

Behavioural, thermal, and metabolic characteristics of a wintering lizard (*Anolis carolinensis*) from South Carolina

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Summary

1. *Anolis carolinensis*, the most northerly distributed member of its neotropical genus, does not hibernate, but facultatively basks during days with direct sunlight throughout the December to March period.
2. Both sexes were primarily inactive (92% of emerged time), infrequently foraging (6.4%), interacting socially (1.3%), or responding to predator threats (<0.1%).
3. Because subjects infrequently moved (averaging 2 cmh⁻¹), apparent thermoregulatory behaviour (i.e. sun/shade shuttling) was rarely observed.
4. Body (T_b) and concurrent air (T_a) temperature relationships for emerged lizards were: maximum T_b s range of 33–34 °C, a mean T_b of 23 °C, and a mean $T_b - T_a$ differential of 2.4 °C (ranging up to 15 °C).
5. Several criteria characterized winter *A. carolinensis* as being passive, thermal generalists.
6. Mean monthly oxygen uptake for wintering *A. carolinensis* was estimated at 0.924 (December), 0.686 (January), 0.884 (February), and 1.118 (March) $\text{ml g}^{-1} \text{day}^{-1}$.
7. The total estimated energy expenditure for the four months by the average male (3.8 g body mass) and female (2.9 g body mass) was 1.99 and 1.52 kcal, respectively, which is equivalent to 0.21 and 0.16 g of lipid metabolized, respectively ($\approx 6\%$ of body mass).
8. Compared to metabolic rates at the species' 32–35 °C preferred T_b range, the 23 °C average T_b of emerged lizards represented a 60% reduction in energy expenditure. We speculate that the observed basking T_b s reflect an adaptive trade-off between non-basking T_b s for minimum metabolic costs and optimally high T_b s to facilitate physiological processes (e.g. gonadal recrudescence), but at a threat to lipid reserves.

Key-words: Energetics, seasonality, social behaviour, thermal regulation, time-budget profile

Functional Ecology (1996) **10**, 201–209

Introduction

The green anole (*Anolis carolinensis* Voigt), the only anoline lizard endemic to the United States, has an unusual distribution. First, *A. carolinensis* occupies the highest latitude ($\approx 36^\circ$) for its large (>250 spp.) neotropical genus (Williams 1969), being found as far north as Tennessee (Conant 1975). Second, it has a very broad distribution, covering the southeastern United States as far west as Texas. Thus, *A. carolinensis*

populations experience a wide range of photoperiods and air temperatures, both annually at a given locality as well as geographically between localities. In response to its seasonal and geographic variation in habitats, the species exhibits interpopulational variability in life-history characteristics, particularly along latitudinal gradients (Michaud & Echternacht 1995), genotypic clines (Wilson & Echternacht 1987), subspecific differentiation (Christman 1980; Wade, Echternacht & McCracken 1983; Wilson & Echternacht 1990), and phenotypic plasticity (Michaud 1990).

With respect to the more temperate populations of *A. carolinensis*, winter conditions impose significant restrictions on an ectotherm's behaviour and energetics. Depending on environmental severity, one would expect a species to respond to winter by either: (1) becoming dormant or (2) maintaining some level

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syringe fitted with a stopcock ('pre-oxygen' sample). The pump was then shut off, the chamber was sealed, and the subject allowed to respire for approximately 50 min. A 10 ml air sample was then taken from the chamber by a syringe with a stopcock ('post-oxygen' sample). For subject replications, the chamber was unsealed, the pump restarted to flush the chamber and re-establish an atmosphere of dry, CO₂-free air, then the chamber resealed for another reading. The pre- and post-oxygen syringe samples were run through the oxygen analyser with a syringe pump (Razal, Model AE; Razal Scientific Instruments); oxygen consumed was the difference between the two samples. Ambient temperature, thermostatically controlled by the metabolic chamber, and barometric pressure were recorded from a mercury-filled thermometer and barometer (Princo, Model 453; Princo Instruments). Metabolic rate was calculated with the following formula:

$$V_{O_2} \text{ (ml g}^{-1} \text{ h)} = (\text{vol} \times \text{STP} \times \text{oxy}) / (\text{lizard mass} \times \text{respiration time}),$$

where $\text{vol} = (\text{chamber volume} - \text{lizard volume})$, $\text{STP} = (\text{atmospheric pressure}/760) \times (273/\text{air temperature} + 273)$, and $\text{oxy} = (\text{pre-oxygen sample} - \text{post-oxygen sample}) / (1 - \text{post-oxygen sample})$.

