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Thermal Biology and Temperature Selection in Juvenile Lizards of Co-occurring Native and Introduced *Anolis* Species

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ABSTRACT.—**Microhabitat selection is critical to thermoregulation in ectotherms, particularly in small-bodied organisms for which low thermal inertia can impose rapid acquisition of thermal equilibrium with the environment. Although thermal microhabitat selection is often included in studies of niche partitioning among lizard species these investigations typically address only adult thermoregulation and, therefore, potentially neglect age classes in which thermal microhabitat selection could be especially consequential. We measured thermal time constants for juveniles of the lizard *Anolis carolinensis* and compared thermal microhabitat selection of this species with that of an invasive co-occurring congener, *Anolis sagrei*. In keeping with the exceptionally low mass of these lizards, heating and cooling rates were found to be extremely high and more similar to those of some insects than to other terrestrial vertebrates. On laboratory thermal gradients juvenile *A. carolinensis* tended to select warmer temperatures than *A. sagrei*, a pattern that is opposite to that observed for adults of these species. Because the rate of core temperature change was found to be an order of magnitude higher in juveniles than in adults and because the interspecific pattern of temperature selection is categorically different, these results suggest that investigation of juvenile anole thermoregulation could be of particular importance in developing an accurate characterization of resource partitioning among these model species.**

In ectotherms, temperature is a principal quantity linking whole animal biological functioning and the environment and, therefore, has been a preeminent concern in ecology (Angilletta, 2009). Heat exchange governs behavioral, physiological, and chemical processes connected to resource acquisition (Beaupre et al., 1993; Belliure et al.; 1996; Ayers and Shine, 1997), growth (Avery, 1984), development (Bull, 1980; Georges et al., 2005), performance (Bennett, 1990; Angilletta et al., 2002), and ultimately survival and reproduction (Dawson, 1975; Spotila and Standora, 1985). In some cases, environmental temperature appears to be a primary direct determinant of animal movement, habitat selection, and territory establishment (Kearney, 2002; Kearney et al., 2003; Downes and Bauwens, 2004). Additionally, via indirect effects arising through its influence on sympatric species, environmental temperature can mediate a large portion of an animal's ecological interactions. Environmental temperature, therefore, serves as a major axis defining the fundamental multidimensional niche (Hutchinson, 1957; Magnuson et al., 1979).

Caribbean lizards of the genus *Anolis* have been studied in regard to ecological differentiation and multidimensional niche partitioning (Roughgarden, 1995; Losos, 2009). This work has resulted in the classic conceptualization of *Anolis* species recurrently evolving toward occupancy of a distinct set of niches (Losos et al., 2003), each associated with a specific ecomorph, or suite of morphological and ecological characteristics (Williams, 1983). Sympatric *Anolis* appear to partition resources predominantly along only three axes: prey size, structural habitat, and thermal environment (Schoener, 1974). In general, optimal range of body temperatures and precision of thermoregulation varies according to season, species, sex, reproductive status, and age (Huey and Pianka, 1977; Patterson and Davies, 1978; Van Damme et al., 1986; Ming-Chung and Hutchison, 1994; Diaz et al., 2006). Most studies of niche partitioning among anoles, and particularly those regarding thermal habitat, however, have focused exclusively on adults (Hertz, 1992; Jenssen et al., 1996; Huey and Webster, 1976). Because body size is expected to have major effects on heat flux with the environment (Stevenson, 1985), thermoregulation in other age classes could differ substantially from that described in current characterizations of *Anolis* ecology and niche partitioning.

In this study, we examined heat flux in juvenile anoles and compared thermal microhabitat selection in juvenile *Anolis carolinensis* and *Anolis sagrei*. Since its introduction to the southeastern United States in the 1940s (Lee 1985), the Cuban Brown Anole, *A. sagrei*, has expanded its range steadily into that of its native congener, the Green Anole, *A. carolinensis* (Campbell, 1996, Turnbough, 2006), presenting an excellent opportunity for direct investigation of the processes that shape anole communities. The similarly sized, common, and abundant *A. carolinensis* and *A. sagrei* are characterized as occupying substantially overlapping structural habitat niches (Williams, 1969). Therefore, the degree to which these formerly allopatric and potentially competing congeners differ in the full fundamental niche has become a question critical to an understanding of their ongoing interaction. Tested on laboratory thermal gradients, adult *A. carolinensis* select body temperatures between 28°C and 36°C with a mean near 31°C (Licht, 1968; Brown and Griffin, 2005). Field body temperatures for this species can average somewhat higher and overlap with those recorded for *A. sagrei* (Lister, 1976). However, adult *A. sagrei* occupy the most open, insolated habitats and are observed to maintain body temperatures higher than those of sympatric congeners with mean selected temperatures as high as 33°C (Lister, 1976). Because thermoregulatory behavior in the juvenile life stage of these model species has not been studied previously, our goals were (1) to quantify heat flux (heating and cooling) relative to body mass in extremely small-bodied lizards, (2) to compare thermal preference of *A. carolinensis* and *A. sagrei* juveniles, and (3) to contrast the results of these investigations with those for adult *A. carolinensis* and *A. sagrei* in the context of the abiotic niche and interspecific resource partitioning.

