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**FIRST STUDIES ON THE THERMAL ECOLOGY OF *CERATOPHORA TENNENTII*:
(SAURIA: AGAMIDAE) INHABITING THE CLOUD FORESTS OF KNUCKLES MASSIF,
SRI LANKA**

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INTRODUCTION

The leaf nose lizard *Ceratophora tennentii* (Günther and Gray 1861) is a relic agamid inhabiting the Knuckles Massif and one of five species of *Ceratophora* found in Sri Lanka (Pethyagoda & Manamendra-Arachchi, 1998). This agamid was first described by Günther and Gray in 1861 in Sir Emerson Tennent's book 'Sketches of the Natural History of Ceylon'. The distribution of the genus in Sri Lanka is of interest as it encompasses the three distinct massifs: the Knuckles, Central and Rakwana mountain ranges. The status of the five species varies; *C. erdeleni* and *C. karu* have only small populations and is known only from few forests (Morningside Forest Reserve), whereas *C. aspera* and *C. stoddartii* occur in appreciable populations in a wider area of occupancy, the populations are highly fragmented. The fifth species, the slow moving *C. tennentii* is known only from the cool mountain forests of the Knuckles Massif. Its natural habitats were greatly disturbed and altered during the past two centuries from extensive clearing of the Knuckles for coffee and tea. Subsequently the habitat was further disturbed when large scale cultivation began in the late 1960's. *C. tennentii* is considered an Endangered agamid (IUCN Red Data Book, 2002) and Endangered (CAMP Report, De Silva, Molur & Walker, 2000). Animals with limited distributions are often sensitive to changes in habitat structure and it is important that key aspects of *C. tennentii* biology and ecology are known. Thermoregulation is central in this respect, since most physiological processes are temperature dependent (Avery, 1982; Huey 1982), and may influence habitat selection and adaptation, but the degree to which thermal concerns dominate reptile ecology may differ between species (Gans & Dawson, 1976). Information on thermal ecology is also necessary for habitat management decisions particularly if the species is vulnerable to anthropogenic disturbance.

Several studies of thermoregulation have been conducted on Sri Lankan reptiles but have mainly dealt with *Varanus salvator* and *V. bengalensis* (Dryden & Wikramanayake, 1991; Dryden, Green, Wikramanayake & Dryden, 1993; Rathnayake et al., 2003; Wikramanayake & Green, 1989; Wikramanayake & Dryden, 1993; Wikramanayake, 1995). The mountain forests of Sri Lanka are similar to the well studied forests of Central and South America in that they present particular problems for thermoregulating reptiles (see review in Smith and Ballinger, 2001). They

often have closed canopy with only limited sunlight penetration and are frequently covered in cloud. Current theory predicts that reptiles living under such conditions will, to some extent, abandon thermoregulation and allow body temperatures to track environmental temperatures (Huey, 1982). The reasons for this may vary, but usually concern the distances and time involved in accessing the limited sunlit patches to raise body temperatures; if environmental temperatures are sufficiently high for activity it may be more economical for a reptile to abandon active thermoregulation and track the temperatures in the immediate vicinity. However, such temperatures can be below those required for optimum physiological performance but optimal in an ecological context (Huey, 1982). This paper is the first investigation of the thermoregulatory habits of *C. tennentii* and has been undertaken with the aim of providing a basis for future more in-depth studies.

METHODOLOGY

One hundred and sixty-five lizards were captured and immediately measured for body temperatures with handling. Simultaneously, in most instances, associated air ($n = 151$) and substrate ($n = 140$) temperatures were recorded. Substrate temperatures were those immediate to the location of the lizard and could be either soil or tree bark temperatures and air temperatures were taken 1.5 m above the ground at the location of the lizard. The main results presented here are based on cloacal temperatures by inserting a digital thermometer (infra-red Pyrometer) (130 mm stainless steel sensor probe model ST-9263A/B/C) into the cloaca but in anticipation of future studies skin surface temperature was also measured using an infra-red Pyrometer. The pyrometer detects infra-red energy by focusing onto a germanium filter (emissivity of reptiles = 0.95 (Tracy, 1982)). This instrument has a residual error of $\pm 0.1^\circ\text{C}$ but needs to be applied close to the lizard - within approximately 15cm of skin surface, to give an accurate reading.

Four basic behaviours were identified and recorded simultaneously with body temperatures. They were defined in the following way: (i) basking – located in an area with either full or dappled sunlight with the lizard normally inactive but some postural movement may have occurred i.e. opening of the mouth, changing the angle to the sun, feet movement etc; (ii) shade – located in an area with no sunlight and basically no movement; often located at the root base or the stem of cardamom or other vegetation; (iii) active – involved in some form of locomotory movement; (iv), feeding – in the act of securing or consuming a prey item.

