

THERMOREGULATION OF MONITOR LIZARDS IN AUSTRALIA: AN EVALUATION OF METHODS IN THERMAL BIOLOGY¹

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Abstract. The aims of this paper are to compare the thermal ecology of four species of varanid lizards that occupy a range of habitats and climatic regions, and to assess the efficacy of methods for evaluating the extent to which ectothermic animals exploit their thermal environments. Hertz et al. (1993) have proposed several indices of thermoregulation, and these are evaluated with respect to our data from varanid lizards.

The thermoregulatory characteristics of three tropical monitor lizards (*Varanus panoptes*, *V. gouldii*, and the semiaquatic *V. mertensi*), and the temperate-zone *V. rosenbergi* were studied throughout the year. Radiotelemetry was used to measure the body temperatures (T_b 's) of free-ranging animals, and microclimatic data were collected to determine the range of possible T_b 's that an animal could achieve. Operative temperatures (T_e 's) were estimated by biophysical models for each set of animal characteristics and microclimatic conditions. The T_b 's selected by animals in a laboratory thermal gradient were used to determine the set-point range of T_b 's that the animals voluntarily select.

Plots that superimpose T_b 's, T_e 's, and the set-point range across the day are extremely useful for describing the thermoregulatory characteristics of ectotherms. These plots can be used to determine the extent to which the animals exploit their thermal environment: we define an index of thermal exploitation (Ex) as the time in which T_b 's are within the set-point range, divided by the time available for the animal to have its T_b 's within the set-point range.

Only *V. mertensi* was active throughout the year. In general, during seasons of inactivity, the T_b 's of inactive species fell outside the set-point range, but during periods of activity all species selected T_b 's within their set-point range. The temperate-zone species (*V. rosenbergi*) thermoregulates very carefully during periods when environmental conditions allow the animals to attain the set-point range, and *V. gouldii* also thermoregulates carefully in the wet season. *V. mertensi* selects T_b 's that are significantly lower than the other species both in the field and in the laboratory, and thermoregulatory indices of this species were intermediate relative to the other species. The amount of time spent in locomotion each day was not correlated with the indices of thermoregulation: the most active species, *V. panoptes*, was, with respect to several indices, the least careful thermoregulator.

The type of question that is being addressed, with respect to the interactions between an animal's thermal environment and its thermoregulatory behavior, determines the appropriateness of the various indices of thermoregulation. The Ex index describes the thermoregulatory characteristics of ectotherms in a heterogeneous thermal environment, and in such an environment a large amount of information can easily be interpreted graphically. This index is less useful in a thermally homogeneous environment.

Key words: Australia; biophysical ecology; body temperature; lizards; monitor lizards; seasonality; thermal environment; thermoregulation; tropics, wet-dry tropics; *Varanus*.

INTRODUCTION

Studies of thermoregulation by reptiles span the fields of community ecology, physiological ecology, and physiology (Heath 1964, Huey and Slatkin 1976, Bartholomew 1982, Huey 1982, 1991, Tracy and Christian 1986, Peterson 1987, Hertz 1992a, b). Some of the central questions related to thermoregulation have also been among the most elusive, partly because the ques-

tion of how carefully an animal thermoregulates is actually a suite of questions (Hertz et al. 1993). To address these questions requires an integration of an animal's thermoregulatory behavior, the availability of thermal opportunities, and the physiological and morphological properties that allow an animal to exploit its thermal environment (Hertz et al. 1993). Once the complex question regarding thermoregulation is broken into its discrete components, then the appropriate questions can be addressed to explore fully the ecological, physiological, and evolutionary aspects of thermoreg-

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ulation. Hertz et al. (1993) have suggested a conceptual framework for exploring thermoregulation by comparing the body temperatures (T_b) selected by an ectotherm to the available thermal environment and the preferred body temperature range of the animal in a thermal gradient. They developed several indices that compare and combine these elements to address different components of the broad question of how carefully an animal thermoregulates. One of the aims of this paper, in addition to comparing the thermal ecology of four closely related species, is to evaluate the efficacy of these indices of thermoregulation (Hertz et al. 1993) in describing the thermoregulation of the species we studied. We also present an additional thermoregulatory index based on a graphical presentation of data.

To fully understand thermoregulation by animals in their natural environments, it is necessary to measure the available range of thermal options. It is possible to address this by determining the operative temperature of an animal under the range of environmental conditions in its habitat (Porter and Gates 1967, Bakken 1981, 1992, Tracy 1982, O'Conner and Spotila 1992). Operative temperatures can be determined by using biophysical models in conjunction with microclimatic data (reviewed by Tracy 1982, Bakken 1992, O'Conner and Spotila 1992), or physical models with thermal properties similar to those of the study animal (reviewed by Bakken 1992). These techniques allow investigators to address questions central to our understanding of thermoregulation, such as determining whether or not an animal can possibly attain its preferred body temperature in a given environment (Christian et al. 1983, Peterson 1987, Hertz 1992a, b) and the cost/benefit relationships of body temperature selection (Huey and Slatkin 1976, Christian et al. 1984, Tracy and Christian 1986, Grant 1990).

Here we report the results of extensive radiotelemetry studies of field body temperatures and activity of four species of varanids (monitors or goannas) from temperate and tropical regions of Australia. Varanid lizards are typified as being active foragers with high aerobic capacities (Bartholomew and Tucker 1964; but see Christian and Conley 1994), but Shine (1986) has suggested that the morphological similarity of varanids belies interesting ecological variability. The thermal biology of several species of varanid lizards has been studied in temperate regions (Stebbins and Barwick 1968, King 1977, 1980, Weavers 1983, Pianka 1994) and tropical areas (King et al. 1989, Wikramanayake and Green 1989, Green et al. 1991, Wikramanayake and Dryden 1993), but the diversity of techniques makes an in-depth comparison of these species difficult. Using data from the literature, King (1991) concluded that terrestrial varanids thermoregulate at high T_b 's regardless of body size, but he tentatively suggested that semiaquatic species thermoregulate at lower T_b 's.

We studied *Varanus gouldii*, *V. panoptes*, and *V.*

mertensi in the tropics, and *V. rosenbergi* in temperate Australia. A comparison of these species provides an opportunity for unique comparisons between closely related tropical and temperate species of similar size, and among tropical species that inhabit the same region but select different habitats within the region (woodlands, open floodplains, and in and around water). Simultaneous measurements of the microclimate allow an evaluation of the T_b measurements with respect to the operative temperatures (T_e ; Bakken 1981) as determined by the interaction of the physical environment with morphological characteristics of the animals. Here we use plots that superimpose T_b 's, T_e 's, and the set-point range across the day to determine the extent to which the animals exploit their thermal environment: we define an index of thermal exploitation (EX) as the time in which T_b 's are within the set-point range, divided by the time available for the animal to have its T_b 's within the set-point range. This index is easily interpreted and, in the appropriate circumstances, yields a large amount of information about how ectothermic animals interact with their thermal environments. The daily and seasonal activity patterns are also examined and compared to the thermoregulatory patterns.

MATERIALS AND METHODS

Study areas and species

Phylogenetically, the varanids are grouped into four major lineages, and the four species studied here are closely related in the "*Varanus gouldii* group" (Baverstock et al. 1993). Three species of varanid lizards were studied in tropical Australia during the wet (summer), dry (winter), and late dry (spring) seasons. *Varanus gouldii* and *V. panoptes* were studied at the Kapalga Research Station in Kakadu National Park and *V. mertensi* was studied at Lake Bennett, 80 km south of Darwin, Northern Territory. These two sites (between 12°30' and 13° S latitude) are ≈140 km apart and experience the same seasonally monsoonal climate. The mean maximum air temperatures in this area range from 30.4°C in July (dry season) to 33.1° in November (early wet season) and the mean minimum temperatures for these months are 19.3 and 25.3° respectively (Bureau of Meteorology, Darwin, Northern Territory, Australia, unpublished data). A fourth species, *V. rosenbergi*, was studied at Flinders Chase National Park, at the western end of Kangaroo Island, South Australia (36° S) which experiences a cool-temperate climate, with maximum rainfall in winter (Burrows 1979). The mean daily maximum air temperatures range from 21.5° in January (midsummer) to 14.4° in July (midwinter), and the mean daily minimum air temperatures for those months are 14.2 and 9.4°, respectively (Burrows 1979). Table 1 shows the tropical and temperate seasons considered in this study, describes the typical environmental conditions during these seasons, and gives a

TABLE 1. The months during which data were collected and the corresponding seasons in the tropics and temperate zones of Australia. Brief descriptions of the prevailing climatic conditions and typical behavior of the lizards during each season are also listed. The species are abbreviated as follows: *V. panoptes*, (Vp); *V. gouldii*, (Vg); *V. mertensi*, (Vm); and *V. rosenbergi*, (Vr).

Seasons	Observation months	Typical environmental conditions	Typical lizard behavior
Tropical			
Wet	November through February	high temperatures, monsoonal rains	Vg and Vm active, Vp mostly active
Dry	June through July	warm days, cool nights, dry	Vp, Vm active, Vg inactive
Late dry	September	high temperatures, dry	Vm active, Vp, Vg inactive
Temperate			
Summer	January	warm temperatures, dry	Vr active
Winter	June through July	cold temperatures, rain	Vr inactive
Spring	September	cool to warm temperatures, some rain	Vr active, particularly on sunny days

brief summary of the behavior of the lizards during each season.

Most of the data presented here have been collected from lizards of all four species with a fresh mass of ≈ 1.5 kg. However, some species can exceed this size; e.g., male *V. panoptes* can grow to a fresh mass of 6 kg. All species are diurnal heliotherms that eat a variety of invertebrate and vertebrate prey (Shine 1986, Green et al. 1991). *V. mertensi* is a semiaquatic species that forages in and around permanent water (Shine 1986). *V. panoptes* inhabits woodlands and floodplains in the study area. *V. gouldii* is found sympatric with *V. panoptes* in woodlands with sandy soils, but this species is not found on floodplains (K. Christian, *personal observation*).

