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## THERMAL BIOLOGY AND MICROHABITAT USE IN PUERTO RICAN EYESPOT GECKOS (*SPHAERODACTYLUS MACROLEPIS MACROLEPIS*)

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**Abstract.**—The thermal environment of ectotherms affects every aspect of their life history and many ectotherms must keep their body near an optimal temperature range through some form of thermoregulation. Because of the small size of geckos in the genus *Sphaerodactylus*, they are highly susceptible to overheating and desiccation. Also, because of their small size, they are assumed to conform quickly to environmental temperatures, leaving them no option but to exploit microhabitats with temperatures as close as possible to their optimal range. We used a thermal gradient to find the preferred temperature of *S. macrolepis* in the lab and thermal imaging and data loggers in the field to explore their thermal ecology and microhabitat selection. Our data suggest that all of the microhabitats available within our study sites are outside of the preferred temperature range of *S. macrolepis* during the hottest parts of the day. The layer of leaf litter closest to the ground had the highest humidity and lowest, most stable temperatures. However, geckos ranged into a nearby grassy field where temperatures and humidity were sub-optimal. Although these geckos quickly conform to the temperature of their microhabitat, they appear to adjust activity periods to exploit suitable environmental temperatures when they are available.

**Key Words.**—activity time; body temperature; humidity; rapid heat exchange; thermal environment; thermal imaging

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### INTRODUCTION

Every aspect of the life history of ectothermic animals is directly affected by body temperature (Stevenson et al. 1985; Shine et al. 1997). Consequently, the ability to keep body temperatures within or near an optimal range is essential for survival (Gans and Pough 1982). Ectothermic reptiles often accomplish this through behavioral thermoregulation. Such behaviors include changes in activity time (e.g., Huey and Pianka 1977), shuttling between sun and shade (e.g., Cowles and Bogert 1944), changes in posture (e.g., Muth 1977), and shifting microhabitats (e.g., Angilletta et al. 2009).

Body size directly affects the ability of an ectotherm to thermoregulate. Heat transfer theory predicts that larger animals will exhibit greater differences between body and environmental temperatures than smaller animals and that this is largely attributable to thermal inertia (Muth 1977). The effects of convective heat loss also are much greater for smaller organisms as a result of their small surface area to volume ratio, rendering them more likely to conform rapidly to available environmental temperatures (Stevenson 1985).

Puerto Rican Eyespot Geckos (*Sphaerodactylus macrolepis*; Fig. 1) are small (to about 34–35 mm Snout-Vent Length [SVL]) tropical sphaerodactylids widely distributed across the Puerto Rican Bank (Schwartz and Henderson 1991). Because of their small size, sphaerodactyls exhibit high surface area to volume ratios

and are highly susceptible to desiccation (Leclair 1978; Snyder 1979; Nava 2006; Steinberg et al. 2007). Snyder (1975) determined that 94% of total water loss in *S. macrolepis* was cutaneous. Because of this high susceptibility to desiccation, sphaerodactyls frequently are restricted to relatively cool and moist microhabitats (Steinberg et al. 2007).

Maintaining relatively low body temperatures would appear to be important for sphaerodactyls to avoid overheating or excessive desiccation. However, largely because of their diminutive size and the resulting difficulty in using conventional field methods to obtain body temperatures, references to the thermal biology of West Indian sphaerodactyls usually are extrapolated from information on habitat (summarized in Henderson and Powell 2009). The only recorded habitat or body temperatures for any species were by Breuil (2002; of *S. sputator* under rocks on St. Martin in direct sunlight during the day at temperatures of 27–33° C) and Howard et al. (2001; body and substrate temperatures of 28.1° C for the same species on Anguilla at night). Using a thermal gradient, Bentz et al. (2011) determined preferred temperatures of 25.3° C for *S. kirbyi* on Union Island, St. Vincent, and the Grenadines. In this study, we used thermal imaging technology to determine a preferred temperature range for *Sphaerodactylus macrolepis*, evaluate the rate at which they heat and cool to ambient conditions, and test the hypothesis that their small size leaves them no alternative but to regulate body temperatures by exploiting suitable microhabitats



FIGURE 1. Adult female Puerto Rican Eyespot Gecko (*Sphaerodactylus macrolepis*) from Guana Island, British Virgin Islands. (Photographed by Robert Powell).

and/or adjusting activity periods to avoid suboptimal environmental temperatures.

#### MATERIALS AND METHODS

**Study sites.**—We conducted fieldwork on Guana Island, British Virgin Islands, from 13–18 October 2013. We located two primary study sites (ca. 3 × 3 m) near coordinates 18°28'31.86"N 64°34'33.32"W (WGS84) in Seagrape (*Coccoloba uvifera*) along the coast between White Beach and a mowed grassy area (Fig. 2). Both sites were characterized by shaded *Coccoloba* litter on a sandy substrate (Fig. 3). In addition, we regularly monitored a 180-m transect (18°28'31.86"N 64°34'33.32"W to 18°28'26.45"N 64°34'27.52"W) along the grassy side of the forested area (Fig. 4).

