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Eric D. Wikramanayake; Gil L. Dryden

*Copeia*, Vol. 1993, No. 3. (Aug. 18, 1993), pp. 709-714.

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## Thermal Ecology of Habitat and Microhabitat Use by Sympatric *Varanus bengalensis* and *V. salvator* in Sri Lanka

ERIC D. WIKRAMANAYAKE AND GIL L. DRYDEN

Habitat and microhabitat use by *Varanus bengalensis* and *V. salvator* differ considerably; *V. bengalensis* ranged further inland from aquatic habitats than the semiaquatic *V. salvator*, which was found mostly in riparian and aquatic habitats. When active, *V. bengalensis* used warm, open microhabitats, but inactive animals either took refuge in structures such as tree hollows, termite mounds, and burrows or remained in microhabitats which provided some cover but little protective refuge. The temperatures in refuges were stable but lower than daytime air temperatures, whereas the temperatures in the latter microhabitats were unstable. The habitats and microhabitats of *V. salvator* were, however, thermally stable and cooler than microhabitats of active *V. bengalensis*. *Varanus salvator* also used burrows for refuge. The body temperatures of the two species reflected their differential use of thermal habitats and microhabitats; active *V. bengalensis*, which used warm open microhabitats, had a high active body temperature, but inactive animals in refuges had low body temperatures. *Varanus salvator*, which used cooler microhabitats during activity and inactivity, maintained a stable but low body temperature. Its body temperature also approximated the ambient temperatures in the riparian and aquatic habitats. Thus, the two species had different thermoregulatory behaviors which required use of habitats and microhabitats with different thermal regimes.

MANY reptiles thermoregulate behaviorally by selecting appropriate habitats, microhabitats, and activity times (Huey, 1982; Pianka, 1986). Differences in thermoregulatory behavior among sympatric lizards can reflect thermal niche partitioning, which is manifested along the spatial and temporal resource axes (Magnuson et al., 1979; Tracy and Christian, 1986). However, unless the immediate history of activity and microhabitat use of an animal is known, observations of thermoregulatory behavior can be misleading (Avery, 1982). This is especially true with large lizards because of the thermal inertia associated with body size and their ability to exert some control over body heat flux by vasomotor adjustments (Brattstrom, 1973; McNab and Auffenberg, 1976; Earll, 1982).

Limited data on sympatric *V. bengalensis* and *V. salvator* in Sri Lanka suggest that their thermoregulatory behaviors are different and that there are some differences in habitat use and activity times (Wikramanayake and Green, 1989). Both species are relatively large, with adult *V. bengalensis* and *V. salvator* attaining snout-vent lengths exceeding 0.5 m and 1.0 m, respectively (Deraniyagala, 1953; Wikramanayake and Dryden, unpubl. data). Both are widely foraging predator-scavengers with overlapping, catholic diets (Deraniyagala, 1953; Losos and Greene, 1988; pers. obs.).

In this study we investigated the thermal correlates of habitats and microhabitats used by sympatric *V. bengalensis* and *V. salvator*, to determine whether their different thermoregulatory behaviors require use of space and time with thermal regimes which may reflect thermal niche partitioning.

### STUDY SITE

The study was conducted at Uda Walawe National Park (UWNP; 6°30'N, 80°52'E), Sri Lanka between April and Oct. 1989. A few observational data points on habitat and microhabitat use (see Methods) were also gathered on the Panadura River near the southwestern coast, about 15 km south of Colombo.

The park is located immediately south of the central hills, and straddles the wet and dry zones. Its habitat consists of tropical monsoon forest, riparian forest (bordering the Walawe River and confluent streams), scrub jungle, savannah, isolated rocky outcrops, and numerous ephemeral ponds. The monsoon forest consists of small patches surrounded by sparse scrub jungle and grassland/savannah. The major tree species in the riparian forest, *Terminalia arjuna* and *Hopea cordifolia*, are confined to this habitat and form a dense, high canopy. Detailed descriptions of the park habitat are given in Nugegoda et al. (1987) and Dryden and Wikramanayake (1991).

## METHODS

We used radiotelemetry to continuously monitor habitat use, microhabitat use, and activity of both species. Temperature-sensitive transmitters also allowed us to measure the lizards' microhabitat temperatures. These data were then used to confirm other observational data on habitat and microhabitat use, activity, and body temperatures.

Microhabitat is defined as the animal's immediate physical environment and is described by further qualifying the habitat types according to whether the animal was in shade or sun and above or on the ground. "Microhabitat temperature" was measured by the radio transmitter as the shaded ambient temperature immediately above the dorsal, pelvic region of the animal. This was an air temperature if the animal was in a terrestrial habitat or the water temperature if in an aquatic habitat. Outside air temperature was measured with a Schultheis thermometer as the shaded bulb temperature 1 m above ground level in an open, sunny area.

