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Physiological Ecology of the Mangrove-Dwelling Varanid *Varanus indicus*

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ABSTRACT

Some species of terrestrial lizards in wet-dry tropical climates reduce their body temperatures (T_b 's) and activity and lower their metabolic rates during the dry season when food and water resources are scarce. However, semiaquatic lizards have access to water and presumably food throughout the year, so it is possible that they will not have the seasonal response seen in terrestrial species. We studied the thermal biology, energetics, and water flux of *Varanus indicus*, a semiaquatic, mangrove-dwelling varanid in tropical northern Australia. Although *V. indicus* remained active all year, they reduced their activity in the dry season, but not to the extent of terrestrial varanids. *Varanus indicus* field metabolic rates decreased by 38% in the dry season mostly as a result of the reduction in activity. Although food and water depletion are the driving forces behind decreases in dry season T_b selection and energetics for many varanids, *V. indicus* appears not to be subject to these pressures to the same extent. Thermoregulatory indices indicate that *V. indicus* actively thermoregulate in the wet and dry seasons, but they do not fully exploit the available thermal resources. These lizards are unusual among varanid lizards in that their midday T_b 's are relatively low (about 31°C) despite the availability of thermal resources that would allow them to attain substantially higher T_b 's.

Introduction

Lizards worldwide inhabit a wide range of habitats and climates (Pianka and Vitt 2003) and are therefore subject to a variety of seasonal and thermal conditions. The extent to which species and individuals respond to these thermally variable conditions varies from complete thermoconformity, usually in places where temperatures are relatively high and constant (Lee 1980; Rummery et al. 1995), to the maintenance of high and relatively stable body temperatures (T_b 's) using complex thermoregulatory behaviors (Diaz 1992; Villavicencio et al. 2007). In highly seasonal climates, many species use a combination of behavioral and physiological mechanisms to conserve energy when food and water are limited (Stanner and Mendelssohn 1991; Christian and Green 1994; Pianka 1994; Thompson et al. 1998; Heger 2000; Guarino et al. 2002).

Studies of seasonal energetics of lizards in the wet-dry tropics have revealed varying responses to the slightly lower ambient temperatures and lower availability of food and water that characterize the dry season (Christian et al. 2003). Reptiles in the wet-dry tropics of Australia have lower nighttime T_b 's in the dry season because of the passive effects of cooler conditions (Christian et al. 1999b), some species actively select lower T_b 's during the day (Christian et al. 1983, 1999a; Christian and Bedford 1995, 1996), some depress their metabolic rate (Christian et al. 1996b, 1996c, 1999a), and most species decrease their activity during the dry season (Christian and Weavers 1996). Consequently, the field metabolic rates (FMRs) of lizards in the wet-dry tropics of Australia are lower in the dry season than in other seasons (Christian and Green 1994; Christian et al. 1995, 1996b, 1996c, 1996d, 1999a, 2003). The fact that *Varanus panoptes* living near water sources do not use these energy-saving mechanisms, whereas those in woodland habitats without water employ all of these mechanisms during the dry season, is evidence that these behavioral and physiological responses are the result of decreased levels of food and water (Christian et al. 1995).

Although some species select lower T_b 's during the day, it is important to note that the thermal environment in the wet-dry tropics allows for lizards to attain high T_b 's throughout the year (Christian and Bedford 1995, 1996; Christian and Weavers 1996). In contrast, the semiaquatic varanid *Varanus mertensi* does not change its seasonal T_b 's, resting metabolic rates, or activity levels considerably between seasons (Christian and Weavers 1996; Christian et al. 1996d). Although the FMRs of *V. mertensi* are lower in the dry season than in the wet season, this seasonal difference is largely attributable to the passive consequences of lower nighttime T_b 's (Christian et al. 1996d).

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Varanus mertensi may be less affected by seasonal changes in the wet-dry tropics because the habitats it occupies provide it with year-round access to water and food (Christian et al. 1996d). To further examine seasonal trends in semiaquatic, tropical zone lizards, we investigated the thermoregulation and energetics of *Varanus indicus* (Daudin 1802), a semiaquatic varanid that occupies mangrove systems in the wet-dry tropics of northern Australia and other parts of Asia. Given that *V. indicus* also inhabits habitats that are ostensibly productive year-round, we hypothesized that they would remain active throughout the year without the striking metabolic and behavioral adjustments of terrestrial species in response to the dry season conditions. Because other semiaquatic varanids appear to select lower T_b 's than terrestrial species of similar size (Wikramanayake and Green 1989, 1993; King 1991; Traeholt 1995; Christian and Weavers 1996), we also hypothesized that *V. indicus* would thermoregulate at relatively low T_b 's.