**Preferred temperatures.**—To determine thermal preferences, we used methods of Bauwens et al. (1995) modified to accommodate small animals (Bentz et al. 2011). On 9–11 October in an air-conditioned laboratory in Villanova, Pennsylvania, we placed 14 (seven male and seven female) *Sphaerodactylus macrolepis* captured on Guana Island in October 2012 individually into a thermal gradient. We maintained a temperature range of 21.1–38.9° C by placing a dark-purple filtered heat lamp over and a heating pad under one end of a 20-gallon aquarium with a uniformly dry sand substrate too shallow to allow geckos to burrow. Because *S. macrolepis* in the Virgin Islands is thought to be diurnal (Seaman 1961), we conducted all trials between 1230 and 1830. We monitored the temperature of the substrate with a thermal camera (TiR FLUKE thermal imaging camera; Fluke Corp., Everett, Washington, USA) and recorded thermal images of each individual after 45 min. Because body and substrate

temperatures were measured with a thermal camera, we provided no cover objects; consequently, we did not take temperatures at intervals during the trials to avoid disturbing the animals. We changed the sand substrate after each trial to avoid the possible effects of scent marking.

Thermal imaging cameras combine infrared and visible light images, using a color gradient to show a range of temperatures superimposed on a digital image. Thermal images were accurate to within 0.5° C when we compared thermal images of substrates with measurements taken with a quick-reading electronic thermometer with a type K thermocouple (Fluke Corp., Everett, Washington, USA). We used “SmartView” thermal imaging software (Fluke Corp., Everett, Washington, USA) to analyze images.

**Thermal environment.**—We placed 14 iButtons (DS1922L and DS 1923-Hygrochron; Embedded Data Systems, Lawrenceburg, Kentucky, USA) wrapped in leaves or embedded in clumps of grass at varying depths in the leaf litter at both sites and in different microhabitats representing varying degrees of shade and sun exposure along the transect. Microhabitats included the top, middle, and bottom of leaf litter (ranging in depth from 5–15 cm), in dense grass on a dirt substrate, in thin grass on a sand substrate, under leaves on grass, and on open sand (although we saw geckos on open sand only when disturbed; they would have to traverse such areas to move from clump to clump or from the shaded areas into the grassy sites). We programmed iButtons to record temperature data to 0.5° C every half an hour. We collected temperature data for five days at the study sites and temperature for one full day and two half days along the transect. We also collected humidity data to 0.001% RH every 10 min for one full day and two half



**FIGURE 2.** Aerial view of Guana Island, British Virgin Islands (courtesy of Guana Island and Privateislandsmag.com). The arrow indicates the location of White Beach, illustrated below in the Google Earth® image showing the dense Seagrape (*Coccoloba uvifera*) stand separating the beach from a regularly mowed grassy area. The two white Xs mark the approximate locations of the two study sites (18°28'31.86"N 64°34'33.32"W; WGS84) and the white line marks the approximate location of the transect paralleling the Seagrape stand.

days in the two sites and along the transect for six ecologically relevant microhabitats including the top and bottom of leaf litter, dense grass on a dirt substrate, thin grass on a sand substrate, and under leaves on grass, and open sand. We used a thermal imaging camera to record thermal images of geckos and substrates in various microhabitats, and recorded date, time, location, and sex of the gecko for each image.

**Activity periods.**—Observations of lizards in the grassy area at varying distances from the forest edge triggered questions of how far away from shade they would move and at what times they would do so. We recorded the distance of lizards from the forest edge at 0730, 0930, 1130, 1400, and 1700 on 15 October and opportunistically on the previous and following days. We measured distances from where a gecko was first sighted in the short grass to the closest shaded site with elevated vegetation (i.e., trees or shrubs). For each sighting, we recorded time of day, degree of insolation (full sun, sun-shade mosaic, or full shade), sex of the lizard, and the type (dense grass, sand/grass,

grass/leaves, or sand) and temperature of the substrate. When possible, we recorded thermal images of the gecko.

**Heating and cooling rates.**—We generated heating and cooling curves at ambient temperatures on an artificial substrate (a large plastic container) in a non-air-conditioned room on 17–18 October. As for determining preferred temperatures, we provided no cover objects as they would have precluded the use of the thermal camera. We placed three adult geckos under a heat lamp for one minute until they reached temperatures of 34–35° C and three juveniles for 30–40 sec until they reached temperatures of 31–35° C. We also placed six adult and three juvenile geckos in a refrigerator for 3–4 min until they reached temperatures



**FIGURE 3.** Study sites 1 (top) and 2 (bottom) in Seagrape (*Coccoloba uvifera*) between White Beach and a mowed grassy area on Guana Island. Leaf litter ranged in depth from 5–15 cm. (Photographed by Kaitlin E. Allen).



