



Institute of Biodiversity and Environmental Conservation

**Spatial Ecology, Thermal Biology and Prey Behaviour of the Bornean
Keel Pit-viper, *Tropidolaemus subannulatus* (Reptilia: Squamata:
Viperidae)**

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Thermoregulation and Activity of the Bornean Keeled Pit-viper,
Tropidolaemus subannulatus (Reptilia: Squamata: Viperidae)

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DECLARATION

I declare that the work in this thesis was carried out in accordance with the regulations of Universiti Malaysia Sarawak. Except where due acknowledgements have been made, the work is that of the author alone. The thesis has not been accepted for any degree and is not concurrently submitted in candidature of any other degree.



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ABSTRACT

The Bornean Keeled Pit-viper, *Tropidolaemus subannulatus* is a relatively common and widespread species of venomous snake of medical importance in south-east Asia. Nonetheless, knowledge of its biology had remained largely unknown, representing a challenge for both conservation and management on one hand, and public health on the other. This study aims to contribute to the knowledge of a tropical ectothermic vertebrate, leading to an enhanced understanding on its spatial biology, foraging behaviour and thermoregulation. A total of 21 snakes were encountered at Kubah National Park, Sarawak, East Malaysia (Borneo), during the study period (June 2018 to October 2021). Seven of these were qualified for tracking, based on mass and other telemetric limitations, and five (three females and two males) tracked between October 2019 and January 2020. Each individual was implanted with a temperature-sensitive radio-transmitter to locate individuals, as well as to record microhabitat use and internal body temperature. Microhabitat assessments were conducted during these field study. Analysis of feeding behaviour was conducted in a controlled environment in the lab. An ethogram was prepared based on video footage captured with a HDD camera. All individuals of *T. subannulatus* tracked revealed a relatively small home range (mean 100% MCP 303.51 m²), as well as limited movement (mean horizontal = 20.89 m, mean vertical = 13.03 m). Horizontal displacements were limited, while vertical movements were relatively more substantial, albeit challenging, with visuals of snakes bearing transmitters difficult to obtain at times due to dense vegetation, especially when snakes used high canopy microhabitats of tall trees, including *Xanthophyllum griffithii* and those of the genus *Shorea*. Apart from occasional changes in posture, *T. subannulatus* can remain motionless for days or weeks. There are no significant differences in movement and home range between the sexes of *Tropidolaemus subannulatus*.

This study found that the pit-vipers were found to utilize tree branches, saplings, twigs and ferns, while over 80% of the time were found on tree branch. Males were found to only utilized tree branches and saplings, probably due to their pronounced sexual dimorphism. Thermal studies showed a wide temperature variation, between 22.97°C and 30.56°C. Core body temperature and body surface temperature displayed significant differences ($P < 0.001$), suggestive of a thermoconformer rather than a thermoregulator, as may be expected of many ectothermic tropical vertebrates that are nocturnal. Although weakly correlated, there was a significant relationship between ambient temperature with core body temperature ($r = 0.209$) and surface body temperature ($r = 0.298$). Substrate temperature have significant relationship with core body temperature ($r = 0.671$) and surface body temperature ($r = 0.993$), with stronger correlation compared to ambient temperature. *Ex-situ* feeding behavioural experiments showed eight common predatory behaviour (head shift, eye fix, approach, strike, wait, upper jaw retraction, gape, tongue flick) that can be classified into three different phases, namely, pre-capture, feeding, and post-feeding phases, during experiments with new-born *Rattus norvegicus*. Understanding spatial use, thermoregulation, the foraging and prey-handling behaviour are critical. These can provide important insights into evolutionary fitness, as well as the biotic and abiotic factors associated with the focal species. Such studies of tropical snakes of medical importance are vital for development of effective plan of action for conservation as well as public health.

Keywords: Ethogram, home range, movement, snake, thermoregulation

Ekologi Ruang, Biologi Terma dan Tingkah Laku Mangsa Ular Kapak, *Tropidolaemus subannulatus* (Reptilia: Squamata: Viperidae)

ABSTRAK

Ular kapak, *Tropidolaemus subannulatus* merupakan spesis ular berbisa yang mempunyai kepentingan perubatan yang biasa serta meluas di Asia Tenggara. Namun begitu, pengetahuan biologi mengenai spesis ini masih tidak diketahui, ini mewakili cabaran bagi pemuliharaan dan pengurusan, serta kesihatan awam. Kajian ini bertujuan untuk menyumbang kepada pengetahuan mengenai vertebrata ektotermik tropikal, membawa kepada pemahaman yang lebih baik tentang biologi spatial, tingkah laku mencari makanan, dan termoregulasi. Sebanyak 21 ekor ular telah ditemui di Taman Negara Kubah, Sarawak, Malaysia Timur (Borneo), sepanjang tempoh kajian (Jun 2018 hingga Oktober 2021). Tujuh daripada semua layak untuk penjejakan, berdasarkan had jisim serta telemetrik yang lain, dan lima (tiga perempuan dan dua lelaki) dijejak antara Oktober 2019 dan Januari 2020. Setiap individu telah diimplan dengan pemancar radio sensitif suhu bagi mengesan individu, serta untuk merekodkan penggunaan mikrohabitat dan suhu badan dalaman. Penilaian mikrohabitat telah dijalankan sewaktu kajian lapangan ini. Analisis tingkah laku pengendalian mangsa telah dilakukan dalam persekitaran terkawal dalam makmal. Etogram telah disediakan berdasarkan rakaman video yang telah ditangkap dengan kamera HDD. Seluruh individual *T. subannulatus* yang dijejak menunjukkan julat rumah yang agak kecil (min 100% MCP 303.51 m²) serta pergerakan yang terhad (min mendatar = 20.89 m, min menegak = 13.03 m). Anjakan mendatar adalah terhad manakala pergerakan menegak adalah lebih besar secara relatif, walaupun mencabar, visual bagi ular-ular yang diimplan dengan pemancar sukar diperoleh pada masa-masa tertentu disebabkan oleh tumbuhan-tumbuhan pokok yang tebal, terutamanya apabila ular-ular tersebut menggunakan