Material and Methods

Study Site

Varanus indicus was studied in a discrete patch (27.2 ha) of mature mangrove forest lining the estuarine (northern) section of the Adelaide River, approximately 70 km east of Darwin, Northern Territory (12°33'20"S, 131°22'28"E). The climate in this region is characterized by distinct wet (December through March) and dry (May through September) seasons. During the wet season, there are warm air temperatures (mean maximum of 31.7°C and mean minimum of 25.7°C in January in Darwin), high humidity, and frequent rainfall. Dry season days are generally warm, with cooler nights (mean maximum of 30.4°C and mean minimum of 19.3°C in July), low humidity, and little or no rain (Taylor and Tulloch 1985). Data were collected during two dry seasons and two wet seasons (2003–2004). The climatic conditions during these years and seasons were typical in that the rainfall and mean temperatures were within the 95% confidence intervals of measurements between 1940 and 2004 (data from the Australian Government Bureau of Meteorology).

Radiotelemetry

The lizards were captured using baited pipe traps as outlined by Smith (2004), placed in individual bags, and transported to Charles Darwin University, Darwin. Within 2 d of capture, temperature-sensitive radio transmitters (model SB-2; Holohil Systems, Carp, Ontario) were implanted intraperitoneally. Beforehand, transmitters were calibrated at 5°C increments between 5° and 40°C in a water bath (Grant, Chesterland, OH) using a reference mercury thermometer traceable to the National Institute of Standards and Technologies. The final mass of transmitters ranged between 4 and 13 g, and all implanted transmitters weighed <3% of the animals' body masses. Transmitters were surgically implanted in 20 *V. indicus* (682–2,173 g), with 10 each in the wet and dry seasons. Not all of these

were recaptured for FMR measurements, and T_b data were successfully collected from nine individuals in each season.

Thermoregulation

We recorded T_b 's of free-ranging *V. indicus* by using an automated system with a fixed antenna, receiver, and digital processor (Telonics, Mesa, AZ) connected to a data logger (CR10X; Campbell, Logan, UT) in 2003 and a coupled Advanced Telemetry Systems (Isanti, MN) data logger (model R2100) and receiver (model D5041A) in 2004. Both digital processors and data loggers were calibrated in the laboratory before taking measurements in the field. The T_b 's of multiple individuals were recorded at the same time at 15-min intervals. Hourly and grand means were calculated for each individual for all *V. indicus* sampled in a season.

The set point range has been defined as the "preferred" T_b of an animal, as measured in the laboratory without other ecological demands of the environment that may influence T_b (Hertz et al. 1993; Christian and Weavers 1996). The upper and lower limits of the set point range for *V. indicus* was estimated using the central 50% of the T_b measured in a thermal gradient (Hertz et al. 1993). A wooden thermal gradient (4 m × 1.5 m) was constructed and housed in an air-conditioned room. Two 60-W heat lamps (0.5 m above the bottom of the container and connected to timers) were spaced 0.5 m apart from one end of the container, thus providing a continuous gradient of substrate temperatures that ranged from 19° to 42°C during the daytime hours (0700–1800 hours). Individual *V. indicus* ($n = 6$) were placed one at a time inside the gradient with a thermistor inserted ~50 mm inside the cloaca. The thermistor was attached to a HOBO XT temperature data logger (Onset Computer, Bourne, MA), which was calibrated, and taped to the side of the tail using an adhesive bandage. The T_b of each *V. indicus* was recorded every 15 min over a 2-d period, resulting in 38 measurements per individual during daytime hours, excluding the first 1.5 h after the heat lamps came on. These lizards were fasted 48–72 h before being placed in the thermal gradient.

We recorded microclimate data as described by Christian and Weavers (1996). Various environmental temperatures (air in shade, mud, water, inside hollow temperatures) were measured every 15 min for 2 wk each season. All measurements were recorded with HOBO Pro Series data loggers (Onset Computer) with a 1.5-m thermistor attached. Shaded air temperatures were measured at 2 m above the ground.

Operative temperatures (T_e) represent the interaction between an animal and its environment by incorporating aspects of the physical characteristics of an animal (e.g., absorptivity and surface areas) and the microhabitat in which it is situated (Porter and Gates 1969; Bakken 1981, 1992; Bakken et al. 1985). The $T_{e_{max}}$ and $T_{e_{min}}$ were calculated from a steady state biophysical model based on equations by Tracy (1982) and similar to models used broadly (Porter and Gates 1969; Porter et al. 1973; Porter and James 1979; Porter and Tracy 1982; Wald-

schmidt and Tracy 1983), including input data based on animal characteristics and microclimate data collected from the study site. An absorptivity value of 87% was measured for *V. indicus* using methods outlined by Christian et al. (1996a). Briefly, the light from a 100-W tungsten halogen bulb was shone through an integrating sphere (model IS-040; Labsphere, North Sutton, NH) containing a Moletron (Portland, OR) broadband pyroelectric detector mounted at a right angle to the optical path. Four diffuse reflectance standards (Labsphere) were sequentially placed over the exit port of the sphere, and the signal from the detector was used to construct a calibration curve corresponding to the absorptance values of the standards (98%, 50%, 25%, and 1%). The dorsal surface of an animal was then placed over the exit port, and the absorptance was determined from the best-fit straight-line calibration curve from the standards.