We estimated a mean daily energy expenditure of wintering adults (December–March). Since metabolic rate is primarily temperature dependent in ectotherms, lizards were assumed to be at air temperature (non-basking) during non-daylight hours (19:00–07:00 h) and during daylight hours for overcast days (07:00–19:00 h). During daylight hours when direct sunlight was partially or fully available for basking, we empirically derived an estimate of the mean T_b above that of concurrent T_a from our thermoregulation data. A mean daily energy expenditure was then generated using: (1) NOAA data for actual hourly cloud cover and hourly air temperatures during December–March 1992, (2) a T_b/V_{O_2} curve extrapolated from our metabolic rate data, and (3) activity estimates from our behavioural profile data; these values were used in the following formula for mean daily energy expenditure:

$$\frac{\sum_{d=1}^{122} \sum_{h=1}^{24} (V_{hd} + V_{hd,2.4})}{122},$$

where V_{hd} is the metabolic rate during an hour (h) of a day (d) at the air temperature corresponding to T_b during a period when basking did not occur, $V_{hd,2.4}$ is the metabolic rate during an hour (h) of a day (d) at the corresponding basking body temperature ($T_b = T_a + 2.4^\circ\text{C}$), summed across each day (d) for 122 days (December–March). To convert metabolic rates among units of O₂ and CO₂, we assumed 4.8 kcal l⁻¹ O₂ (McDonald 1976) in which primarily lipids, but some liver glycogen (Gist 1972), were oxidized;

20.08 J ml O₂⁻¹ and 25.1 J ml CO₂⁻¹ were used as energy equivalents (Congdon & Tinkle 1982).

Results

BEHAVIOURAL PROFILE

To ensure that the lizard behaviour was not inhibited by low T_b , observations were conducted between 10:00–15:00 h (mean start time of 12:30 h) in sunny weather (mean sun index = 3.4, range 1–4) with mild to warm T_a (mean = 22.2°C, range 12–32°C). No significant differences in the sun index or T_a existed between the 53 male and 30 female records (Kruskal–Wallis tests, χ^2 values 2.47 and 3.33, respectively; $P > 0.05$). During the observation periods, lizards averaged 66.8% of their time in the sun, with males and females having similar values (64 and 68%, respectively; Kruskal–Wallis test, $\chi^2 = 0.15$, $P = 0.70$).

Lizards averaged 92.2% of their emergence time at rest (i.e. stationary), with foraging behaviour (6.4%) being the second most observed category (Fig. 1). The remaining categories of recorded behaviour were agonistic interactions, courtship, and predator avoidance, averaging 1.1, 0.2, and <0.1% of the observation periods, respectively. No behaviours showed a significant difference between males and females (Kruskal–Wallis tests, χ^2 values were in the range 0.08–1.74, P levels were in the range 0.78–0.19).

Because lizards were mostly stationary, the hourly rate of distance moved was extremely low. Males moved an average of 2.53 cm h⁻¹ which was significantly further than the 1.28 cm h⁻¹ mean for females (Kruskal–Wallis test, $\chi^2 = 4.02$, $P = 0.04$). Not surprisingly, Spearman rank tests positively correlated movement with foraging and agonistic activities ($r_s = 0.37$ and 0.32, respectively, $P < 0.004$) and negatively with being stationary ($r_s = -0.39$, $P < 0.001$). No

