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Thermal biology of *Lanthanotus borneensis* (Lanthanotidae) in Sarawak, Borneo

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Abstract. *Lanthanotus borneensis*, the Bornean earless monitor, is a monotypic member of the family Lanthanotidae, and restricted to the island of Borneo. Little has been published on its field ecology. This study investigated aspects of its thermal biology through an analysis of surface body temperatures of free ranging individuals against corresponding environmental temperatures, in order to explore aspects of microhabitat utilisation in relation to thermoregulation. A generalised linear mixed model shows significant effect of air and substrate temperatures, but not of water temperature. Further, the fixed effects of substrate temperature (coefficient estimate 0.396; $P < 0.05$) versus ambient temperature (0.264; $P < 0.05$), is suggestive of thigmothermy as the primary mode of thermoregulation. The species does not appear to utilise specific microhabitat structures to thermoregulate, the results of these observations suggesting that it is a thermoconformer.

Keywords: Bornean Earless monitor, microhabitat, thermoconformer, thigmothermy.

Introduction

Thermoregulation is an often complex behavioural and physiological process by which ectothermic organisms regulate their body temperature (T_b) to maintain it within a range optimal to corporal functions, such as locomotion, reproduction, growth and defensive attempts (Carrascal et al., 1992; Brewster et al., 2013). Thermoregulation in squamate reptiles cannot be defined simply by analysing numerical data, but requires the integration of understanding on the behavioural ecology of a species (Huey and Slatkin, 1976). Studies on the behavioural thermoregulation in lizards (Huey and Slatkin, 1976; Muñoz et al., 2016; Yang et al., 2020) bring to the fore the diversity of mechanisms, with individual lizard species adopting different behavioural buffering strategies to counteract daily and annual temperature fluctuation. These include postural changes, alternating between microhabitats and adjusting activity periods (Adolph and Porter, 1993; Kearney, 2001; Chukwuka et al., 2020). Nonetheless, Díaz et al. (2022) reported that the ability to change thermoregulation related strategies is threatened by rising global temperatures. As the physiology and behaviour of a lizard have a strong dependence on ambient temperatures, an individual lizard's thermal type can also influence its selection of microhabitats (Michelangeli et al., 2018). In ectotherms, squamate reptiles typically rely on external sources of heat and behavioural strategies to thermoregulate. The evolving adaptational strategies observed in lizards yields a continual platform of possible research that can be done on their thermal ecology. Such research is lacking for most parts of the tropics, such as Borneo, which has a rich herpetofaunal diversity.

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Nocturnal reptiles residing in tropical forests behaviourally thermoregulate by seeking appropriate thermal refugia (Nordberg and Schwarzkopf, 2019). Other behaviours include nocturnal 'basking' observed in a species of freshwater turtles (McKnight et al., 2023). It is also known that nocturnal lizards are capable of switching thermoregulation strategies depending on the available thermal environment and the cost of thermoregulating (Arenas-Moreno et al., 2021). At night, a tropical ecosystem can sustain a thermal environment that is cooler and less heterogenous, with dense canopy covers acting as a buffer against strong solar radiation by day. Nocturnal lizards have evolved a physiological adaptation to tolerate these cooler environmental temperatures using minimal locomotion cost (Autumn et al., 1999; Bertoia et al., 2021), and also conform to the restricted thermal availability at night (Tan and Schwanz, 2015; Arenas-Moreno et al., 2018) and tend to be thermoconformers (Pianka et al., 2017). Thermoconformers are more passive within their environment, exhibiting the ability to conform their T_b with surrounding temperatures, that show a relatively wide range (Angilletta et al., 2002). With no known local thermoconformer species reported, it is left in speculation whether the rapid rate of habitat degradation poses a greater threat to the herpetofauna species on Borneo than expected.