Because of the relatively large size of *V. indicus*, the animals do not change T_b instantly. Therefore, T_e 's alone are not sufficient as an index of T_b 's as the animals move through a thermally complex environment (Christian et al. 2006). Thus, to develop thermoregulatory indices, we used the null model-based approach of Christian et al. (2006), a synopsis of which is given below. A null distribution of predicted T_b ($\text{pred}T_b$) between the maximum ($T_{e_{\max}}$) and minimum ($T_{e_{\min}}$) operative temperatures was generated (in True BASIC). The $\text{pred}T_b$ represents the T_b 's achievable by the animal on the basis of body size of *V. indicus*, T_e , and the T_b of the animal in the recent past (as the animal is warming or cooling). To calculate $\text{pred}T_b$, a random starting place was assigned (corresponding to a site in which the microclimate at that time is between $T_{e_{\max}}$ and $T_{e_{\min}}$), and a random length of time for the modeled animal to remain in that spot was also assigned. The $\text{pred}T_b$ was calculated for the animal in that place for each minute that the animal remained there. This was done using T_e as the driving force and the thermal time constant τ (taken from regression equations generated from data in Dzialowski and O'Connor 2001) to incorporate body mass. The form of the equation is

$$\text{pred}T_b = T_0 + (T_e - T_0) \times e^{-t/\tau},$$

where T_0 is the temperature at the time the animal first enters the new place. Different time constants were used for warming (32.8 min) and cooling (47.0 min). The program then assigned a new random place and time, calculated the corresponding $\text{pred}T_b$, and continued these steps over the course of the whole day (24 h), repeating this process for 1,000 d to generate a null distribution of random $\text{pred}T_b$ achievable throughout the day.

Using this null distribution, we determined a number of thermoregulatory indices for any time during the day. We calculated the mean $\text{pred}T_b$ for each hour of the day and then compared these values with the actual animal T_b (as measured by telemetry) at each hour using the indices of Hertz et al. (1993). The mean deviation of an animal's field-active T_b 's from its set point (or preferred) range, \bar{d}_b , as defined by Hertz et al. (1993), was calculated. This index is an indication of the accuracy of thermoregulation. A measure of the thermal quality

of the animal's environment (\bar{d}_e), which is the mean deviation of T_e from the animal's set point range (Hertz et al. 1993), was also calculated. For large ectotherms, it is appropriate to substitute the mean achievable T_b ($\text{pred}T_b$) for mean T_e to calculate \bar{d}_e .

The "effectiveness" of thermoregulation, as defined by Hertz et al. (1993) as

$$E = 1 - \frac{\bar{d}_b}{\bar{d}_e},$$

was calculated, where a value for E of 0 indicates a random selection of thermal environments and a value for E of 1 indicates perfect thermoregulation. An alternative to this index, simply $\bar{d}_e - \bar{d}_b$, was suggested by Blouin-Demers and Weatherhead (2001). The "exploitation" of the thermal environment (Ex) was calculated as the amount of time an animal has a T_b within its set point range divided by the amount of time during the day in which it is possible for the animal to achieve its set point range (Christian and Weavers 1996).

