter season.

Effect of temperature and season on standard metabolic rate.—I measured standard metabolic rates of adult male and non-gravid female *S. lateralis* in July (n = 21) 2012 and January (n = 21) 2013 as rates of oxygen consumption ($\dot{V}O_2$) at four discrete temperatures (24, 28, 32, 36 °C) using an Oxzilla II oxygen analyzer (Sable Systems, Las Vegas, Nevada, USA) and flow-through respirometry. I acclimated lizards to seasonal temperature conditions (described above) prior to measurement of $\dot{V}O_2$. I fasted lizards for 48 h prior to measurement of $\dot{V}O_2$ to ensure a post-absorptive state (Robert and Thompson 2000; Iglesias et al. 2003). I allocated four to five lizards to each temperature treatment, and I only used lizards once in each temperature treatment. All measurements were conducted during the evening between 2100–0100. I placed lizards in a 90 mm long plastic chamber in a constant temperature incubator for 60 min at each test temperature prior to measurement (Cartland and Grimmond 1994). I used a Sable Systems sub-sampler to maintain a constant flow rate of 5.0 ml min^{-1}. To monitor the baseline oxygen concentrations, I placed a reference (blank) chamber within the incubator. I recorded and analyzed data using Sable System Software and I calculated mean $\dot{V}O_2$ (ml O_2 h^{-1}) from a minimum of 5 min of steady state oxygen consumption (Hare et al. 2006).

Comparisons of rates of heating, cooling, and water loss.—I determined total evaporative water loss (ml H_2O g^{-1} h^{-1}) at 28, 32, 36 °C in August 2012 by measuring the change in lizard mass over time at each temperature. I fasted lizards (n = 17, 0.4–1.2 g) for 48 h, weighed them to the nearest 0.001 g, and placed them in mesh bags (50 mm × 90mm) in a controlled constant temperature incubator at 35% relative humidity for 4 h. If lizards urinated or defecated after initial weighing or while in mesh bags, I did not include the individuals in analyses. Lizards were not otherwise restrained during the measurement period, and I collected all data between 1200–1700. After the allotted time, I removed lizards and re-weighed them. I calculated total evaporative water loss as the difference in initial lizard mass from final mass. I randomly assigned lizards to one of the three temperature treatments and I only used each individual once in each temperature trial.

I measured heating and cooling rates of male and female *S. lateralis* (n = 14, 0.7–1.5 g) in dry air (35% relative humidity) and under humid (90–98% relative humidity) conditions. I determined rates of heating and cooling using a step change in temperature (15–33 °C) under each condition. To prevent lizards from escaping, I placed skinks in open-ended aluminum chambers (100 × 25 mm) with a small amount of cotton inserted into each end. To determine rates of heating and cooling under humid conditions, I sealed skinks contained within the aluminum cylinder inside a plastic aquarium (290 × 220 × 220 mm) to which I added a small volume of water to elevate the relative humidity to 90–98%. I monitored relative humidity using a SPER Scientific Mini Environmental Quality meter (model no. 850070; Sper Scientific, Scottsdale, Arizona, USA). I determined heating and cooling rates of skinks in dry air in similar fashion except that I placed skinks within an aluminum cylinder and then sealed inside a dry plastic aquarium with a ventilated top to prevent moisture condensation. Humidity in dry chambers ranged from 28–36%. Skinks were first equilibrated to a body temperature of 15 °C in a Percival programmable environmental chamber (Percival Scientific, Perry, Iowa, USA). I measured rates of heating and cooling under each moisture condition by transferring skinks equilibrated to 15 °C

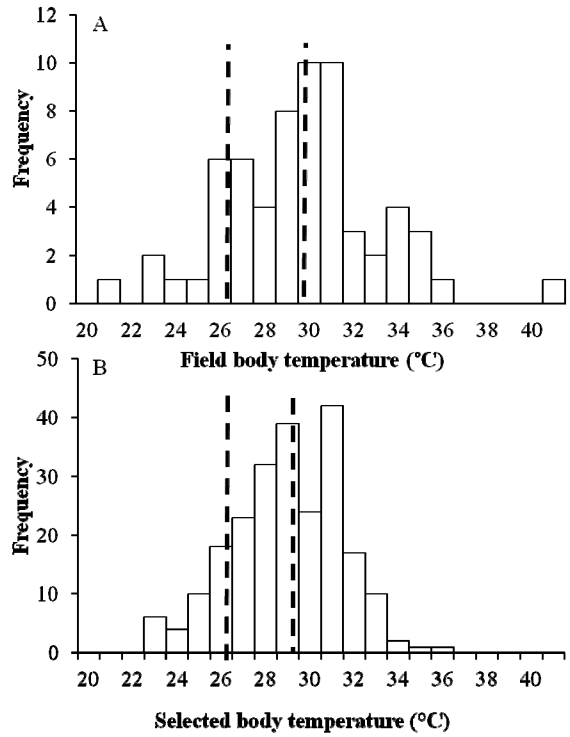

FIGURE 2. Field and selected substrate temperatures of *Scincella lateralis* in South Carolina. (A) Field body temperatures (T_{bf}) measured May 2012-December 2012. (B) Selected substrate temperatures (T_{sel}) measured in laboratory thermal gradients during July-November, 2012. Dashed vertical lines are central 50% of body temperatures (T_{set}).

immediately to a separate environmental chamber set at 33 °C. Using a copper constantan thermocouple probe inserted approximately 5 mm into the cloaca, I measured body temperature continuously during heating and cooling. I recorded body temperatures (nearest 0.01 °C) using a Sper Scientific temperature data logger (model no. 800024C) calibrated against a National Institute of Standards and Technology (NIST)- certified thermometer. Rates of heating (T_h) and cooling (T_c) were expressed as thermal time constants according to the methodology used by Smith (1976).