Behavior was classified as (1) active—animals observed foraging, walking, or basking in open, exposed microhabitats; or (2) inactive—animals resting in microhabitats affording shade and cover (e.g., tree branches with overhead vegetative cover) or in refuges.

We identified four habitat types as follows: (1) refuge—physical structures such as burrows, termite mounds, tree hollows, etc., which provided protection; (2) inland—all terrestrial/arborescent habitats such as monsoon forest, scrub jungle, grassland/savannah located inland from the riparian forest; (3) riparian—all riverine forest, which varied in extent depending on the location but was demarcated by a sharp transition from high forest to scrub or grassland/savannah; and (4) aquatic—any aquatic habitat including the river, streams, lakes, ponds, etc.

*Radio-tagged animals.*—Five animals of each species were captured and equipped with temperature-sensitive radio transmitters (=radio-tagged animals). The transmitters (11–13 g), weighed less than 1% of the body weight of the smallest animal of either species so equipped. Each transmitter was sewn onto a piece of Cordura nylon material (7 × 10 cm), which was then contact cemented onto the dorsal surface of the animal's pelvic region. The transmitters were positioned such that the thermistor probes were exposed to ambient conditions but were shaded from incident sunlight. Radio-tagged animals were released at their respective capture points

and allowed 18 h to seven days of acclimation before being radio tracked.

Each animal was tracked continuously from 0600–1800 h for three consecutive days, during which time we determined activity, habitat type, microhabitat (in each habitat), microhabitat temperature, air temperature, behavior, time of day, and weather condition. These data were obtained every 15 min throughout the tracking period. Animals were observed, with binoculars when necessary, from 25–100 m depending on the habitat, and we took precautions to avoid disturbing or alarming them. At the end of each tracking period, the animals were recaptured to remove the transmitters and released.

*Non-radio-tagged animals.*—Habitat, microhabitat, and temperature data were also obtained for other animals which were not radio tagged (nontagged animals). We searched extensively for animals throughout the different habitat types in the study site and examined potential refuges such as tree hollows, dens, and termite mounds. Searches covered all hours between 0600 h and 1800 h. When an animal was spotted, we recorded its habitat, microhabitat, microhabitat temperature, behavior, air temperature, time of day, and weather. The microhabitat temperature was recorded at the exact spot (trunk position) that the animal was first sighted. Other variables were recorded as for the radio-tagged animals. The microhabitat data include multiple observations on some animals but none on the same day; thus multiple observations were considered to be independent. Data from these nontagged animals were treated separately from the radio-tagged animals during the analysis.

*Body temperature.*—Animals of both species were also captured throughout the study to determine body temperatures. Body temperature was obtained immediately after each capture, and capture times did not exceed 10 min. Because prior experiments on heating and cooling have shown considerable thermal inertia in large varanids (Brattstrom, 1973, McNab and Auffenberg, 1976; Earll, 1982), we assumed there would be no substantial change in body temperature during the capture period. To ensure that a deep cloacal temperature was obtained, we first inserted a stiff plastic tube (8 cm) into the cloaca, and the Schultheis thermometer was inserted through this tube until the bulb emerged from the opposite end. Along with each body temperature, we obtained the cor-

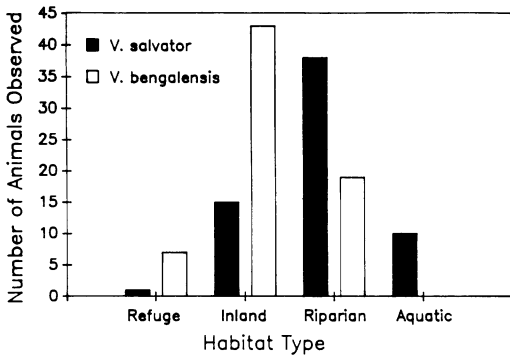


Fig. 1. Distribution of *Varanus bengalensis* and *V. salvator* in the four habitat types. Habitat categories are defined in Methods.

responding air temperature and recorded time of capture to generate body temperature profiles during the day for each species. Body temperature data were obtained more than once for recaptured animals, but because there was an interval of at least two days between captures, the multiple body temperatures obtained from the same animal were considered independent.