mikrohabitat kanopi tinggi bagi pokok-pokok tinggi seperti *Xanthophyllum griffithii* dan pokok-pokok genus *Shorea*. Selain daripada perubahan postur sekali-sekala, *T. subannulatus* mampu kekalkan pergerakan selama beberapa hari atau minggu. Tiada perbezaan yang ketara dalam pergerakan dan julat rumah antara jantina. Kajian ini mendapati ular ini didapati menggunakan dahan pokok, anak-anak pokok, ranting-ranting serta paku pakis dan lebih daripada 80% ditemui pada dahan-dahan pokok. Ular jantan ditemui hanya menggunakan dahan-dahan pokok dan anak-anak pokok, ini mungkin disebabkan oleh dimorfisme seksual. Kajian terma menunjukkan variasi suhu yang lebar iaitu antara 22.97°C dan 30.56°C; oleh itu, berpotensi untuk fleksibel, barangkali untuk keperluan fisiologi. Suhu badan teras dan suhu permukaan badan menunjukkan perbezaan yang ketara ($P < 0.001$), mencadangkan termokonformer berbanding termoregulasi, seperti yang dijangkakan daripada banyak vertebrata tropika ektotermik yang hidup pada waktu malam. Walaupun berkorelasi lemah, terdapat hubungan yang signifikan antara suhu persekitaran dengan suhu badan dalaman ($r = 0.209$) dan suhu permukaan badan ($r = 0.298$). Suhu substrat mempunyai hubungan yang signifikan dengan suhu badan dalaman ($r = 0.671$) dan suhu permukaan badan ($r = 0.993$) dengan korelasi yang lebih kuat berbanding dengan suhu persekitaran. Eksperimen tingkah laku pengendalian mangsa *ex-situ* menunjukkan lapan tingkah laku pemangsa (anjakan kepala, tumpuan pada sasaran, pendekatan, serangan, menunggu, penarikan rahang atas, ternganga, jentikan lidah) yang boleh dikelaskan kepada tiga fasa berbeza, iaitu, fasa pre-tangkapan, suapan, dan selepas suapan, semasa kajian dengan menggunakan *Rattus norvegicus* yang baru lahir. Memahami penggunaan spatial, termoregulasi, tingkah laku pemangsa dan pengendalian mangsa adalah kritikal. Ini mampu memberikan cerapan penting mengenai kecergasan evolusi, serta factor-faktor biotik dan abiotik yang dikaitkan dengan spesis fokus. Kajian

tentang ular-ular tropikal yang mempunyai kepentingan perubatan adalah penting bagi pembangunan pelan tindakan yang berkesan untuk pemuliharaan serta kesihatan awam.

Kata kunci: *Etogram, julat rumah, pergerakan, termoregulasi, ular*

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LIST OF ABBREVIATIONS

asl	Above sea level
GPS	Global Positioning System
ha	Hectare
HW	Head Width
IUCN	International Union for Conservation of Nature
JW	Jaw Width
km	Kilometre
m	Metre
MCP	Minimum Convex Polygon
MDD	Mean Daily Displacement
mm	Millimetre
SE	Standard Error
SVL	Snout-vent-length
T _a	Ambient temperature
T _b	Core body temperature
T _{bs}	Body surface temperature
T _s	Substrate temperature
ToL	Total Length
VES	Visual Encounter Survey

CHAPTER 1

INTRODUCTION

1.1 General Introduction to Viperidae

Pit-vipers are members of the family Viperidae, and are currently classified as a subfamily, Crotalinae (Stuebing et al., 2014). They possess a heat-sensitive pit behind the nostrils, on each side of the snout, the source of the English common name. All pit-vipers are venomous and are equipped with prominent fangs that are particularly long and comprise hollow teeth that rotate through remarkably large angles (Lillywhite, 2014). A majority are ovoviviparous and the typical pit-vipers appeared as short and bulky bodied with a distinct triangular head (Das, 2018).

Compared to active foraging snakes, such as cobras and rat snakes, vipers and pit-vipers are ambush foragers and practice the ‘sit-and wait’ technique. Viperid snakes have been commonly reported to prey on mammal or avian groups. Unlike other non-viper snakes, they often swallow relatively large prey (Lillywhite, 2014), and incredibly, can transport prey approximately three times the relative mass of prey ingested compared to non-vipers (Cundall & Deufel, 2006). For instance, Pough and Groves (1983) summarised that the largest prey swallowed by a viper was 36% of its body mass, while the largest prey swallowed by a non-viper was a mere 14% of its mass. However, there are findings that shows relatively smaller prey categories such as insects, reptiles and carrion being consumed by some vipers.

Over 300 species of pit-vipers are now known (Uetz et al., 2021). Of these, 102 are found in Asia and six occur on Borneo. Five of these show a prehensile tail and are mostly

arboreal. To date, there are no recorded human mortalities resulting from pit-viper bites on Borneo. Nevertheless, bites must be treated as medical emergencies.

Table 1.1: List of pit-vipers (Serpentes: Viperidae: Crotalinae) on Borneo, along with their IUCN Red List Status and geographical distribution.

No.	Species	IUCN Status	Status in Borneo
1	<i>Garthius chaseni</i>	Least Concern	Sabah and northern Sarawak
2	<i>Parias malcolmi</i>	Near Threatened	Sabah
3	<i>Parias sumatranus</i>	Least Concern	Widespread
4	<i>Popeia sabahi</i>	Least Concern	Widespread
5	<i>Craspedocephalus borneensis</i>	Least Concern	Widespread
6	<i>Tropidolaemus subannulatus</i>	Least Concern	Widespread

In the Laws of Malaysia, Act 716, Wildlife Conservation Act 2010, only three species (*Parias sumatranus*, *Craspedocephalus borneensis* and *Tropidolaemus subannulatus*) are mentioned and all are categorized under the Protected Wildlife status. The rest remain unlisted as it is most probably not updated in the species checklist during the gazettelement of the law. In addition to the Wildlife Conservation Act 2010, *Parias sumatranus* has been listed as *Trimeresurus sumatranus*, *Craspedocephalus borneensis* as *Trimeresurus borneensis*, and *Tropidolaemus subannulatus* as *Tropidolaemus wagleri*. An updating of the law in terms of both biological status of species and nomenclature are needed to play a part in protecting these species and to ensure success in conservation.