Statistical analyses.—I conducted statistical analyses using SAS statistical software package (SAS Institute, Cary, North Carolina, USA). I analyze the effect of month on T_{bf} using one-way analysis of variance (ANOVA) and the effect of time of day on T_{sel} using repeated measures ANOVA with time of day as a factor and individual skink as the repeated measure. I analyzed metabolic rate using a two-way ANCOVA with temperature and season as factors and body mass as the covariate. I analyzed evaporative water loss using a one-way ANCOVA with temperature as a factor and initial body mass as a covariate. Preliminary analysis indicated that males and females did not differ in T_{sel}, therefore data from both sexes were combined in all subsequent analyses. I analyzed rates of heating and cooling in dry versus humid air using a paired *t*-test. Before using ANCOVA, I tested the assumption of homogeneity of slopes and I tested the assumption of normality for ANOVAs and ANCOVAs using the Proc Univariate procedure in SAS (all P values > 0.05). For all ANCOVAs, I made post hoc pair-wise comparisons using a least significant difference test on least squared means. For all ANOVAs, I used a Tukey's honestly significant difference test as the post hoc pair-wise comparison. I considered indices of thermoregulation, data on microhabitat temperatures, and assessment of skink activity (based on time of capture) as descriptions and were not compared statistically. I reported data as the mean ± SEM unless otherwise reported, and probability values ≤ 0.05 were considered significant.

RESULTS

Thermoregulation: field and selected substrate temperatures.—Overall field body temperatures (T_{bf}) of *S. laterialis* ranged from 20.4–40.5 °C and selected substrate temperatures in thermal gradients (T_{sel}) ranged from 22.5–35.3 °C (Fig. 2a, b). Central 50% of T_{bf} ranged from 26.8– 30.4 °C (mean 29.1 ± 0.42), whereas thermogradient T_{set} was 27.1–29.7 (mean: 28.8 ± 0.22 °C). Central 50% of T_{bf} was greater during November/December (26–31 °C) than in June/July (27.5–31 °C). Mean T_{bf} did not vary significantly over the eight-month study period (Table 1).

Overall T_{bf} did not vary significantly over the daily activity period (0900–2000, $F_{3,60}$ = 0.14, P = 0.931, Fig. 3), however, T_{sel} in thermal gradients was significantly higher in late afternoon (29.2 °C) compared to the morning (27.6 °C), or evening (28.1 °C; $F_{3,16}$ =5.19, P = 0.002, Fig. 3). Skinks were active throughout the day during springtime as evidenced by the distribution of T_{bf}s recorded as a function of time of day, but activity was limited primarily during the morning and late afternoon or early evening during summer. During autumn and

TABLE 1. Mean (mean ± SE) and sample size (n) of field body temperatures (T_{bf}) of *Scincella lateralis* in South Carolina, measured during May-December (August omitted), 2012, and results of One way ANOVA testing differences among months.

May	June	July	Sept	Oct	Nov	Dec	Result
29.9 ± 0.8 (8)	29.9 ± 0.7 (20)	29.5 ± 0.3 (5)	28.3 ± 1.1 (5)	29.3 ± 1.3 (11)	27.3 ± 1.4 (9)	27.3 ± 2.1 (6)	$F_{6,57}$ = 0.96, P = 0.46

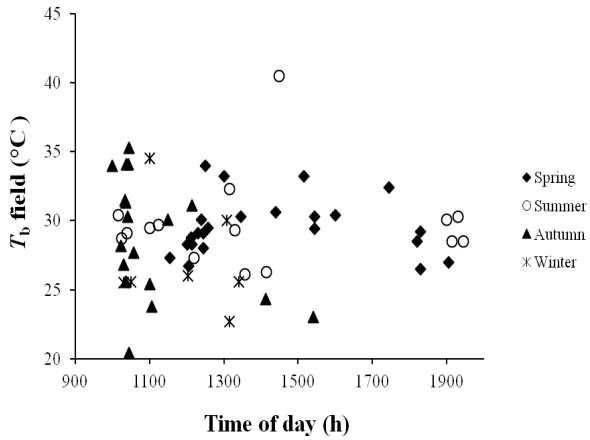

FIGURE 3. Mean field (open circles) and selected substrate temperature (filled circles) of adult *Scincella lateralis* in South Carolina as a function of time of day. M: morning, A: afternoon, LA: late afternoon, E: evening. Error bars are ± one standard error. Asterisks indicate significant difference in body temperature among time of day ($P < 0.05$).

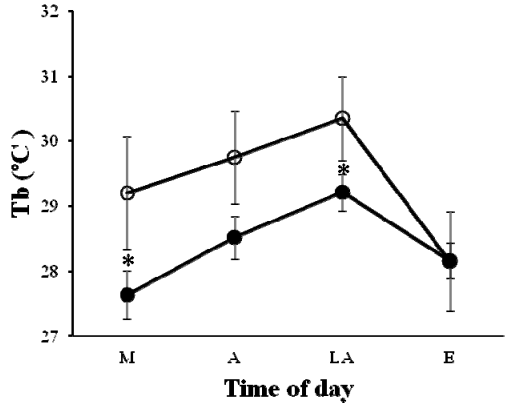

FIGURE 4. Field body temperatures of *Scincella lateralis* in South Carolina as a function of time of day and season. Filled diamonds: spring; open circles: summer; filled rectangles: autumn; asterisk: winter. ○ = Tb Field, ● = TSEL, * = outlier.

winter skink T_{bf}s were recorded primarily during the morning and early afternoon suggesting skinks were preferentially active during this time (Fig. 4).