Field Metabolism and Water Flux

The doubly labeled water ($^3\text{H}-\text{H}_2^{18}\text{O}$) technique (Lifson and McClintock 1966) was used to measure the FMR and water flux of free-ranging animals over a mean period of 21 d in the wet season and 31 d in the dry season. Blood samples (0.3 mL) were taken from the caudal vein before injections of 440 μL (mean value) of H_2^{18}O (95% atoms excess) and 1 mL of tritiated water (20 MBq mL^{-1}), 8–12 h after injection, and on recapture. Concentrations of H_2^{18}O after equilibration were 70 times background levels, and recapture concentrations were 10.2 times background levels. Isotopic samples were measured at the Division of Sustainable Ecosystems, Commonwealth Scientific and Industrial Research Organization, Canberra. The techniques for sample analysis to determine isotopic measurements of the FMR and water flux are described in detail elsewhere (Christian et al. 1995, 1996d; Christian and Weavers 1996) but will be described briefly here. Blood samples were stored frozen in plastic vials until vacuum distilled in the laboratory. A liquid scintillation counter (model LS2800; Beckman, Palo Alto, CA) was used to measure tritium in subsamples of extracted water (20 μL). Other subsamples of extracted water (20 μL) were equilibrated with standard CO_2 charges at 80°C in Urey exchange tubes, after which $^{18}\text{O} : ^{16}\text{O}$ ratios were determined by isotopic ratio mass spectrometry (V. G. Optima, Cheshire). We assumed that any changes in body mass and water pools were linear and that mass-specific water pools were stable during the experimental period. Body water pool sizes were calculated from the dilution of H_2^{18}O in the equilibrated blood samples compared with standard dilutions (50 μL in 100 mL). Changes in the concentrations of the isotopes during the release periods were used to calculate rates of CO_2 production and water flux

Table 1: Set point ranges and mean T_b 's (as measured in the lab) for *Varanus indicus* and other varanid lizards from the same region (from Christian and Weavers 1996)

Species	Set Point (°C)		Mean T_b in Lab (°C)
	Lower	Upper	
<i>V. indicus</i>	30.9 (3.7)	33.5 (4.1)	32.3 (3.8)
<i>Varanus panoptes</i>	35.8	37.6	36.7
<i>Varanus gouldii</i>	34.0	36.3	35.1
<i>Varanus mertensi</i>	33.1	35.5	34.2

Note. For *V. indicus*, $n = 6$. Values in parentheses are SDs.

(Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980).

For comparison, we used the empirical equation for reptiles (Nagy et al. 1999) to predict the FMR of *V. indicus*, using the mean mass of the animals we sampled in each of the two seasons, and this was compared with the 95% confidence interval around the mean measured values from *V. indicus*. Allometric equations for reptiles from arid and tropical regions (Nagy 1982b) were used to calculate predicted water flux rates for comparison with the 95% confidence interval around the mean measured values from *V. indicus*.

Energy Budget Calculations

Energy expenditure was derived from field CO_2 estimates using a thermal equivalent of $25.7 \text{ kJ L}^{-1} \text{ CO}_2$, assuming an average respiratory quotient of 0.75 (Nagy 1982a). FMR was partitioned into components due to T_b and activity for each season by combining field and laboratory data. Schultz (2002) measured the standard metabolic rate (SMR) of 10 *V. indicus* (mean mass = $997 \pm 204 \text{ g}$) at four temperatures as follows: at 18°C , $\text{SMR} = 16.0 \text{ mL O}_2 \text{ h}^{-1}$ (SD = 3.6); at 24°C , $\text{SMR} = 30.2 \text{ mL O}_2 \text{ h}^{-1}$ (SD = 5.7); at 30°C , $\text{SMR} = 52.0 \text{ mL O}_2 \text{ h}^{-1}$ (SD = 9.8); at 36°C , $\text{SMR} = 90.7 \text{ mL O}_2 \text{ h}^{-1}$ (SD = 16.5). A regression equation was derived relating T_b and body mass to resting metabolism: $\text{SMR} = -1.86M^{0.75} \times 10^{0.044T_b} \text{ mL O}_2 \text{ h}^{-1}$ (Schultz 2002). Using these metabolic data, field T_b 's from the day (0900–1800 hours) and night (the remaining 14 h) were used for both seasons to estimate the total resting metabolism (TRM) under field T_b conditions (Benabib and Congdon 1992). The oxygen consumption values were converted to units of energy using the energy equivalent of $20.08 \text{ kJ L}^{-1} \text{ O}_2$ (Benabib and Congdon 1992).

The difference between the FMR and TRM provides an index of the amount of energy expended in activities such as locomotion, digestion, and reproductive costs (van Marken Lichtenbelt et al. 1993), and it has been termed the activity respiration (AR; Benabib and Congdon 1992). The percentage of the total field metabolism allocated to activity (%AR) is calculated as $\text{AR}/\text{FMR} \times 100$ (Anderson and Karasov 1981). The field maintenance scope is derived from the ratio of FMR/TRM

(Congdon and Tinkle 1982), and if the animal's body mass changes $<1\%$ per day, this can be termed the sustained metabolic scope (SusMS; Peterson et al. 1990).