Five of six species of Bornean pit-vipers are found in Sarawak, namely *Garthius chaseni*, *Parias sumatranus*, *Popeia sabahi*, *Craspedocephalus borneensis* and *Tropidolaemus subannulatus*. Being a rather elusive species and with the lack of research on snakes, not much is known about the pit-vipers on Borneo. Despite the ‘Least Concern’ status in the IUCN Red List, these forest obligate species are susceptible to deforestation in Sarawak. In some areas, deforestation is intense with the purpose of converting the land for agriculture and logging activity. Due to lack of data, their population trends remain unknown. Among the four species, *Tropidolaemus subannulatus* appears to be most common and widespread on Borneo.

1.2 Ecological Roles and Cultural Use of Snakes

There are 3,956 snake species reported globally (Uetz et al., 2021) that can be found in a vast variety of habitats and environments around the world. They live in climates ranging from the tundra to the tropics, and from the dry arid desert to the open ocean (Hsiang et al., 2015), and compared to lizards, snakes can be found in more habitat types (Campbell & Campbell, 2001). Over 200 species of snakes are found on the island of Borneo, occupying marine, freshwater, and terrestrial habitats, ascending to at least 2,000 m on mountain-tops (Stuebing et al., 2014). Aquatic snakes can be found in wetlands, including swamps, swift rocky streams, muddy rivers, shallow coastal areas and around coral reefs.

Snakes can be both prey and predator of vertebrates and invertebrates are often placed as secondary or top predators in the trophic webs, making their ecological roles distinct and substantial (Campbell & Campbell, 2001). For instance, Voris and Voris (1983) reported about one-third of Indo-Australian fish families form the food base of 39 species of sea snakes. Despite the known importance of snakes in the ecosystem, many are listed as

threatened in the IUCN Red List, and even more are Data Deficient, and clearly in need of more study.

Depending on the culture or tradition of the places, snakes can either be an object of fascination or feared, idolized or loathed (Pough et al., 1998; Campbell & Campbell, 2001). For example, in some African societies, the African rock python (*Python sebae*) and the Royal python (*Python regius*) are worshipped and killing them is taboo (Cansdale & Wood, 1961; Alves et al., 2012). The god of Nile River in Egypt was a god-serpent who represented power of the Pharaohs (Moreno et al., 2006). Having such positive belief would have increased the likelihood survival of these species especially in human-dominated landscapes where people would be obliged to protect them. Snakes are also equally often connected with negative emotions, which makes them prone to be feared or hated (Dodd, 1993; Vizotto, 2003; Alves et al., 2010; Ceríaco, 2010; Alves et al., 2012). At the end of the day, humans tend to have opinions about snakes based on exposure, which can be different for everyone. Consequently, their attitudes towards snakes can potentially affect the likelihood of believing snakes are worth saving (Campbell & Campbell, 2001).

Snakes have influenced many aspects of human life, such as for in the medicinal sciences, magico-religious practices, as pets, and dangers to human populations (Alves et al., 2012). Reports show that snakes had been exploited in many forms for human use. Eggs, shells, meat, blood, oil, skins, bones, and other body parts of reptiles had long been exploited for food and as materials for creating tools, ornaments, medicine and religious objects (Alves et al., 2012).

Alves et al. (2012) mentioned that the use of snakes in medicinal practices had existed in ancient Greece, as Asklepios, the god of medicine related to snakes. Since then, snakes have been used in a plethora of healing practices and rituals. Use of snakes for these

medicinal practices can be in many ways and forms as treatment. For example, in Andalusia, Spain, snakes have a high influence in medicinal and magico-religious. According to Benítez (2011), reptiles make up of 23% of the animals use in the said practice, and snakes have been used to treat various type of diseases, such as cephalgia (Benítez, 2011), erysipelas (Sezik et al., 1997), back pain (El-Kamali, 2000), and many others. Utilisation can be by consuming the meat, eating the skin mixed with food or herbs, rubbing the fat externally, and rubbing or hitting live snakes in areas of body which are aches or injury, as a form of imitational magic (Benítez, 2011).

Superstitious influences are strong in Borneo amongst the indigenous tribes. Instead of being idolized or worshipped, the snake motif spikes fear amongst a majority of the community. The fear of snakes can be severe, to the point that a mere picture or mention of the word triggers fear and alarm. With the intense fear comes exaggeration in story and tales, particularly amongst the inhabitants of longhouses. Folklore, urban legends and personal experiences of a person are often passed from one person to another orally. The feeling of dread and horror someone have towards snakes have a biased opinion on how the story proceeds.

In Borneo, the local Chinese use '*Lau Zhua*' as someone who is sly or deceitful, the usual depiction of snakes in the Bible (Genesis 3). Although not of evil intention, there is also a local Malay word, '*Mengular*', directly translated, is 'snaking', which means being lazy. This word often comes from the representative of how a snake tends to linger around a location for a long time after a meal.

Snakes sometime serve as food among certain local communities. Although not a common cuisine in urban areas, it is widely consumed in rural ones, either as a source of protein or out of curiosity for taste of an exotic fare. The most common snake targeted on

Borneo are pythons (*Malayopython reticulatus* and *Python breitensteini*), mainly due to their delicate and appealing flavour (Stuebing et al., 2014) and the Elephant Trunk Snake (*Acrochordus javanicus*), the latter species probably because they are commonly caught incidentally by fishermen in nets, large size and unprotected status.

Traditional medicines and other remedies derived from snakes are in high demand among urban residents. On Borneo, parts such as meat, skin, blood and gall bladder have been reported to be used as ingredients to treat illness such as asthma, poor eyesight, arthritis and many more (Stuebing et al., 2014). Snakes commonly targeted for such purposes consist of pythons (*Malayopython reticulatus* and *Python breitensteini*) and the Sunda Spitting Cobra (*Naja sumatrana*).

1.3 Objectives

The present study is aimed to gain new data on the field ecology of *Tropidolaemus subannulatus* through four broad topics, including:

i) Spatial movement

Determining the home range and movement pattern of *Tropidolaemus subannulatus*

- What movement pattern does this species show and how large is their home range, vertically as well as horizontally? Are there significant differences in movement and home ranges between the sexes? What are the factors that affect movement (including breeding season, body size and environmental factors)?

ii) Microhabitat utilization

Determine microhabitat selection in *Tropidolaemus subannulatus*.

- What are the critical microhabitats utilised by *Tropidolaemus subannulatus*? Are there sexual differences in the same, and different microhabitats associated with different activities (such as refugia, foraging and breeding activities)?

iii) Thermoregulation

Determine the thermal range of *Tropidolaemus subannulatus*.