Lanthanotus borneensis Steindachner, 1877 is a subfossorial and semi-aquatic squamate, inhabiting localized streams within lowland hill dipterocarp forests of western Borneo (Das, 2010). As the sole living representative of the family Lanthanotidae and an endemic of the island, much interest exists on its biology and conservation. Poorly-known for the first century of its description, this species resurfaced in the pet trade within the last decade, at which time, sporadic information on its biology and trade started to emerge (Janssen, 2018; Das and Auliya, 2021; Mebs et al., 2021). Furthermore, although the lineage has been shown to be sister to the clade comprising the essentially diurnal varanids (Branch, 1982; Ast, 2001), *L. borneensis* is unique in being strictly nocturnal.

Details of thermal range, use of thermal resources and thermal strategies in *L. borneensis* have remained largely unknown, apart from an anecdotal observation by Langner (2017), who mentioned a value of 26.0°C, and to date, is the only publication that contains in situ observations of the species. Harrisson (1961) reported that, based on the observations of a number of individuals maintained in captivity, this species displays temporally indistinct activity patterns, showing no evidence of basking and remaining hidden for long periods of time. As an inhabitant of tropical rainforests of Borneo, areas threatened by both logging and climate-change, studies on its thermal requirements become important.

In this study, we present an in-situ report on the thermal ecology of free-ranging individuals of *L. borneensis*. We established two primary objectives in this study: 1) to determine mode of thermoregulation used by the lizard, and 2) to evaluate if there are possible association between microhabitat utilisation and thermoregulation. Much like most tropical nocturnal reptiles, we predict that in this species, thermal ecology is directed towards thermoconformation, based on the slope of the regression line between body and environmental temperatures. We used radio telemetry techniques, comprising temperature-sensitive transmitters to assess the surface T_b of *L. borneensis* and to test for relationships with surrounding temperatures.

Materials and methods

Study areas and sampling periods

We studied two populations of *L. borneensis*, located ca. 85 km apart. These are located at remnant secondary and primary forests adjacent to logging camps within the Kapit region of Upper Baleh, north of Kapit (ca. 1.95°N, 112.32°E) in central Sarawak, Borneo. Access to these camps is controlled by respective landowners, and the coordinates kept confidential for security and conservation reasons. We tracked a total of nine individuals in this study, comprising one male and two females at site A, and four males and two females at site B. We observed both sites to be similar in habitat structure and were located at elevational ranges between 115-200 m asl, within lowland mixed dipterocarp forests and regenerating secondary forests dominated by *Alseodaphne*, *Macaranga*, *Glochidion* and *Shorea* species of trees. The landscape included rocky streams with widths ranging between 1-2 m and depths ranging from a few centimetres to scattered pools that deepen to ca. 80 cm. The geological formation of the area consists of sediments of slate, silt, sandstone and mud clast conglomerate (Muol and Noweg, 2018). We established one transect at each site (ca. 200 m) along rocky streams and conducted data collection from November 2019 to August 2022, totalling a period of 151 days.

Sampling procedures and data collection

We carried out active searches and tracking from 0900 to 1400 h, and from 1800 to 2100 h. When encountered, we hand-caught individuals and noted the date and time. Each individual was provided with a distinct identification number (e.g., LB01, LB02) and a radio transmitter attached before release at the point of encounter. We recorded relocation positions using a Handheld Global Positioning System (Garmin™ GPS Map64s).

In instances where direct observations were not possible, such as locations within deep rock crevices, we used an endoscope (Depstech™ DS450) to locate the lizards and concomitantly, behaviours were observed and recorded. Environmental parameters, including ambient temperature (T_a) and substrate temperature (T_s), were recorded with an environmental meter (Extech™ 510N) and a thermal gun (Fluke 62 MAX). Ambient temperature refers to as air temperature which we recorded within a few centimetres from substrate. We recorded water temperature (T_w) when an individual was found submerged in water, whereby substrate temperatures were not taken. We recorded T_b retrieved from transmitters (see *Radio telemetry and harnessing technique*). We also recorded microhabitat or refugia descriptions.

