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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

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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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of activity through facultative basking during favourable periods (e.g. Ballinger & Congdon 1981; Congdon, Ballinger & Nagy 1979; Parker 1965; Pearson & Bradford 1976; Vitt 1974). In the first response, winter dormancy carries minimal energetic costs, and would be expected when stored energy reserves and feeding opportunities are limited. In the second response, the energetic penalty for activity during the winter increases with latitude (and elevation) because of the increase in length of the inactive period. Perhaps constrained by primary adaptations of its genus for tropical habitats, *A. carolinensis* appears to be an obligate practitioner of the second response. Thus, wintering *A. carolinensis*, particularly its northern populations, presents an opportunity to examine the behavioural and energetic compensations of a subtropical species at its climatic fringe.

Our study quantifies the behavioural, thermal, and metabolic variables of a northern population of wintering *A. carolinensis*. Where possible, these data are compared with information from other anolines and conspecifics of different populations and seasons.

Materials and methods

STUDY SITE AND SEASONALITY

Data were collected from an *A. carolinensis* population on the Savannah River Site (SRS), approximately 20 km south of Aiken, South Carolina. The site (33.5° latitude, 82° longitude, and 171 m elevation) was situated in a mature oak-pine community (Workman & McLeod 1990). Climatological data (NOAA 1992) taken for Augusta, Georgia (29 km west of our study site) showed an annual rainfall of 107 cm, with the wettest and driest months being July (17.8 cm) and October (1.4 cm), respectively; the average daily air temperature was 17°C, with mean monthly extremes being 28°C (July) and 8°C (January).

We collected behavioural, thermal, and metabolic data for wintering lizards. Statistical comparisons between samples used non-parametric tests (Siegel 1956), and were performed with the SAS (1985) software package. The null hypothesis was rejected at a probability level of $P \leq 0.05$ (or less in the case of multiple correlations). Variables and procedures are as follows.

BEHAVIOURAL PROFILE

During November 1987 to mid-April 1988, focal observations (i.e. continuous observation of an individual; Altmann 1974) were made on each of 30 female and 53 male lizards. The behaviour of each lizard was observed during a 0.5 h observation period from a distance of ≥ 7 m using binoculars when necessary. Data were recorded by hand on preprinted data sheets. Variables recorded were: relative cloud cover ('sun index'), air temperature, time spent in the sun,

frequency of movement, and distance moved. The observation time was partitioned among the following categories: stationary (surveying the immediate habitat and possibly basking without perch-changing movements), foraging (detecting, pursuing, and eating prey), predator avoidance (detecting, moving to cover, and hiding from potential predators), courtship (male–female displaying and/or chasing), and agonistic (males or females chasing and/or displaying at conspecifics). If the subject acted as if it were concentrating its attention on (or avoiding) the observer, the observations were stopped and data discarded. Because direct sunlight and basking affect lizard body temperature and the propensity for activity, we ranked the availability of ambient sunlight during a observation period with a 'sun index', where 1 = overcast, 2 = mostly cloudy, 3 = partly cloudy, and 4 = sunny.

THERMAL BIOLOGY

The cloacal temperatures of 525 lizards were taken between 09:00–16:00 h from November 1987 to April 1988. Subjects were either noosed or caught by hand and their body temperatures measured (within 0.1°C) with a quick reading mercury thermometer (Miller^R; Miller & Weber Inc.). For most body temperature (T_b) data, air (T_a) and site (T_s) temperatures were available from a data logger (Model 21X; Campbell Scientific Inc.), where fixed-site thermocouples recorded T_a (shaded locality 2 m above the ground) and T_s from 12 localities about the collecting area. The 'sun index' variable was also recorded for each T_b observation.