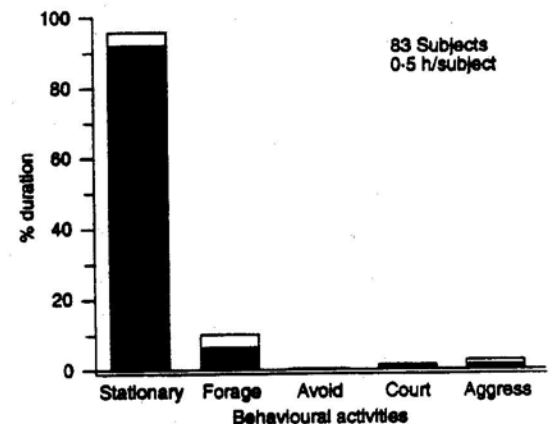


Fig. 1. Mean percentage total duration (black bars) for five behaviours (those being: stationary, foraging, avoiding predators, courting and agonistic interactions) observed during 30-min periods for 83 *Anolis carolinensis* during November–April on the Savannah River Site, Aiken, South Carolina; white bars indicate the magnitude of two standard errors of the mean.

on V_{O_2} ($df = 5, 1, 5$; F values = 24.7, 8.1, and 3.2; P levels = 0.0001, 0.006, and 0.008; respectively).

Mean daily oxygen uptake rates were calculated using the above metabolic, behavioural, and thermal biology data sets. Because lizards fed only rarely and were motionless for more than 90% of their activity period (only moving about 2cmh^{-1}), the resting V_{O_2} for winter *A. carolinensis* was a reasonable estimate of winter field metabolic rates. Field V_{O_2} rates were taken from the V_{O_2}/T_b relationship (Fig. 5), as extrapolated from Fig. 4. To estimate hourly T_b and corresponding V_{O_2} for 'an average lizard', T_a was converted to T_b for each hour of each day (NOAA data, Augusta, GA, December–March, 1992) by the following rules: (1) $T_a = T_b$ if hour were

Table 2. Six-way Spearman correlation (r) and probability level (P) of body temperature (T_b), air temperature (T_a), site temperature (T_s), $T_b - T_a$ differential, hour of day (HR), and sun index (SI) for *Anolis carolinensis* at the Savannah River Site, Aiken, South Carolina, during November–April. All temperatures are $^{\circ}\text{C}$

Variable	T_b	T_a	T_s	$T_b - T_a$	HR	SI
T_b (r)	—	0.84	0.99	0.51	0.01	0.09
(P)		0.001*	0.001*	0.001*	0.89	0.10
T_a (r)		—	0.96	0.03	0.01	-0.07
(P)			0.001*	0.51	0.83	0.19
T_s (r)			—	-0.26	0.10	-0.08
(P)				0.001*	0.16	0.30
$T_b - T_a$ (r)				—	0.01	0.24
(P)					0.96	0.001*
HR (r)					—	-0.07
(P)						0.16
SI (r)						—
(P)						

* Statistically significant ($P < 0.001$).