Radio telemetry and harnessing technique

We used temperature sensitive transmitters (BD-2T; 0.85 g; battery life: four weeks; Holohil Systems, Ltd., Carp, Ontario, Canada). We calibrated transmitters using a water bath 2-3 days before travel to study sites for accurate readings of surface body temperatures. Following Knapp and Owens (2005), we attached the transmitters dorsally, on the mid-pelvic region of the target species using fishing materials (fig. 1). After release, we tracked each individual to their next re-location position. The signals or 'pings' that we received from the transmitters were then recorded as the time taken to complete 11 pings for three iterations. We then took the mean reading and compared these with the calibration curve obtained during the calibration of transmitters in the lab to get a body temperature reading.

Figure 1. An adult female *Lanthanotus borneensis* with a harnessed transmitter attached to the sacral region.

Data analysis

We selected surface body temperature for analyses, as the focal species was typically associated with hard-to-reach refugia. This made accurate cloacal body temperature measurements without causing stress a challenge. The Generalised Linear Mixed Model (GLMM) was the primary analysis for this study. Surface T_b of the tracked individuals was analysed to examine relationships with T_a, T_s and T_w. For GLMM, T_a, T_s and T_w were considered as fixed effects, T_b as the response variable, and lizard ID as a random factor. As a preliminary study, following Huey and Slatkin (1976), the regression equations resulting from T_b correlations with the fixed effects were examined to evaluate thermoregulation in *L. borneensis*. This was done by evaluating the slope of the regression line, where if the slope approaches 0, thermoregulation is suggested, whereas if the slope is approaching 1, this is suggestive of thermal passivity. Microhabitat types were analysed against T_b of individuals using GLMM, with T_b as the response variable, microhabitat types as fixed factors and lizard ID as a random factor. All values are reported as mean ± SE. Statistical analyses were conducted using the IBM's Statistical Package for the Social Sciences (SPSS), version 26.0.

Results

We recorded thermal data of each individual over a period of 66 days. Mean T_b for tracked individuals was 25.63 ± 0.08°C (n = 120, range 22.82-28.00°C). The mean for T_a observed was 27.17 ± 0.12°C (n = 160, range 24.0-31.7°C). Mean T_s observed was 23.98 ± 0.13°C (n = 99, range 18.9-27.2°C), and the mean for T_w was 23.98 ± 0.13°C (n = 54, range 24.50-28.30°C). We further visualised the thermal data to show a comparison of body temperatures between sexes (fig. 2, table 1).

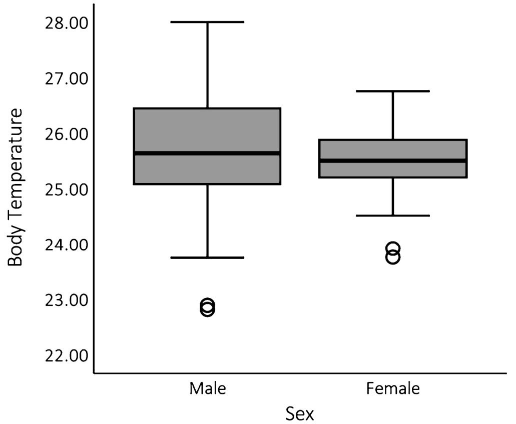

Figure 2. Boxplot of body temperatures for males and females of *Lanthanotus borneensis*.

We found that GLMM indicated that T_w does not have a statistically significant effect on T_b ($P = 0.587$). However, variables T_a and T_s demonstrated significant associations with T_b as the associated P-values were lower than the predefined significance threshold of $\alpha = 0.05$. The regression line revealed slopes for T_a and T_s with T_b that approach 1 (fig. 3).

We made a total of 119 observations on microhabitat occupancy on the nine tracked individuals for this thermal study. A total of six microhabitat types were found occupied from our field observations (fig. 4). The tracked lizards were observed to alternate between microhabitats, with intervals of 1-8 days spent at one location before moving on to the next location, eight days being the longest period we observed an individual residing in a particular refugium. We observed females occupying six microhabitat types, and males occupying four. GLMM results indicate that body temperatures are not predicted by microhabitat type ($P = 0.515$). Ranges of body temperatures observed in each microhabitat type are presented in fig. 5.