- Is there behavioural control of body temperature?
- Does ambient and substrate temperatures effect body temperature?

1.4 Conservation Importance

Being a relatively common species on Borneo, *Tropidolaemus subannulatus* is a suitable model to represent tropical snake species. This study is expected to contribute to our knowledge of a tropical ectothermic vertebrate, leading to a better understanding on its spatial biology, feeding behaviour and thermoregulation. A better understanding of how snakes work is significant considering the group plays a vital role in the ecosystem as both predator and prey. Finally, this research will provide critical knowledge for both conservation of snakes and other ectothermic animals, as well as provide information on public health to a range of professions who venture into forests and fields, either for work or for recreation. Furthermore, there are records of the *T. subannulatus* being collected for both the international and local pet trades (Sy, 2018; Amarga & Supsup, 2020), and it is hoped that scientific knowledge gained on its field biology will be useful for its conservation and management.

1.5 Significance of Study

Snakes being an important part of our natural ecosystems, as both prey and as predator, can perform as a bioindicator of environmental health (Campbell & Campbell,

2001; Barnes et al., 2017). Snakes play major roles in the ecological community and have the potential to help understand the dynamics of ecosystems (Bouskila, 1995, Luiselli, 2006). They are more diverse in the tropical regions compared to temperate ones (Brown et al., 2005), yet there is a shortage of studies on tropical snakes. With contemporary technology, such as radiotelemetry, studies of animal ecology have now become possible.

Tropidolaemus subannulatus, as a member of the Viperidae, is a venomous species, and responsible for a number of bites annually, which makes them of medical importance. Medical attention will be required if they are being bitten as it could be life threatening and victims will experience excruciating pain. Hence, knowledge of their life history is important for those who venture out, be they foresters, hikers, or members of the general public.

CHAPTER 2

LITERATURE REVIEW

2.1 General Review of Ecology

2.1.1 Spatial Biology and Movement

Knowledge of the natural habitat of an organism is vital for understanding its biology. Understanding the utilisation of space is needed for addressing broader questions of ecology, distribution, behaviour and conservation, and nature of life history is instructive in understanding movement patterns and spatial biology (Wakso & Sasa, 2009). Despite being a biodiversity hotspot, the primary forests of south-east Asia are under severe anthropogenic threats (Barnes et al., 2017; Hughes, 2017), while details of the spatial ecology of their inhabitants remain largely unavailable (Brown et al., 2005).

Size requirements of habitats as well as habitat and microhabitat type requirements vary across taxa. Reptiles, such as snakes, are sensitive when it comes to temperature, being ectothermic organisms. Other factors, such as local weather conditions, prey availability, predation pressure, mating opportunity and intrasexual competition play an important key role in determining species presence (Daltry et al., 1998; Brown et al., 2005). Patterns of movement are affected by multiple environmental and social variables, as well as dispersion of potential prey and predator species (Schwaner, 1991; Houston & Shine, 1994). Thus, it is crucial for an animal to balance between risks and rewards of potential cost of foraging behaviour, as predation potential increases with movement and foraging activities (Gerritsen & Strickler, 1977; Barnes et al., 2017).

Their life history, presence and absence of predators, food and water availability, reproduction stage, and seasonal change can determine spatial and geographical movement

or migration. Lunar cycle too can affect movement and activities in several species, including snakes (Houston & Shine, 1994). The last mentioned study demonstrated a strong lunar effect on activity, with significantly less movement on moonlit nights. It was assumed that moonlight probably increases possibility of detection by predators, the results therefore consistent with the predator avoidance hypothesis.

The home range of an organism typically refers to areas it travels in search of food and mates (Burt, 1943; Todd & Nowakowski, 2020). Size of home range varies with snake species. The constant need for thermoregulation certainly plays an important role for habitat utilization, such as thermal tolerance. Unlike endotherms, such as mammals and birds, home range area in snakes relate to body size, and in general, male snakes show larger home ranges than females (Todd & Nowakowski, 2020).

Sex of individuals have also been shown to play a role in movement and spatial use: Barnes et al. (2017) demonstrated that male *Trimeresurus macrops* displays larger home ranges than shown by the female, and adult of the two sexes may confront specific challenges which may be reflected in behaviour, movement and the use of space (Madsen, 1987; Shine, 2003; Barnes et al., 2017). Males may display greater movement than females in requirement for finding a mate and to reproduce. Barnes et al. (2017) showed that females of *Trimeresurus albolabris* exhibit larger home ranges than males, while Wakso and Sasa (2009) found that movement pattern and home range of the Fer-de-lance (*Bothrops asper*) were unaffected by sex. The different stage of reproductive phase may also affect locomotion, as studies had shown that gravid snakes tend to move less frequent and smaller distances compared to non-gravid female snakes (Johnson, 2000; Barnes et al., 2017). However, these generalisations are not universal: Brown et al. (2005) showed that the most extensive movements were displayed by four gravid females of *Stegonotus cucullatus*

compared to a non-gravid female that generally moved over shorter distances than did larger males.

Snakes are typically secretive (Wakso & Sasa, 2009), which make them challenging to study in the wild. Some of the difficulties have been overcome with the use of radiotelemetry. Given the fact that south-east Asia is a biodiversity hotspot, the data of snake fauna for even the most abundant and widespread snake species remain scarce, with much potential for future research, using radiotelemetry and other emerging technologies.

The tropical forests often show a great diversity of snake species compared to temperate regions (Pough et al., 2001). Movements and spatial patterns of vipers in temperate regions regularly depend on daily thermal refugia (Brown & Lillywhite, 1992, Beaupre, 1995) or overwintering hibernacula (Macartney et al., 1988). Tropical species are potentially less affected by daily or seasonal thermal constraints (Shine & Madsen, 1996; Luiselli & Akani, 2002). Despite this, foraging behaviour may still differ throughout the year in response to shifting prey availabilities (Madsen & Shine, 1996; Sant'Anna & Abe, 2007). Unlike temperate regions, many tropical regions are hot all year round, yet exhibit significant seasonal variation in precipitation regimes which became one of the important components of the habitat (Brown et al., 2005). The seasonal variation in precipitation may also influence the spatial ecology of some organisms. Individual *Stegonotus cucullatus* are known to shift their home range size between wet- and dry-seasons, no spatial overlap between home-ranges in these two seasons (Brown et al., 2005).