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MATERIALS AND METHODS

Collection and Maintenance of Study Subjects.—Juvenile anoles were obtained from eggs hatched in the laboratory. Adult reproductive female *A. carolinensis* and *A. sagrei* were collected in Jacksonville, Duval County, Florida in June 2005. In July 2005, additional adult female *A. carolinensis* were collected by a commercial supplier (Candy's Quality Reptiles) from a single population in LaPlace, Saint John the Baptist Parish, Louisiana. Adult anoles were housed individually at the University of Tennessee, Knoxville, in screen-topped 3.8-L glass enclosures containing wooden dowels for perching, large leaves for cover, and a calcium carbonate sand substrate (Zoo Med Vita-Sand) of approximately 3 cm depth. Light was provided in all enclosures by UVB full spectrum (Reptisun 5.0) and cool white 40-W fluorescent bulbs on a 14 : 10 h light : dark cycle. Temperature in the enclosures ranged from 22°C during the night to 27–31°C during the day. Anoles were misted with water at least twice daily and fed vitamin-dusted crickets ad libitum. Each adult anole was housed in the laboratory for 4–10 weeks. Female anoles retain sperm and produce viable eggs throughout a breeding season when housed in isolation following mating. Every two days, the substrate of each enclosure was thoroughly searched for eggs. Eggs visible on the surface between searches were immediately removed from the enclosure for incubation. All eggs were incubated at 30°C in sealed 250-mL, opaque, plastic containers in a mixture of 20 g vermiculite and 20 mL water.

Prior to testing, juveniles were housed individually in screen-topped 10.6-L glass enclosures containing wooden dowels for perching and sphagnum moss for cover. Housing enclosures for juveniles received UVB full spectrum and cool white fluorescent illumination on a 12 : 12 h light : dark cycle. Temperatures in enclosures followed a diel cycle, with daily highs of 32–34°C in light and 28–30°C in shade and nightly lows of 23–25°C. Juvenile enclosures were misted with water several times daily, and juveniles were provided with an ad libidum supply of flightless fruit flies and pinhead crickets. No food was available to juveniles in the 12 h prior to testing of thermal microhabitat selection.

Measurement and Analysis of Thermal Time Constants.—Heating and cooling curves following step transfer of juvenile *A. carolinensis* between differing thermal environments were inspected to determine the specific temporal relationship between core body and environmental temperatures and to inform subsequent examination of environmental temperature selection. Both a cooling and a heating curve were recorded for each of 17 anoles (age range = 1–24 days; mass range = 0.247–0.741 g) obtained in the laboratory from Louisiana females. Because of the prohibitive difficulty in accurately and humanely measuring core body temperature in live lizards of the size examined in this study, cooling and heating were measured for animals freshly euthanized by isoflurane inhalation. Each anole was equilibrated to an initial core body temperature of 28°C and then transferred to a substrate in a temperature gradient chamber of either 18°C or 38°C (for details of thermal gradient chamber construction and temperature gradient regulation, see Goodman and Walguarnery, 2007). Core body temperature was recorded every 10 sec until an apparent point of equilibrium was obtained using a single-channel digital microprocessor thermometer (Omega HH23, OMEGA Engineering, Inc, Stamford, CT) attached to a thermocouple probe inserted into the cloaca.

Thermal time constants were determined from the heating and cooling curves. A thermal time constant is the time over which a body progresses through $(1 - 1/e) \approx -63\%$ of the difference between its starting temperature and its equilibrium temperature under the conditions into which the body has been transferred. The thermal time constant is invariant with size of the temperature step and, therefore, is more useful for comparative purposes than are other metrics of the rate of temperature change. We determined thermal time constants and calculated equilibrium body temperatures simultaneously according to the iterative curve-straightening approach of Bakken (1976b). Time constants obtained from heating and cooling curves were compared and regressed against body mass to determine the relationship between body size and the rate at which equilibrium is attained. These analyses were conducted in the statistical computing environment R (R Development Core Team 2005).