Statistical Analyses

Seasonal means were compared using ANCOVA with body mass as a covariate. Differences between means were considered statistically significant when $P \leq 0.05$, and means are presented $\pm 1 \text{ SD}$. We report results of new statistical analyses of FMR, water flux, and water economy index (WEI) comparing *V. indicus* with other species of *Varanus* of similar size from the same region using data collected in previous studies (Christian et al. 1995, 1996d) using ANCOVA with post hoc t -test comparisons. A repeated-measures ANOVA was used to compare

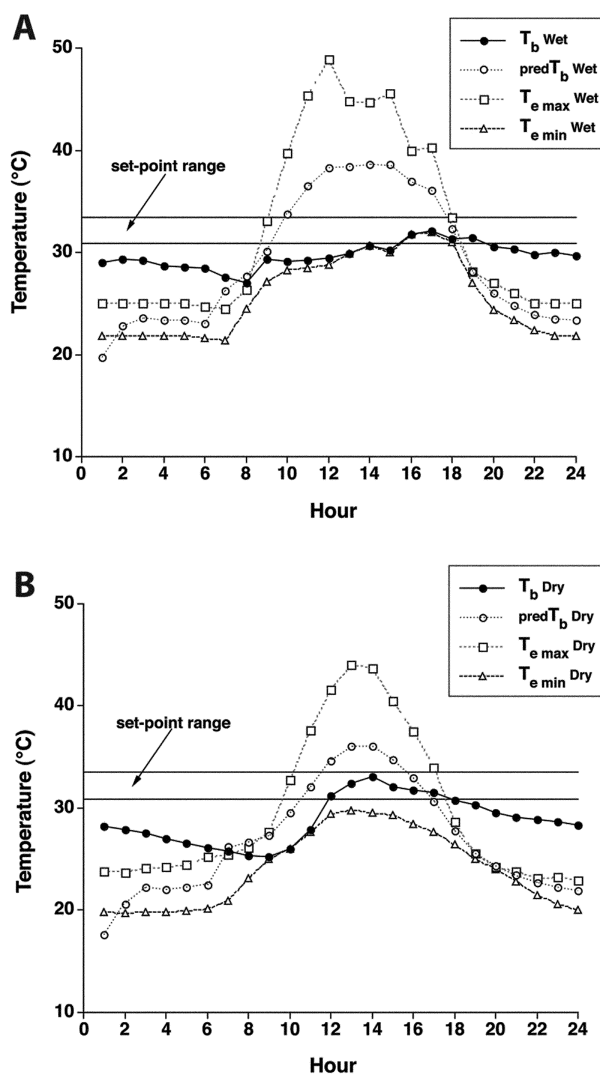


Figure 1. Grand mean body temperatures (T_b ; as measured by radio-telemetry), predicted T_b ($\text{pred}T_b$), set point range, and operative temperatures ($T_{e \text{ max}}$ and $T_{e \text{ min}}$) as a function of time of day for free-ranging *Varanus indicus* during the wet season (A) and dry season (B).

Table 2: Summary of body temperature (T_b) data and thermoregulatory indices of *Varanus indicus* (this study) and three other varanids from the same region (Christian and Weavers 1996) during the wet and dry seasons

Species	Grand Mean T_b (°C)	Midday T_b (°C)	\bar{d}_e	\bar{d}_b	$\bar{d}_e - \bar{d}_b$	E	Time Set Point Range (h)		
							Possible	Exploited	Ex (%)
Wet season:									
<i>V. indicus</i>	30.3	30.6	3.5	.9	2.6	.75	10	2.6	26
<i>Varanus panoptes</i>	36.4	35.2	7	1.5	5.5	.79	8.7	1	12
<i>Varanus gouldii</i>	35.9	35.9	6.4	.2	6.15	.96	9.1	8.7	96
<i>Varanus mertensi</i>	34.0	34.0	8.9	.5	8.45	.95	11.3	8.1	72
Dry season:									
<i>V. indicus</i>	29.7	31.4	1.4	1.0	.4	.30	8	5.1	64
<i>V. panoptes</i>	36.2	36.2	2.1	.9	1.28	.60	7.3	5	68
<i>V. gouldii</i>	28.2	28.2	1.9	5.7	-3.75	-2.0	7.8	0	0
<i>V. mertensi</i>	33.4	33.4	1.4	1	.48	.34	8.1	6	74

Note. Data from *V. indicus* were collected from nine individuals in the wet season and nine different individuals in the dry season. Ex = exploitation.

the midday T_b 's of *V. indicus* with those of another semiaquatic varanid in the same region, *Varanus mertensi*, using data from Christian and Weavers (1996).