METABOLISM

From December 1987 through January 1988, newly captured lizards were used to make 509 metabolic determinations (31 females and 43 males) at seven ambient temperatures (8, 13, 18, 23, 28, and 33°C). The lizards were collected from the field and acclimated on a standardized 12:12 light/dark photoperiod for 3–10 days before testing (Art & Claussen 1982). Metabolic rates were measured an average of seven times (range of 3–16) at a given temperature; a mean value represented a subject's metabolic rate for that temperature. Individuals were not tested across temperature treatments.

Following the procedures of Gatten (1985), a lizard was acclimatized for 72 h without food and transferred to a darkened plexiglass metabolic chamber approximately 18 times the body volume. During a 2 h pre-reading period, an external pump pulled air through drierite and ascarite (to remove water and CO₂, respectively) and into the subject's metabolic chamber. Simultaneously, an Amtex oxygen analyser (Model S3A/II; Amtex Instruments) received dry, CO₂-free air from outside the chamber at 131 kPa and 10 ml min⁻¹. To initiate a metabolic determination, a 10-ml air sample was taken from the chamber using a

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

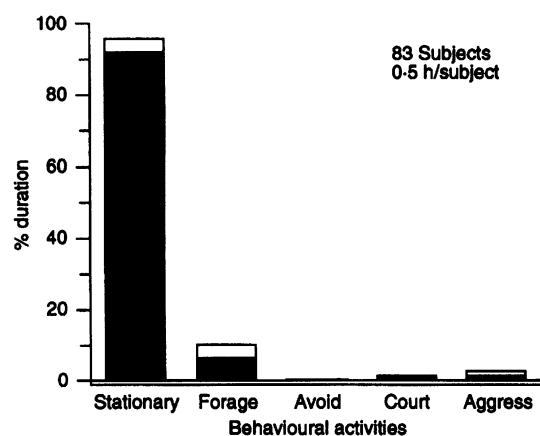


Fig. 1. Mean percentage total duration (black bars) for five behaviours (those being: stationary, foraging, avoiding predators, courting and agonistic interactions) observed during 30-min periods for 83 *Anolis carolinensis* during November–April on the Savannah River Site, Aiken, South Carolina; white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

other significant correlations occurred among variables, including the behaviour events with the environmental variables (i.e. sun index and T_a).

Lizard behaviour may have been influenced by the approach of the breeding season during the latter part of our study period. To determine if lizard behaviours changed with the chronology of the observational records, we divided the observations into November–February (34 subjects) and March–April (49 subjects) periods. Except for distance moved per hour, no significant differences were detected between the two periods for any of the observed behaviours (Kruskal–Wallis tests, $P > 0.05$). For the one significant variable, lizards moved further during the November–February period (mean = $2.66 \pm \text{SE } 0.45 \text{ cm h}^{-1}$) than the March–April period (mean = $1.68 \pm \text{SE } 0.31 \text{ cm h}^{-1}$).

THERMAL BIOLOGY

As long as the sky was not completely overcast, wintering *A. carolinensis* were able to raise their body temperatures (T_b) above air temperatures (T_a) by basking (Table 1). For all observation periods, the

Table 1. Sun index, ranked overcast (1) to full sun (4), and corresponding *Anolis carolinensis* body temperature (T_b), air temperature (T_a), $T_b - T_a$ differential, and selected site temperatures (T_s) during November–April at the Savannah River Site, Aiken, South Carolina. Data are mean, standard error (SE), and sample size (n)

Sun index	T_b (°C) Mean (SE) n	T_a (°C) Mean (SE) n	$T_b - T_a$ (°C) Mean (SE) n	T_s (°C) Mean (SE) n
1	13.9 (1.04) 20	13.1 (0.96) 20	0.8 (0.16) 20	11.7 (0.24) 16
2	23.7 (0.49) 86	22.6 (0.43) 86	1.1 (0.22) 86	22.8 (0.73) 46
3	20.0 (0.56) 65	18.7 (0.45) 65	1.4 (0.31) 65	18.6 (0.51) 38
4	22.1 (0.44) 206	19.4 (0.39) 206	2.7 (0.23) 206	17.6 (0.53) 85
All	22.2 (0.30) 407	19.9 (0.26) 407	2.3 (0.16) 407	18.6 (0.39) 185