**FIGURE 4.** A section of the transect paralleling the Seagrape (*Coccoloba uvifera*) in a mowed grassy area. Microhabitats along the transect included dense grass on a dirt substrate, thin grass on a sand substrate (inset), under leaves on grass, and open sand. (Photographed by Kaitlin E. Allen).

of 21–22° C. We subsequently monitored the temperatures of each gecko on the artificial substrate at ambient temperature using the FLUKE thermal imaging camera until the gecko was no longer visible on the camera screen (which we interpreted as the lizard reaching ambient temperature). We recorded sex, SVL (the distance from the tip of the snout to the vent in mm), time, temperature, and the time elapsed until an individual reached ambient temperature, and we then marked each gecko to ensure that no individual was subjected to heating or cooling more than once.

**Statistical analyses.**—We performed Shapiro-Wilk tests to determine whether data were normally distributed. We used student’s t-tests,  $\chi^2$  analyses, linear regression, and ANOVA to test our hypotheses on normally distributed (and equal variances) data and a Mann-Whitney U-test on data that were not normally distributed. We analyzed all data in R statistical programming language (R version 3.0.2; R Development Core Team, [www.r-project.org/](http://www.r-project.org/)). All means are presented  $\pm$  1 SD. For all statistical tests,  $\alpha = 0.05$ .

## RESULTS

**Preferred temperatures.**—Mean preferred temperature for *Sphaerodactylus macrolepis* in the lab was  $25.34 \pm$

$2.65^\circ$  C. The mean preferred temperature of males ( $24.91 \pm 2.50^\circ$  C) was slightly but not significantly lower than that of females ( $25.77 \pm 2.93^\circ$  C;  $t = -0.588$ ,  $df = 12$ ,  $P = 0.567$ ). However, geckos in the field attained temperatures in the leaf litter that were outside their preferred temperature range for most daylight hours (Fig. 5; Fig. 6).

**Thermal environment.**—All microhabitats available to geckos in leaf litter at our study sites and along our transect were outside the preferred temperature at some times of day (Fig. 7). Even the deepest layer of leaf litter was warmer than preferred temperature between 1200 and 1730. All microhabitats, however, were within the preferred range between 2300 and 0800 (Fig. 7). Humidity was significantly different across all six of the tested microhabitats on 17 October ( $F_{1,5} = 65.38$ ,  $P < 0.001$ ). Relative humidity was both highest and most stable under the leaf litter throughout the day (mean  $97.92 \pm 0.98\%$ ). Relative humidity on top of the leaf litter had the lowest average ( $78.39 \pm 9.31\%$ ), and relative humidity on sand was the most variable ( $79.67 \pm 21.30\%$ ). Between 2100 and 0800, relative humidity remained high and stable across all microhabitats (on litter:  $86.23 \pm 2.41\%$ , under litter:  $98.48 \pm 0.81\%$ ); however, during the day, between 0800 and 2100, it became much more variable (sand:  $64.68 \pm 18.62\%$ ; under litter:  $97.43 \pm 0.87\%$ ).

**Activity time.**—Unless disturbed, geckos were not active on the surface of leaf litter during the day, and efforts to assess activity within the litter were impossible without disturbing both the habitat and the lizards. Therefore, because geckos were largely absent from the grassy field under hot, sunny conditions, we assumed that they were moving into the field only when conditions were moderated by weather or time of day. Consequently, we used the number of geckos found in clumps of grass or under leaves in the field along the transect as an indicator of activity. Gecko activity away from deep shade was low (essentially zero on sunny days) until 1600 when it increased dramatically (Fig. 8). Juveniles tended to venture away from shade more frequently than adults during the early morning and evening (Fig. 8), but differences were not significant. Distances from the shaded vegetation throughout the day exhibited a small spike beginning around 0700 and a larger increase in the evening beginning at 1600, the latter corresponding to the increase in the total number of geckos found in the grassy area (Fig. 9). Distances of juveniles and adults from shaded vegetation did not differ significantly ( $W = 307.5$ ,  $P = 0.106$ ).