Discussion

This study reports a close relationship of T_b of *Lanthanotus borneensis* with both ambient and substrate temperatures, while varanids, its closest relatives, show body temperatures 5°C higher on average (Harlow et al., 2010). Compared to the known T_b range of another Bornean varanoid lizard, *Varanus salvator* (26.3-28.4°C; Traeholt, 1997), *L. borneensis* showed a mean T_b of 25.6°C, range 22.8-28.0°C), which places it closest to the cooler end of the thermal range within the lineage. These two sister groups, Lanthanotidae and Varanidae, do not share similar behavioural thermoregulation strategies, the former being nocturnal, the latter mainly diurnal. As opposed to varanids (Al-Razi et al., 2014; Turner, 2019), no evidence of basking or heliothermic thermoregulation could be found in *L. borneensis*. This was expected, as nocturnal animals tend to avoid high temperatures during the day and carry out activities at night (see

Table 1. Body temperatures of sexes of *Lanthanotus borneensis*. Number of observations (*n*).

Lizard ID	Tracking period	T_b (°C)	*n*	Range	Mean
Male			76	22.82-28.00°C	25.72 ± 0.12°C
LB04	18-26 April 2021	25.13-26.11			
LB05	12-24 April 2021	22.82-24.79			
LB09	11-26 April 2021	24.70-28.00			
	29 September – 16 October 2021				
LB12	22-26 May 2022	22.89-26.32			
LB13	20 July – 13 August 2022	24.37-27.05			
Female			44	23.76-26.76°C	25.48 ± 0.09°C
LB02	15-20 September 2020	25.25-26.41			
	1-24 May 2022				
LB06	16-26 April 2021	24.93-26.76			
LB10	1-26 April 2021	23.76-25.61			
	29 September – 1 October 2021				
LB11	1-26 May 2022	24.86-26.01			

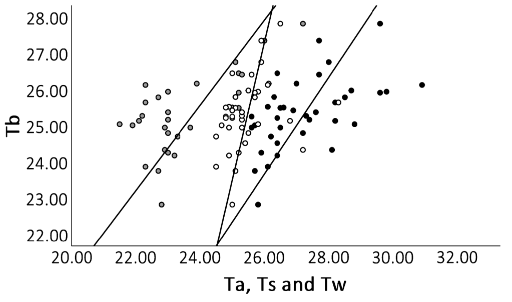

Figure 3. Generalised linear mixed model of body temperatures of *Lanthanotus borneensis* against associated environmental temperatures. T_b against T_a, $F_{1,32} = 11.549$, $P < 0.05$, $y = 8.28 + 0.75 * x$; T_b against T_s, $F_{1,32} = 37.856$, $P < 0.05 y = 2.34 + 0.85 * x$. Black represents ambient temperatures; grey represents substrate temperatures; white represents water temperatures.

Walsberg, 2000). Furthermore, being a relatively sedentary species, the lack of behavioural regulation suggests that the target species is a thermoconformer, as strongly implied by the lack of relationship between T_b and T_w, and the slopes for regressions between T_b with T_a and T_s approaching 1 (Huey and Slatkin, 1976). The stronger correlation of T_b with T_s, rather than T_a and T_w, suggests that the species obtains heat from substrate surfaces, behaviourally closer to being a passive thigmotherm. However, the narrow T_b range (22.82-28.00°C) suggests that this species is a thermal specialist, that may imply active thermoregulation to some extent, perhaps via careful microhabitat selection.