2.1.2 Prey Handling

The different stage of an organism's life history may require a different diet, such as how a juvenile may have a different diet requirement compared to the adults. One such aspect is their feeding strategy. While some animals practice active foraging method to look for

food, some settle for a passive ‘sit-and-wait’ approach, as an increase in movement increases the chance of exposure to predators (Barnes et al., 2017). The diet of a species can be affected by aspects such as sex, reproductive stage, seasonal variation, life stage, body weight, body size and food availability (Brischoux & Lillywhite, 2013). Dietary shifts in ontogeny are also widespread in ectothermic species, as is variation in feeding, as described in the Green turtle (*Chelonia mydas*), typically a herbivore, with reports of some adults exhibiting carnivory (Hatase et al., 2006; Zanden et al., 2013), indicating plasticity in dietary regimes, depending on the environment.

Ectotherms such as snakes possess low metabolic rates, as well as the capability to withstand long periods without the need to feed, which, in turn, allows the exploitation of ephemeral food resources (Lillywhite & McCleary, 2008), as opposed to strategies in endothermic animals. Brooks et al. (2009) showed variation in feeding frequency between the sexes, which was also dissimilar between the seven snake species at their study site. In one out of seven species, the females did not feed during their gravid stage. Both behaviours demonstrate that sexual differences and a particular reproductive stage can influence feeding decisions. Kupfer et al. (2005) demonstrated that diet composition of a caecilian larva (genus *Ichthyophis*) differs spatially and temporally, which suggest a dependence on food availability.

As expected, the larger the animal, the larger the prey size, the higher the feeding frequencies and greater the number of stomach parasites (Brischoux & Lillywhite, 2013). This correlation is significant in snakes, as many large-growing snakes are distributed predominantly in the tropical regions (Shine & Madsen, 1996; Shine et al., 1998). Correlated to body size, head width and size is prey size selected, as displayed in larval Tiger salamanders, *Ambystoma tigrinum* (Brophy, 1980), and *I. cf. kohtaoensis* and other

caecilians with aquatic larval stages (Kupfer et al., 2005). Prey to predator size relationship is also related to jaw gape-limit of predators, whereby morphology may hinder the processing of food before ingestion. However, not all species are affected by such factors. For example, the Yellow-bellied sea snake (*Hydrophis platurus*) does not display ontogenetic shift in prey size, despite having a relatively large adult body size (Brischoux & Lillywhite, 2013). Species may display a variety of feeding behaviours. They can be active hunters, sit-and-wait predators or opportunist feeders.

Predatory strikes are executed more carefully and accurately than defensive strike as the strike is intended to capture a prey to feed (Lillywhite, 2014). Lillywhite (2014) also stated that behaviour of sensing and trailing of envenomated prey by snakes enables them to identify specific prey, since prey can sometimes move a certain distance before succumbing to the venom. Previous study on the Timber rattlesnake (*Crotalus horridus*) showed that mammalian prey that is potentially dangerous to the snake is usually released immediately after striking (Chiszar et al., 1982; Stiles et al., 2002; Rudolph et al., 2004). However, research by Martins et al. (2002) on arboreal snakes reveal that strike and release would give significant difficulties in volant prey even for short distances. Predatory behaviour can differ between venomous and non-venomous snakes. Poor knowledge of the life history of the target species, it was thought that understanding details of its predatory behaviour is critical for comprehending its ecological requirements.

2.1.3 Thermoregulation in Ectotherms

Unlike endotherms, ectothermic organisms experience more immediate effect from the thermal environment (Corkery et al., 2018). Ectotherms, such as reptiles and amphibians, have body temperatures that depend primarily on heat absorbed from the environment via radiation, conduction and convection. In other words, they are highly dependent on the

physical exchange with the environment (Brown & Shine, 2002). Different ectotherms show varying levels of thermal tolerance that potentially affect their rate of biochemical reactions such as enzyme reaction and physiological process (including respiration, excretion and digestion). For an example, an increase in temperature can contribute to changes in water regulation, oxygen uptake, emergence, mating, development, metamorphosis, growth and even sex reversal in amphibians (Feder & Burggren, 1992, Bickford et al., 2010). Although some species may have a common thermoneutral range, others may show the contrary trend. Geographical distribution contributes to thermal tolerance and thermoregulatory behaviour of species or populations within a species, so it can be generalised that ectotherms are influenced by thermal landscapes (Refsnider et al., 2019).

In short, ectothermic animals regulate their body temperature through exploitation of thermal resources of the surrounding environment, albeit thermoregulatory behaviour varies between species. In some, the substrate temperature is more important than radiant energy from surrounding. It is significant especially when radiant energy is unavailable. Corkery et al. (2018) stated that the role of thermal environment has received rising attention due to global warming. Considering the large differences in inter- and intra-specific variation of thermal tolerances among amphibians and reptiles, the rise in global warming undoubtedly will affect these organisms in a way that is poorly or too subtle to be currently understood (Bickford et al., 2010).

Shifting away from heliothermic behaviour to gain heat from substrate is an example of thermoregulatory behaviour, in order to maintain optimal body temperature. However, some reptiles with a wide range of temperature preference, may move less since they do not require much to regulate body temperature to prevent wide fluctuations. Therefore, ectotherms are not entirely limited by ambient temperatures (Corkery et al., 2018).

Thermoregulatory behaviour-imposed costs such as energy loss, predation risk and missed opportunities for foraging and breeding (Huey & Slatkin, 1976; Sears et al., 2016).

Taking advantage of modern technology, the existence of temperature-sensitive radio transmitters has allowed researchers to record body temperatures of target organisms without the need to disturb them.

2.2 Biological Review of *Tropidolaemus subannulatus*

2.2.1 Geographical Distribution

Tropidolaemus subannulatus is known from Sulawesi, southern Philippines, and is widespread on Borneo. This species can be found four countries- Indonesia (Kalimantan), parts of Philippines, Brunei Darussalam, and Malaysia (Labuan, Sarawak and Sabah) (Stuebing et al., 2014; Das & Charles 2015). A sister-species, *T. wagleri* is known from Sumatera (Indonesia), Peninsular Malaysia (Malaysia), Singapore, Thailand, and Vietnam (Vogel et al., 2007). These two species are therefore geographically allopatric.