Thermoregulation: seasonal changes.—Deviation of T_{bf} from T_{set} was lower during spring /summer (d_b = 0.93) compared to autumn/winter (d_b = 2.4, Table 2). Likewise, deviation of T_e from T_{set} was also lower in spring/summer (d_e = 3) compared to autumn/winter (d_e = 11.4). In contrast, thermoregulatory effectiveness was approximately four times higher during autumn/ winter (d_e - d_b = 9) compared to spring/summer (d_e - d_b = 2.1). These values indicate that while skinks thermoregulated during both seasons, they deviated less from thermoconformity during spring/summer whereas they deviated greatly from thermoconformity (i.e., greater effectiveness) during autumn/winter.

During spring and summer, forest clearings were warmer and had a wider temperature range compared to open forest and dense forest habitats (Fig. 5a). Temperatures in closed forest were coolest and least variable of the three habitat classes. Although all three habitats showed some overlap with the preferred range of lizard T_{bf}, temperatures in open forest had the greatest overlap with lizard preferred T_{bf} (central 50% open forest: 26.5–32 °C vs. lizard T_{set}: 27.5–31 °C). In contrast, during winter, the central 50% of temperatures in forest clearing and open forests were similar, although open forests had the widest range in temperature of the three habitat classes (Fig. 5b). Winter temperatures in dense forest were generally cooler and least variable of the habitat classes. Moreover, during winter there was no overlap between central 50% of any of the three habitat classes and lizard T_{set}.

Effect of temperature and season on standard metabolic rate.—Temperature had a significant effect on rate of oxygen consumption in *S. lateralis* ($F_{3,33}$ = 9.34, P < 0.001) with metabolic rate at 24 °C significantly lower than at 28, 32, and 36 °C (Fig. 6). Correspondingly, metabolic rate during both summer and winter was most temperature sensitive between 24–28 °C (Q_{10} = 5.8) and relatively temperature insensitive between 28–33 °C (Q_{10} = 1.1). Overall Q_{10} was 2.4 over the entire temperature range. Season had a significant effect on metabolic rate ($F_{1,33}$ = 6.0, P = 0.022) with summer metabolic rates approximately twice as high at 28 and 36 °C during spring/summer than those in the autumn/winter (Fig. 6).

Comparisons of rates of heating, cooling, and water loss.—Statistical contrast of the ratio of thermal time constants for heating and cooling (T_h/T_c) indicates that *S.*

TABLE 2. Mean seasonal field body temperature (T_{bf}), seasonal environmental temperatures (T_e), accuracy of thermoregulation (d_b), thermal quality of habitat (d_e), and thermoregulatory effectiveness (d_e - d_b) for *Scincella lateralis* in South Carolina. Values are means ± SE and sample sizes (n) for seasonal field body temperature. T_e and d_e data are grand means from hourly substrate temperature measurements collected during the daily activity period from May-September (0900–2000) and October-December (0900–1800), 2012.

Season	T_{bf}	T_e	d_b	d_e	d_e - d_b
Spring/Summer	29.6 ± 0.42 (38)	30.0 ± 1.8	0.93 ± 0.32	3.0 ± 0.93	2.07
Autumn/Winter	27.8 ± 0.84 (26)	15 ± 0.84	2.4 ± 0.38	11.4 ± 0.50	9.0

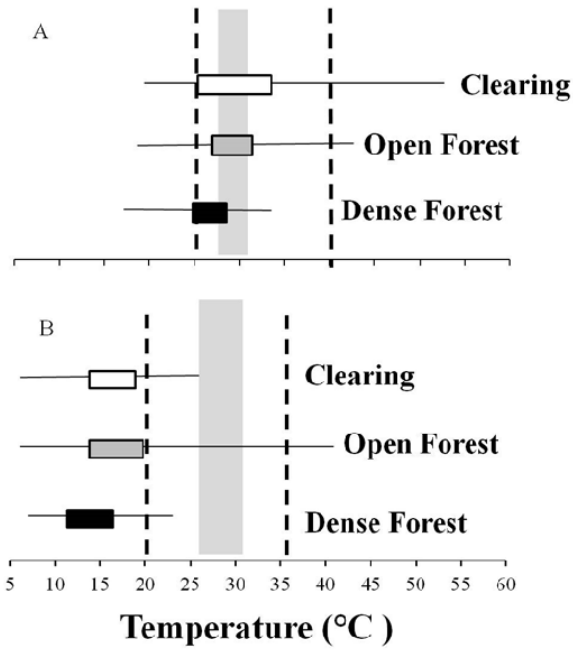

FIGURE 5. Set point temperature (T_{set}, shaded vertical bar) and range (dashed vertical lines) of field body temperatures for *Scincella lateralis* in South Carolina and operative environmental temperatures (horizontal bars) during summer (A) and Winter (B). Horizontal bars are central 50% of operative environmental temperatures in clearing (open bar), open forest (light shaded) and dense forest (dark shaded) environments. Solid horizontal lines are the range in operative temperature recorded in each environment.