Results

Thermoregulation

The set point range selected by *Varanus indicus* was $30.9^\circ \pm 3.7^\circ$ to $33.5^\circ \pm 4.1^\circ\text{C}$ (Table 1). In the wet season, *V. indicus* grand mean T_b overlaps the set point range for 4.5 h (1530–2000 hours), and in the dry season, grand mean T_b overlaps the set point range for 6 h (0100–1900 hours; Fig. 1). The midday (1100–1600 hours) grand means in the wet season (30.6°C) versus the dry season (31.4°C) were very similar, as were the nighttime grand means (29.5° and 28.0°C , respectively). Maximum temperatures selected by *V. indicus* during the wet and dry seasons were very similar (35.8° and 35.7°C , respectively), and there was only a 1.8°C difference between the wet season (27.0°C) and dry season (25.2°C) minimum temperatures. The midday T_b 's of *V. indicus* were significantly lower than those of *Varanus mertensi* ($F_{1,70} = 7.8$, $P = 0.007$).

Table 2 shows various thermoregulatory indices and the number of hours per day that *V. indicus* can, and do, achieve their set point range. During the hours before and after sunset, in both the wet and dry seasons, the T_b 's of *V. indicus* are higher than either T_e value, indicating that the animals are in tree hollows (also supported by radiotelemetry observations), which provide a warmer microhabitat than ambient external temperatures (Christian and Weavers 1996).

Field Metabolism, Water Flux, and Energy Budget

Six lizards were recaptured after injection with isotopes in the wet season, and four were recaptured in the dry season. Recaptured wet season lizards significantly gained mass (a mean of 10.8%; $t_5 = 4.35$, $P = 0.007$), and dry season animals lost a mean of 2% body mass, but this decrease was not significant

($t_3 = 0.78$, $P = 0.49$). Total body water estimates, expressed as a percentage of body mass (TBW), remained the same in the wet and dry seasons (Table 3). Water influx rates were significantly lower ($F_{1,7} = 34.7$, $P = 0.0006$) in the dry season, representing a 43% decrease in water flux. The predicted water influx rates for lizards in arid and tropical zones (Nagy 1982b) were lower than the 95% confidence intervals around the water influx for *V. indicus* in the wet season. However, in the dry season, the predicted water influx rates for tropical lizards was within the 95% confidence interval of water influx for *V. indicus*. ANCOVA was used to compare species within each season. During the dry season, *V. indicus* water flux was significantly lower than that of *V. mertensi* ($F_{3,24} = 5.5$, $P = 0.005$) but not different from those of *Varanus panoptes* or *Varanus gouldii*. During the wet season, *V. indicus* water flux was significantly higher ($F_{3,20} = 6.1$, $P = 0.004$) than those of *V. panoptes* and *V. gouldii* but not different from that of *V. mertensi*.

The WEI is the ratio of water flux to FMR (mL kJ^{-1} ; Nagy and Peterson 1988). During the wet season, WEI was significantly higher (64%; $F_{1,7} = 9.1$, $P = 0.02$) than the dry season value. There was a significant difference among the four similarly sized varanids of the region during the dry season with respect to WEI ($F_{3,22} = 7.3$, $P = 0.002$), with the values of *V. indicus* being lower than those of *V. mertensi* but not those of *V. gouldii* or *V. panoptes*. During the wet season, the WEI of *V. indicus* was higher ($F_{3,20} = 4.4$, $P = 0.016$) than in *V. gouldii* but not different from those of *V. panoptes* or *V. mertensi*.

The FMR was significantly lower in the dry season than in the wet season (Table 4; $F_{1,7} = 10.3$, $P = 0.01$), representing a 38% (69.6 kJ d^{-1}) reduction in FMR. The decrease in dry season FMR is due in part to lower nighttime temperatures (3%) but mostly to a decrease in activity (97%). The FMR of *V. indicus* was not different from those of *V. gouldii*, *V. panoptes*, and *V. mertensi* in the dry season ($P > 0.09$), but during the wet season, the FMR of *V. indicus* was significantly greater than that of *V. mertensi* ($F_{3,20} = 4.2$, $P = 0.02$). All other indices (AR, SusMS, and AS) were higher in the wet season than in the dry season

Table 3: Water flux rates, total body water (TBW) as determined from isotopic analysis, and water economy index (WEI) for field active *Varanus indicus* during wet and dry seasons

	Wet Season ($n = 6$)	Dry Season ($n = 4$)
Mass (g)	1,210 (580)	1,242 (618)
Water influx (mL d ⁻¹)	83.4 (9.4)	35.8 (10.8)
Predicted:		
Arid (mL d ⁻¹)	24.4	25
Tropical (mL d ⁻¹)	51	51.9
Water influx (mL kg ⁻¹ d ⁻¹)	81.3 (32.6)	32.2 (13.3)
TBW (%)	71.2 (3.0)	70.0 (2.7)
WEI (mL kJ ⁻¹)	.50 (.14)	.32 (.05)

Note. TBW = % body mass, derived from ¹⁸O dilution. Sample sizes and masses are as in Table 4. Values in parentheses are SDs. The rates of water flux predicted by the allometric equations for arid and semiarid zone reptiles and for tropical and subtropical zone reptiles (Nagy 1982b) are also shown.