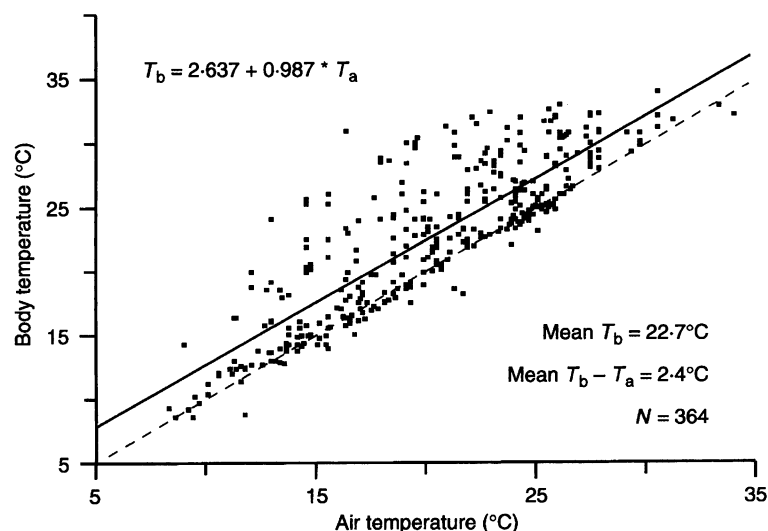


Fig. 2. Body temperature (T_b) regressed on air temperature (T_a) (dashed line) for 364 *Anolis carolinensis* measured on days with partial or full sunlight during November–April on the Savannah River Site, Aiken, South Carolina. Solid line indicates the mean $T_b - T_a$ differential.

mean T_b for winter *A. carolinensis* was 22.7°C , and averaged 2.4°C ($\pm \text{SE } 0.17$) above T_a . These averages appear to reflect active thermoregulation.

Lizards were able to generate $T_b - T_a$ differentials as great as 15°C (Fig. 2). Although the magnitude of $T_b - T_a$ was positively correlated with sun index (Spearman, $r_s = 0.24$, $P < 0.001$; Table 2), a plot of elevated T_b s in Fig. 2 shows that the lizards approached but did not exceed their maximum voluntary T_b of 34°C (Wilson & Echternacht 1990). In addition, T_b and $T_b - T_a$ values were independent of hour of day (Spearman, $r_s = 0.01$, $P = 0.89$ and $r_s = 0.01$, $P = 0.96$, respectively; Table 2), in spite of T_a being correlated with the hour of day (Spearman, $r_s = 0.57$, $P < 0.001$; Table 2). The plot of mean hourly T_b and T_a indicated that 23°C represents the central tendency for lizard body temperatures during each hour of the activity period in spite of rising air temperature across the same time span (Fig. 3).

The effects of sex and season were also examined. No intersexual differences were detected for T_b and T_a for all observations (Kruskal–Wallis tests, $\chi^2 = 1.93$ and 2.39 , $P = 0.166$ and 0.122 , respectively). Neither were there significant intersexual differences within each hourly sample (09:00–16:00 h) for T_b , T_a , or $T_b - T_a$ (Kruskal–Wallis tests, χ^2 values were in the range 3.10 – 0.009 , P levels were in the range 0.08 – 0.98). There was a season effect, however, when comparing data from the three coolest months (December–February) with those from the three warmer months (November and March–April) of our sample. Both T_b and T_a were significantly different across the two subseasonal data sets (Kruskal–Wallis test, $\chi^2 = 58.84$ and 64.32 ; $P = 0.0001$ and 0.0001 , respectively). The mean T_b and T_a for the cool subseason months were 21.0 (SE 0.35) and 18.7°C (SE 0.29), respectively, and for the warmer subseason months were 25.5°C (SE 0.44) and 22.7°C (SE 0.37).