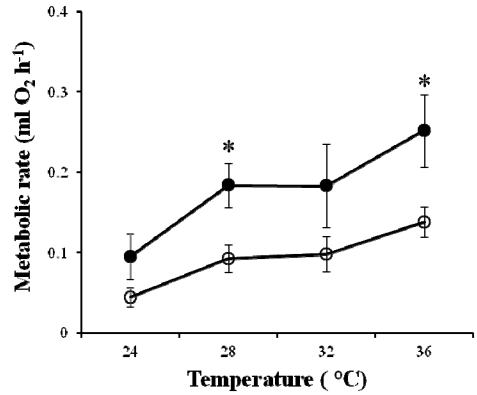

FIGURE 6. Mean oxygen consumption of adult *Scincella lateralis* at 24, 28, 32, and 36 °C measured in summer (filled circles) and winter (open circles). Error bars are ± one standard error. Asterisks indicate temperatures at which rate of oxygen consumption differs between summer and winter ($P < 0.05$). ● = MR Summer, ○ = MR Winter.

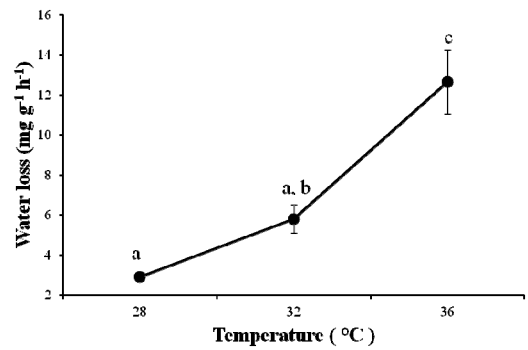

FIGURE 7. Mean total water loss of *Scincella lateralis* at 28, 32, and 36 °C and 35% relative humidity. Error bars are ± one standard error. Different letters above symbols indicate significant difference in evaporative water loss among temperature treatments ($P < 0.05$).

lateralis takes longer to heat than to cool in dry, compared to humid air ($t = 3.13$, df = 6, $P = 0.023$; Table 3). In dry air, thermal time constants for heating were approximately 1.4 times longer than that of cooling. In contrast, thermal time constants for heating and cooling were approximately equal when lizards were maintained at 90–98% relative humidity.

Temperature had a significant effect on total water loss ($F_{2,14} = 24.4$, $P < 0.001$, Fig. 7). Total water loss was higher at 36 than at 32 and 28 °C (Tukey's HSD, $P < 0.05$) but did not differ between the 28 °C vs. 32 °C treatments. Water loss was approximately three times higher in the 36 °C compared to the 28 °C treatment.

DISCUSSION

Thermal biology.—*Scincella lateralis* in South Carolina maintains T_bs between approximately 26 and 31 °C throughout the year. These values are similar to those reported in populations of *S. lateralis* in Texas (25–30 °C; Hudson and Bertram 1966) and Oklahoma (23–34 °C; Smith 1997). The T_b of *S. lateralis* is thus several degrees lower than that of the majority of North American skink species, which typically maintain relatively warm average T_bs of approximately 31–33 °C (Fitch 1954; Brattstrom 1965; Pentecost 1974). The relatively low preferred T_b of *S. lateralis* may be one reason for the marked variation in daily activity patterns

TABLE 3. Mean ± SE and sample size (n) of thermal time constants (minutes) for heating (T_h), and cooling (T_c) of *Scincella lateralis* in dry (relative humidity 24–35%) and humid air (relative humidity 90–98%). Temperature step 15–33 °C. Both values of τ_h/τ_c were significantly different ($P < 0.05$) between means (paired t-tests).

Dry air				Humid air			
Lizard mass (g)	τ_h	τ_c	τ_h/τ_c	Lizard mass (g)	τ_h	τ_c	τ_h/τ_c
0.911 ± 0.085 (7)	5.61 ± 0.75 (7)	4.04 ± 0.37 (7)	1.38 ± 0.12 (7)	0.944 ± 0.112 (7)	3.58 ± 0.274 (7)	3.92 ± 0.367 (7)	0.93 ± 0.065 (7)

across seasons. During spring, for example, skinks are observed throughout most of the day. As air temperatures increase in June, overall activity of *S. lateralis* is primarily limited to morning and evening hours suggesting that high temperatures during late spring and summer may preclude activity on the surface of the ground during the afternoon (Smith 1997). Relatively cool micro-habitats in densely forested habitats, however, may allow skinks to remain active for longer periods in summer. During autumn and winter, skinks are active on sunny days primarily in the morning and early afternoon. Small size and relatively low preferred T_b are characteristics often associated with lizard species with year round activity patterns (Huey and Pianka 1977). The small size and relatively low T_b of *S. lateralis* is therefore likely advantageous particularly under cool conditions by allowing rapid heat exchange with the environment (Fraser and Grigg 1984). During winter, for example, rapid heating allows skinks to warm quickly and remain active even on relatively cool days. Small body size, high surface to volume ratio and relatively cool preferred T_b are thus likely traits which permit individuals of *S. lateralis* to remain active during winter in South Carolina.