Measurement and Analysis of Selected Thermal Microhabitats.—Four thermal gradient chambers were used to test anole selection of thermal microhabitat. These chambers allowed anoles free, undisturbed movement over a 100-cm linear thermal gradient (18 to 46°C) and permitted simultaneous observation of anole position and substrate temperature. For each temperature preference trial, a single anole (age range: 8–13 days) was placed haphazardly within one randomly selected temperature gradient chamber between 1030 and 1100 h local time and allowed to acclimate for one half hour. Following the acclimation period, an observation was made of the anole's position along the gradient and the temperature at that point at every half hour for four hours. During trials, the temperature gradient chamber was uniformly and diffusely illuminated by 40-W overhead florescent lamps, and ambient laboratory temperature was maintained between 25.5°C and 26.5°C. Lizards were each tested once for thermal preference, and no more than one juvenile from each mother was included in this study to prevent influence of any potential maternal effects.

Temperature selection by each species was quantified according to mean selected temperature and the lower and upper limits of the interquartile range (IQR) of selected temperatures. The IQR for an individual was defined as the difference between the closest two observations demarcating at least the middle 50% of observations for that individual. *T*-tests were used to examine differences between the two species in these metrics of thermoregulation. Data normality and equality of variances between groups were verified prior to application of *t*-tests.

A study of juvenile *A. carolinensis* from the same laboratory and time period as this study showed no effect of sex on temperature selection in that species (Goodman and Walguarnery, 2007). Accordingly, and because *A. sagrei* cannot be reliably sexed as juveniles, sex was not included in any analysis in the current study. To examine any possible effect of body mass on temperature preference, mean selected temperatures were regressed on individual mass to test for a linear relationship with body size. Analysis of selected thermal microhabitats was conducted in NCSS (2001).

RESULTS

Thermal time constants calculated for juvenile anoles were inversely proportional to mass and ranged from approximately 27 to 109 sec. Regressions of log time constant on log mass were not significantly different for heating and cooling curves ($P = 0.694$, Fig. 1).

TABLE 1. Mean (°C), standard error (°C), and sample size for the mean selected temperature and interquartile range limits selected temperatures of juvenile *Anolis carolinensis* and *Anolis sagrei* tested in a thermal gradient. Results of *t*-tests comparing means of the metrics are also presented.

	Anolis carolinensis			*Anolis sagrei*			*t*-test	
	Mean	SE	*N*	Mean	SE	*N*	*t*	*P*
Mean	29.66	0.63	26	27.61	0.79	21	2.07	0.044
Upper limit IQR	32.55	0.69	24	30.11	1.09	21	1.94	0.059
Lower limit IQR	27.66	0.88	24	24.84	0.87	21	2.27	0.028

The mean selected temperature and IQR lower limit were higher in *A. carolinensis* than those in *A. sagrei* (Table 1, Fig. 2). The IQR upper limit also tended to be higher in *A. carolinensis*, although only marginal statistical significance was observed for this difference between the two species ($P = 0.059$).

The regression of individual mean selected temperature on body mass was not significant for either species (*A. carolinensis*, $P = 0.308$; *A. sagrei*, $P = 0.296$).

DISCUSSION

According to our heating and cooling curve experiments, juvenile anoles can change core body temperature according to time constants of less than 30 sec. To our knowledge, these lizards are the smallest for which rates of heat flux have been examined in the laboratory, and the observed cooling and heating rates are among the lowest reported for vertebrates. Because heat flux in lizards is typically examined in adults, the body mass of subjects in similar studies is generally two to four orders of magnitude greater than that of the animals in this study. Study of thermal biology in other vertebrate ectotherms of comparable size to juveniles examined in this study is extremely limited, but sub-adult African Reed Frogs (*Hyperolius viridiflavus*) of masses as low as 0.35 g have been shown to have thermal time constants of 29 ± 9 sec in moving air (Kobelt and Linsenmair, 1995). Thermal time constants for ectotherms of body masses equivalent to those of juvenile anoles are actually reported more frequently in studies of insect thermal biology, although even these exceed values determined in the present study. For example, dragonflies with body masses within this range have been found to change temperature in air according to time constants ≥ 60 sec (May 1976), and hoverflies of 0.15–0.20 g exhibit thermal time constants ≥ 85 sec (Bressin and Willmer, 2000). These disparities in time constants highlight the underlying complexity of biophysical interactions affecting heat flux and suggest that extrapolations across taxa should be made with caution.