**Microhabitat selection.**—Active microhabitat selection was evident along the transect where geckos had to choose between dense grass, sand/grass, sand and

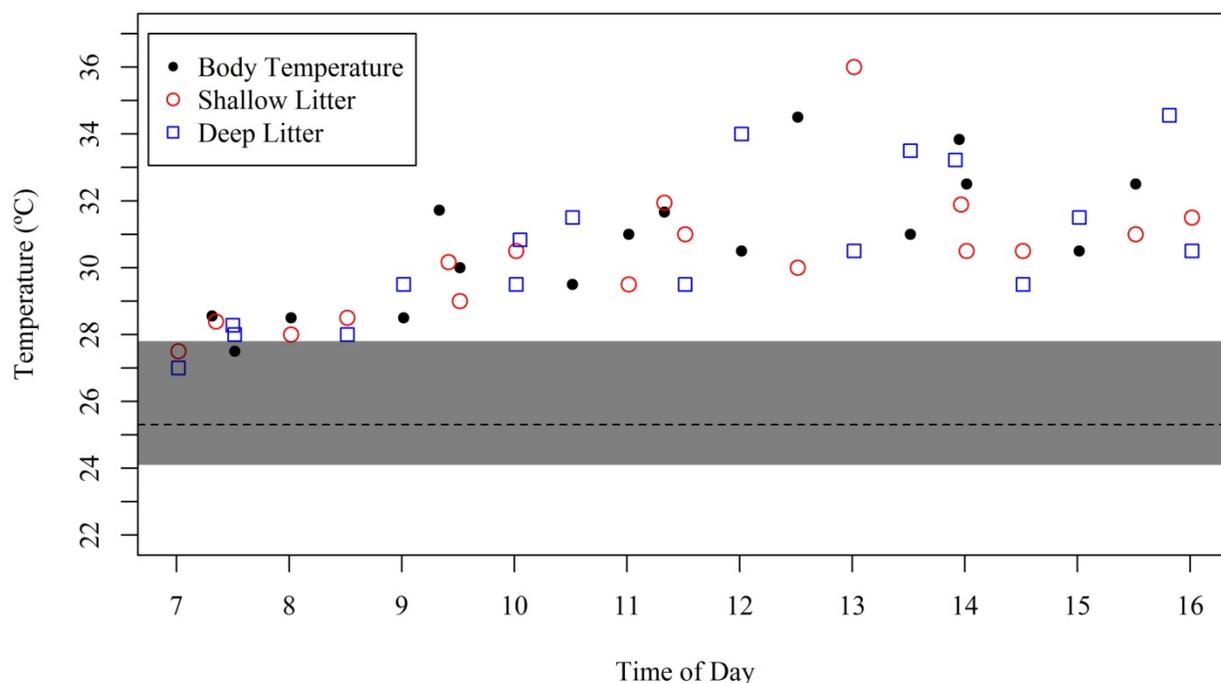


FIGURE 5. Body temperatures of *Sphaerodactylus macrolepis* at site 1 compared to temperatures at the top and bottom of the leaf litter on 15 October 2013. Body temperatures of geckos (solid dots) were measured using a TiR FLUKE thermal imaging camera. Temperatures at the top of the leaf litter (red circles) and bottom of the leaf litter (blue squares) were measured using iButtons. The dotted line represents the mean preferred body temperature and the gray bar the central 50% of preferred temperatures as measured in the lab.

grass/leaves ( $\chi^2 = 12.35$ ,  $df = 3$ ,  $P = 0.006$ ).