RESULTS

Behaviour. Basking in dappled or sunlit patches accounted for 45.7% of observations with 32.2% of lizards found in shaded areas on leaf litter on the forest floor or low growing vegetation. Locomotory activity was observed 13.8% of the time and feeding 8.5%.

Body temperatures. Figure 1 shows box-plots of *C. tennentii* body temperatures ($mean = 21.8 \pm 2.2^\circ\text{C}$, $range = 17 - 30^\circ\text{C}$, $n = 165$) with corresponding substrate ($mean = 19.9 \pm 1.7^\circ\text{C}$) and air temperatures ($mean = 21.0 \pm 2.1^\circ\text{C}$). Body temperatures were significantly higher than both substrate and air temperatures (substrate, $F_{(1,254)} = 42.03$, $p < 0.0001$; air, $F_{(1,327)} = 8.34$, $p = 0.004$).

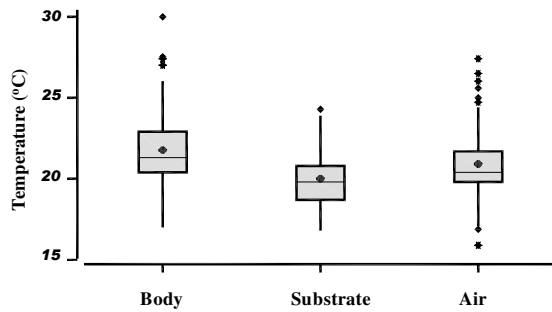


Figure1. Box plots of *C. tennenti* body temperatures shown with substrate and air temperatures. The boxes represent the interquartile ranges with the means shown as solid circles and medians as horizontal bars. The vertical lines either side of the interquartile ranges represent the general ranges of the data. Diamonds indicate outliers – data that are between 1.5 to 3 times from the interquartile ranges.

Body temperatures (T_b) were plotted against corresponding air (T_a) and substrate temperatures (T_s) in a test for thermoregulation. Corrected r^2 values were calculated to estimate the amount of variation in body temperature that can be explained by variation in air or substrate temperature. This gave, for air temperature, the regression (with standard error):

$$T_b = 2.6 + 0.91 \pm 0.04 T_a, r^2 = 75.4\% \quad (1)$$

The 0.91 regression coefficient is significantly different from the theoretical value of 0 required for thermoregulation ($t = 22.3, p > 0.0001$) and also the value of 1 for thermoconformity ($t = 2.25, p < 0.05$). The r^2 value does nevertheless indicate body temperature changes with changing air temperature although this is not necessarily a causal relationship. A plot of air temperature against the differences between air and body temperature (Fig. 2) suggests that the lizards were elevating body temperatures above air temperatures (*mean* difference = $0.8 \pm 1.1^\circ\text{C}$ above) irrespective of how high or low air temperatures were. The regression for substrate temperatures gave:

$$T_b = 1.1 + 1.02 \pm 0.1 T_s, r^2 = 52.3\% \quad (2)$$

The regression coefficient here is in good agreement with thermoconformity. However, the low r^2 value and the standard error (about 10% compared to that for air temperature of around 4%) indicates that substrate temperatures are a less important influence on body temperatures than air temperatures.

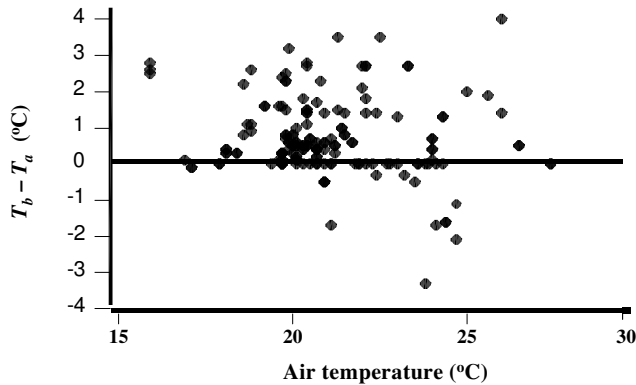


Figure 2. Graph showing the differences between body temperature and air temperature ($T_b - T_a$). This shows that most body temperatures were above air temperatures (see text for further information).