(Table 4). The predicted value of the FMR for a reptile (Nagy et al. 1999) was lower than the 95% confidence interval of the FMR for *V. indicus* in the wet season, but the predicted value was within the 95% confidence interval of the FMR for *V. indicus* in the dry season.

Discussion

Thermoregulation

The midday T_b 's selected by *Varanus indicus* were 3.4° and 2.0°C lower in the wet and dry seasons than the midday T_b 's of the semiaquatic *Varanus mertensi*, which selects significantly lower T_b 's than do two terrestrial varanids (*Varanus panoptes* and *Varanus gouldii*) from the same area (Christian and Weavers 1996).

During the dry season, the \bar{d}_c of *V. indicus* is less than half of what it was in the wet season, indicating that dry season conditions are favorable for allowing the lizards to stay within their set point range. Indeed, in the dry season, *V. indicus* exploits 64% of available time in its set point range, whereas in the wet season, *V. indicus* spends very little time ($E = 26\%$) within its set point range. Thus, *V. indicus* is a less effective thermoregulator in the wet season than in the dry season ($E = 0.30$ and 0.75 , respectively). During the wet season, *V. indicus* has the lowest E index of the four similarly sized tropical Australian varanids studied to date (Table 2), indicating that this species is the least effective at selecting optimal microhabitats to stay within its set point range of T_b 's.

If *V. indicus* were inactive throughout the dry season, in order to maximize their savings of energy and water, they could select deep shade for the entire day in order to achieve the coolest T_b 's possible. However, Figure 1B shows that around 0900 hours, T_b 's are the same as $T_{c_{min}}$, but T_b 's rapidly increase from 1100 hours until they are within their set point range; then, T_b 's gradually decrease from around 1400 hours for the remainder of the day, suggesting that *V. indicus* remain active during the dry season. Radio tracking data also showed that

the lizards were active during dry season days (J. G. Smith, unpublished data). Furthermore, the T_b pattern shown in Figure 1B suggests that these lizards are actively thermoregulating in the dry season, albeit not to the maximum extent possible in their thermal environment. They could emerge, bask, and achieve their set point range 1.5 h earlier in the dry season if they exploited their thermal environment to the fullest (Fig. 1B).

The mangrove forests *V. indicus* inhabit are generally heavily shaded, and although thermal microhabitats are present all year that would enable their set point temperatures to be attained, it is possible that *V. indicus* selects lower T_b 's because the effort required to shuttle between these patches of sun may outweigh the advantages of higher T_b selection (Huey and Stevenson 1979; Hertz et al. 1993). However, during the dry season in northern Australia, one species of large, deciduous mangrove tree (*Xylocarpus mekongensis*) loses its leaves (Brock 2001), creating numerous larger sun patches that would provide easier access to warmer microclimates. An example of a lizard from northern Australia that does not actively seek sun patches is *Hypsilurus spinipes*, an agamid that lives in deeply shaded rain forest and is a complete thermoconformer (Rummery et al. 1995). It is clear from the temperature patterns in Figure 1B that *V. indicus* is not a complete thermoconformer, but the extent to which the effort required to thermoregulate to higher T_b 's in the shady mangrove forest influences the low daytime T_b 's of this species is not known. Similarly, it is not known whether there is a causal link between the low daytime T_b 's and the semiaquatic habitat of *V. indicus*. It is interesting that semiaquatic varanids tend to select lower T_b 's than do terrestrial species (Wikramanayake and Green 1989, 1993; King 1991; Traeholt 1995; Christian and Weavers 1996; Wikramanayake and Dryden 1999; this study). Different species of semiaquatic varanids have evolved from different varanid lineages (Ast 2001), but a formal comparative analysis is needed to determine the relative importance of phylogeny and ecological habitat with respect to these T_b trends.

Table 4: Carbon dioxide production, field metabolic rates (FMRs), and mean body mass of free-ranging *Varanus indicus* during the wet and dry seasons

	Wet Season (<i>n</i> = 6)	Dry Season (<i>n</i> = 4)
Mass (g)	1,210 (580)	1,242 (618)
CO ₂ (mL g ⁻¹ h ⁻¹)	.26 (.05)	.16 (.06)
FMR (kJ kg ⁻¹ d ⁻¹)	161.4 (31.4)	98.7 (35.3)
FMR (kJ d ⁻¹)	184.4 (71.8)	114.8 (45.1)
Predicted FMR (kJ d ⁻¹)	107.8	110.4
RMA (kJ kg ⁻¹ d ⁻¹)	11.1	11.2
RMI (kJ kg ⁻¹ d ⁻¹)	14.9	13.0
TRM (kJ kg ⁻¹ d ⁻¹)	26.0	24.2
AR (kJ kg ⁻¹ d ⁻¹)	135.4	74.5
%AR	83.9	75.5
SusMS	6.2	4.1
AS	13.2	7.6