Because free-ranging *Varanus* are somewhat difficult to capture and our sample sizes for body temperatures are low, we incorporated data from a previous study conducted at Ambalantota, about 40 km south of UWNP, but also along the Walawe River (see Wikramanayake and Green, 1989), into the analysis. A regression of body temperature versus air temperature confirmed (ANCOVA; *V. bengalensis*:  $n = 26$ ,  $F = 0.094$ ,  $df = 1$ ,  $P = 0.76$ ; *V. salvator*:  $n = 24$ ,  $F = 0.110$ ,  $df = 1$ ,  $P = 0.74$ ) that there were no intersite differences in the temperature relationships for each species.

## RESULTS

*Habitat/microhabitat use and temperature.*—There was a marked interspecific difference in habitat and microhabitat use by the two species. *Varanus salvator* was most often found in riparian and aquatic habitats, whereas *V. bengalensis* ranged further from the river and was more frequently found in inland habitats (Fig. 1). Those *V. bengalensis* found in riparian habitats were usually smaller animals, presumably juveniles and subadults. *Varanus bengalensis* also occupied refugia such as termite mounds, small burrows, tree hollows, etc., whereas *V. salvator* took refuge in extensive burrow systems and dense thickets close to aquatic habitats.

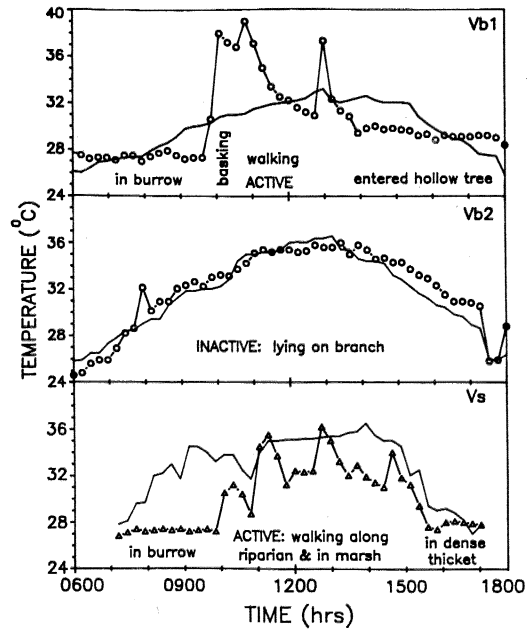


Fig. 2. Microhabitat-behavior profiles for radio-tagged *Varanus bengalensis* (Vb1 and Vb2) and *V. salvator* (Vs). Microhabitat temperature profiles are indicated by the lines with symbols and air temperature profiles by the plain lines. Temperatures were recorded every 15 min from 0600–1800 h.

Radiotelemetry indicated differences in microhabitat temperature regimes between the two species, as represented by the microhabitat-behavior profiles for two *V. bengalensis* and one *V. salvator* in Figure 2. Active *V. bengalensis* were mostly in microhabitats where temperatures were higher than air temperatures. The microhabitat-behavior profile for an active animal (Fig. 2, Vb1) shows that, after the animal emerged from its overnight burrow, it basked near the burrow entrance before walking toward and into a patch of forest. The ambient temperature inside the forest was lower than the outside air temperature. The animal finally entered a hollow tree trunk where the microhabitat temperature was stable. The temperatures in microhabitats occupied by inactive animals out of refuges fluctuated closely with air temperatures (Fig. 2, Vb2). Thus, inactive *V. bengalensis* were in microhabitats where temperatures either approximated, or were lower than, air temperatures (Fig. 2).

In contrast, active *V. salvator* tended to remain in microhabitats that were cooler than the daytime air temperature, and these microhabitat temperatures showed little variability relative to the air temperature (Fig. 2). The spikes

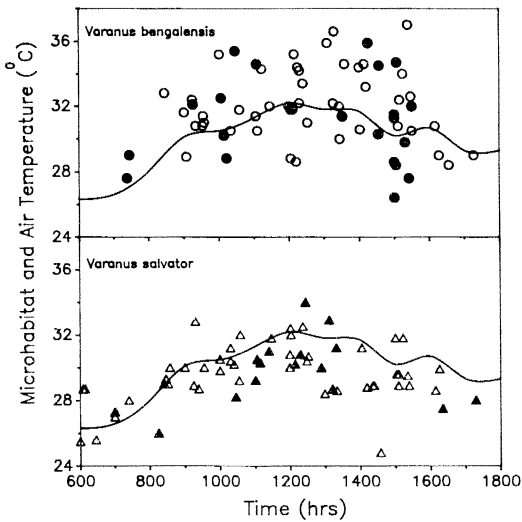


Fig. 3. Microhabitat temperatures for nontagged *Varanus bengalensis* (circles) and *V. salvator* (triangles) during the day. Active animals (walking, foraging, basking in open) are indicated by open symbols and inactive animals (in refuges, lying in shade) by shaded symbols. The daytime air temperature profile is represented by the solid line.

in the microhabitat temperature profiles for *Vs* in Figure 2 occurred when the animal crossed open stretches (e.g., elephant crossings at the river) in the riparian. Like the burrows, the dense thickets used by *V. salvator* were also thermally stable.