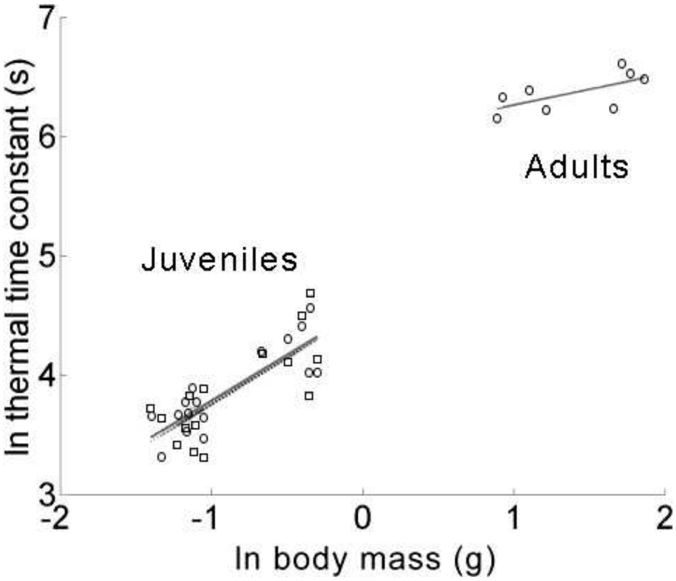

FIG. 1. Relationships between thermal time constant and body mass for juvenile and adult *Anolis carolinensis*. Observations for heating curves are shown as circles with fitted regressions as solid lines. Observations for cooling are shown as squares with the fitted regression as a dashed line. Adult heating data are from Claussen and Art (1981).

Although heat capacitance is a constant property of an animal, both the overall conductance and the operative environmental temperature are properties arising from the interaction of the animal and a specific environment. Convective heat exchange is affected by wind speed, and conduction is affected by the composition and surface of the substrate (Bakken, 1976a). Relative to the exclusively radiative and convective heating in the typical heliothermy assumed of basking lizards, thigmothermy (acquisition of heat from substrates) has been shown to lead to higher rates of heating in small lizards, presumably attributable to the combined effects of rapid direct conduction through the substrate and radiative heating from the warmed air of the boundary layer in contact with the substrate (Bakken, 1989; Belliure and Carrascal, 2002). The typical body proportions and postures of terrestrial vertebrate ectotherms, including reptiles and amphibians, place a large portion of the body surface in contact with the substrate and, therefore, in a role of conductive heat transfer. Indeed, during our temperature selection experiments, anoles rested with the entire venter in contact with the substrate except when moving between positions on the thermal gradient. The resultant close connection between core body temperature and substrate temperature, as well as the extremely rapid convergence of these temperatures on our experimental gradients, both

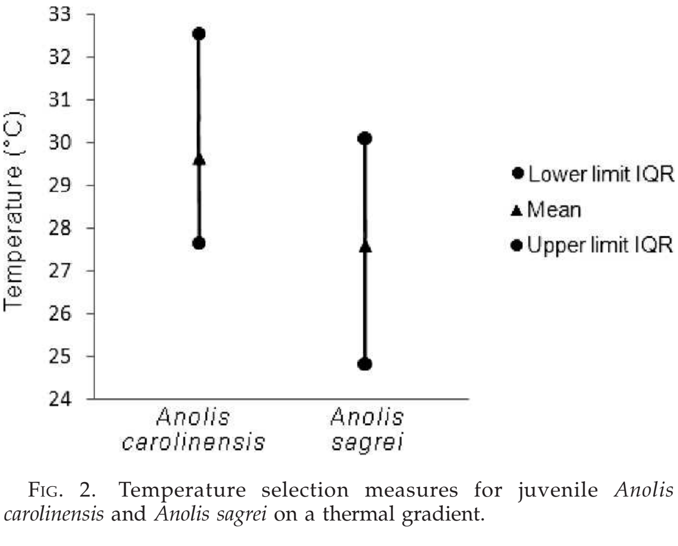

FIG. 2. Temperature selection measures for juvenile *Anolis carolinensis* and *Anolis sagrei* on a thermal gradient.

validates our use of selected substrate temperature as a proxy for selected body temperature in juvenile lizards and demonstrates the potentially critical importance of microhabitat selection to these animals.