Energy exchange model

Microclimatic measurements and lizard morphological measurements (size, absorptances to solar radiation) were combined in an energy exchange model used to calculate an equilibrium temperature that the animal would attain under a given set of environmental conditions (T_e ; Bakken 1981, 1992, Bakken et al. 1985). We used a model designed and applied in studies of lizards similar in size to the varanids in this study (Christian and Tracy 1981, Tracy 1982, Christian et al. 1983, 1984). Because the model has been detailed in these earlier reports, we will only describe the specific adaptations used in this study.

T_e values were calculated at hourly intervals for the two most extreme microhabitats: full sun and deep shade (Christian and Tracy 1981). We assumed that the lizards could achieve any T_b between these two extremes by shuttling and selecting sites of partial shade (Cowles and Bogert 1944, Christian et al. 1983). A third T_e value was calculated for each hourly interval, which assumed that the animals were one-half in sun and one-half in shade. This corresponds to either an animal spending 50% of its time in each of sun and shade, or to an animal being half in sun and half in shade at a given time.

We used hourly means of the microclimatic data as input for the biophysical model. In general, the thermal environments were similar from day to day within a

season for each site. Kangaroo Island differed in so far as the days on which measurements were made in spring varied from very cool and overcast to sunny and warm. Measurements from this season were divided into two groups: cloudy spring days and sunny spring days.

We used a lizard fresh mass of 1.5 kg and a snout-to-vent length of 46 cm in calculations of T_e . The solar absorptivity for each species was measured using an integrating reflectance sphere (Christian and Tracy 1981, Porter and Tracy 1983). The mean values of solar absorptivity for the dorsal surfaces of *V. rosenbergi*, *V. mertensi*, *V. panoptes*, and *V. gouldii* were 0.93, 0.93, 0.86, and 0.78, respectively (Christian et al. 1996).

Indices of thermoregulation

Exploitation index.—Hertz et al. (1993) emphasized the importance of relating the T_b 's of an animal in the field to the T_b 's of the animal in a simple environment such as a laboratory thermal gradient. Measurements from the thermal gradient are used to determine the set-point range of T_b 's that an animal would strive to maintain in the absence of conflicting variables present in the natural environment (Huey and Slatkin 1976, Gans and Pough 1982, Huey 1982, Withers and Campbell 1985, Peterson 1987, Hertz et al. 1993). Here we present an index of thermoregulation in which the amount of time the lizards spend in the set-point range is expressed as a percentage of the time available for them to achieve T_b 's within the set-point range for a given season (as determined by the relevant T_e 's). This is an index of the extent to which the lizards exploit the available thermal environment and is symbolized by Ex (for exploitation). A similar approach has been used to examine thermoregulation by garter snakes (Huey et al. 1989).

Indices of Hertz et al. 1993.—Indices to evaluate temperature regulation and the relationship between T_b 's and T_e 's have been proposed by Hertz et al. (1993). Their method evaluates thermoregulation within the framework of the animal's environment. They suggested evaluating a lizard's thermal preference using several indices to address the separate components of

TABLE 2. Definitions of the indices and other symbols used in this paper.

Index or symbol	Definition
T_b	Body temperature
T_e	Operative temperature: This is the equilibrium temperature that the lizards would attain in a given microclimate. In this study T_e has been calculated using a biophysical model in conjunction with animal characteristics and hourly microclimatic data.
T_{set}	Set-point range of T_b s: This is taken to be the central 50% of the T_b s selected in a laboratory thermal gradient.
d_b	An index of field body temperatures relative to the set-point range as measured by the mean of the absolute value of the deviations of field active T_b s from T_{set} .
d_e	An index of the average thermal quality of a habitat as measured by the mean of the deviations of T_e from T_{set} .
E	Effectiveness of temperature regulation: $E = 1 - (d_b/d_e)$
suffix all	Refers to indices calculated across all periods from which data were collected
suffix set	Refers to indices calculated across periods when it was possible for the animal to achieve a T_b within its set-point range
Ex	Exploitation of the thermal environment: This is calculated as the time in which an animal's T_b s are within T_{set} , divided by the time available for the animal to have its T_b within T_{set} .

the complex question of "How carefully does an ectotherm thermoregulate?" These authors suggested that their indices should be adapted to specific circumstances rather than used only in the original form. Two aspects of our study required alterations of the indices proposed by Hertz et al. (1993): we used a biophysical model to calculate T_e 's and we calculated the indices for each individual rather than an entire population.

As originally proposed by Hertz et al. (1993), the indices of thermoregulation (d_b , d_e , and E ; defined in the three subsections immediately following) were calculated for all periods for which data were collected, and these indices are designated with the suffix "all." Additionally, indices were calculated for the period of the day during which the animals could achieve the set-point range as indicated by the T_e 's. These indices are designated by the suffix "set."

Definition of d_b index.—After determining the set-point range in the laboratory, field measurements of T_b can be compared to it (Licht et al. 1966) by calculating the absolute values of the deviations from this set-point range. For instance, a T_b that is within the set-point range is assigned a deviation value of 0 (Hertz et al. 1993). We calculated the mean of the deviations (d_b) for each individual during each season.

Definition of d_e index.—Analogous to the index of d_b , the mean deviation between the T_e 's and the set-point range can be used as an index, d_e , of the thermal quality of the habitat (Hertz et al. 1993). A small d_e

implies that optimal microclimatic conditions are abundant in the habitat, but if d_e is large the animals must thermoregulate carefully to stay within the set-point range. This index was originally defined using physical models to determine T_e 's and d_b 's (Hertz et al. 1993) rather than mathematical calculations of T_e . The use of multiple physical models allowed Hertz et al. (1993) to measure the availability of different T_e 's in the habitat of small, relatively sedentary *Anolis* lizards. To calculate d_e 's using the mathematical models requires that some estimate of the availability of different thermal environments be incorporated into the index.

The varanid lizards in this study are mobile with home ranges that encompasses many types of microhabitat (Green and King 1978, Shine 1986, Christian and Weavers 1994). It is reasonable to assume that an individual of these species of varanids could easily select either extreme (sun or shade) microhabitat. It would be extraordinarily difficult to further subdivide the availability of microhabitats of the varanids for a number of reasons: there is a large amount of heterogeneity of microhabitats within the large home ranges occupied by the lizards; they use innumerable cracks in the soil and burrows as thermal refugia; and the use of water by *V. mertensi*. Thus, in calculating d_e , we used both extremes of T_e for a given time of day to calculate the mean of T_e in sun and T_e in shade. We recognize that this use of the d_e index does not have the same resolution with respect to the heterogeneity of thermal microhabitats (which would be important for small, less mobile species) as originally described (Hertz et al. 1993), but it nevertheless serves as an index of thermal quality that is determined by microclimatic conditions and animal properties. The direct comparison of d_b with d_e serves as an indicator of thermoregulation. If $d_b < d_e$, then the animals select thermal environments that result in T_b 's within the set-point range more often than would be achieved by selecting random thermal environments and are, by definition, thermoregulating (Hertz et al. 1993).

Definition of E , an index of effectiveness of thermoregulation.—The third index proposed by Hertz et al. (1993) is an indication of the effectiveness of thermoregulation: $E = 1 - (d_b/d_e)$. This value will generally range from 0 (indicating no thermoregulation) to 1 (indicating very precise thermoregulation), but theoretically it is also possible for an animal to have a negative E if it actively avoids microsites with thermal conditions that would result in a T_b within the set-point range.

The indices and other symbols used in this paper are listed in Table 2.

Analyses.—Values for d_b and E were calculated for each individual during each season, allowing a comparison of seasons within a species and between species within each season by ANOVA. The amount of activity (in minutes per day) was analyzed by repeated measures ANOVA using the activity measurements col-

lected during each of three days of telemetry for each individual.

Measurement of set-point temperatures in the laboratory

Set-point temperatures were measured by allowing post-absorptive goannas with temperature-sensitive transmitters to move about freely in a photo-thermal gradient. Their T_b 's were recorded at 15-min intervals. The thermal gradient consisted of an air conditioned room (4 × 4 m) with fluorescent lights on the ceiling and heated by a series of 150 W heat lamps concentrated in one corner and one lamp near the center of the room. This provided a continuous temperature gradient as indicated by floor temperatures that ranged from 22° to 50°. The relationship between light and heat in photo-thermal gradients has been discussed by Sievert and Hutchison (1989), and although the separate effects of heat and light were not experimentally determined here, we judged that the thermal gradient was appropriate for determining the set-point range because these are heliothermic species. Measurements were taken over an entire day for each lizard. Five individuals of each of the three tropical species were measured. Set-point temperatures for *V. rosenbergi* were taken from King (1977), who used a similar study design. The bounds of the central 50% of the observed T_b 's were used to estimate the set-point range (Hertz et al. 1993) for each of five individuals for each species, then a mean lower and upper set-point was calculated from these individual measurements.

Temperature transmitters

Radio transmitters (Telonics, Tempe, Arizona; Austec, Edmonton, Alberta, Canada; and AVM Instruments, Livermore, California) were attached to the side of the base of the tail of the lizards to remotely measure body temperatures (T_b) and the activity of free-ranging animals. The transmitters were fitted to the animals for periods of 7–10 d and were glued directly to the side of the tail, then wrapped with adhesive bandage (total mass of package ranged from 30 g for smaller animals to 50 g for larger individuals). The temperature transmitter included a probe that extended from the transmitter and was inserted 8 cm through the cloaca into the lower gut. On a few occasions, the probes did not remain in place, and the data from those animals have been excluded from the analyses. The transmitters were calibrated in a water bath against a standard thermometer before and after use, and they remained accurate within 0.2°. On days when temperature and activity measurements were recorded, animals were monitored between sunrise and ≈30 min after sunset. During this period T_b 's were recorded every 15 min.

Activity transmitters

Activity-sensitive transmitters were attached to the opposite side of the tail from temperature transmitters.