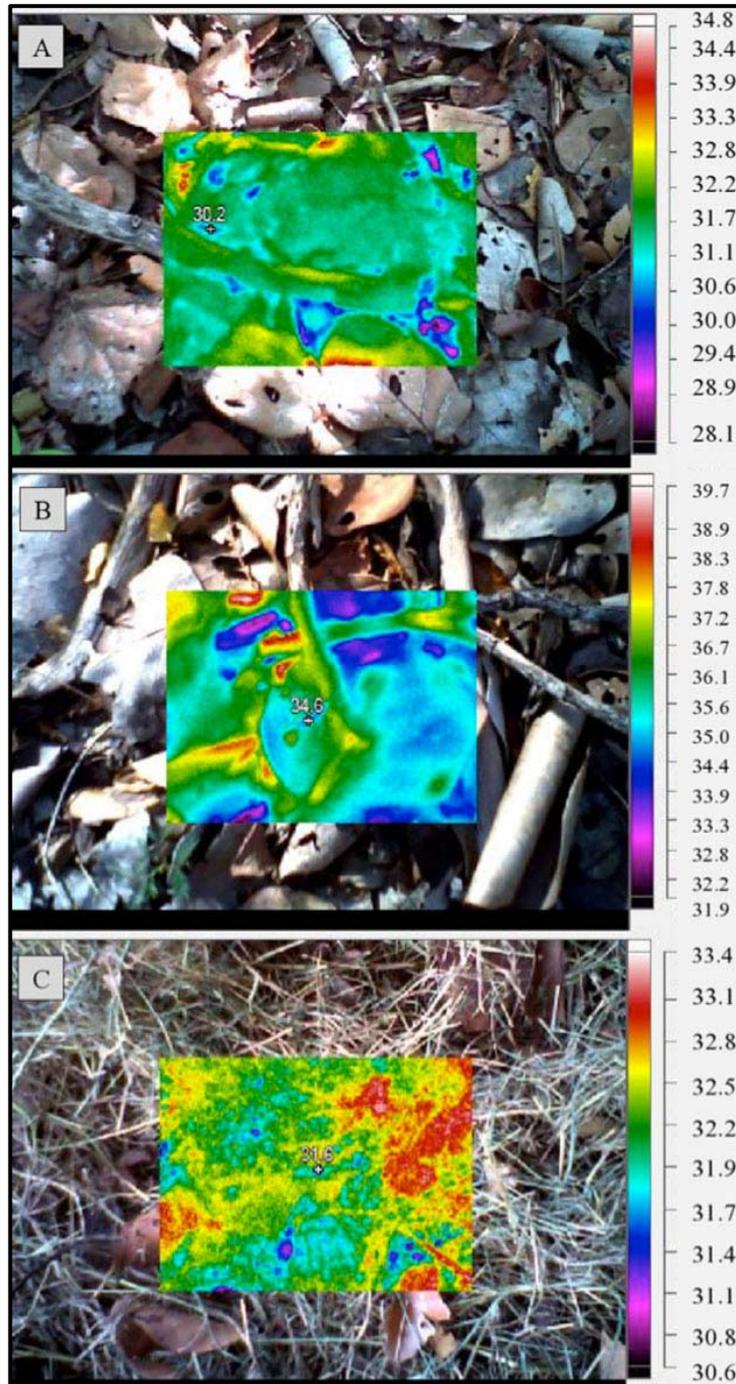
Geckos most frequently chose dense grass and grass covering sand. Geckos along the transect (with only one exception) were in shaded areas under trees, observed under cloudy conditions, or encountered early in the morning before sunlight reached the area. Microhabitats used by juveniles and adults differed significantly along the transect, with adults more frequently in dense grass ( $\chi^2 = 7.20$ ,  $df = 2$ ,  $P = 0.007$ ) and juveniles more frequently in grass/sand ( $\chi^2 = 6.23$ ,  $df = 2$ ,  $P = 0.013$ ). Although grass/sand was significantly warmer than dense grass ( $t = -14.86$ ,  $df = 143$ ,  $P < 0.001$ ), grass/sand had significantly higher humidity throughout the day ( $t = -32.82$ ,  $df = 143$ ,  $P < 0.001$ ). We encountered a greater but non-significant proportion of adults than juveniles venturing out into the grassy area (adults: 28, Juveniles: 17,  $\chi^2 = 2.69$ ,  $df = 2$ ,  $P = 0.101$ ).

**Heating and cooling rates.**—The mean heat gain rate of artificially cooled adults ( $0.717 \pm 0.221^\circ \text{C}/\text{min}$ ; Fig. 10a) was significantly less than that for juveniles ( $1.286 \pm 0.509^\circ \text{C}/\text{min}$ ;  $t = -2.438$ ,  $df = 7$ ,  $P = 0.045$ ). No significant association was evident between the rate of cooling and SVL in adults or juveniles (adults:  $F_{1,4} = 2.818$ ,  $P = 0.169$ ; juveniles:  $F_{1,1} = 10.31$ ,  $P = 0.192$ ); however, this is likely attributable to small sample sizes (adults:  $n = 6$ , juveniles:  $n = 3$ ). The mean heat loss rate

of artificially heated adults ( $0.649 \pm 0.093^\circ \text{C}/\text{min}$ ; Fig. 10b) did not differ significantly from that of juveniles ( $1.089 \pm 0.379^\circ \text{C}/\text{min}$ ;  $t = -1.950$ ,  $df = 4$ ,  $P = 0.123$ ). We observed no significant association between adult or juvenile SVL and the rate of heat loss (adult:  $F_{1,1} = 0.101$ ,  $P = 0.804$ ; juvenile:  $F_{1,1} = 2.807$ ,  $P = 0.343$ ), but this also might have been a reflection of small sample sizes (adults:  $n = 3$  and juveniles:  $n = 3$ ). Heating and cooling rates for adults or juveniles did not differ significantly (adults:  $t = 0.495$ ,  $df = 7$ ,  $P = 0.636$ ; juveniles:  $t = 0.537$ ,  $df = 4$ ,  $P = 0.620$ ).

## DISCUSSION

Although thermal camera images cannot precisely measure internal body temperatures, images showing temperatures of disturbed geckos corresponding to the microhabitats where they originated before disturbance and the rapid rate at which individuals reached ambient temperatures during the heating and cooling trials strongly suggest that *Sphaerodactylus macrolepis* at our study site conformed to the temperatures of their microhabitats. Mean preferred temperature ( $25.34^\circ \text{C}$ ) was lower than expected given the available environmental temperatures, but similar to the preferred temperature of  $25.3^\circ \text{C}$  for *S. kirbyi* on Union Island, St.