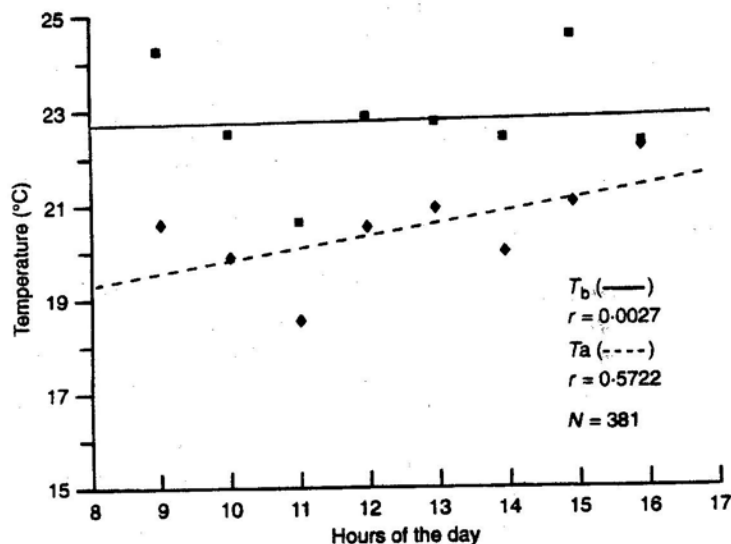


Fig. 3. Linear regressions of body temperature (T_b) (solid line) and corresponding air temperature (T_a) (dashed line) on hour of day measured for 381 *Anolis carolinensis* during partial to full sunlight from November to April on the Savannah River Site, Aiken, South Carolina. The square and diamond symbols indicate mean hourly T_b and T_a , respectively.

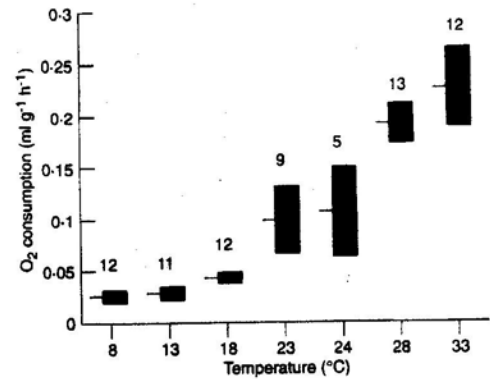


Fig. 4. Mean oxygen uptake for six ambient temperature treatments from 509 determinations using 74 *Anolis carolinensis* during December–January on the Savannah River Site, Aiken, South Carolina. Ends of black bars indicate ± 2 standard errors of the mean (horizontal line).

night time or hour were daylight with 100% cloud cover; or (2) $T_a + 2.4^{\circ}\text{C} = T_b$ if daylight hour had partial or no cloud cover, where 2.4°C was empirically derived as the mean increment above a corresponding T_a because of basking.

The mean hourly oxygen uptake for a wintering adult in 1992 was estimated at $0.026\text{ ml (g h}^{-1}\text{)}$ (SE 0.0004) during the night-time hours of 19:00–06:59 h ($N = 1452$ h) and $0.049\text{ ml (g h}^{-1}\text{)}$ (SE 0.002) during the daylight hours of 07:00–18:59 h ($N = 1452$). Monthly rates varied significantly (Kruskal–Wallis test, $\chi^2 = 17.51$, $df = 3$, $P = 0.0006$) because each month reflected a different combination of photoperiod, ambient temperatures, and cloud cover; monthly daily averages were estimated to be 0.924 (SE 0.026), 0.686 (SE 0.008), 0.884 (SE 0.018), and 1.118 (SE 0.030) $\text{ml O}_2\text{ g}^{-1}\text{ day}^{-1}$ during December, January, February, and March ($N = 31, 29, 31, \text{ and } 31$ days), respectively. January had the lowest mean total daytime O_2 uptake ($0.398\text{ ml g}^{-1}\text{ 12 h}^{-1}$, SE 0.006, $N = 29$), being only 37% more than the night-time estimated value ($0.289\text{ ml g}^{-1}\text{ 12 h}^{-1}$, SE 0.024). At the other extreme, the March day/night differential was 252% (0.801 and $0.318\text{ ml g}^{-1}\text{ 12 h}^{-1}$; SE 0.084 and 0.010, respectively; $N = 31$).

Ambient conditions during the majority of each 24-h period during winter kept lizards at a relatively low T_b , and resulted in a relatively modest daily energy expenditure. Daily T_a for the region (NOAA) during December through March averaged $10.2, 7.9, 10.6, \text{ and } 12.4^{\circ}\text{C}$, respectively. Low metabolic rates ($< 0.05 V_{O_2}$, Fig. 5) were associated with the low T_a s and the non-basking T_b s. The inclusion of basking T_b s into the metabolic profile did not substantially increase the mean estimated energy expended during the winter. Using the mean daily (24 h) oxygen uptake value (0.903 ml g^{-1} , or 4.33 calories) for 121 days (December–March) multiplied by body mass, resulted in 1.99 and 1.52 kcal for the average adult male and female, respectively (equivalent to 0.21 and 0.16 g of lipid metabolism, respectively).