These included a mercury switch that, when moved, produced a signal, audible from the telemetry receiver. This technique for measuring activity was developed and used on *V. varius* by Weavers (1983), who determined that monitors cannot walk without moving the tail to a degree that produced the activity signal. Activity in the present study is, therefore, defined as the locomotion of the animal. We typically monitored the locomotory activity of three animals at a time. The three activity frequencies were programmed into a separate Telonics radio receiver from the one used to measure T_b 's, and the three frequencies were continuously scanned with the receiver automatically moving to the next frequency after 5 s. Thus, each of the three animals was sequentially sampled for 5 s and then the 15-s cycle began again. Activity during the 5-s sample was taken to represent 15 s of activity and activity was therefore recorded in blocks of 15, 30, 45, and 60 s·min⁻¹·animal⁻¹.

Microclimate

Microclimate data were collected simultaneously with telemetry measurements. Solar radiation was measured with a Middleton pyranometer in conjunction with an integrator (Middleton, BWD Proprietary, Limited, Melbourne, Australia). Environmental temperatures (air, soil surface in the sun, and soil surface in the shade) were measured hourly with 30-gauge type K thermocouples with their sensing tips painted white to reduce radiation errors (Christian and Tracy 1985a). Wind speed at lizard height (8 cm) was measured with a miniature cup anemometer (Rimco, Analite Proprietary, Limited, Melbourne, Australia) on some days and was qualitatively described on other days at hourly intervals. The reflectivity of ground surfaces was measured by inverting the pyranometer (30 cm above the ground) and expressing the inverted measurement as a fraction of the upright reading (Christian and Tracy 1981).

RESULTS

Over 8000 T_b 's were measured on 203 lizard-days from 57 lizards. Table 3 shows the number of lizards and lizard-days from which T_b and activity data were recorded for each species and season.

Mean midday T_b 's and set-point ranges

The midday (1100–1600) mean T_b 's as measured in the laboratory thermal gradient and the corresponding set-point ranges for each species are given in Table 3. Table 3 lists the midday grand mean T_b 's measured in the field for each species during the different seasons. A repeated measures ANOVA comparison of the three tropical species reveals that *V. panoptes* selected a significantly higher T_b in the thermal gradient than did *V. mertensi*, but *V. gouldii* selected T_b 's that were not different from the other two species. Although individual measurements are not available for *V. rosenbergi* (from King 1977) to include this species in the analysis, the

TABLE 3. A) Summary of body temperature data from four species of varanid lizards as measured in a laboratory thermal gradient and in the field during different seasons. Body temperature (T_b) data from the field are given as grand mean midday (1100–1600) T_b s, and the number of lizards (n) and lizard-days during which measurements were made are given for each species and season. The set-point range of T_b s as determined in a laboratory thermal gradient is also given for each species. One standard error is given in parentheses. Laboratory measurements for *V. rosenbergi* are from King (1977), and, because individual measurements were not available from this species, the laboratory data were not included in the statistical analysis. B) A summary of the analysis (repeated measures ANOVA) of midday field T_b s and laboratory measurements.

A) Summary of body temperature data					
Species/season	n	Field		Laboratory	
		Lizard-days (no.)	Midday T_b (°C)	Set-point range (°C)	Méan (°C)
<i>V. panoptes</i>					
wet (all)	6	19	35.2 (0.76)	35.8–37.6	36.7 (0.51)
wet (active)	4	11	36.4 (0.76)		
dry	6	20	36.2 (0.67)		
late dry	6	14	32.9 (0.69)		
<i>V. gouldii</i>					
wet	5	16	35.9 (0.27)	34.0–36.3	35.1 (0.51)
dry	4	14	28.2 (0.68)		
late dry	4	11	32.9 (0.58)		
<i>V. mertensi</i>					
wet	4	12	34.0 (0.28)	33.1–35.5	34.2 (0.32)
dry	5	15	33.4 (0.62)		
<i>V. rosenbergi</i>					
summer	8	42	36.3 (0.31)	34.0–36.5	35.2
winter	5	20	17.4 (0.53)		
spring (cloudy)	4	12	25.5 (1.22)		
spring (sunny)	4	8	34.8 (0.86)		
B) Summary of statistical analyses					
Field T_b s: Comparing seasons for each species:					
<i>V. panoptes</i>	dry > late dry; $F_{2,11} = 5.22, P = 0.03$				
<i>V. gouldii</i>	wet > late dry > dry; $F_{2,8} = 36.56, P < 0.0001$				
<i>V. mertensi</i>	no significant differences; $F_{1,6} = 3.42, P = 0.11$				
<i>V. rosenbergi</i>	summer > winter and cloudy spring; $F_{2,14} = 241.85, P < 0.0001$				
<i>V. rosenbergi</i>	summer and spring > winter (sunny spring not different from summer); $F_{2,14} = 201.70, P < 0.0001$				
Field T_b s: Comparing species for each season:					
wet/summer	V_g, V_r and $V_p > V_m$; $F_{3,17} = 366, P = 0.03$				
dry/winter	$V_p > V_m > V_g > V_r$; $F_{3,13} = 214.50, P < 0.0001$				
late dry/spring	V_g and $V_p > V_r$ (cloudy); $F_{2,8} = 72.97, P < 0.0001$				
late dry/spring	V_r (sunny) not different from other species; $F_{2,8} = 0.36, P = 0.70$				
Laboratory T_b s: Comparing the tropical species:					
	$V_p > V_m$ (V_g not different from other two); $F_{2,9} = 4.86, P = 0.037$				

laboratory means and set-point ranges of *V. gouldii* and *V. rosenbergi* (King 1977) are virtually identical (Table 3).

Comparing the midday mean T_b 's measured in the field for each species over three seasons (Table 3) reveals a general pattern of significantly lower T_b 's during periods of inactivity. This is true both for *V. rosenbergi*, which experiences winter inactivity, and the two terrestrial tropical species that have periods of inactivity during the dry season (*V. gouldii*) and the late dry season (*V. gouldii* and *V. panoptes*). The aquatic *V. mertensi*, however, did not show a seasonal decrease in activity or in T_b . During spring, *V. rosenbergi* experience extremely variable climatic conditions. On cloudy days in this season, the midday mean T_b 's were not different from winter T_b 's. On sunny spring days,

however, the midday mean T_b 's were not significantly different from the summer mean (Table 3).

During the dry/winter season, all four species had significantly different midday T_b 's in the following order from the lowest to the highest: the temperate-zone *V. rosenbergi*, the inactive *V. gouldii*, the active *V. mertensi*, and the extremely active *V. panoptes*. During the late dry/spring, using only sunny spring days for *V. rosenbergi*, mean midday T_b 's do not differ among the species despite the fact that *V. gouldii* and *V. panoptes* spend much of the time underground during this period, while *V. rosenbergi* emerge from their burrows every day. On cloudy spring days, *V. rosenbergi* had significantly lower T_b 's than did *V. gouldii* and *V. panoptes* at the same time of year. During the wet/summer season, when all species are active, *V. mertensi* had