On the island of Borneo, *Tropidolaemus subannulatus* can be found at 20 and up to 1,400 m elevation (Auliya et al., 2012), in both primary and secondary forests. This pit-viper is commonly sighted at several sites on Borneo, including Kubah National Park, Bako National Park, and the alluvial forests of Gunung Mulu National Park. Although it is a common and widespread species, there have been rather few observations in the wild. Aspects of their biology, including habitat utilization, movement, diet, reproductive behaviour, thermoregulation and related life history aspects had remained unknown till now.

2.2.2 Taxonomy Identification

The Bornean keeled pit-viper (*Tropidolaemus subannulatus*) is an ovoviviparous, venomous snake, and till the early part of the century, was confused with *T. wagleri*. Vogel

et al. (2007) reviewed the genus and demonstrated the distinctness of *T. subannulatus* from *T. wagleri*. Firstly, the internasals are not in contact, being separated by two (rarely, one) scale(s). Secondly, the strong ontogenetic shift in colouration and pattern that occur in female *T. wagleri*, in which the adult females are mostly black (not green), with yellow crossbands. This is in contrast to the green ground colour of both male and female adult *T. subannulatus*. Thirdly, the supralabial scales of *T. subannulatus* is typically separated from the suboculars which in contrast to about one third of cases in *T. wagleri*. Characteristics of the species include a flat-topped and steep-sided head, in addition to its distinctive triangular shape, the rear of head wider than the neck. The scales on the throat are enlarged and are keeled.

Stuebing et al., (2014) described that in juveniles, males and females are similar in morphology, both having a slender body, and therefore, may be visually unsexable. As they mature, male and female become sexually dimorphic as well as dichromatic. While males are relatively slender, females are heavy-bodied, longer, and heavier than males. Females can grow up to 1 meter in length, whereas males grow under half that size. The obvious variation displayed by the species is in colouration among the females. Some appear yellow-green, with bluish crossbands, while some other turn blue-black, with small yellowish green dots arranged in a crossband pattern. This is in contrast to the adult males that displays a green ground colour, with rows of red spots on each side of the flanks, that either fade or turn blue.



Figure 2.1: Reproduction of *Tropidolaemus subannulatus* (Gray, 1842) published by Motley and Dillwyn (1855) in what may be the first account of the natural history of Borneo's vertebrate fauna, entitled 'Contributions to the natural history of Labuan and adjacent coasts of Borneo'.

2.2.3 General Ecology

The target species occupies lowland forests in Borneo, where they are arboreal and associated with low vegetation, and sometimes, on trees over 2 m above ground. They are known from lowland dipterocarp forests, and other habitats in the plains, particularly in the vicinity of water bodies (Das & Charles, 2015).

The Bornean Keeled Pit-viper is an ambush forager as they practice the ‘sit-and-wait’ technique. Unlike active foragers, vipers are adapted better in intraoral prey transport compared to other snakes (Cundall & Deufel, 2006). Vipers are significantly exceptional based on ratios of snake body length to prey length and maximum diameter of prey (Pough & Groves, 1983; Cundall & Deufel, 2006), and known to swallow prey 36% of its mass, the largest prey swallowed by any snake, while the largest prey devoured by a non-viper is approximately 14% of its mass. This indicates that their morphological features reduce the handling costs for prey as well as increasing the maximum size of prey that a pit-viper can swallow (Pough & Groves, 1983). The diet of the target species consists of small mammal and birds for adult individual, while the juveniles and half-grown individuals consumes lizards and frogs (Stuebing et al., 2014).

The venom of *T. subannulatus* is haemotoxic, with the property to destroy red blood cells, and this species is known to be medically significant, although there are no recorded human mortalities from its bite. A Study by Tan et al. (2017) on venomics of the congeneric *T. wagleri* reported that its venom is rather different among many pit-vipers, containing abundant neurotoxic peptides but little hemotoxic proteinases. According to the Clinical Toxinology Resources Website (2018), the venom of *T. subannulatus* was found to contain a mixture of procoagulants with the possibility of having anticoagulants and haemorrhagins properties. Ismail et al. (2023) reported that the bites from this species are often minor.

However, it may cause moderate to severe local effects. Generally, it does not induce necrosis or coagulopathy and the treatment is supportive and symptomatic without the specific venom.

CHAPTER 3

METHODS AND MATERIALS

3.1 Study Site

3.1.1 Geology and Topography

Gazetted on 17 November 1988 (Forest Department Sarawak, 2020), Kubah National Park covers an area of 2,230 ha, and is located in the Matang Range of western Borneo, in the State of Sarawak, East Malaysia. The Park is situated approximately 20 km north-west of Kuching City, the state capital. It is the closest National Park from the city, and therefore easily accessible compared to others in Sarawak. The three major peaks within the Range include Gunung Serapi, Gunung Sendok and Gunung Selang. Gunung Serapi is the highest, at 911 m asl. The range has a rather hilly and steep terrain which consist of mud and sand deposited alluvium, along with water body such as streams and drains on the flanks. Hazebroek and Morshidi (2000) described the geology of the Park, which is made up of a variety of soft podzolic soils that are of different colours such as red-yellow and grey-white, lowland podzols on soft old alluvium, soft upland podzols and concentrated alluvial soils. The forest vegetation primarily consists of mixed dipterocarp, with small areas of scrub forest and patches of Kerangas (or Bornean heath). The variation in topology and geology is thought to be associated with the rich species richness of the flora and fauna of the Park.

3.1.2 General Introduction to Habitat

The Park's vegetation mainly comprises undisturbed natural forests, with five major types of vegetation- alluvial forest, mixed dipterocarp forest, heath (Kerangas) forest, submontane forest and secondary forest, with patches of scrub forest (Hazebroek &

Morshidi, 2000). Due to its location, Sarawak has an equatorial climate, characterized by heavy precipitation, consistent high temperatures, and relatively high humidity (Whittow, 1984; Singh, 2012). These factors collectively have resulted in an abundance of species richness of flora and fauna.

At least 100 palm species (Pearce, 1992), many species of wild orchids and ferns (Vermeulen & Lamb, 2011) and 12 timber-producing tree species of commercial value (Bukhori et al., 2019) have been recorded from Kubah. A total of 19 species of wild mammals (Mohd-Azlan et al., 2018), 69 species of amphibians (Das et al., 2018) and 155 species of birds (Lepage, 2021) have been recorded, further suggesting high biological richness of the Park. This is associated to Kubah being an active ecotourism spot and familiar to researchers and the general public who visit the Park in large numbers. Lihan et al. (2014) studied soil sample collected at the Park and detected antimicrobial activity with the potential to develop antimicrobial compound for battling infectious bacterial agents. The interaction between biotic and abiotic components in Kubah National Park is thus vast, complex, and requires more study.