Consistent relationships between thermal time constants and body mass of ectotherms have been observed from regressions in previous studies (Claussen and Art, 1981). The simplest effective models explaining these relationships consider relative rates of heat transfer at the surface and within the body as well as the scaling of various dimensions with mass. For small animals in air, these models simplify to a proportional relationship dependent on a length measurement (the thickness of the layer separating the surface of the animal and its isothermal core); therefore, time constants are expected to scale approximately as mass$^{1/3}$ (Grigg et al., 1979). For animals in water, heat exchange at the surface is much greater than for animals in air; surface temperature approximates ambient temperature; and thermal time constants scale according to the allometric relationship between surface area and mass. Based on measurements for several species across greater than three orders of magnitude in body mass, Grigg et al. (1979) observed an exponent of 0.69 relating surface area to mass in lizards. Log–log regression of heating time constants on body mass for our data on juvenile anoles yielded an exponent of approximately 0.77. This regression is much closer to that predicted for heating in water than for heating in air (Grigg et al., 1979) and is significantly different from that describing the relationship in adult anoles ($t = 4.044$, df $= 15$, $P = 0.001$). We take this result as an indication of the predominance of substrate conduction rather than heat transfer to air in the observed overall heat flux in these very small lizards and an indication of the importance of examining thermal interactions across both differing environmental conditions and age classes in describing a species' thermal biology.

Differences between thermal biology of *Anolis* species were apparent from comparison of temperatures selected by juvenile anoles on a laboratory gradient, but differences between mean temperatures selected by *A. carolinensis* and *A. sagrei* were in the opposite direction of those in adults of these species. Adults of *A. carolinensis* tend to select cooler temperatures than those of *A. sagrei* (Licht, 1968; Lister, 1976; Brown and Griffin, 2005), whereas juveniles of *A. carolinensis* tend to select warmer temperatures than those of *A. sagrei*. Mean selected temperature differed by about 2°C between species. This difference in selected temperature is of similar magnitude to that among adult lizards concluded to partition thermal resources in other studies (Vitt and de Carvalho, 1995; Grover, 1996). However, the overlap between species along the temperature gradient (Fig. 2) suggests that separation in fundamental thermal niche is less than complete and that competition might nevertheless occur over access to microhabitats of particular thermal characteristics.

Hertz (1992) suggested that the ability of two species to partition thermal resources would depend not only on the difference between the species in preferred body temperature but also on the scale of variation in the spatial distribution of thermal microhabitats. For species to partition habitat, thermal heterogeneity of the habitat would have to be coarse-grained relative to territory size (i.e., territories would have to differ in mean operative environmental temperature rather than encompassing similar arrays of environmental temperatures and, therefore, similar thermoregulatory opportunities). Patterns of resource heterogeneity and partitioning have been documented among some anoles (Rand, 1964). However, Hertz (1992) concluded that such patterns would not permit thermal resource partitioning in other ecologically similar anoles because (1) spatial heterogeneity in thermal resources at the scale of territories was low and (2) observed interspecific differences in mean body temperature were no larger than seasonal differences in mean body temperature within species. Consideration of these points suggests that juvenile anoles would be far more likely than adults to partition thermal resources because the thermal heterogeneity of the habitat as encountered by juveniles would be substantially more coarse-grained. Anoles increase in size (mass) by an order of magnitude from hatching to adulthood, and as juveniles, anoles use only a fraction of the total habitat used by adults (Schoener, 1968; Jenssen et al., 1998). Total temporal heterogeneity of thermal resources would also be lower in juveniles because this age class represents only a fraction of the entire life of the animal. Interspecific differences among juvenile anoles in thermal resource use, relative to intraspecific differences, should be proportionally greater than these differences among adults. Therefore, characterization of the multidimensional niche based only on observation of adult anoles could lead to potentially erroneous conclusions concerning resource partitioning in other age classes. Because acquisition of resources during early life stages can have compounding effects on growth and resource acquisition in later life stages, understanding juvenile habitat preferences could be of particular importance in accurately determining patterns of overall resource partitioning and competition among species.

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Erratum

In the article, "Thermal Biology and Temperature Selection in Juvenile Lizards of Co-occurring Native and Introduced *Anolis* Species," by Justin W. Walguarnery, Rachel M. Goodman, and Arthur C. Echternacht, which appeared in Vol. 46, No. 4, on pages 620–624 of the *Journal of Herpetology*, there was an error in the first sentence of the Results section. The sentence stated: "Thermal time constants calculated for juvenile anoles were inversely proportional to mass and ranged from approximately 27 to 109 sec." It should have stated: "Thermal time constants calculated for juvenile anoles were proportional to mass and ranged from approximately 27 to 109 sec."