Despite maintaining relatively consistent T_bs while active, there was a trend of increasing T_{bf} beginning in the morning and peaking in late afternoon. Similarly, in the thermal gradient, skinks selected significantly higher temperatures during late afternoon (29.2 °C) compared to morning (27.6 °C) and evening (28.2 °C) paralleling the trend observed in the field. These observations suggest that skinks in the field tend toward actively selecting higher T_bs in late afternoon as opposed to passively letting T_b vary with the environment. Selection of higher T_b in late afternoon could represent a circadian-mediated shift in thermoregulatory behavior which reflects a period of increasing activity late in the afternoon when environmental temperatures rise or fall within their preferred range (Ellis et al. 2006). Slight variation in T_b during the daily activity period is not uncommon among thermoregulating reptiles (Clark and Kroll 1974; Huey and Pianka 1977). In Australian Sleepy Lizards (*Tiliqua rugosa*), for example, T_b peaks late in the afternoon despite overall thermoregulatory behaviors that maintain T_b between 33–35 °C (Firth and Belan 1998).

Evaluation of thermoregulatory behavior.—The hypothesis that *S. lateralis* is a thermoconformer in the field was not supported. Costs of thermoregulation for small reptiles are predicted to be higher in forested environments because of the limited availability of sunlight patches compared to open locations (Huey and Slatkin 1976; Hertz et al. 1993). Accordingly, forest-dwelling lizards could mitigate increased cost of thermoregulation in shady forested environments by allowing body temperature to fluctuate passively with environmental temperature (i.e., thermoconformity). Indeed, this pattern appears to be true for several forest-dwelling species (Alcala and Brown 1966; Rummery et al. 1995; Huey et al. 2009). In contrast, results of this study indicate that *S. lateralis* is an effective thermoregulator. First, *S. lateralis* selects a relatively narrow range of body temperatures between approximately 26–31 °C both in the field and in laboratory thermal gradients. Second, skinks are able to maintain these preferred temperatures in the face of daily and seasonal variation in thermal environment. Finally, indices measuring precision of thermoregulation of *S. lateralis* in relation to quality of the thermal environment indicate that skinks select temperatures non-randomly with respect to that available in the environment.

The quality of thermal environment in the study area varied greatly between summer and winter, yet skinks were able to thermoregulate effectively during both seasons. Thermoregulatory effectiveness (d_b - d_e) ranged from approximately 2.1 in summer to 9.0 in winter indicating that skinks invested more in thermoregulation during winter than in summer. For *S. lateralis*, the physiological disadvantage of less effective thermoregulation is likely to be relatively low in spring and summer since there are a variety of microhabitats available to skinks where T_e corresponds closely to T_{set} (d_e = 3). For example, the central 50% of temperatures in the three habitat classes (forest clearing, open forest, and dense forest) had considerable overlap with T_{set}. During late spring and summer, skinks largely ceased activity during the afternoon (pers. observ.), and thus avoided times when high air temperatures greatly exceeded T_{set}. Conversely, during late autumn and winter, the thermal environment was far more challenging (d_e = 11.4), however, skinks nevertheless thermoregulated much more effectively than in spring/summer. During autumn/winter, there was no overlap in central 50% of environmental temperatures in the three habitats and skink T_{set}. Despite this constraint, however, skinks were able to maintain T_bs within the preferred range (26–31 °C) and attain approximately the same maximum T_b in both winter and summer. During winter, the cost of thermoconformity would likely be substantial since non-thermoregulating skinks would have low T_b and correspondingly poor physiological performance (Blouin-Demers and Nadeau 2005; Herczeg et al. 2006). The results of the present study are consistent with previous work on Black Rat Snakes (*Pantherophis obsoleta*) where individuals from a cool high latitude, and presumably high-cost thermal environment, have comparable thermoregulatory effectiveness (d_e - d_b ≈ 3.1; Blouin-Demers and Weatherhead 2001) to spring/summer-active *S. lateralis* (d_e - d_b ≈ 2.1).

Lizards employ a combination of behavioral strategies and physiological mechanisms to thermoregulate (Huey and Pianka 1977). Unlike relatively large lizards (i.e. > 5 g) with greater thermal inertia, shuttling between sun and shade as a primary means of thermoregulation may be problematic for *S. lateralis* because T_b is likely to fluctuate widely between these two environments. Similarly, it seems unlikely that *S. lateralis* could use physiological mechanisms to modify heat exchange such as alteration of cutaneous circulation to either reduce or enhance heat loss (Fraser and Grigg 1984). In light of these constraints, *S. lateralis* appears to thermoregulate primarily by using different microhabitats (e.g. forest clearings, open forest, dense forest) and by regulating time of activity on a daily and seasonal basis. Differential use of various elements of structural microhabitat habitat is one strategy used by lizards to maintain T_bs within preferred ranges (Grant and Dunham 1988; Adolph 1990). The phrynosomatid lizard *Sceloporus occidentalis,* for example*,* selects more arboreal perches during summer in hot desert environments where thermal microenvironments are cooler than those close to the surface of the ground (Adolph 1990). Because *S. lateralis* is almost entirely terrestrial and rarely climbs (Conant and Collins 1998), it is likely that skinks can also thermoregulate by using different structural elements of the ground substrate (e.g. leaves, grasses, debris) within their environment. The extent to which *S. lateralis* uses subsurface environments is not known, but these environments could be an important thermal resource, particularly during summer when ground temperatures may preclude activity on the surface for at least part of the day.