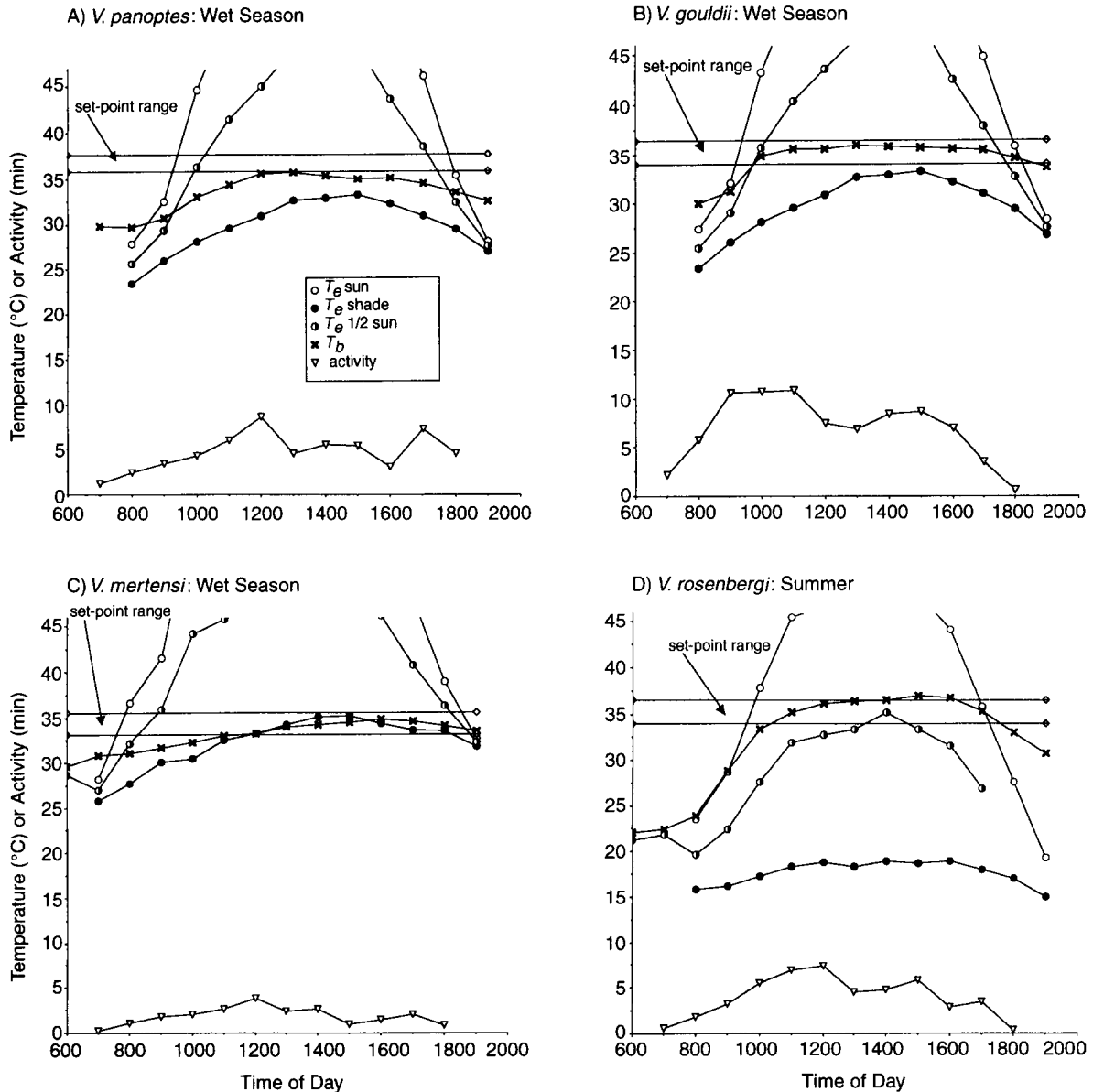


FIG. 1. Grand mean body temperatures (T_b ; as measured by radio telemetry), operative temperatures (T_e 's), and time spent in locomotory activity as a function of time of day of free-ranging varanid lizards during the wet/summer season. Plots are shown for (A) *V. panoptes*, (B) *V. gouldii*, (C) *V. mertensi*, and (D) *V. rosenbergi*. Operative temperatures are as calculated from a biophysical model in conjunction with microclimatic data: T_e sun is for an animal that remains in full sun, T_e shade is for an animal that remains in deep shade, and T_e 1/2 sun is for an animal half in sun and half in shade. Only T_e 's $< 45^\circ\text{C}$ are shown to preserve resolution in these plots. The first and last records of locomotory activity approximate the times the animals emerge from and retreat to their overnight shelters. The set-point range of body temperatures, as measured in a laboratory thermal gradient, is delineated by the horizontal lines.

significantly cooler T_b 's than did the other three species, which did not have different T_b 's from each other.

The field midday mean T_b 's generally fall within the set-point range during periods when the animals are active, but they are lower than the set-point range during periods of inactivity. If only the midday T_b 's of active animals are considered, the grand mean T_b for *V. panoptes* in the wet season is higher and within the set-point range (Table 3).

Operative temperatures (T_e 's)

Figs. 1, 2, and 3 show the T_e 's in sun, in shade, and in 50% sun throughout the day for each species for the different seasons. Data were only collected for *V. mertensi* during the wet and dry seasons. The hourly grand mean diurnal T_b 's, as measured by telemetry, are also plotted on these graphs, along with the hourly grand mean activity (in minutes). In some cases, early and late in the day the T_b 's are warmer than either T_e . This

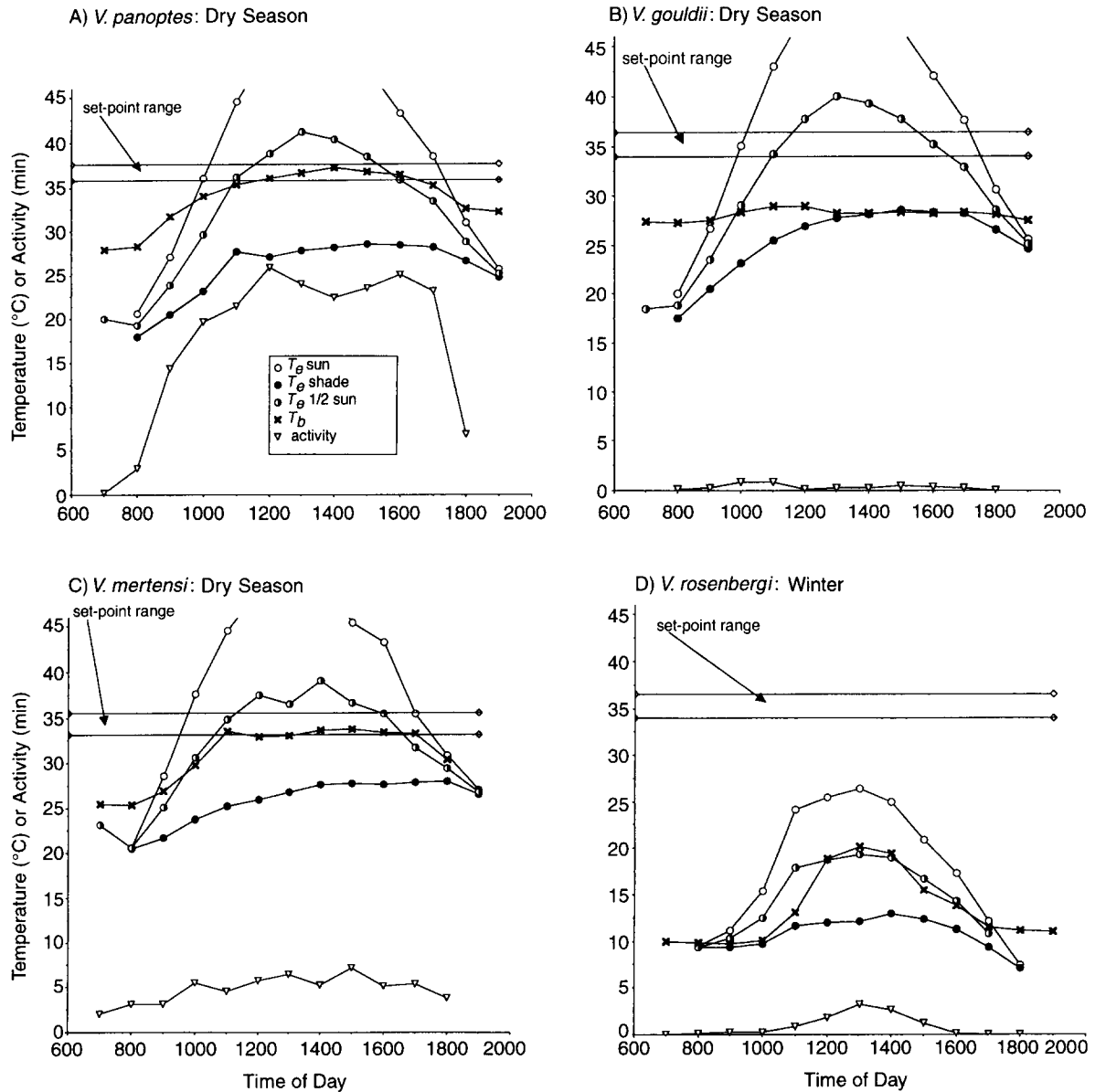


FIG. 2. Grand mean body temperatures, operative temperatures, and time spent in locomotory activity as a function of time of day of free-ranging varanid lizards during the dry/winter season. See Fig. 1 legend for details.

suggests that the animals are inside burrows, which are warmer microhabitats than are aboveground microhabitats at these times (Christian et al. 1984).

During the hotter times of the year, the T_e in areas receiving the full radiant energy of the sun reach extremely high temperatures ($>70^\circ\text{C}$ in some cases); at these times, the observed T_b 's are generally very close to the much lower shade T_e , indicating that the animals spend much of their time in the shade or the water.

The calculated T_e 's in these figures are derived from microclimatic data collected from days that were considered to be "typical" days during each season. During spring on Kangaroo Island the thermal environment is variable, depending on cloud cover, and we

have made separate calculations of T_e 's and divided the observed T_b 's and activity for cloudy days (Fig. 3C) and sunny days (Fig. 3D). The calculated T_e 's for *V. rosenbergi* in winter suggest that this species cannot attain the set-point range because of limitations of the thermal environment on typical days. King (1977) reported two instances (out of 15 d of radiotelemetry of five lizards) in which individuals of this species attained high T_b 's on sunny days during winter. Both our data and those of King (1977, 1980) suggest that this species is only occasionally able to attain the set-point range on unusually warm days during winter.

The pattern of activity across the day in each season can be related to the T_b 's and the T_e 's (Figs. 1–3).