**FIGURE 6.** Thermal images taken from each of the field sites and the transect on 15 October 2013. Smart View Thermal Imaging software was used to center the digital marker over the body of the gecko (the outline of each gecko’s body is visible in each image) and analyze the body temperature (°C). Body temperature is shown for a gecko at (A) Site 1 at 0925, (B) Site 2 at 1600, and (C) in the transect at 1420. Temperature ranges are represented by color gradients with red being the warmest and purple the coolest relative to the average temperature in the rest of the image.

Vincent and the Grenadines (Bentz et al. 2011). suggests that they restrict activity to periods when Environmental temperatures were higher than preferred temperature during much of the day, even under the leaf litter where these geckos spend much of their time. This suitable temperatures are available, possibly becoming nocturnal when both temperature and humidity are closer to optimal, as predicted by the “Bogert Effect” (see

discussion in Huey et al. 2012). Although preferred temperature and activity temperature often are co-adapted in lizards, this pattern does not apply to many geckos (Huey et al. 1989). Therefore, to what extent these high environmental temperatures affect the physiology of sphaerodactyls is unknown, and no information is available on the performance curve of this species or any lizard in the genus *Sphaerodactylus*.

Because of their small size and susceptibility to desiccation, relatively cool moist microhabitats are extremely important to the thermal ecology of these

geckos. Choosing habitat that is protected from direct sunlight by a dense forest canopy and deep leaf litter is a tactic commonly used by sphaerodactyls to avoid overheating and desiccation (López-Ortiz and Lewis 2004). We determined that deep leaf litter was the most stable thermal environment with the highest, most stable humidity and was closest to the preferred temperature throughout the day. This would suggest that these geckos spend much of the day evading stressfully hot temperatures, presumably by varying their position in the litter.

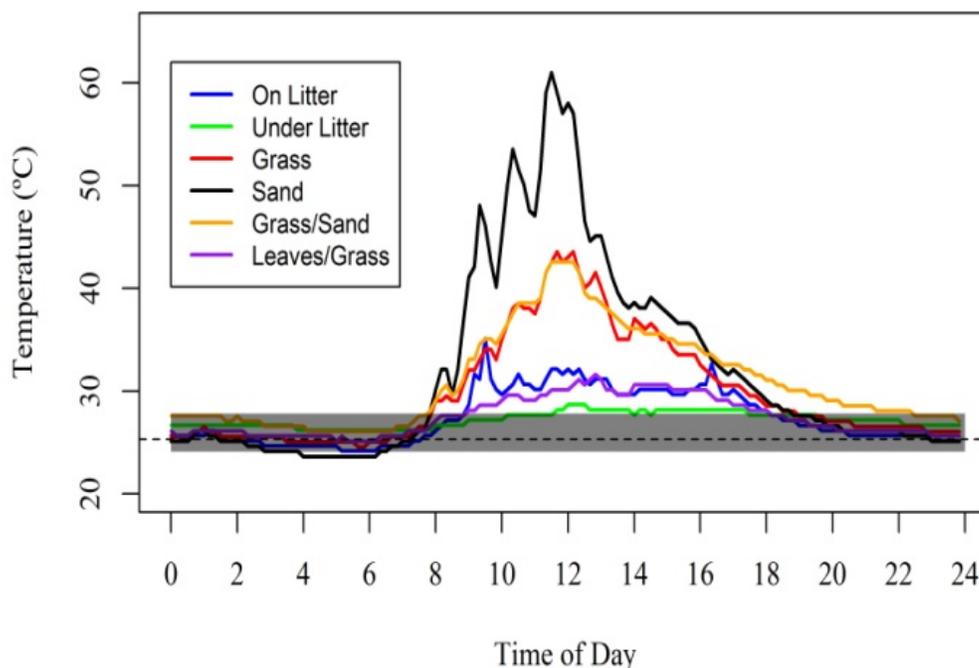


FIGURE 7. Thermal environments available to *Sphaerodactylus macrolepis* on and in the leaf litter at site 2 and in ecologically relevant microhabitats along the transect throughout the day on 17 October 2013. Data were gathered using iButtons. The dotted line represents the mean preferred body temperature and the gray bar the central 50% of preferred temperatures as measured in the lab.