Influence of temperature and season on metabolic rate.—The observed increase in $\dot{V}O_2$ as a function of T_b and overall Q_{10} of approximately 2 is typical of many diurnal lizard species (Bennett 1982; Pough and Andrews 1985). The rate of oxygen consumption in *S. lateralis*, however, does not vary significantly from 28 to 36 °C, suggesting that metabolic rate is independent of temperature over the range of temperatures commonly achieved in the field. Moreover, during both summer and winter, metabolic rate was temperature insensitive between 28–33 °C with Q_{10} values of approximately one recorded over this temperature range. This range in temperature also corresponds closely to the central 50% of temperatures skinks adopted in the field and laboratory. The marked increase in $\dot{V}O2$ (and hence Q_{10} values) at 24 and at 36 °C (though non-significant) may indicate threshold temperatures at which temperature-dependent shifts in metabolic physiology occur. The hypothesis that S. *lateralis* exhibits a compensatory increase in winter metabolic rate compared to that of summer, as predicted for some winter-active lizard species (Tsuji 1988) was rejected. Overall, summer metabolic rates at 24, 28, 33, 36 °C were approximately double that of lizards measured in winter. The lower overall metabolic rates in winter likely reflect reduced energetic demands associated with absence of reproduction, and reduced overall activity time (Beyer and Spotila 1994). Seasonal hormone profiles have not been measured for *S. lateralis*, however, it is also likely that seasonal changes in hormone concentrations such as thyroxine or corticosterone may contribute to the increased metabolic rate during spring and summer and reduced metabolic rate during winter (John-Alder 1984, 1990).

Heating, cooling, and water loss.—The hypothesis that heating rate is reduced by evaporative cooling was supported. When maintained in dry air, individuals of *S. lateralis* heat more slowly (mean $T_h = 5.6 \pm 0.75$ °C min^{-1}) than they cool (mean $T_c = 4.04 \pm 0.37$ °C min^{-1}). This effect was eliminated when skinks were maintained under conditions of high relative humidity (98% RH: $T_h = 3.58 \pm 0.12$ °C min^{-1} vs. 98% RH: $T_c = 3.92 \pm 0.37$ °C min^{-1}). These observations indicate that evaporative cooling is likely responsible for the slower rate of heating in dry compared to humid air. Similarly, at a relative humidity of 47%, the Australian skink, *Lampropholis delicata* (approx 0.9 g) also heated more slowly ($T_h = 4.23$ °C min^{-1}) than they cooled ($T_c = 3.24$ °C min^{-1}; Fraser and Grigg 1984). In contrast, thermal heating constants are approximately twice as high for a typical medium sized skink *Eulamprus tympanum* (12.8 g, $T_h = 11.0$; Fraser and Grigg 1984). While the reduced heating rate observed in small lizards as a result of evaporative cooling is likely attributable to their high surface to volume ratio rather than to direct physiological control, evaporative cooling may nonetheless help buffer lizards from rapid over heating when active on the surface of the ground. A reduced heating rate would be advantageous for small lizards like *S. lateralis*, which are likely to encounter hot sunny open environments when foraging or traversing across habitat patches.

Evaporative water loss is typically high in small lizards (Heatwole and Veron 1977) suggesting that access to moist microenvironments may be important for small lizard species including *S. lateralis*. At 36 °C, water loss was approximately 13 mg H_2O g^{-1} h^{-1} corresponding to loss of approximately 28% of body mass per day. Direct comparisons of rates of evaporative water loss with other lizard species is difficult due to variation in methodology used by different researchers. Nonetheless, evaporative water loss of *S. lateralis* (mean mass: 0.79 g) measured at 28 °C and 35% relative humidity in this study are comparable to that of the gecko *Sphaerodactylus cinereus* (mean mass 0.6 g) measured at 30 °C and 0% relative humidity. Individuals of *S. lateralis* lost

approximately 3.5 mg H_2O g^{-1} h^{-1} corresponding to 13.5% of body mass day $^{-1}$ compared to a loss of 16.8 % body mass day^{-1} in *S. cinereus* (Dunson and Branham 1981). Collectively, these observations suggest that environmental moisture as well as temperature may constrain distribution and activity pattern of *S. lateralis*.

Implications for distributional patterns and thermoregulation.—Physiological requirements of *S. lateralis* likely influence its habitat use and distributional pattern across the landscape. A patchy matrix of open and shaded environments allows skinks to maintain body temperature and water balance within preferred ranges despite relatively wide variation in seasonal temperature and presumably, moisture conditions. In addition, food availability as well as competition and predation (e.g., Huey and Slatkin 1976) likely interact with temperature and moisture to influence habitat selection (Huey 1982).

The results of the study also underscore the importance of considering potential costs of thermoconformity versus advantages of thermoregulation particularly for small species inhabiting environments that undergo relatively extreme temperature fluctuations. For *S. lateralis*, thermoconformity would risk individuals experiencing dangerously high T_b in summer whereas passively maintaining low T_b in winter would limit functions such as locomotor performance, assimilation, as well as severely constrain activity time (Blouin-Demers and Nadeau 2005; Vickers et al. 2011). In contrast, thermoconformity would appear to be most advantageous for species inhabiting tropical forests where temperatures under the canopy are relatively mild and invariant year round (Inger 1959; Alcala and Brown 1966). In these environments, thermoregulatory opportunities are limited and temperature extremes are rare. Accordingly, under these conditions, costs of thermoconformity are likely to be relatively low. The thermoregulatory behavior observed in *S. lateralis* support the model that precision of temperature regulation is a malleable trait that varies according to seasonal changes in costs and benefits in the environment.