Commonly encountered in tropical nocturnal species, shuttling between microhabitats at night is a strategy to regulate body temperature for physiological demands (Nordberg and Schwarzkopf, 2019). Field data taken of activities and behaviours demonstrate that the Bornean Earless Lizard is relatively sedentary, remaining at a refugia with unvarying substratum temperatures for up to eight days before transiting to the next. The results from the current study demonstrate that the species is not a perfect thermoconformer, and does not specifically utilize microenvironments for thermoregulation, and it is suggested that periods of inactivity observed is unrelated to active thermoregulation. This behaviour has been observed in

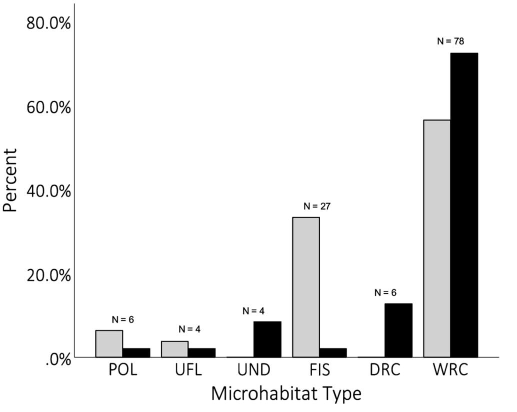

Figure 4. Microhabitat use in *Lanthanotus borneensis*. Abbreviations: WRC: Rocks (underwater); DRC: Rocks on dry streambank; FIS: Within fissures of exposed bedrock; UND: Underground in loose soil; UFL: Under fallen logs; POL: Isolated, shallow water pools. Black represents females; light grey represents males.

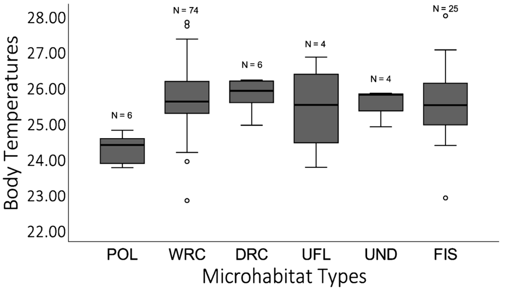

Figure 5. Boxplots on the distribution of body temperatures of nine individuals of *Lanthanotus borneensis* across microhabitats occupied. $N = 119$. Abbreviations used: POL: Isolated, shallow water pools. WRC: Rocks (underwater); DRC: Rocks on dry streambank; UFL: Under fallen logs; UND: Underground in loose soil; FIS: Within fissures of exposed bedrock.

the Shinisauridae (Yang et al., 2020) and in members of the Helodermatidae (Holcomb, 2017). Since thermoregulation is evident to some degree in all living organisms, subsequent studies that include thermal preferences, thermal performance curves, operative temperatures, and available environmental temperatures are required to enhance our comprehension of the thermal biology of *L. borneensis*.

The lack of relationship between T_b and T_w suggests that *L. borneensis* does not utilise aquatic resources for thermal regulation. The lizard may be in water for the purpose of foraging since it is known to feed on aquatic prey, such as small crustaceans (Losos and Greene, 1988). However, we believe that hydric conditions may be significant for other physiological processes, such as rate of evaporative water loss, accounting for the observations we made of different individuals remaining underwater for several hours. Rozen-Rechels et al. (2019) considered hydric conditions to be an important factor when ascertaining how it influences the thermal biology of ectotherms, in this case, a semi-aquatic lizard, since thermoregulation can be affected by the restriction of water. As *L. borneensis* is a stream obligate, further studies on its thermal biology should address these questions to examine its response to water with and without restrictions such as drought, or disturbances caused by anthropogenic activities.

Lizards provide a significant service as bioindicators and their thermal biology has been increasingly recognized as important by ecologists (Silva et al., 2020). With the demonstrated increase in land temperatures as a result of global climate change (Munawar et al., 2022), tropical lizards are expected to be vulnerable (Huey et al., 2009). Moreover, fossorial lizards have a higher risk of extinction with persisting habitat modifications compared to arboreal and terrestrial species (Theisinger and Ratinarivo, 2015), an unsettling reality that could possibly affect the future of the focal species of this study, given that its thermal sensitivity remains largely unknown.

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