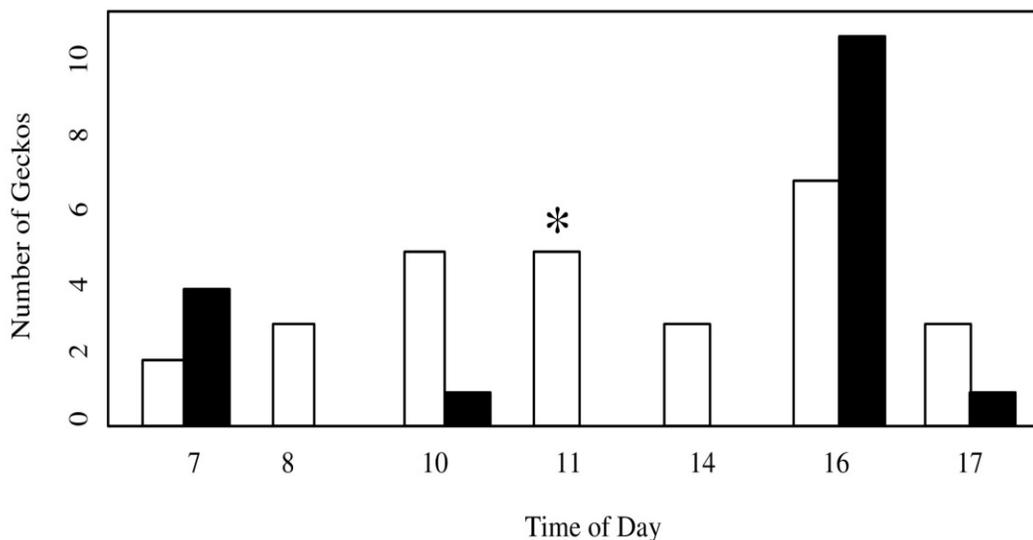


FIGURE 8. Numbers of geckos found along the transect throughout the day on 15 October 2013. White bars represent adults and black bars represent juveniles. A significant difference ( $P = 0.025$ ) between adults and juveniles at 1100 is denoted by the asterisk (\*).

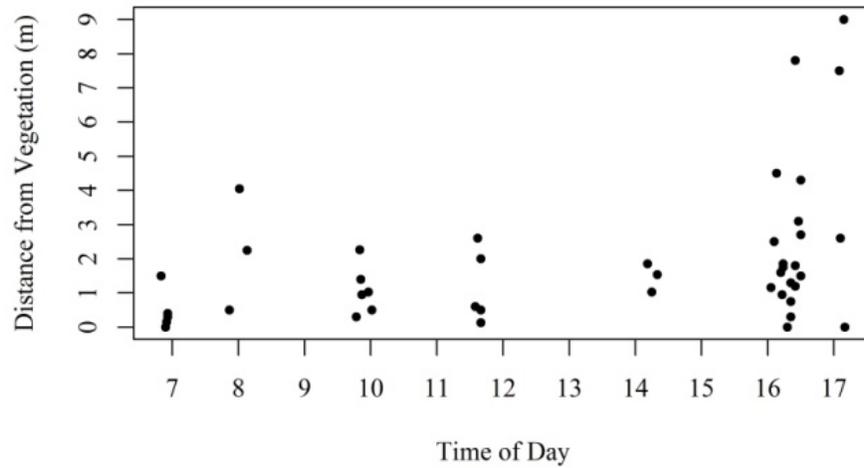


FIGURE 9. Distances of geckos along the transect from the nearest point of shaded forest cover on 15 October 2013.