Variance in body and environmental temperatures. A further test of thermoregulation was made using a comparison of the equality of body and environment temperature variances using an F -test. Variance as a method of determining thermoregulatory precision (Huey & Slatkin, 1976) assumes that the lizards were regulating around a mean value and has been the subject of much discussion since there is some evidence that reptiles regulate between lower and upper set points (Berk & Heath, 1975; Barber & Crawford, 1977). Variance in body temperature may however provide insight for predicting whether a reptile can achieve greater body temperature precision by restricting activity to microenvironments with limited thermal variance (Hertz & Huey, 1981) or has access to a greater range of thermal resources. The null hypothesis of the F -test is that the variances are equal and that the lizards are not attempting to thermoregulate precisely. The results supported the null hypothesis for air temperature ($F = 1.09$, $p = 0.58$) but not for substrate temperature $F = 1.66$, $p = 0.008$, where body temperatures had significantly greater variance.

Relationship between skin surface and cloacal temperature. Regression analysis of cloacal temperature (T_b) with skin surface temperature (T_{ss}) gave

$$T_b = -0.71 + 1.1 \pm 0.16 T_{ss} (r^2 = 66.5\%) \quad (3)$$

This suggests that skin surface temperature gives a reasonable indication of cloacal temperature. The error in the equation is about 14.5% and hence skin surface temperature may be a moderately useful measurement for future studies of continuous observation of individuals, since it is non-invasive and less likely to influence behaviour than cloacal measurement.

DISCUSSION AND RECOMENDATIONS

The preliminary results presented here have shown that *C. tennentii* operates at relatively low body temperatures that closely track air temperatures. The time spent basking appears to explain the approximate 2°C difference that body temperatures were maintained above substrate/ air temperatures, which, although small, is fairly consistent across the temperature ranges. This is unusual in a species that spends time basking. Most heliothermic lizards, for example, maintain

greater differences between body and environmental temperatures at low temperatures, this then becomes progressively smaller as environmental temperatures increase (Huey, 1982; Avery, 1982). The majority of basking did occur in dappled sunlight, which is less effective in raising body temperature; seeking out full sunlit patches or increasing basking intensity may be too costly in an ecological context. However, it should be noted that by basking *C. tennentii* differs from many other forest lizards. For example, *Anolis gundlachi* in the forests of Puerto Rico does not bask or regulate its time of activity (Heatwole, et. al., 1969) nor does *Hypsilurus spinipes* in Australian forests (Rummery et al., 1994). Research in natural enclosures on tropical forest species have given similar results- for instance in the giant Solomon Island skink *Corucia zebrata* (Mann and Meek, 2004) but basking and partial basking similar to *C. tennentii* was found in *Physignathus cocincinus* (Meek, 1999).

It is of interest that the body temperatures of *C. tennentii* were significantly lower than either body (two-sample $t = 5.78$, $p < 0.0001$, $d.f. = 31$) air ($t = 6.01$, $p = 0.0001$, $d.f. = 23$) or substrate ($t = 5.5$, $p < 0.0001$, $d.f. = 15$) temperatures associated with the sympatric agamid *Calotes liocephalus*. Why do the lizards not select these warmer microhabitats or select higher body temperatures? One possible explanation is inter-specific competition from *C. liocephalus*, perhaps in the form of restricting access to prime basking areas or areas with higher environmental temperatures. Variance in body temperature is also significantly greater in *C. liocephalus* ($F = 0.36$, $p < 0.0001$) perhaps suggesting less precise thermoregulation, but could also indicate access to a larger range of thermal resources (Huey, 1982). *C. liocephalus* is usually found higher in the canopy and on tree trunks or branches without cover than *C. tennentii* and it may be that here air temperatures and availability of sunlight patches are greater. These results suggest that the Knuckles forest, with limited basking areas, could intensify competition for thermal resources. Competition of this kind has been found in *Anolis* lizards. For instance, species that occur on islands without congeners are active over broader temperature ranges than those in complex anole communities (Ruibal and Philibosian, 1970; Huey and Webster, 1975) although this may not always be the case (Hertz, 1980).

Several studies have assessed the impact of habitat change on thermal biology of lizard populations (See Smith and Ballinger, 2001 for review) and whilst it was found, for example, that timber practices altered the thermal characteristics of habitats favouring heliothermic species in some instances (Vitt et al., 1998; Klingenbock et al., 2000) this may not always be the case (Vitt et al., 1998). In non-basking species, particularly those that operate at low body temperatures, excessively hot habitats may exceed temperatures for physiological thresholds. This could influence activity times, metabolic rates and reproduction amongst other things and with the decline of *C. tennentii* in previously occupied habitats as a consequence of anthropogenic activities, this suggests that new detailed research on the species ecology should be given a priority.

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