METABOLIC RATE

The rate of resting metabolism (V_{O_2}) showed a significant increase (Kruskal–Wallis test, $df = 5$, $\chi^2 = 61.62$, $P = 0.0001$) over the six ambient temperature treatments (Fig. 4). The temperature groups 8 – 18 , 23 , and 28 – 33°C were significantly different from one another (Tukey's Studentized Range test, $df = 60$, $P < 0.05$). Within each of the six temperature groups, males and females did not significantly differ in V_{O_2} or mass (Kruskal–Wallis tests, χ^2 values ranged 2.19 to <0.01 , P values ranged from 0.14 to 0.99), nor was there a significant difference in the body mass of subjects among temperature treatments (Kruskal–Wallis test, $df = 5$, $\chi^2 = 9.08$, $P = 0.17$). Using residuals, a multiple regression analysis (SAS 1985; GLM procedure) indicated that temperature and, to a lesser extent, mass and a mass/temperature interaction had significant effects

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 ($P < 0.001$).

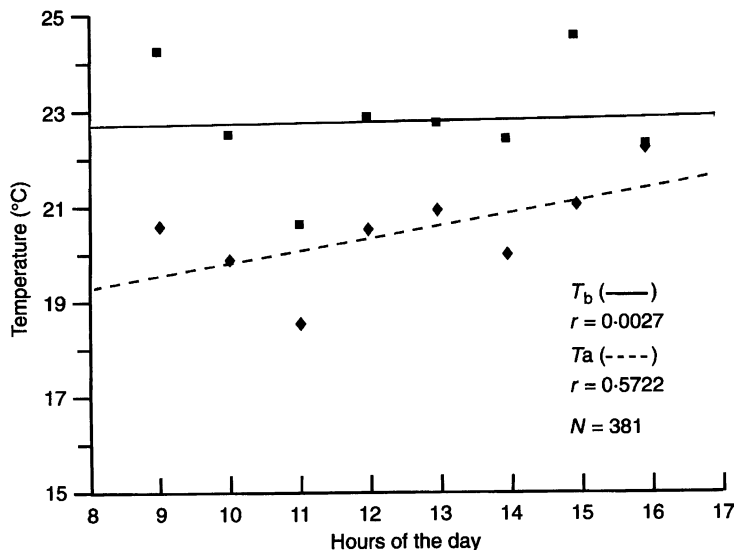


Fig. 3. Linear regressions of body temperature (T_b) (solid line) and corresponding air temperature (T_a) (dashed line) on hour of day measured for 381 *Anolis carolinensis* during partial to full sunlight from November to April on the Savannah River Site, Aiken, South Carolina. The square and diamond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

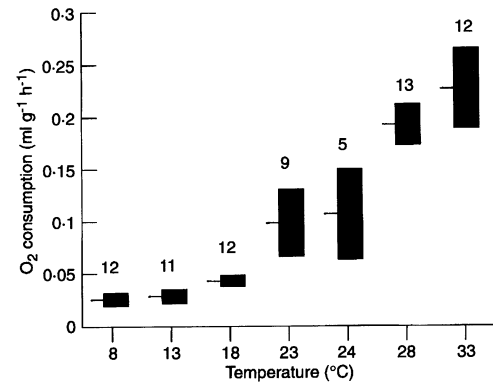


Fig. 4. Mean oxygen uptake for six ambient temperature treatments from 509 determinations using 74 *Anolis carolinensis* during December–January on the Savannah River Site, Aiken, South Carolina. Ends of black bars indicate ± 2 standard errors of the mean (horizontal line).

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 , and 12.4°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).