Note. Values in parentheses are SDs. Predicted FMR was calculated with the equation for reptiles from Nagy et al. (1999). The total resting metabolism (TRM) was calculated using field body temperatures in the laboratory-defined equation relating body temperature to resting metabolism, summed over 24 h, and it can be divided into resting metabolism during active periods (RMA) and resting metabolism during inactive periods (RMI). The amount of energy expended in activity (AR) is estimated as the difference between the FMR and TRM. The sustained field metabolic scope (SusMS) is calculated as FMR/TRM. The percentage of the total field costs allocated to activity (%AR) is calculated as AR/FMR × 100. The field activity scope (AS) is (FMR – RMI)/RMA.

Water Flux

Water influx rates of *V. indicus* were much higher in the wet season than those predicted for lizards in arid and tropical zones (Nagy 1982*b*), but in the dry season, the influx rates were less than the predicted value. *Varanus mertensi* has greater rates of water flux than those predicted by Nagy (1982*b*) in both the wet and dry seasons (Christian et al. 1996*d*). However, the wet-dry tropics of northern Australia do not fit neatly into the categories defined by Nagy (1982*b*), because although the wet season is humid and could be classed as tropical, the dry season has characteristics similar to those in the arid zone.

Given that *V. indicus* inhabit environments that abut water bodies (floodplains and river systems) year-round, it is reasonable to assume that they have access to water throughout the year and therefore obtain at least part of their water from sources other than food. To cope with estuarine environments, they may possess specialized salt secretory glands like another Australian varanid mangrove specialist, *Varanus semiremex* (Dunson 1974). The dry season water flux rates of *V. indicus* are lower than those of *V. mertensi* but not different from those of the similar-sized terrestrial species studied to date (Christian et al. 1995, 1996*b*). *Varanus mertensi* (which is also active year-round) showed no seasonal change in water flux rate, whereas, like *V. indicus*, *V. panoptes* and *V. gouldii* (which reduce their activity for some months) had dry season water flux rates that were half their wet season values.

The WEI (Nagy and Peterson 1988) assesses the water fluxes of animals relative to their energy expenditure. The lower the

ratio, the less water animals use for the same energy output, and thus desert animals tend to have lower WEIs than non-desert species. As noted above, the dry season WEI for *V. indicus* was lower than that for the semiaquatic *V. mertensi*. Furthermore, the dry season WEI for *V. indicus* was lower than those for the semiaquatic *Varanus salvator* and the terrestrial *Varanus bengalensis* (calculated from Dryden et al. 1992). All of these species inhabit areas with abundant water supplies. It is not known why the WEI of *V. indicus* in the dry season is low relative to the WEIs of these other semiaquatic varanid species, but examination of the numerator and denominator of this index (Tables 3, 4) shows that the decrease in dry season water flux is greater than the decrease in dry season FMR. Although water is always available for *V. indicus*, this decrease in water flux suggests that, for whatever reason, *V. indicus* consume less food and water in the dry season, which is also supported by the fact that the dry season lizards sampled in the doubly labeled water experiment tended to maintain or decrease body mass, whereas wet season lizards gained mass.

FMRs and Seasonal Energy Budgets

The extent of seasonal metabolic reduction exhibited by *V. indicus* (38%) during the dry season is low compared with those of other varanid species in the region, except *V. mertensi* (33%; Christian et al. 1996*d*). In *V. mertensi*, the reduction is due to the passive consequence of lower nighttime temperatures, whereas this phenomenon accounts for only 3% of the dry

season reduction in *V. indicus*, the remainder being due to decreased activity. This is in support of other (unpublished) radio tracking data indicating that *V. indicus* is less responsive to seasons than the savannah species but more so than *V. mertensi*. So far, all lizards studied in the Australian wet-dry tropics exhibit lower FMRs in the dry season, but the relative contributions of the behavioral and physiological mechanisms to achieve this varies among species (Christian et al. 2003).

Varanus indicus shows generally intermediate physiological responses to seasonal changes between the semiaquatic *V. mertensi* that remains active year round and the terrestrial *V. gouldii* and *V. panoptes* that spend at least some of their time inactive during the driest part of the year. An investigation of the seasonal productivity of the mangrove system along Adelaide River (particularly with regard to the prey of *V. indicus*) would help to determine the causes of their reduced activity and energy expenditure in the dry season.

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