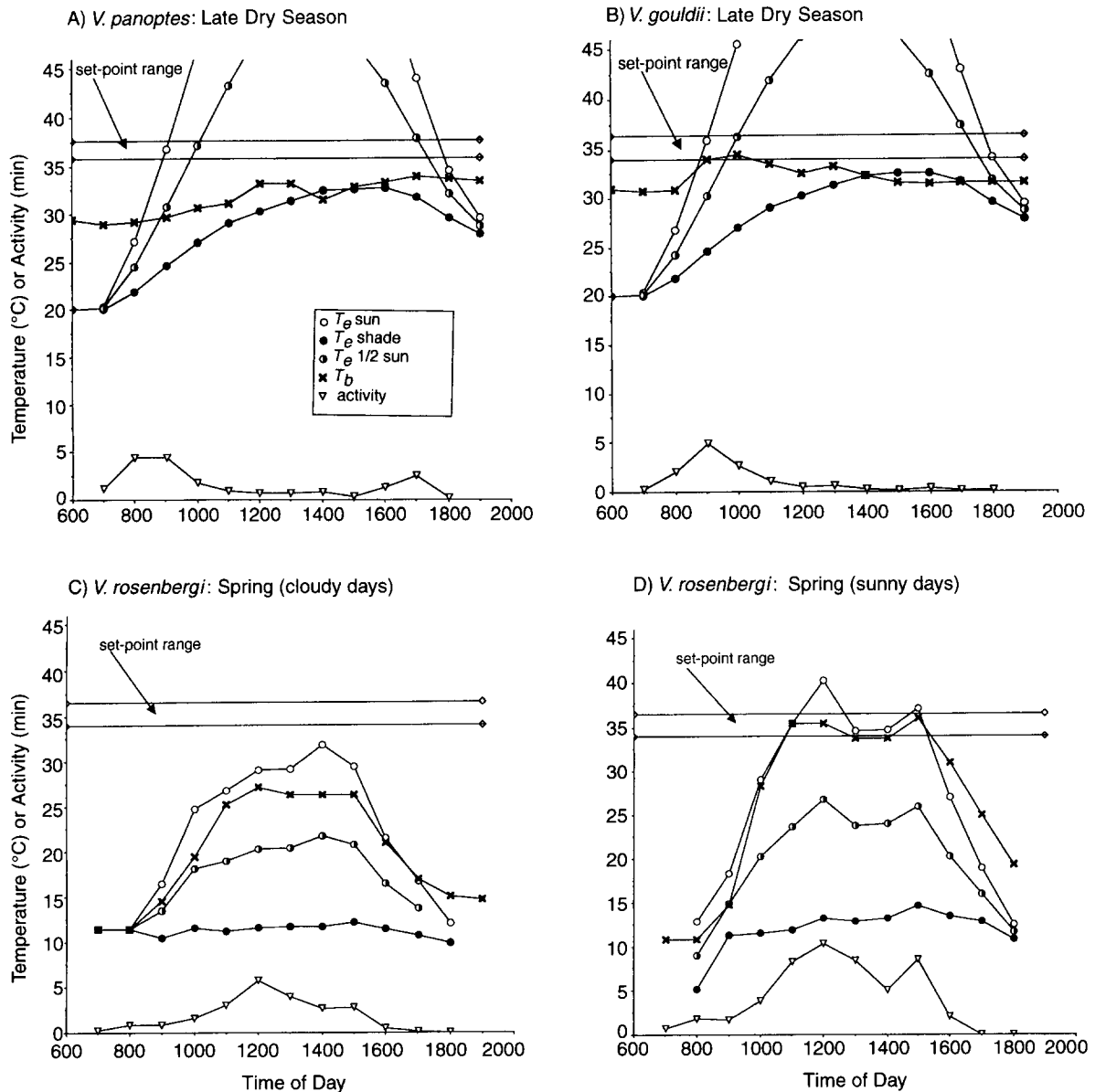


FIG. 3. Grand mean body temperatures, operative temperatures, and time spent in locomotory activity as a function of time of day of free-ranging varanid lizards during the late dry/spring season (see Fig. 1 legend for details). No data were collected for *V. mertensi* during this season. The data for *V. rosenbergi* during this season are divided into (C) cloudy days and (D) sunny days.

During the seasons when the lizards are most active (the wet/summer for all species, and the dry season for *V. panoptes* and *V. mertensi*) their pattern of activity is relatively evenly distributed across the day. During seasons when lizards are generally inactive, there is either virtually no activity at all (*V. gouldii* in the dry season) or there is a small peak of activity in the morning (*V. gouldii* and *V. panoptes* in the late dry). Under cool to cold conditions (spring and winter for *V. rosenbergi*) the lizards have a midday peak in activity.

Exploitation of the available time in the set-point range (Ex)

Table 4 shows the number of hours per day that a lizard in a given season can possibly achieve its set-point range, the number of hours per day that the lizards do achieve the set-point range (based on grand mean T_b 's as measured by telemetry), and the index Ex which is the ratio of these two time intervals and represents a measure of the exploitation of the available thermal environment. This index can range from 0 to 100%, and the full range is represented in Table 4.

TABLE 4. The hours per day during which it is possible to attain the set-point range of T_b s, the hours that the set-point is actually achieved based on grand mean T_b s for each species during the various seasons, and the index Ex, which is the ratio of the two preceding columns ($\times 100$) and represents the percentage of the available time in the set-point range that is exploited by the lizards.

Species	Season	Time set-point range possible (h)	Time set-point range exploited (h)	Ex
<i>V. panoptes</i>	wet (all)	8.7	1.0	12
	wet (active)	8.7	5.7	66
	dry	7.3	5.0	68
	late dry	9.0	0.0	0
<i>V. gouldii</i>	wet	9.1	8.7	96
	dry	7.8	0.0	0
	late dry	9.1	1.4	15
<i>V. mertensi</i>	wet	11.3	8.1	72
	dry	8.1	6.0	74
<i>V. rosenbergi</i>	summer	7.7	7.3	95
	winter	0.0	0.0	0
	spring (cloudy)	0.0	0.0	0
	spring (sunny)	4.6	4.6	100

In *V. panoptes*, Ex ranges from 0 to only 68%. This is the lowest maximum found for any of the four species, suggesting that this species does not exploit its thermal environment to the extent of the other species studied. During the wet season this species only exploits 12% of the time available to achieve the set-point range, and this is due in part to the fact that on some days in this season the animals remain in their burrows despite favorable thermal conditions and despite (or perhaps due to) an abundance of prey in this season (Christian et al. 1995). If only days when the animals are active in the wet season are considered, *V. panoptes* remain in the set-point range 5.7 h, which corresponds to an Ex value of 66%. This species is generally inactive in the late dry, resulting in an Ex value of 0%. The Ex indices for *V. gouldii* range from 0% in the dry season to 96% in the wet season. During the late dry season Ex is low (15%) due to general inactivity, although a small peak in morning activity corresponds with the time the set-point range is reached (Fig. 3B). *V. mertensi* does not have a season of inactivity, and its Ex indices only range from 72 to 74%. In *V. rosenbergi*, the index ranges from 0% in winter and on cloudy spring days to 95% in summer and 100% on sunny spring days.

In the wet/summer season all species except *V. panoptes* have high Ex indices. In the dry/winter season *V. mertensi* and *V. panoptes* have moderately high values, but the other two species have Ex indices of 0%.

Field thermoregulation relative to the set-point range (d_b)

Fig. 4A shows the mean d_b indices calculated by comparing the field T_b 's with the set-point body tem-

perature range selected in the laboratory. The figure legend summarizes the statistical comparisons of the means of the d_b set values. The d_b set index was not calculated for *V. rosenbergi* during winter or on cloudy spring days because the animals cannot achieve their set-point range under these conditions. Comparing d_b set indices for the different seasons within each species shows that *V. panoptes* and *V. gouldii* have significantly higher values of d_b set during the late dry season and, for *V. gouldii*, during the dry season. These higher values of d_b set correspond to periods of reduced activity, with the animals spending many days in their burrows. For *V. mertensi*, which does not have a season of inactivity, the d_b set indices are not significantly different between the wet and dry seasons. Similarly, mean d_b set indices do not differ for *V. rosenbergi* on sunny spring days and summer days, which are the periods when this species is most active.

Comparing the d_b set indices of species within each season demonstrates larger deviations from the set-point range in periods of relative inactivity, but during the wet/summer season (when all species are generally active), *V. panoptes* has a significantly higher index than all other species. During the late dry/spring season the active *V. rosenbergi* had smaller deviations from the set-point range (considering sunny days only) than *V. panoptes*, which were inactive. The d_b set index of *V. gouldii* was not significantly different from either *V. panoptes* or *V. rosenbergi* in the late dry/spring season. The stability of the temperature inside the underground refugia of *V. gouldii* results in T_b 's close to the set-point range, giving the incorrect impression of relatively careful thermoregulation. *V. panoptes* also spends much of its time underground during this season, and the two species experience similar T_b 's (Fig. 3). However, in this season *V. gouldii* has a lower d_b set index than *V. panoptes* because *V. gouldii* has a set-point range that is lower and closer to the T_b 's experienced by the lizards in their natural burrows.

d_b indices compared to d_e indices

The indices of the thermal quality of the habitat, d_e all and d_e set, are shown for each species and season in Fig. 4B. These indices were calculated assuming equal access to sun and shade in the habitat, but d_e set was not calculated for *V. rosenbergi* during winter or cloudy spring days because the set-point range could not be achieved with the prevailing environmental conditions. The d_e set value for sunny spring days in the environment of *V. rosenbergi* is the highest calculated for all four species, and this reflects low environmental temperatures and solar radiation levels that result in low T_e 's compared to the set-point range. For the three tropical species, the d_e set values were highest during the hotter times of the year (the wet and late dry seasons) when the hot environmental conditions resulted in high T_e 's compared to the set-point range.

A d_b value that is less than the corresponding d_e value

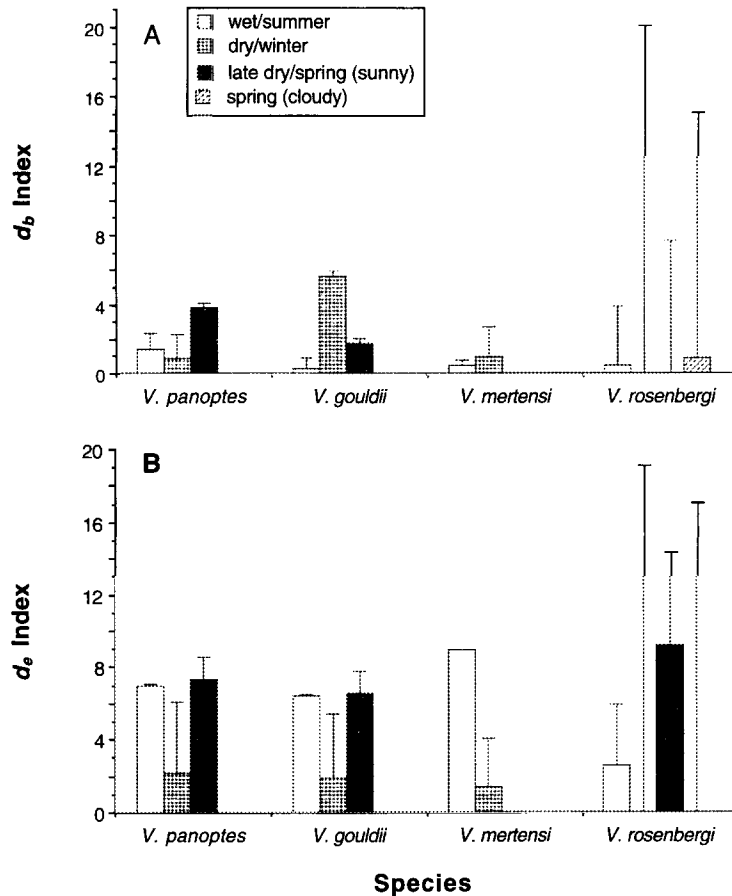


FIG. 4. Means of (A) the d_b index indicating the degree to which the animals experience T_b 's outside the set-point range, and (B) the d_e index of the quality of the thermal environment. The bars represent indices that have been calculated using only those hours during which the set-point range could be attained ("set"), and the lines extending above the bars represent indices calculated for all hours for which data were collected ("all"). The summary statistics (below) refer to the indices calculated over periods when the set-point range was possible. There are no summary statistics for d_e because only one value was calculated for each species during each season.