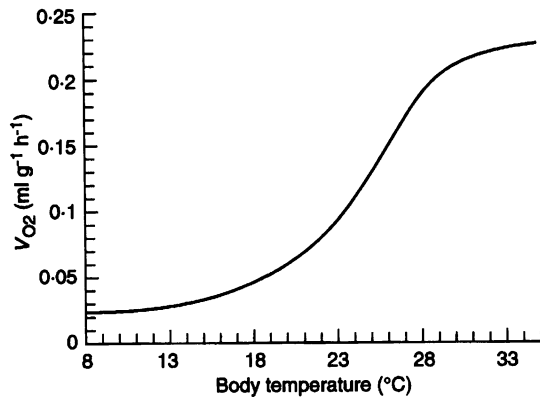


Fig. 5. Resting metabolism/temperature relationship for *Anolis carolinensis* based on the data of Fig. 4.

Discussion

BEHAVIOURAL PROFILE

Wintering *A. carolinensis* predictably emerged on days with direct sunlight and appeared to thermoregulate, spending 67% of their time in sunlight. However, because lizards did not seem willing to move far from their nighttime refugia, thermoregulating behaviour appeared to be limited. Frequently the movement of the sun (rather than the movement of the lizard) shifted a lizard's exposure between sun and shade.

A number of time budget and behavioural performance analyses have been made on anoles (e.g. Andrews 1971; Fleming & Hooker 1975; Jenssen, Greenberg & Hovde 1995; Lister & Garcia Aguayo 1992; Losos 1990a, b; Moermond 1979a, b; Pounds 1988; Talbot 1979). From these studies, dry season *A. nebulosus* has been labelled the most sedentary of lizards, travelling an average distance of 64–78 cm h⁻¹ with 97–99% of their time 'resting/hiding' or 'scanning/foraging' (Lister & Garcia Aguayo 1992: their Tables 5 and 6). However, wintering South Carolina *A. carolinensis* was as sedentary as *A. nebulosus*, being motionless in the 'stationary' mode for 92.2% of their activity period. When activity did occur, *A. carolinensis* moved far less than *A. nebulosus*; distance travelled averaged only 1.5 (females) to 2.5 (males) cm h⁻¹.

In the winter period, *A. carolinensis* is one of the most inactive anoles, devoting little to no time toward social activities of any type ($\approx 1.3\%$ of total observation durations). Then by late April, our *A. carolinensis* population becomes one of the most active of anoles (Jenssen *et al.* 1995). From May through July male *A. carolinensis*, for example, are territorial, reproductive, travel an average of 27 m h⁻¹, display 100 times per hour, and spend approximately two thirds of their day in social activity (Jenssen *et al.* 1995). Beginning in August, the male activity profile precipitously shifts once more; males are no longer territorial or sexually active, they double their feeding rate, move far less (8 m h⁻¹), and infrequently display (six displays per

hour) (Jenssen *et al.* 1995).

In comparison with other congeners, *A. carolinensis* seems to have a 'boom-or-bust' annual cycle to its social behaviour. Because the majority of anoline social behaviour (i.e. territoriality, courtship) is associated with reproductive activity, the annual extremes of the *A. carolinensis* behavioural profile is probably accentuated by the temperate climate. The low winter temperatures at our study area drastically reduce the microhabitat, a dependable food source, and the conditions for ectothermic activity; these are all prerequisites for successful reproduction. In contrast, anoles of more tropical climes can potentially reproduce the year around; however, some may exhibit a varying degree of seasonality in reproduction because of an annual dry season (reviewed in Jenssen & Nunez 1994).

THERMAL BIOLOGY

The mean T_b for our wintering *A. carolinensis* in South Carolina (23 °C) was considerably lower than the March–April data collected in Brazos County, Texas (28 °C; Clark & Kroll 1974), and much lower than the March data collected in Miami, Florida (30 °C; King 1966). The $T_b - T_a$ differential for our data (2.4 °C) was also much narrower than that for the Texas data (6.3 °C; Clark & Kroll 1974). The mean T_b of our wintering anoles (23 °C) was 3.5 °C below the lower end of the estimated *A. carolinensis* activity range for Miami (26.5 °C; King 1966). All three data sets, however, recorded maximum field T_b around 35 °C, a value which is close to the voluntary maximum T_b (36 °C) under laboratory conditions (Wilson & Echternacht 1990).