Most nontagged animal data were for active animals, which were foraging, walking, or basking and therefore easier to spot. From late morning to midafternoon, most microhabitat temperatures of active *V. bengalensis* fall above the daytime air temperature profile (Fig. 3). Microhabitat temperatures for *V. salvator*, however, are mostly below the air temperature profile (Fig. 3). Thus, during the day, active *V. bengalensis* occupied warmer microhabitats than did active *V. salvator* (Table 1). There were no statistical differences in microhabitat temperatures between inactive *V. bengalensis* and *V. salvator*.

**Body temperatures.**—The daytime body temperature profiles of each species reflect their respective microhabitat temperature profiles. Like its microhabitat temperature profile (Fig. 3), the body temperatures of *V. bengalensis* were higher during midday hours but lower during the early morning and evening hours (Fig. 4). Body temperatures of *V. bengalensis* extricated from refuges were lower than of animals out of refuges ( $29.9\text{ C} \pm 2.1$  and  $33.1\text{ C} \pm 3.3$ , respectively;

TABLE 1. TEMPERATURES (C MEANS  $\pm$  SD; n) OF MICROHABITATS OCCUPIED DURING ACTIVITY AND INACTIVITY FOR NONTAGGED *Varanus bengalensis* AND *V. salvator*. Active animals were walking, foraging, and basking in open microhabitats. Inactive animals were either resting in shaded microhabitats that provided cover or were in refuges. Statistical comparisons were by t-test.

	<i>V. bengalensis</i>	<i>V. salvator</i>	P
Active	32.1 $\pm$ 2.14; 47	29.7 $\pm$ 1.77; 46	<0.01
Inactive	31.5 $\pm$ 2.78; 15	29.6 $\pm$ 2.06; 18	n.s.
Refuge	30.2 $\pm$ 2.61; 7	28.2; 1	

$\bar{x} \pm \text{SD}$ ;  $t = 2.217$ ;  $df = 24$ ;  $P = 0.036$ ) regardless of time of day. In contrast to *V. bengalensis*, the profile for *V. salvator* showed relatively constant body temperatures throughout the day (Fig. 4).

The daytime body temperatures of *V. salvator* ( $30.4\text{ C} \pm 2.1$ ) were also much lower than those of active and inactive *V. bengalensis* out of refuges ( $33.1\text{ C} \pm 3.3$ ) ( $t = 3.15$ ;  $df = 42$ ;  $P = 0.002$ ). The slope of the regression between the body temperature and air temperature was higher for *V. bengalensis*, than that for *V. salvator* (Fig. 5; ANCOVA  $n = 50$ ;  $F = 14.879$ ;  $df = 1$ ;  $P = 0.000$ ).

## DISCUSSION

The two species of monitor lizards exhibit some spatial segregation. *Varanus bengalensis* ranges further from aquatic habitats and is active in warmer microhabitats than *V. salvator*, which is most frequently found in the cooler riparian or aquatic habitats.

The radio-tracking data confirmed the observations of habitat/microhabitat use and microhabitat temperatures of nontagged *V. bengalensis* during activity and inactivity. *Varanus bengalensis* is active during the midday hours and was frequently observed basking, walking, and foraging in warm, open microhabitats where temperatures often exceeded air temperature. Activity in such open, terrestrial habitats may facilitate achieving a high, active body temperature by this species. This relationship between body temperature of active *V. bengalensis* and air temperature is similar to that of other terrestrial varanids, which also tend to maintain higher-than-ambient body temperatures when active (Stebbins and Barwick, 1968; King, 1980; Auffenberg, 1981). However, inactive animals seek refuges which are cooler than ambient air temperatures or remain inactive in microhabitats that afford some cover (tree branches and

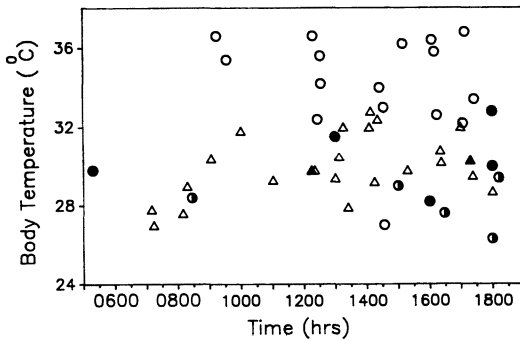


Fig. 4. Body temperatures for *Varanus bengalensis* (circles) and *V. salvator* (triangles) captured during the day. Fully shaded symbols indicate animals extricated from refugia (burrows, tree hollows, etc.), and partly shaded circles indicate inactive *V. bengalensis* caught while resting in shaded microhabitats (mostly branches) out of refugia.

similar perches) where temperatures fluctuate with air temperature. Body temperatures of inactive animals tend to be lower than those of active animals. Thus, *V. bengalensis* tends to occupy microhabitats with a wide range of temperature regimes, a behavior which is reflected in its body temperature profile.