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LITERATURE CITED

Ackerman, E.A. 1941. The Köppen classification of climates in North America. Geographical Review 31:105–111.

Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Adolph, S.C., and W.P. Porter. 1993. Temperature, activity, and lizard life histories. The American Naturalist 142:273–295.

Alcala, A.C., and W.C. Brown. 1966. Thermal relations of two tropical lizards on Negros Island, Philippine Islands. Copeia 1966:593–594.

Aleksiuk, M. 1971. Temperature-dependent shifts in the metabolism of a cool temperate reptile, *Thamnophis sirtalis parietalis*. Comparative Biochemistry and Physiology 39A:495–503.

Andrews, R.M. 1994. Activity and thermal biology of the Sand-swimming Skink *Neoseps reynoldsi*: diel and seasonal patterns. Copeia 1994:91–99.

Andrews, R.M., and F.H. Pough. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology 58:214–231.

Angilletta, M.J. 2001. Variation in metabolic rate between populations of a geographically widespread lizard. Physiological and Biochemical Zoology 74:11–21.

Bakken, G.S., W.R. Santee, and D.J. Erskine. 1985. Operative and standard operative temperature: tools for thermal energetics studies. Integrative and Comparative Biology 25:933–943.

Bakken, G.S., and M.J. Angilletta, Jr. 2014. How to avoid errors when quantifying thermal environments. Functional Ecology 28:98–107

Basundhara, C., S. Bhupathy, and B.K. Acharya. 2010. Distribution pattern of reptiles along an eastern Himalayan elevation gradient, India. Acta Oecologica 36:16–22.

Bělehrádek, J. 1930. Temperature coefficients in biology. Biological Reviews 5:30–58.

Bennett, A.F. 1982. The energetics of reptilian activity. Pp. 155–199 *In* Biology of the Reptilia. Gans, C., and F.H. Pough (Eds.). Academic Press, New York, New York, USA.

Bennett, A.F., and W.R. Dawson. 1976. Metabolism. Pp. 159–223 *In* Biology of the Reptilia, Physiology. Gans, C., and F.H. Pough (Eds.). Academic Press, London, UK.

Beyer, E.C., and J.R. Spotila. 1994. Seasonal variation in metabolic rates and maintenance costs of the Eastern Fence Lizard, *Sceloporus undulatus*. Comparative

Biochemistry and Physiology A: Physiology 109:1039–1047.

Blouin-Demers, G., and P.J. Weatherhead. 2001. Thermal ecology of Black Rat Snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology 82:3025–3043.

Blouin-Demers, G., and P. Nadeau. 2005. The cost benefit model of thermoregulation does not predict lizard thermoregulatory behavior. Ecology 86:560–566.

Brattstrom, B.H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376–422.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. The American Naturalist 124:255–279.

Cartland, L.K., and N.M. Grimmond. 1994. The effect of temperature on the metabolism of juvenile Tuatara, *Sphenodon punctatus.* New Zealand Journal of Zoology 21:373–378.

Clark, D.R., Jr., and J.C. Kroll. 1974. Thermal ecology of anoline lizards: temperate versus tropical strategies. The Southwestern Naturalist 19:9–19.

Conant, R., and J.C. Collins. 1998. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. 4th Edition. Houghton Mifflin, Boston, Massachusetts, USA.

Daut, E.F., and R.M. Andrews. 1993. The effect of pregnancy on thermoregulatory behavior of the viviparous lizard *Chalcides ocellatus*. Journal of Herpetology 27:6–13.

Dawson, W.R., V.H. Shoemaker, and P. Licht. 1966. Evaporative water losses of some small Australian lizards. Ecology 47:589–594.

Dunson, W.A., and C.R. Bramham. 1981. Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: *Sphaerodactylus cinereus*, *S. notatus*, and *Anolis sagrei*. Physiological Zoology 54:253–259.

Dutton, R.H., and L.C. Fitzpatrick. 1975. Metabolic compensation to seasonal temperature in the rusty lizard, *Sceloporus olivaceus*. Comparative Biochemistry and Physiology Part A: Physiology 51:309–318.

Ellis, D.J., B.T. Firth, and I. Belan. 2006. Circadian rhythm of behavioral thermoregulation in the Sleepy Lizard (*Tiliqua rugosa*). Herpetologica 62:259–265.

Fitch, H.S. 1954. Life history and ecology of the Five-lined Skink, *Eumeces fasciatus*. University of Kansas Publications, Museum of Natural History 8:1–156.

Firth, B.T., and I. Belan. 1998. Daily and seasonal rhythms in selected body temperatures in the Australian lizard *Tiliqua rugosa* (Scincidae). Physiological Zoology 71:303–311.

Fraser, S., and G.C. Grigg. 1984. Control of thermal conductance is insignificant to thermoregulation in small reptiles. Physiological Zoology 57:392–400.

Grant, B.W, and A.E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami.* Ecology 69:167–176.

Hare, K.M., S. Pledger, M.B. Thompson, J.H. Miller, and C.H. Daugherty. 2006. Daily patterns of metabolic rate among New Zealand lizards (Reptilia: Lacertilia: Diplodactylidae and Scincidae). Physiological and Biochemical Zoology 79:745–753.

Heatwole, H., and J.E.N Veron. 1977. Vital limit and evaporative water loss in lizards (Reptilia, Lacertilia): a critique and new data. Journal of Herpetology 11:341–348.