3.1.3 Location of Study

Field work was carried out at Kubah National Park at six existing trails (Belian Trail, 1.5 km, Summit Trail, 5 km, Selang Trail, 1.6 km, Main Trail, 1.9 km, Rayu Trail, 3.8 km and Waterfall Trail, 1.6 km). A paved tar road reaches the summit of Gunung Serapi, and is within the Summit Trail, its purpose being to access the telecommunication and observation tower at the peak and is about 3–4 m in width and about 5 km long.



Figure 3.1: Location of Kubah National Park, in western Sarawak. Source: Google Maps.

3.2 Data Collection

The Visual Encounter Survey (VES) technique (Doan, 2003) was used along the existing trails at the study site. Pit-vipers were located visually and individuals weighing 5% or less of the respective radio-transmitter weight were used, the transmitter implanted and radio tracked. A total of 12–15 days were devoted to field data collection each month, and 8–9 hours spent per day, involving four persons, both by day and at night. A total of 21 snakes were encountered during the study period (June 2018 to October 2021). Seven individuals were studied for tracking and five successfully tracked between the period of October 2019 to January 2020. Three males and two females were implanted with temperature-sensitive radio-transmitters and data obtained for analyses. Environmental data,

such as ambient temperature, humidity, and light intensity, were recorded with a 4-in-1 Environmental Meter (EXTECH 45170). Quantification of canopy cover was made by digital photography estimates (DPE), via the grid method, using Adobe Photoshop 2021 (version 22.5.1.441).

Ethograms of feeding behaviour was done in a controlled environment in the lab. All activities were recorded with a Sony HDR-XR350, 7.1 Mega Pixels Handycam video camera recorder and the behaviour analysed via the video editing software, Lightworks (version 2021.1).

3.2.1 Climatic Data

Sarawak's latitudinal position in north-western of Borneo is within the humid tropics which gives it a year-round equatorial climate (Singh, 2012), and the lowland of the State has uniform high temperature and humidity nearly throughout the year. The temperature can be within the range of 23°C during early mornings, to 32°C at other times of the day (Sarawak Government, 2018). Although the humidity is constantly high in the lowlands (80–90% relative humidity), the precipitation and advent of the monsoons vary. In north-east Sarawak, the monsoons typically extend between November and February, bringing heavy precipitation (Sarawak Government, 2018). Depending on locality, average precipitation per year is between 3,300 mm and 4,600 mm. With such variation in climatic conditions, it is significant to study the ecology of ectotherms since they are sensitive to environmental, particularly thermal, change.

3.2.2 Radio Telemetry

Being an ambush forager, *Tropidolaemus subannulatus* tends to spend much of the time at a single location without moving and can be secretive and rather difficult to observe

in the wild. The use of radio telemetry in wildlife study had progressed much since its first use in the 1960s (Cochran & Lord, 1963). Since then, it has opened a vast opportunity of topics for ecological studies. The continuous advancement in wildlife radio telemetry technology has enabled researchers to obtain data such as home range size, movement, migration and dispersal, habitat preference, microhabitat use and thermoregulation (Habib et al., 2014).

Unlike other reptiles, attaching radio transmitters to snakes presents special challenges, for lack of limbs, ability of the body to extend after a large meal and typically, a smooth body contour, permitting slippage of external harnesses. Thus, most transmitters are attached internally via surgical implantation. Internal attachment also enables core body temperature readings to be obtained by the temperature sensitive transmitter.

Two models of radio transmitter were used in this study, Holohil BD-2 and Holohil SB-2 (Holohil Systems Ltd, Canada) due to the contrast in weight between two sexes. Holohil BD-2 was implanted in males and Holohil SB-2T in females. Compared to Holohil BD-2 which has a lifespan of 10–20 weeks, Holohil SB-2T has a lifespan of 3–6 months, being larger, and therefore, housing a larger battery. Transmitters were encased with multiple layers of a biologically inert butyl rubber compound in order to prevent tissue reaction. Both models had frequency ranges up to 151 MHz. Thermal data obtained in this study include body surface temperature (T_{bs}) and surface temperature (T_s), recorded with a thermal gun (Fluke 62 MAX, 62 MAX+ Infrared Thermometer).

Locations of encounter were recorded with a Global Positioning System (GPS) of (GarminTM Map60CSx), and home ranges maps were prepared. A laser distance meter (Leica model DistoTM D2) was used to estimate spatial displacement. Individuals implanted with transmitters were radio-tracked at least 12 days per month. In tropical rainforests, radio-

tracking can be a challenge, especially in study sites with dense vegetation, presence of physical barriers such as boulders and large fallen logs, along steep terrain.

3.2.3 Temperature and Thermoregulation

Ectotherms in the wild experience temperature shift depending on the environment, movements and activities, its study potentially leading to increasing of our understanding of their life history and thermal tolerance. A number of methods have been used to study body temperature and thermoregulation of ectotherms. Cowles and Bogert's (1944) pioneering work of thermal requirements in desert reptiles took body temperature through cloacal, which are now thought to potentially differ from actual readings, as it involves handling of the animal. Obtaining core body temperatures of an animal by implanting data loggers and temperature sensitive radio transmitter does not require handling or disturbing of the target animal, and therefore, yields more accurate data. Adam et al. (2016) recorded body temperature in Koalas (*Phascolarctos cinereus*) via surgically implanting temperature-sensitive transmitters and data-loggers, and reported that the body temperature reading between the two did not exceed 0.3°C, with about 85% of the data typically within a difference of 0.1°C.