ciated with optimal body temperatures for recrudescence are almost certainly not compensated by food intake. In addition, feeding during the winter may result in mortality from putrefaction of gut contents during prolonged periods of low temperatures (Scott *et al.* 1995). There is also evidence that foraging and predator escape behaviour, where glycolysis-powered sprinting is employed, is depressed in wintering lizards (Gatten, Echternacht & Wilson 1988). Therefore, we propose that wintering *A. carolinensis* of northern populations (e.g. South Carolina and Tennessee) strike a compromise, where basking T_b s are voluntarily restricted to reduce metabolic costs, while still being sufficient to facilitate gonadal recrudescence.

When compared with their summer activity profile (Jenssen *et al.* 1995), wintering *A. carolinensis* do little more than remain stationary and bask (see above, Behaviour Profile, Stationary). Wintering *A. carolinensis* do not hibernate (Gordon 1956), but emerge during warm days and stay close to their refugia (Ragland, Wit & Sellers 1981; Gatten *et al.* 1988; present study). Despite the ability to markedly raise its T_b (e.g. $T_b - T_a$ up to 15 °C), *A. carolinensis* seems to behave like a passive, thermal generalist (*sensu* Hertz, 1974; Huey & Slatkin 1976) which is not 'precisely' regulating its body temperature. Huey & Slatkin (1976) and Huey (1982) offered two criteria for measuring the relative intensity of thermal regulation: (1) the frequency of thermoregulatory behaviour and (2) the relative slope of the linear regression of T_b on T_a . With regard to the first criterion, *A. carolinensis* occupied sunny perches for two thirds of our observation periods, but they also showed almost no perch changes to track moving sunlight patterns. Therefore, there was little evidence that lizards were precisely thermoregulating by shuttling between the available patches of sunlight and shade. The second criterion (T_b/T_a regression slope), if equal to 1, suggests thermal conformity of T_b with ambient conditions (thermal passivity) and, if equal to zero, an independence of T_b from ambient conditions (precise thermoregulation). With a slope of 0.99, our data indicated that the population was frequently passive to ambient temperature conditions. However, these criteria alone can have limitations in interpretation (e.g., Huey 1982; Dreisig 1984). van Damme, Bauwens & Verheyen (1987) found that seasonal effects still might cause a thermoregulating species to generate a T_b/T_a slope near 1; they suggested the *y*-intercept from the T_b/T_a regression as an added criterion, such that the greater the *y* value is from zero, the more evidence for thermoregulation. A *y*-intercept of 2.4 °C for our wintering *A. carolinensis* provides evidence of some thermoregulation as does the consistency of mean hourly T_b s across the activity period (Fig. 3).

To summarize thermoregulatory behaviour within the winter context, *A. carolinensis* was observed to bask. However, the analysis of the sun/shade

shuttling, regression slope, and *y*-intercept criteria indicated a 'thermal passive' characterization (Hertz 1974, 1979; Huey 1982). Lizards were not seen to move far from their winter shelters, thus diminishing their ability to precisely thermoregulate. This reluctance to move, however, should not be viewed as missed opportunities to raise T_b s, but rather as a part of an adaptive compromise. Should wintering anoles precisely thermoregulate to optimize gonogenesis and behavioural activity at T_b s of 32–35 °C, a 2.5-fold metabolic cost would occur over that of the 23 °C mean T_b of our sample of emerged lizards (Fig. 5). With few foraging opportunities and limited lipid reserves, high T_b s would be deleterious.