Some anoles, whose populations are altitudinally distributed between a range of thermal environments, maintain similar T_b s by adjusting their activity periods, microhabitat use, and basking rates (Hertz & Huey 1981). However, this does not seem the case for early spring *A. carolinensis*; comparisons between populations showed a substantial difference in mean T_b s as reported from the sources cited above (locality, latitude, and mean T_b : Miami, 26°, 30 °C; Brazos, 30°, 28 °C; SRS, 33.5°, 23 °C, respectively). There appeared to be a negative relationship with latitude; if this is a robust trend, then the Knoxville, Tennessee population (latitude 36°) should have the lowest mean basking T_b for wintering *A. carolinensis*.

If there is a latitude effect on mean winter T_b , it is not a simple relationship. On one hand, high T_b s during winter may prepare *A. carolinensis* for breeding; lab experiments (Noeske & Meier 1977; Licht 1971, 1973) indicate that seasonal gonadal recrudescence is facilitated by high T_b (approximately 32 °C) and daily temperature fluctuations. In spite of low spring T_a s, basking can expedite gonadal recrudescence, but at an energetic cost that increases with elevated T_b . However, at higher latitudes the T_a in winter months reduces food availability. Thus, metabolic costs asso-

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

of fasted Panamanian *Anolis limifrons* to be 0.08 and 0.23 ml O₂ g⁻¹ h⁻¹ at 20 and 30 °C, respectively, very similar to that of our fasting *A. carolinensis* (0.06 and 0.21 ml O₂ g⁻¹ h⁻¹ at 20 and 30 °C, respectively; Fig. 5). However, if lizards were fed, a likely field condition during the winter in Panama but not in South Carolina, the metabolic rate of *A. limifrons* almost doubles (0.13 and 0.44 ml O₂ g⁻¹ h⁻¹ at 20 and 30 °C, respectively; Andrews & Asata 1977). *Sceloporus jarrovi* is an iguanid lizard of about 15 g body mass that basks during sunny winter days in the Chiricahua Mountains of southeastern Arizona. Field metabolic rates of *S. jarrovi*, determined with doubly labelled water (Congdon *et al.* 1979), were higher during the early portion of winter (0.077 ml CO₂ g⁻¹ h⁻¹) when they basked most frequently, and similar (0.034 ml CO₂ g⁻¹ h⁻¹) during the late portion of winter when they basked less frequently) to those of wintering *A. carolinensis* (0.037 ml O₂ g⁻¹ h⁻¹).

CONCLUSIONS

Anolis carolinensis, belonging to a large genus of tropically adapted species, is the most northerly distributed anoline lizard. Within high latitude *A. carolinensis* habitats, winter temperatures reduce the availability of preferred microhabitats, food, and opportunities for maintaining elevated body temperatures. Possibly because of phylogenetic constraints, *A. carolinensis* does not hibernate in response to low ambient temperatures, but appears to conserve energy by other means.

South Carolina *A. carolinensis* experience low T_a s during December–March (10.2 °C mean, NOAA), with limited direct sunlight for thermoregulation during the majority of each 24-h period. When the sun was available, lizards emerged, but few raised their T_b s to the 32–35 °C range where foraging activity, digestion, and gonadal recrudescence would be maximally facilitated (Licht 1971, 1973; Windell & Sarokon 1976; Gatten *et al.* 1988). Energy input appeared insignificant because few feeding opportunities were observed, and if a lizard were to eat, gastric inhibition experienced during cold nocturnal and overcast periods could be detrimental. Lizards appeared to compensate for the increased metabolic costs associated with facultative basking activities by limiting their thermoregulatory behaviour and by being extremely sedentary.

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