Herczeg, G., A. Gonda, J. Saarikivi, and J. Merila. 2006. Experimental support for the cost-benefit model of lizard thermoregulation. Behavioral Ecology and Sociobiology 60:405–414.

Hertz, P.E., R.B. Huey, and R.D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. The American Naturalist 142:796–818.

Hudson, J.W., and F.W. Bertram. 1966. Physiological responses to temperature in the Ground Skink, *Lygosoma laterale.* Physiological Zoology 39:21–29.

Huey, R.B., C.A. Deutsch, J.J. Tewksbury, L.J. Vitt, P.E. Hertz, H.J. Álvarez Pérez, and T. Garland, Jr. 2009. Why tropical lizards are vulnerable to climate warming. Proceedings of the Royal Society B 276:1939–1948.

Huey, R.B., and M. Slatkin. 1976: Costs and benefits of lizard thermoregulation. The Quarterly Review of Biology 51:363–384.

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25–91 *In* Biology of the Reptilia. Gans, C., and F.H. Pough (Eds.). Academic Press, New York, New York, USA.

Huey, R.B., and E.R. Pianka.. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. Ecology 58:1066–1075.

Iglesias, S., M.B. Thompson, and F. Seebacher. 2003. Energetic cost of a meal in a frequent feeding lizard. Comparative Biochemistry and Physiology 135:377–382.

Inger, R.F. 1959. Temperature responses and ecological relations of two Bornean lizards. Ecology 40:127–136.

John-Alder, H.B. 1984. Seasonal variation in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. Journal of Comparative Physiology B 154:409–419.

John-Alder, H.B. 1990. Effects of thyroxine on standard metabolic rate and selected intermediary metabolic enzymes in field-active lizards *Sceloporus undulatus*. Physiological Zoology 63:600–614.

Kearney, M., and W.P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. Ecology 85:3119–3131.

Lewis, T.H. 1951.The biology of *Leiolopisma laterale* (Say). American Midland Naturalist 45:232–240.

Lillywhite, H.B. 2006. Water relations of tetrapod integument. Journal of Experimental Biology 209:209–226.

Litzgus, J.D., and W.A. Hopkins 2003. Effect of temperature on metabolic rate of the Mud Turtle (*Kinosternon subrubrum*). Journal of Thermal Biology 28:595–600.

Mautz, W.J. 1980. Factors influencing evaporative water loss in lizards. Comparative. Biochemistry and. Physiology A 67:429–437.

Murrish, D.E, and V.J. Vance. 1968. Physiological responses to temperature acclimation in the lizard *Uta mearnsi*. Comparative Biochemistry and Physiology 27:329–337.

Neilson, K.A. 2002. Evaporative water loss as a restriction on habitat use in endangered New Zealand endemic skinks. Journal of Herpetology 36:342–348.

Parker, S.L., and R.M. Andrews. 2007. Incubation temperature and phenotypic traits of *Sceloporus undulatus*: implications for the northern limits of distribution. Oecologia 151:218–231.

Pentecost, E.D. 1974. Behavior of *Eumeces laticeps* exposed to a thermal gradient. Journal of Herpetology 8:169–173.

Quirt, K.C., G. Blouin-Demers, B.J. Howes, and S.C. Loughheed. 2006. Microhabitat selection of Five-lined Skinks in northern peripheral populations. Journal of Herpetology 40:335–342.

Robert, K.A., and M.B. Thompson. 2000. Influence of feeding on the metabolic rate of the lizard, *Eulamprus tympanum*. Copeia 2000:851–855.

Robert, K.A., M.B. Thompson, and F. Seebacher. 2006. Thermal biology of a viviparous lizard with temperature-dependent sex determination. Journal of Thermal Biology 31:292-301.

Rummery, C., R. Shine, D.L. Houston, and M. B. Thompson. 1995. Thermal biology of the Australian Forest Dragon, *Hypsilurus spinipes* (Agamidae). Copeia 1995:818–827.

Secor, S.M., and K.A Nagy. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. Ecology 5:1600–1614.

Shine, R., and M. Kearney. 2001. Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? Functional Ecology 15:282–288.

Smith, D.G. 1997. Ecological factors influencing the anti-predator behaviors of the Ground Skink, *Scincella laterlalis*. Behavioral Ecology 8:622–629.

Smith, E.N. 1976. Heating and cooling rates of the American Alligator, *Alligator mississippiensis*. Physiological Zoology 49:37–48.

Stevenson, R.D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. The American Naturalist 125:102–117.

Tsuji, J. 1988. Seasonal profiles of standard metabolic rate of lizards (*Sceloporus occidentalis*) in relation to latitude. Physiological Zoology 61:230–240.

Vickers, M., C. Manicom, and L. Schwartzkopf. 2011. Extending the cost-benefit model of thermoregulation: high-temperature environments. The American Naturalist 177:452–461.

Vitt, L.J., and S.S. Sartorius. 1999. HOBOs, Tidbits, and lizard models: the utility of electronic devices in field studies of ectotherm thermoregulation. Functional Ecology 13:670-647.

Wu, Q., S.L. Parker, and M.B. Thompson. 2009. Selected body temperature, metabolic rate and activity pattern of the Australian fossorial skink, *Saiphos equalis*. Herpetological Journal 19:127–133.

Zaiden, F. 2003. Variation in Cottonmouth (*Agkistrodon piscivorus leucostoma*) resting metabolic rates. Comparative Biochemistry and Physiology A 134:511–523.

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