ENERGETICS

Resting metabolism of *A. carolinensis* has previously been measured at various temperatures (reviewed by Gatten *et al.* 1988). Some of the values from past studies on *A. carolinensis*, with our equivalent measure in parentheses, are as follows: resting metabolism, 0.02 kcal g⁻¹ day⁻¹ at 28 °C (0.022 kcal g⁻¹ h⁻¹) (Dessauer 1953); resting metabolism, 0.028 ml O₂ g⁻¹ h⁻¹ at 10 °C (0.025 ml O₂ g⁻¹ h⁻¹) and 0.219 ml O₂ g⁻¹ h⁻¹ at 30 °C (0.209 ml O₂ g⁻¹ h⁻¹) (Maher & Levedahl 1959); and resting metabolism of cold acclimated (10 °C) subjects, 0.020 ml O₂ g⁻¹ h⁻¹ at 10 °C (0.022 ml O₂ g⁻¹ h⁻¹), 0.063 ml O₂ g⁻¹ h⁻¹ at 20 °C (0.062 ml O₂ g⁻¹ h⁻¹), and 0.182 ml O₂ g⁻¹ h⁻¹ at 30 °C (0.209 ml O₂ g⁻¹ h⁻¹) (Gatten 1985). Concordance of metabolic rates among the various studies, in spite of differences in seasonal and acclimation protocol, is not too surprising; Gatten *et al.* (1988) found that aerobic capacity did not vary with season, and variation among lizards in resting oxygen consumption overlapped broadly among seasons.

In general, the energy expenditure of reptiles is low when compared with endotherms, where the daily metabolic expenditure (mass-corrected energy metabolism) of a free-ranging bird or rodent is 20 to 40 times that of a lizard (Nagy 1983). However, compared with other lizards (Bennett & Dawson 1976), the estimated metabolic cost for wintering *A. carolinensis* was minimal over the 4-month winter season (December–March), and was equivalent to 0.21 g of lipids metabolized for an average adult male (≈6% of body weight).

As a comparison with other anoles, Bennett & Gorman (1979) calculated the resting metabolism of the Caribbean *Anolis bonarensis* at about 0.17 ml O₂ g⁻¹ h⁻¹ at 27 °C (the same as for *A. carolinensis*, Fig. 5), and estimated that a young adult male *A. bonarensis* (similar in mass to our average adult *A. carolinensis*) would expend up to 545 J day⁻¹ if active and 256 J day⁻¹ when at rest. The average energy expenditure for wintering male *A. carolinensis* was 69 J day⁻¹, or 13–27% that of the Caribbean *A. bonarensis*. Andrews & Asata (1977) found the resting metabolism