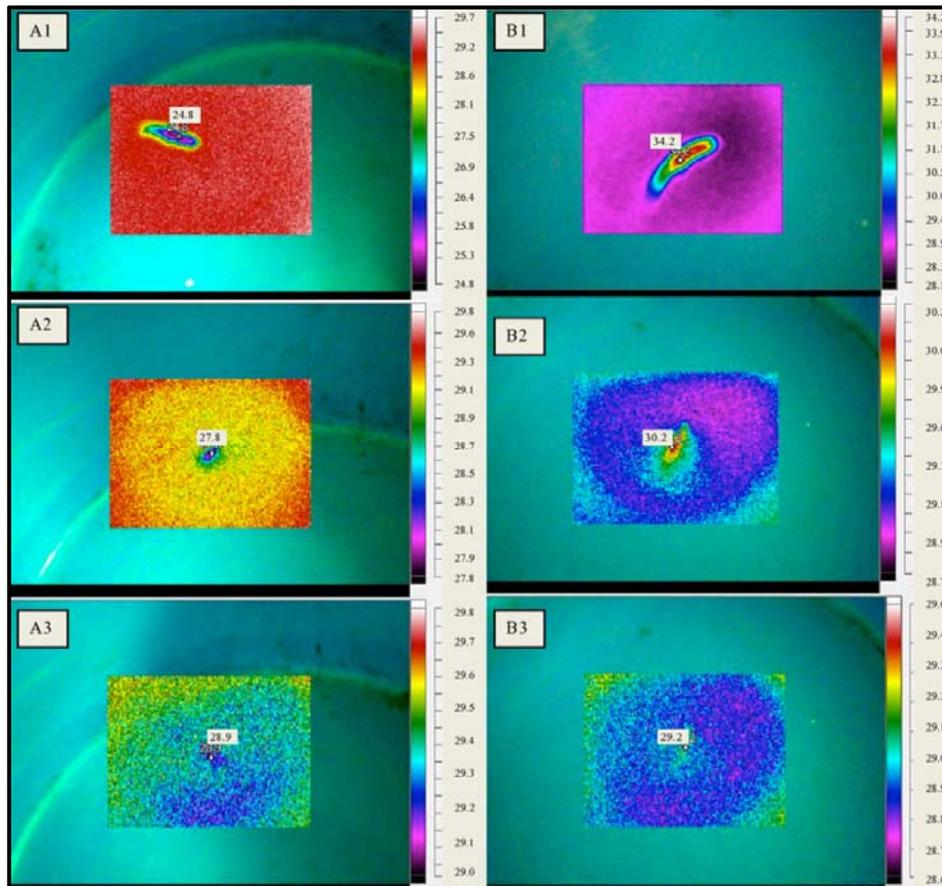


FIGURE 10. Thermal images of heating and cooling trials in a large plastic arena. Each series shows a thermal image from the beginning, middle, and end of each trial. A digital marker is placed over the image of the gecko and the body temperature (°C) is indicated. Series (A): cooling trials. Series (B): warming trials. The background color appears to change because the color range represents temperatures relative to the average temperature of the focal object, with red being warmer and purple being cooler.

However, we also found individuals ranging away from apparently critical microhabitats into an exposed grassy area, but largely before sunrise, after rain, or during cloudy periods. This was unexpected as grass was deemed unsuitable habitat for *S. nicholsi* (López-Ortiz and Lewis 2004) and *S. lewisi* (Meier and Noble

1990), and we could find no previous records of *Sphaerodactylus* active in open grassy fields. Although visual surveys of small, fast, and secretive geckos are unlikely to generate conclusive data and might be biased against smaller juveniles, our observations raise some interesting questions. Why adults primarily used dense grass over a dirt substrate and juveniles were more commonly encountered in sparse grassy cover over a sand substrate is unclear. Because grass on sand remained well outside the preferred temperature for a greater part of the day than dense grass and provided less cover, we doubt that thermal factors or predator avoidance are responsible. However, humidity in grass on sand was significantly higher than in dense grass, and we speculate that humidity might be more critical to the survival of juveniles than an optimal thermal environment. Alternatively, adults might exclude juveniles from more suitable microhabitats, as described for *Anolis aeneus* by Stamps (1990).

Many *Sphaerodactylus* geckos exhibit diurnal activity patterns (e.g., *S. becki*, Powell 1999; *S. nicholsi*, López-Ortiz and Lewis 2004; *S. kirbyi*, Bentz et al. 2011), although Nava et al. (2001) indicated that *S. parvus* activity on Anguilla peaked between 1900 and 2100. The round or oval pupils found in all geckos in the genus *Sphaerodactylus* suggest that they evolved to be primarily diurnal (Röll 2001). In our study sites, we saw no *S. macrolepis* on top of the leaf litter during the day unless the litter was disturbed; however, geckos were in the field along the transect during the day when it was cloudy, after a rain, or in well-shaded areas. The small increase in both numbers of geckos (particularly juveniles) in the grass and their distance from the forest edge during the morning at 0700–0800 and a larger increase in the evening at 1600 are suggestive of crepuscular peaks in activity. These increases in activity correspond more closely with environmental temperatures approaching the preferred temperature than with humidity levels rising to those in the microhabitat under the leaf litter. We did not collect data before sunrise or after dark, so we cannot say whether activity continued into or through the night, but these geckos appear to adjust their activity patterns to take advantage of times when environmental temperatures are closest to the preferred temperature.

Not surprisingly, juveniles gained heat significantly more quickly than adults, but differences in cooling rates were not significant. The difference between heating and cooling rates was not significant for either adults or juveniles, and neither was significantly affected by SVL. These results correspond with those of Fraser and Grigg (1984), who suggested that heating and cooling rates are unimportant to thermoregulation in small lizards because they are unable to control them physiologically like larger ectotherms. Although unable to control heating and cooling rates, the capacity to heat and cool quickly

allows small ectotherms to opportunistically exploit limited optimal environmental temperatures by means of rapid heat exchanges (Fraser and Grigg 1984).

Due to small size and secretive habits, our knowledge of the thermal biology of sphaerodactyls lags far behind that of many other ectotherms. This study confirms assumptions that these diminutive geckos conform rapidly to temperatures of the microhabitat, gain and lose heat quickly, and apparently exploit microhabitats that provide optimal temperatures and tolerable humidity levels at least during some periods. It does, however, raise additional questions regarding how small ectotherms deal with environmental temperatures that frequently exceed apparent optima and what thermal limits can be exceeded when foraging in presumably inhospitable microhabitats. These questions become increasingly important when we consider that global changes in climate are likely to exacerbate the apparent discrepancies between preferred and available temperatures (e.g., Huey et al. 2012). Consequently, we need to explore the nature of performance curves in sphaerodactyls, how changes in temperature affect physiological function, and how available environmental temperatures and relative humidity affect their distributions in nature and activity periods throughout the year.

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