Summary of Statistical Analyses

Species	Seasonal comparisons	Statistics	
<i>V. panoptes</i> (Vp)	late dry > wet and dry	$F_{2,13} = 5.72$	$P = 0.01$
<i>V. gouldii</i> (Vg)	dry > late dry > wet	$F_{2,10} = 64.16$	$P < 0.0001$
<i>V. mertensi</i> (Vm)	no significant differences	$F_{1,7} = 3.71$	$P = 0.10$
<i>V. rosenbergi</i> (Vr)	sunny spring days not different from summer	$F_{1,10} = 2.06$	$P = 0.18$
Seasons	Species comparisons	Statistics	
wet/summer	Vp > Vg, Vm, and Vr	$F_{3,18} = 5.65$	$P = 0.012$
dry	Vg > Vm and Vp	$F_{2,11} = 46.10$	$P < 0.0001$
late dry/spring	Vp > Vr (sunny)	$F_{2,11} = 4.36$	$P = 0.04$

indicates thermoregulation because it implies that the animals have been selective about the microhabitats they used (Hertz et al. 1993). This criterion suggests that there is thermoregulation in all cases for which the indices have been calculated except for *V. gouldii* during the dry season and for *V. rosenbergi* during winter (Fig. 4). During the dry season, *V. gouldii* spends most of the time underground, but this is also true for both

V. gouldii and *V. panoptes* during the late dry season (Christian et al. 1995). However, the warm conditions in their underground refugia during this season, combined with the very hot conditions aboveground, result in d_b values less than the corresponding d_e values. Although *V. rosenbergi* regularly emerge from their burrows during winter (King 1977, Christian and Weavers 1994), they are rarely able to attain their set-point

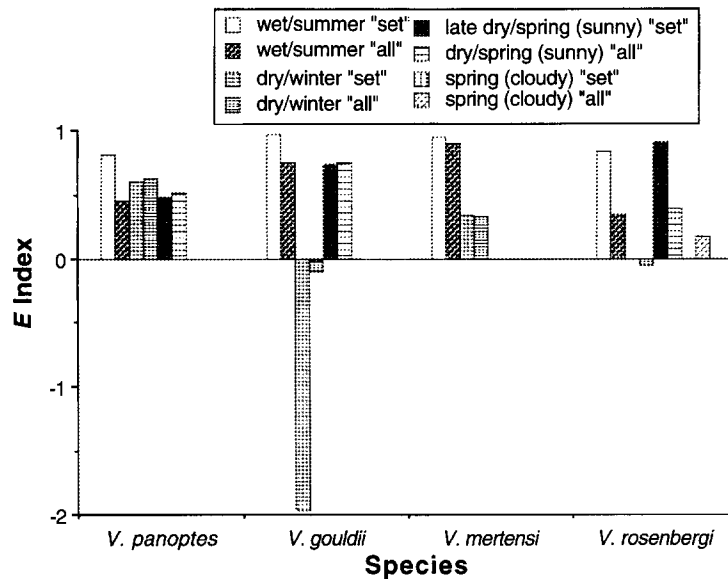


FIG. 5. Means of the E index of the effectiveness of thermoregulation for each species during each season. Indices have been calculated using all hours for which data were collected ("all"), as well as for only those hours during which the set-point range could be attained ("set"). The summary statistics (below) refer to the indices calculated over periods when the set-point range was possible.

Summary Statistics

Species	Seasonal comparisons	Statistics	
<i>V. panoptes</i> (Vp)	no significant differences	$F_{2,13} = 1.33$	$P = 0.30$
<i>V. gouldii</i> (Vg)	late dry and wet > dry	$F_{2,10} = 108.31$	$P < 0.0001$
<i>V. mertensi</i> (Vm)	wet > dry	$F_{1,7} = 13.94$	$P = 0.007$
<i>V. rosenbergi</i> (Vr)	sunny spring not different from summer	$F_{1,10} = 0.98$	$P = 0.35$

Seasons	Species comparisons	Statistics	
wet/summer	Vg and Vm > Vp; Vg > Vr	$F_{3,18} = 3.89$	$P = 0.03$
dry/winter	Vp and Vm > Vg	$F_{2,11} = 43.42$	$P < 0.0001$
late dry/spring	Vr > Vp	$F_{2,11} = 4.62$	$P = 0.03$

range. The fact that the d_b value is less than the d_c value corresponds to our observations that the animals often do not move far from their burrow entrance in this season. The reasons for these animals emerging from their burrows under such conditions are unclear (Christian and Weavers 1994).

Effectiveness of thermoregulation (E)

Fig. 5 shows the indices of the effectiveness of thermoregulation, E_{all} and E_{set} , for each species during each season, and a summary of the results of statistical comparisons of the E_{set} indices within species and within seasons is given in the figure legend. Corresponding statistical comparisons for the E_{all} values yielded similar results except for *V. rosenbergi* on sunny spring days (see Discussion). *V. panoptes* showed no significant difference in E_{set} during different seasons, but *V. gouldii* had a negative E_{set} during the dry season, indicating that they avoid thermally optimal conditions by remaining in their burrows during this season. *V. mertensi* had a significantly greater E_{set} dur-

ing the wet season compared to the dry season. This is, in part, due to the hot conditions in the wet season resulting in a high d_c compared to the less extreme dry season. *V. rosenbergi* have high E_{set} indices that are not significantly different during summer and sunny spring days.

Comparing species within each season (Fig. 5), there is a pattern for the inactive animals to have significantly low E_{set} values implying a lack of thermoregulation. During the wet/summer season, when all species were active, *V. panoptes* had the lowest E_{set} value, *V. mertensi* and *V. gouldii* had the highest, and *V. rosenbergi* had an intermediate value. During the late dry/spring season *V. rosenbergi* had a significantly higher E_{set} than *V. panoptes*, and *V. gouldii* was not different from either of these two species.

Activity

In addition to the daily pattern of activity (shown relative to T_c and T_b in Figs. 1–3), the total locomotory activity (in minutes per day) can be compared for the

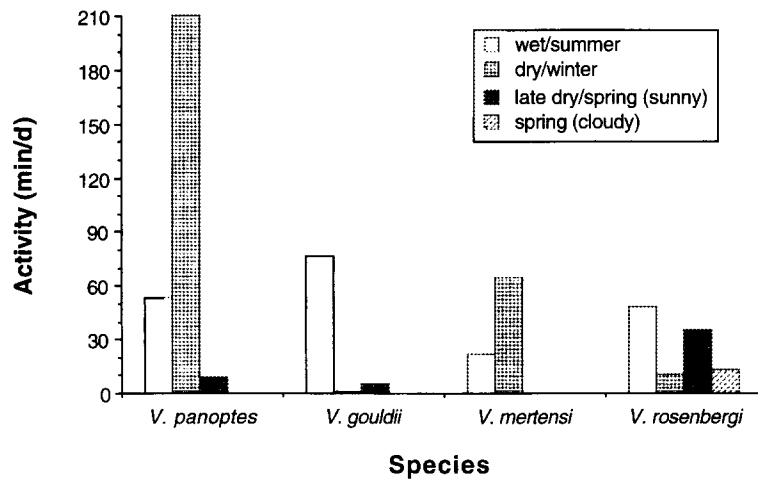


FIG. 6. Grand means of time spent in locomotory activity per day.

Summary of Statistical Analyses (repeated measures ANOVA)

Species	Seasonal comparisons	Statistics	
<i>V. panoptes</i> (Vp)	dry ≥ wet > late dry	$F_{2,19} = 31.18$	$P < 0.0001$
<i>V. gouldii</i> (Vg)	wet > late dry and dry	$F_{2,17} = 7.11$	$P = 0.005$
<i>V. mertensi</i> (Vm)	no significant difference	$F_{1,7} = 2.37$	$P = 0.17$
<i>V. rosenbergi</i> (Vr)	summer, spring (sunny) > winter, spring (cloudy)	$F_{3,14} = 9.14$	$P = 0.001$

Seasons	Species comparisons	Statistics	
wet/summer	no significant differences	$F_{3,19} = 1.69$	$P = 0.20$
dry/winter	Vp ≥ Vm, Vr and Vg	$F_{3,15} = 14.06$	$P < 0.0001$
late dry/spring (cloudy)	no significant differences	$F_{2,20} = 0.58$	$P = 0.57$
late dry/spring (sunny)	Vr > Vp and Vg	$F_{2,20} = 7.64$	$P = 0.003$

different species and times of year. Fig. 6 shows the grand means of the measurements of locomotory activity per day and a summary of the statistical analyses (repeated measures ANOVA) of these data is given in the figure legend. *V. panoptes* are most active during the dry season, least active in the late dry season, and engage in an intermediate amount of activity in the wet season. *V. gouldii* are most active in the wet season and are much less active in the dry and late dry seasons. There was no seasonal difference in the amount of activity per day for the semiaquatic *V. mertensi*. *V. rosenbergi* was significantly more active in summer and on sunny spring days than in winter and cloudy spring days.

Comparing the activity among species within each season revealed no difference among the species in the amount of activity during wet/summer season. During the dry/winter season, however, *V. panoptes* was significantly more active than any of the other species. The least active during this season were *V. gouldii* and *V. rosenbergi* despite the fact that optimal thermal conditions were available to *V. gouldii* but not to the overwintering *V. rosenbergi*. *V. mertensi*'s activity is intermediate during this season compared to the other species. During the late dry/spring season there were no differences among *V. panoptes*, *V. gouldii*, or *V.*

rosenbergi if only cloudy spring days are considered for *V. rosenbergi*. However, if only sunny spring days are considered, this temperate species is significantly more active than *V. panoptes* and *V. gouldii*.