- Huey, R.B. (1982) Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *Journal of Experimental Biology* **7**, 401–409.
- Huey, R. B. & Slatkin, M. (1976) Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* **51**, 363–384.
- Jenssen, T.A. & Nunez, S.C. (1994) Male and female reproductive cycles of the Jamaican lizard, *Anolis opalinus*. *Copeia* **1994**, 767–780.
- Jenssen, T.A., Greenberg, N. & Hovde, K.A. (1995) Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* **9**, 41–62.
- King, F.W. (1966) *Competition between two south Florida lizards of the genus Anolis*. PhD Dissertation. University of Florida, Coral Gables, FL.
- Licht, P. (1971) Regulation of the annual testis cycle by photoperiod and temperature in the lizard *Anolis carolinensis*. *Ecology* **52**, 240–252.
- Licht, P. (1973) Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* **1973**, 465–472.
- Lister, B.C. & Garcia Aguayo, A. (1992) Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* **61**, 717–733.
- Losos, J.B. (1990a) Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* **60**, 369–388.
- Losos, J.B. (1990b) Concordant evolution of locomotor behavior, display rate and morphology in *Anolis* lizards. *Animal Behavior* **39**, 879–890.
- Maher, M.J. & Levedahl, B.H. (1959) The effect of the thyroid gland on the oxidative metabolism of the lizard, *Anolis carolinensis*. *Journal of Experimental Zoology* **140**, 169–189.
- McDonald, H.S. (1976) Methods for the physiological study of reptiles. *Biology of the Reptilia*, Vol. 5, *Physiology A* (eds C. Gans & W. R. Dawson), pp. 19–126. Academic Press, New York.
- Michaud, E.J. (1990) *Demographic variation of life history traits in the lizard, Anolis carolinensis*. PhD Dissertation. University of Tennessee, Knoxville, TN.
- Michaud, E.J. & Echternacht, A.C. (1995) Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* **29**, 86–97.
- Moermond, T.C. (1979a) The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* **70**, 141–167.
- Moermond, T.C. (1979b) Habitat constraints on the behavior, morphology and community structure of *Anolis* lizards. *Ecology* **60**, 152–164.
- Nagy, K.A. (1983) Ecological energetics. *Lizard Ecology: Studies of a Model Organism* (eds R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 24–54. Harvard University Press, Cambridge, MA.
- NOAA (United States National Oceanic and Atmospheric Administration). (1992) Local Climatological Data, Augusta, Georgia. Ashville, NC.
- Noeske, T.A. & Meier, A.H. (1977) Photoperiodic and thermoperiodic interaction affecting fat stores and reproductive indexes in the male green anole, *Anolis carolinensis*. *Journal of Experimental Zoology* **202**, 97–102.
- Parker, R.B. (1965) *The adaptation of the lizard Sceloporus olivaceus (Smith) to the winters of central Texas*. PhD Dissertation. University Texas, Austin, Texas.
- Pearson, O.P. & Bradford, D.F. (1976) Thermoregulation of lizards and toads at high altitudes in Peru. *Copeia* **1976**, 155–170.
- Pounds, J.A. (1988) Ecomorphology, locomotion and microhabitat structure: patterns in tropical mainland *Anolis* community. *Ecological Monographs* **58**, 299–320.
- Ragland, I.M., Wit, L.C. & Sellers, J.C. (1981) Temperature acclimation in the lizards *Cnemidophorus sexlineatus* and *Anolis carolinensis*. *Comparative Biochemistry and Physiology* **70A**, 33–36.
- SAS Institute. (1985) *SAS User's Guide: Statistics, Version 5*. SAS Institute, Cary, NC.
- Scott, D.E., Fischer, R.U., Congdon, J.C. & Busa, S.A. (1995) Whole body lipid dynamics and reproduction in the eastern cottonmouth, *Agkistrodon piscivorus*. *Herpetologica* **51**, 472–487.
- Siegel, S. (1956) *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Talbot, J.J. (1979) Time budget, niche overlap, inter- and intraspecific aggression in *Anolis humilis* and *A. limifrons* from Costa Rica. *Copeia* **1979**, 472–481.
- Vitt, L.J. (1974) Winter aggregations, size classes and relative tail breaks in the tree lizard, *Urosaurus ornatus* (Sauria: Iguanidae). *Herpetologica* **30**, 182–183.
- Wade, J.K., Echternacht, A. C. & McCracken, G. F. (1983) Genetic variation and similarity in *Anolis carolinensis* (Sauria: Iguanidae). *Copeia* **1983**, 523–529.
- Williams, E.E. (1969) The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quarterly Review of Biology* **44**, 345–389.
- Wilson, M.A. & Echternacht, A.C. (1987) Geographic variation in the critical thermal minimum of the green anole, *Anolis carolinensis* (Sauria: Iguanidae), along a latitudinal gradient. *Comparative Biochemistry and Physiology* **87A**, 757–760.
- Wilson, M. A. & Echternacht, A. C. (1990) A comparison of heat and cold tolerance of two morphs of *Anolis carolinensis* (Iguanidae) from Southern Florida. *Journal of Herpetology* **24**, 330–333.
- Windell, J. T. & Sarokon, J. A. (1976) Rate of gastric evacuation in the lizard, *Anolis carolinensis* (Sauria: Iguanidae). *Herpetologica* **32**, 18–23.
- Workman, S. W. & McLeod, K. W. (1990) Vegetation of the Savannah River Site: major community types. Savannah River Site Natural Environmental Research Park Progr., Department of Energy Publication SRO-NERP-19, 1–137.

Received 4 November 1994; revised 12 June 1995; accepted 20 June 1995