Radiotelemetry indicated less daily variability in *V. salvator* microhabitat temperatures, which tend to be below air temperatures. *Varanus salvator* occupies these cooler microhabitats despite the presence of accessible, warmer microhabitats nearby. During the night, when air temperature decreases, *V. salvator* uses dense thickets and aquatic habitats as refugia (Wikramanayake and Green, 1989). The similarity between early morning and midday body temperatures of *V. salvator*, and its use of microhabitats with relatively constant temperatures, suggests that it uses thermally stable microhabitats to regulate body temperature during the day and night. *Varanus komodoensis* and *Varanus giganteus* also use thermally stable, warm, nocturnal microhabitats to maintain high body temperatures (Auffenberg, 1981; King et al., 1989).

The body temperature of active *V. salvator* is lower than the active body temperatures of larger (i.e., *V. komodoensis* and *V. giganteus*) and smaller (i.e., *V. bengalensis*) terrestrial varanids. It is, however, comparable to the body temperature of *V. niloticus*, another semi-aquatic varanid (Hirth and Latif, 1979; Bowker, 1984). Thus, the low body temperature of *V. salvator* probably reflects the use of aquatic habitats. Maintaining a body temperature that approximates the cooler temperatures of aquatic and

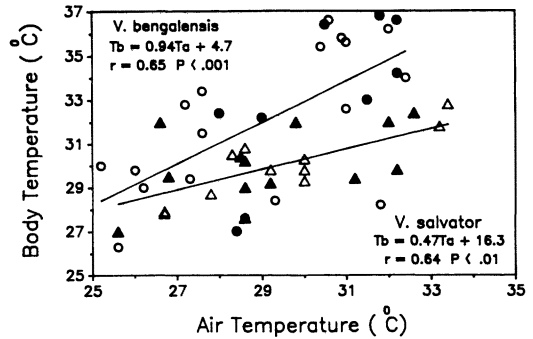


Fig. 5. Regression of body temperature ( $T_b$ ) and air temperature ( $T_a$ ) for *Varanus bengalensis* (circles; upper regression line) and *V. salvator* (triangles; lower regression line). Shaded symbols indicate animals captured at the Ambalantota site.

riparian habitats will enable *V. salvator* to exploit such habitats more efficiently, precluding the necessity for frequent trips to and from basking sites, which can be limiting in the densely canopied riparian habitat. Furthermore, eco-physiological adaptations to a low active body temperature can also allow *V. salvator* to commence activity early in the day, when the air temperature is still relatively low, without having to bask for extended periods to elevate body temperature.

Thus, our data indicate that the thermoregulatory behaviors of *V. bengalensis* and *V. salvator* are different. The two species achieve and maintain their respective body temperatures by using habitats, microhabitats, and activity times with specific thermal regimes, thereby exhibiting some spatial and temporal differences. Other sympatric varanids are also known to segregate along spatial resource axes (Pianka, 1969; Shine, 1986). However, more research is needed to determine whether the differences in the thermal behaviors of *V. bengalensis* and *V. salvator* are associated with interspecific ecological interactions.

#### ACKNOWLEDGMENTS

We thank M. Madawela for permission to work at UWNP, C. Jayawardene and his staff, especially P. Dharmasiri, K. Nandasena, and others at the Veheramankada camp for their hospitality and field assistance, and P. B. Karunaratne for field assistance. Logistical support and advice by D. Marcellini and J. Seidensticker is greatly appreciated. EDW was supported by a Smithsonian Institution Postdoctoral Fellowship. The project was partially funded by

a Friends of the National Zoo (FONZ) grant to EDW.

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- (EDW) DEPARTMENT OF HERPETOLOGY, NATIONAL ZOOLOGICAL PARK/SMITHSONIAN INSTITUTION, WASHINGTON, D.C. 20008; AND (GLD) 9100 SOUTH MILL SITE ROAD, ASHLAND, MISSOURI 65010. Submitted 6 May 1991. Accepted 15 May 1992. Section editor: G. R. Ultsch.