DISCUSSION

Problems in assessing thermoregulation

The indices of thermoregulation used in this study to examine and compare thermoregulation in the field incorporate information obtained from thermoregulating animals in the laboratory. The laboratory measurements of set-point range provide a frame of reference for evaluating field body temperatures (Hertz et al. 1993). Although using laboratory measurements as a reference is a valuable technique, possible problems with this approach are worth mentioning. Implicit in this approach is the assumption that the animals in the laboratory thermoregulate by optimally exploiting the available thermal environment. That is, that the selected T_b 's represent the unencumbered, preferred body temperatures that they would select in an ideal habitat. However, the animals in the laboratory possibly do not thermoregulate in this way either because they are encumbered by unmeasured stress reactions that result in them not thermoregulating in an optimal fashion, or,

although they may thermoregulate optimally, they may have a different thermoregulatory response to the artificial environment in the laboratory compared to the field. A related problem is that the set-point temperature range may change seasonally (Christian et al. 1983, Christian and Bedford 1995). If this were the case, then at least the thermoregulatory indices would indicate a seasonal change even if additional experiments were needed to fully interpret the nature of the change. Thus, some of the seasonal differences discussed could, in part, be due to seasonal shifts in the set-point range. The discussion that follows does not purport to explain all aspects of the thermoregulatory behavior of these four species, but the indices and the temperature graphs (Figs. 1–3) reveal a variety of thermoregulatory responses across seasons and across species.

Thermoregulation during the wet/summer season

Although all four species are considered to be active during the wet/summer season, *V. panoptes* had the lowest *Eset* index, indicating less effective temperature regulation by this species during this season. Also, the mean midday T_b for this species during the wet season was lower than the set-point range, and the *Ex* index was the lowest of the four species during this season. Although generally active, *V. panoptes* were inactive some wet season days (three of six lizards were inactive for at least 1 d, for a total 8 inactive d out of 19 d of telemetry). The animals tended to gain fresh mass during this period, suggesting the possibility that they were inactive not because of adverse conditions, but rather because food is abundant during the wet season and the animals do not need to forage every day (Christian et al. 1995). If only the active days are considered, however, the mean midday T_b is within the set-point range, and *Ex* is 66%. This is considerably higher than the *Ex* of 12% if all days are included in the analysis and is very similar to the *Ex* of 68% for this species during the dry season. However, both of these *Ex* values are lower than those of any other species during active seasons, suggesting that *V. panoptes* is a less careful thermoregulator than the other species.

The *Ex* values for *V. gouldii* and *V. rosenbergi* are similar and very high, suggesting that these species thermoregulate carefully in this season. The thermoregulatory indices of *V. mertensi* are also relatively high in this season, but this species does not reach the set-point range as quickly as *V. gouldii* and *V. rosenbergi* in the mornings (Fig. 1). This may be related to morning activity in the water, and the thermal characteristics of semiaquatic species will be discussed in more detail.

Thermoregulation during the dry/winter season

The two terrestrial tropical species have very different behaviors and activity patterns during the dry

season, when *V. panoptes* is most active and *V. gouldii* is least active. This, however, is also mediated by local conditions. The very active *V. panoptes* live near the floodplain, but those living in the woodland with the *V. gouldii* have activity and energetic patterns similar to *V. gouldii* (Christian et al. 1995). Thus, the availability of food and water near the floodplain during the dry season seems to dramatically influence the seasonal activity patterns of *V. panoptes*.

In the dry/winter season *V. mertensi* and *V. panoptes* have moderately high *Ex* values, but the other two species have *Ex* indices of 0%. It is interesting to note, however, that this value for *V. rosenbergi* is due to the fact that there is no time when the set-point range can be reached, but for *V. gouldii* the *Ex* of 0% is due to the fact that the lizards avoid microhabitats that would result in T_b 's in the set-point range even though the animals could possibly attain the set-point range for 7.5 h/d.

Thermoregulation during the late dry/spring season

The decline of activity in *V. panoptes* living on the floodplain coincides with the complete drying of this area in the late dry season. This is evident in some of their thermoregulatory indices (Figs. 4 and 5, Table 4). The fact that the comparison of d_e with d_b indicates thermoregulation by both *V. panoptes* and *V. gouldii* during the late dry season, when both are underground much of the time, underscores the cautionary note that the thermoregulatory indices need to be used together and in conjunction with observations of the activities of the animals (Heath 1964, Hertz et al. 1993). The activity-sensitive radio transmitters indicated that during the periods of inactivity the lizards did not move around inside the burrows to thermoregulate underground. Thus, the small deviations between T_b 's and the set-point range in these animals simply reflect the fact that the T_e 's inside the burrows at this time of year in the tropical environment are near the set-point range.

In the late dry/spring season *V. panoptes* and *V. gouldii* have very low *Ex* values. On cloudy spring days *Ex* is also low for *V. rosenbergi*, but on sunny spring days this species exploits the available thermal environment to the maximal extent possible.

Thermoregulation in the semiaquatic species

Unlike the two terrestrial tropical species (Christian et al. 1995) and the temperate-zone species (Christian and Weavers 1994), the semiaquatic *V. mertensi* does not have an inactive season. This species shows no seasonal differences with respect to midday body temperatures, activity, or d_b set. The significantly lower *Eset* value during the dry season is the result of a slight (but not significant) decrease in d_b set and a markedly higher quality thermal environment during the dry season (d_e set is only 1.43 compared to 8.90 in the wet

season). The thermal environment of *V. mertensi* during the dry season has the highest thermal quality (lowest d_e) of those measured (Fig. 4B).

The index E contains a ratio and is thus sensitive to extreme values in either the numerator or the denominator. The high quality of the thermal environment in the dry season results in a low E_{set} value suggesting, incorrectly, that *V. mertensi* is an ineffective thermoregulator during this season. One way to correct this anomaly would be to calculate a more complicated d_e that incorporates the water temperatures and the effects of evaporative cooling from recently emerged lizards. This would result in a higher d_e , which would cause a higher E_{set} value. Alternatively, the thermoregulatory characteristics of the water monitors can be determined by inspection of Figs. 1C and 2C and Table 4 which indicate that the grand mean T_b 's of this species are within the set-point range for 8.1 h/d during the wet season (72% of the available time in the set-point range) and 6.0 h/d during the dry season (74% of the available time) despite foraging forays into the water. Thus, we suggest that the seasonal difference in E_{set} is a consequence of the way this index is calculated, and we conclude from inspection of Figs. 1C and 2C that this species carefully thermoregulates in both seasons. Although telemetry measurements were not made during the late dry season for *V. mertensi*, observations of this species revealed definite activity during this period. Both the activity data and the thermoregulatory indices from this species indicated very little difference between the wet and dry seasons with respect to the behavior of these semiaquatic lizards. Their diet consists largely of aquatic organisms (Shine 1986). The availability of water, and presumably therefore food, throughout the year results in a stability of habitat for this species that apparently precludes the need for a period of inactivity.

It is interesting to note that this semiaquatic species has a lower set-point range and lower midday T_b 's in the field than the terrestrial species (during the seasons they are active). Although the midday means we report here for *V. mertensi* (33.4° and 34.0°C for the dry and wet seasons, respectively) are slightly higher than the mean that has been previously reported (32.0°) by King (1977, 1991) for a smaller sample of measurements and individuals from this species, the mean T_b is nevertheless still lower than the terrestrial species we studied, and similar to other semiaquatic varanids (Wikramanayake and Green 1989, King 1991, Wikramanayake and Dryden 1993).

Thermoregulation by temperate and tropical lizards

Given the very different thermal environments in which they live, it is instructive to compare the thermoregulatory characteristics of the temperate-zone *V. rosenbergi* with the tropical species. As discussed, *V. rosenbergi* apparently thermoregulate very carefully on

sunny spring days by remaining in the sun to keep T_b within the set-point range to the extent that $Ex = 100\%$. The indices of thermoregulation also suggest very careful thermoregulation by this species during summer. The exploitation of 95% of the time available to be in the set-point range is the highest for any species during the summer/wet season. In all respects, *V. rosenbergi* is an equal or a more careful thermoregulator than *V. panoptes* when physical conditions allow this species to attain its set-point T_b (summer and sunny spring days). *V. gouldii*, however, is also an effective thermoregulator (higher E_{set} and similar Ex compared to *V. rosenbergi*) during the wet season when environmental temperatures are at their highest. Considering all indices during seasons of activity, the temperate-zone *V. rosenbergi* and the tropical *V. gouldii* are both careful thermoregulators compared to the other two tropical species.

The indices of thermoregulation indicate that *V. panoptes* is the least effective thermoregulator, but it is also the most active (particularly during the dry season). One explanation for this apparent lack of careful thermoregulation when *V. panoptes* is very active is that the animals are forced to be active to obtain food in the dry season and that careful thermoregulation is a secondary consideration. Alternatively, it could be argued that, apart from avoiding extreme T_b 's, careful thermoregulation is simply not a characteristic of this species relative to others. This interpretation is supported by the similarity of the Ex value in the dry season (68%) compared to the wet season when only days of activity are considered (66%). The thermal opportunities exist during both of these seasons for the animals to achieve T_b 's within the set-point range for much of the day (Figs. 1 and 2), but this species consistently fails to fully exploit those opportunities. Although the field data suggests less effective thermoregulation by *V. panoptes*, this conclusion is contradicted by data showing that in the laboratory this species has the narrowest set-point range of the four species studied.

It may be necessary for *V. rosenbergi* to thermoregulate carefully in its temperate environment to attain T_b 's that allow optimal performance (Huey 1982) during active foraging. In the tropical environment, however, it may be possible for lizards to be near the optimal T_b range by simply avoiding extremes. The result indicating that some tropical varanid species appear to thermoregulate more carefully than others in the same habitat is intriguing. This is indicative of differences in behavior and the use of microhabitats, but the ecological and historical causes and effects of the differences in how carefully each species thermoregulates are unknown.

Locomotory activity

Of particular note is the extreme locomotory activity of *V. panoptes* during the dry season (Fig. 6). The mean

amount of time these animals spent in translocation was 3.5 h/d, but on some days some individuals were moving 6.6 h/d. The other species, and *V. panoptes* during other seasons, were active for periods of ≤ 77 min/d (Fig. 6). The Cuban iguana *Cyclura nubila* spent 92 min/d in movement (Christian et al. 1986), and the Galapagos land iguana *Conolophus pallidus* spent ≈ 100 min/d during each of three seasons (Christian and Tracy 1985b). The radiotelemetric measurements of time spent in locomotion do not provide any measurement of the intensity of activity, but with respect to the time spent in locomotion, the only direct measurement of extremely high levels of activity by any varanid is for *V. panoptes* during the dry season (Fig. 6).

The time spent in locomotion is not correlated with the index of effectiveness of thermoregulation (E_{set}) when all values are considered ($P = 0.50$), or when only the seasons when the lizards were active are considered ($P = 0.36$). Similarly, there is no correlation between E_x and time spent in locomotion when all values are considered ($P = 0.10$), or when only seasons when the lizards were active are considered ($P = 0.54$). As discussed, the highly active *V. panoptes* in the dry season have values of all the thermoregulatory indices that indicate only moderately careful thermoregulation.

The period of relative inactivity for *V. rosenbergi* corresponds to winter, but for the tropical species the periods of inactivity correspond to the dry periods of the year when food availability is low (Christian et al. 1995). During the dry season, the *V. panoptes* that live near the floodplain forage near the edge of the remaining water. This requires that they walk several kilometres from the edge of the floodplain, where they spend the nights in burrows, to the edge of the water. This distance, along with their foraging activities at the water's edge (Christian et al. 1995), account for the large amount of time spent in locomotory activity during this season.

Accuracy of thermoregulation

One of the aims in developing the indices of thermoregulation was to split the large, complex question of "How carefully does an animal thermoregulate?" into its distinct components (Hertz et al. 1993). If, as described by Hertz et al. (1993), d_b is calculated across all periods of the day regardless of whether or not the set-point range can be attained, this index is confounded by the limitation of the thermal environment rather than being a measure of the thermoregulatory behavior of the animal. Thus, if an animal is in an environment where its set-point range can only be attained for a short period of the day, then the animal will have a large $d_{b,all}$ if this index is calculated across the entire day. If the animal thermoregulates very accurately within the set-point range during the portion of the day when this is possible, then this careful thermoregulation will be obscured in the $d_{b,all}$ because of the inclu-

sion of the other periods of the day in the calculation of the index. This problem is exacerbated in the calculation of E_{all} because $d_{b,all}$ is used in a ratio. If limitations of the thermal environment are reflected in both the numerator and the denominator of the index, then the index of the effectiveness of thermoregulation is difficult to interpret and potentially misleading. The restriction of the calculations of d_b , d_c and E to the period of the day when the animal can attain its set-point range unambiguously separates the thermoregulatory responses of the animal (d_b) from the quality of the thermal environment (d_c). This case is illustrated by *V. rosenbergi* on sunny spring days. Inspection of Fig. 3D reveals that these animals thermoregulate very accurately within the set-point range during the period of the day when this is physically possible, and the lizards exploit 100% of the available time at T_b 's within the set-point range (Fig. 3D, Table 4). On the basis of these results, we conclude that these animals are thermoregulating very carefully, and, in fact, could do no better given the limitations of the thermal environment. If, on the other hand, we calculated d_b across the entire day, then this index is much higher (8.53 compared to 0.84). Similarly, if d_b and d_c are calculated across the day then E_{all} is lower (0.41 compared to an E_{set} of 0.91) indicating less effective thermoregulation. Inspection of Fig. 3D alone is evidence for careful thermoregulation by *V. rosenbergi* on sunny spring days. Depending on how the indices are calculated, they can either support this conclusion or obscure it. If an investigator collects data for several early morning hours before the period when the set-point range can be achieved, a very different conclusion may be drawn compared to the case where data are collected only a short period prior to the availability of the set-point range. Inconsistencies in the periods during which data are collected relative to times when the set-point range can be achieved could result in differences in $d_{b,all}$ and E_{all} indices that are simply due to arbitrary sampling, and are unrelated to the thermoregulation of the animals. However, if the indices of thermoregulation are limited to periods when the set-point range can be attained, E_{set} is an index of thermoregulation that reflects the thermoregulatory behavior of the animal.

It nevertheless may be interesting to examine how well animals thermoregulate when the set-point range is not achievable, but care must be taken with respect to the sampling periods to obtain meaningful results. The problems outlined pertain primarily to questions related to behavioral selection of thermal sites. By including all hours of information in the analyses, the metrics of Hertz et al. (1993) emphasize the efficacy of the thermal environment. Thus, the indices, as originally proposed by Hertz et al. (1993), are particularly useful for examining questions at the scale of geographic range or habitat selection in which the overall quality of the thermal environment is of primary concern. On the other hand, by limiting the calculations

to periods when the set-point range can be achieved, the emphasis is directed towards the thermoregulatory behavior of the animals. The various metrics of thermoregulation have merit, but the questions being asked will determine which indices are most appropriate for a given study.

The *Eset* index must be used cautiously, however, because of the nature of ratios. For example, the *Eset* of *V. gouldii* during the late dry season (0.74) suggests more effective thermoregulation than that of *V. panoptes* during the dry season (0.60). Inspection of Figs. 3B, 2A, and the corresponding *Ex* values of 15 and 68%, however, indicates that the opposite may be true. In the calculation of *Eset* for *V. gouldii*, the numerator of the ratio is relatively low because the animals spend much of the day near the set-point range even though very little time is spent within the set-point range. The relatively large denominator indicates a relatively harsh thermal environment, and combined with the low numerator yields the *Eset* of 0.74. The numerator is even lower in the calculation for *V. panoptes* during the dry season indicating less variation from the set-point range. The denominator is also relatively low indicating a benign thermal environment. Thus, despite the fact that the lizards spend 5 h/d in the set-point range, the *Eset* value is only 0.60. It might be argued that in this case the index of thermoregulatory effectiveness of *V. gouldii* should be positively weighted to reflect the harsher thermal environment. However, the animals spend most of the day with T_b 's below the set-point range even though the thermal environment is harsh due to extremely high environmental temperatures rather than low environmental temperatures. Thus, the index has not weighted the harshness of the thermal environment in a meaningful way, and it incorrectly indicates more effective thermoregulation in *V. gouldii* in the late dry season compared to *V. panoptes* in the dry season. On the other hand, inspection of Figs. 3B, 2A, and the corresponding *Ex* values readily reveals which of these lizards thermoregulates more effectively.

Much can be learned about a lizard's thermoregulatory behavior by inspecting plots such as Figs. 1–3 that show the range of T_e 's available to the animal as well as the T_b 's selected and the set-point range selected in the laboratory. In fact, with respect to describing the thermoregulatory pattern of a species in a given season, the indices of thermoregulation did not provide any new information that could not be determined directly from the plots of T_e 's and T_b 's (Figs. 1–3). However, this graphical approach to quantifying thermoregulation (including the *Ex* index) may be misleading in some environments. A high *Ex* value correctly indicates careful thermoregulation in an environment in which there are many sites which would result in sub-optimal T_b 's. This would be the case in any relatively open habitat in which T_e in the sun is greater than the set-point range, such as the open woodland and flood-

plains inhabited by the varanid lizards of this study. However, this index alone would not indicate thermoregulation in a homogeneous thermal environment in which T_e 's of most sites were within the set-point range (Christian and Bedford 1995), such as the heavily shaded forests inhabited by *Anolis gundlachi* (Huey 1982, Hertz 1992b).

The phylogenetic history could conceivably influence thermoregulation. For example, the fact that *V. rosenbergi* emerge from their burrows even on the coldest winter days (Christian and Weavers 1994) may be related to some unknown ancestral function rather than to a contemporary function. However, the data presently available for varanids do not suggest that the midday mean, set-point T_b 's, or thermoregulatory indices are related to phylogenetic history. The variability described here for four species that are closely related (Baverstock et al. 1993) suggests that ecological factors rather than phylogeny may determine these thermoregulatory characteristics. The seasonal differences in behavior of individual *V. panoptes* near the floodplain compared to those in the woodland (Christian et al. 1995) also support this conclusion. The fact that the three semiaquatic species for which there are data (King 1991 as well as these results) are members of three different major lineages of varanids (Baverstock et al. 1993) suggests that the relatively low T_b 's selected by semiaquatic species are not related to phylogenetic history.

Despite extensive measurements of T_b 's and microclimatic data and analyses of a variety of indices of thermoregulation in conjunction with biophysical modelling, fundamental questions still remain about these species that are not easily addressed by any of these tools. For example, is the only moderately careful thermoregulation of *V. panoptes* during its season of extremely high activity due to thermoregulation being secondary to other ecological demands that require high activity? Or, apart from avoiding extremes, perhaps careful thermoregulation is not a characteristic of this tropical species. Do physiological factors, ecological factors, or both determine whether a species is a careful thermoregulator or not, and what is the role of phylogenetic history in determining thermoregulatory characteristics? Does *V. panoptes* exhibit variable activity and thermoregulatory behavior during the wet season because food is so plentiful that they need to forage only on some days? If so, why is this not so for *V. gouldii* during the wet season? Why does *V. rosenbergi* emerge from its burrow on winter days even though the lizards can only very rarely achieve the lower set-point T_b ? Why do semiaquatic varanids such as *V. mertensi* select T_b 's (both in the laboratory and in the field) that are lower than terrestrial species even though they have the thermal opportunities to attain similarly high T_b 's? Questions such as these approach the fundamental decision-making processes of thermoregulating reptiles in variable environments, and the

development of the tools needed to answer these kinds of questions represent a challenge for future studies of thermoregulation.

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