3.2.4 Morphometric Measurements

Snakes were put under anaesthesia with the use of isoflurane during the assessment, as a safety precaution, in which the administration of anaesthesia was carried out by a licensed veterinarian. The following body measurements were taken- Snout-vent-length (SVL) and Total Length (ToL), with a measuring tape, while Head Width (HW) and Jaw Width (JW) with a dial caliper (Mitutoyo™, to the nearest 0.1 mm), and weight recorded with an electronic digital scale (MyWeight™ 7001^{DX}, to nearest 1 g). Snakes were sexed

while unconscious. Attempts to sex snakes while conscious proved challenging due to the dangers of handling them as well as on account of the retractive muscle often preventing the extrusion of the hemipenes. Only snakes that weighed 5% or less that of the respective radio-transmitter were selected for the surgical implantation of radio transmitters (Kenward, 1987; White & Garrott, 1990; Rowley & Alford, 2007) Individuals which did not meet the requirements to implant the transmitter are injected with pit tags to mark them. Morphological photos of the snakes are also taken from dorsal, ventral, lateral head views, ventral head view and dorsal head view.

3.2.5 Prey Handling Behaviour

Vipers can strike in less than half a second, and can lunge from a resting position, erect the elongate fangs, inject venom into their prey and return to their original position, presumably to escape retaliation from its victim (Kardong, 1986; Kardong & Bels, 1998; LaDuc, 2002). *Tropidolaemus subannulatus* acquired from the field were placed in a lab setting. A transparent glass tank measuring 90 cm x 45 cm x 45 cm was used. A 5 cm x 5 cm grid was placed on a frontal plane and at the bottom of the tank to estimate distance and for scale. The video recorder was on tripod was placed in front of the setting to record all the activities. Environmental readings such as ambient temperature (T_a) was recorded with 4-in-1 Environmental Meter (EXTECH 45170); body surface temperature (T_{bs}); and surface temperature (T_s) were taken with a thermal gun (Fluke 62 MAX, 62 MAX+ Infrared Thermometer). ‘Pinkies’ (i.e., newborns) of the Brown rat (*Rattus norvegicus*) were used in these experiments, as the diet of the snake has been reported to include small mammals (Stuebing et al., 2014). *R. norvegicus* is amongst the familiar laboratory animals, as well as widespread worldwide, including in Malaysia (Schweinfurth, 2019). The entire sequence of

feeding behaviour was recorded, analysed using Lightwork video editor (version 2021.1), and prey handling behaviour ethogram was prepared.

3.3 Data Analyses

Data such as ambient temperature, substrate temperature, body surface temperature and core body temperatures were tested with regression and correlation analyses to assess the relationship between variables, after transformation to log paper, with significant levels set at 0.05. Analyses of home ranges were done using Biotas (Ecological Software Solutions™; version 2.0) and QGis (version 3.18.3). Independent sample t-test was conducted to find out the significant difference in home range size between different sexes.

Ethograms were analysed from video footages and still images downloaded from the video camera using Lightworks (version 2021.1) video editing software for behavioural descriptions. Other statistical procedures have been described in the respective data chapters.

CHAPTER 4

SPATIAL ECOLOGY OF *TROPIDOLAEMUS SUBANNULATUS*

4.1 Introduction

According to Lillywhite (2014), snakes had evolved into organisms which occupies a vast variety of habitats, from terrestrial to aquatic and from the cold tundras to dry deserts. Their morphological features and physical specialization are adapted to enable them to survive specific habitats. Many snakes are secretive and highly elusive, making them hard to study in the field. Spatial utilization is an important aspect to be understood as it is of great biological significance in understanding an animal's home range (Hayne, 1949). Therefore, an understanding of habitat occupancy and spatial requirements is necessary for enhancing species conservation and management.

Many factors affect animal movement, including environmental and social variables, as well as presence and dispersion of potential predators and prey (Schwaner, 1991; Houston & Shine, 1994). Movements, activities, as well as general spatial patterns of ectotherms such as snakes are affected by a mixture of abiotic and biotic aspects (Gibbons & Semlitsch, 1987; Gregory et al., 1987; Secor, 1994). Wakso (2009) generalised that movement pattern and spatial utilization may be connected to life history parameters, such as reproduction (Gregory et al., 1987; Reinert & Zappalorti, 1988; Shine, 2003), growth (Wharton, 1966; Diller & Johnson, 1988; Bronikowski, 2000) and food acquisition (Secor & Nagy, 1994; Luiselli, 2006).

This study focusses on the Bornean Keeled Pit-viper, *Tropidolaemus subannulatus*, which, while being relatively abundant, remains poorly understood. There is a single field

observation by McKay (2001) that report low activity in six days of observation made on an individual at Bako National Park, Sarawak.

Usage of spatial resources by an animal demonstrates the opportunities these resources provide (Waser & Wiley, 1979), such as food, shelter and mating opportunities (Macartney et al., 1988). Within vipers, home range sizes are known to vary. Reiserer et al. (2018) reported desert-dwelling rattle snakes and other vipers having large home range and are known to displace over 2 km in a few days. Relatively small home range among vipers have also been demonstrated. Lillywhite and McCleary (2008) found snakes occupying areas near bird rookeries that have small home ranges (0.01 to 0.02 km²), showing little spatial displacement as they forage nocturnally below rookery trees.

Although the climate of the tropical island of Borneo has been generalised as being with uniformly high temperature and humidity all year round, certain biotic or abiotic factors contribute to changes in behaviour of movement/displacement or activity, such as such as during the reproduction season and/or the monsoonal months. The active search for mates, shift in local rate of precipitation, and the dynamics of prey abundance over time are examples of motivation that affect the behavioural movement of an animal, and consequently, affect the rate of spatial utilization.

The introduction of radio telemetry has allowed researchers to study the ecology of the most secretive of species that are difficult to observe in nature. Radio telemetry provides the opportunity and access to a myriad of ecological data that enable researchers to understand critical aspects of an organism's life history, such as home range, movement, migration and habitat utilization.

4.2 Specific Objectives

Questions developed for the chapter on the field ecology of *Tropidolaemus subannulatus* include determination of movement pattern and use of spatial resources by the species.

1. How large is the home range and what movement pattern does this species demonstrate, vertically as well as horizontally?

Are there significant differences in movement and home ranges between the sexes?

4.3 Methodology

4.3.1 Transmitter Types

Two types of radio transmitter were used in this research, namely Holohil BD-2 and Holohil SB-2 (Holohil Systems Ltd, Canada) radio transmitters. This is due to the difference in body mass between the sexes of the target species. Holohil BD-2 transmitters weigh 1.2 g and was implanted in males; Holohil SB-2T transmitters weigh 3.6 g and were implanted in females. Holohil BD-2 has a lifespan of 6–10 weeks, while corresponding figures for SB-2T were 3–6 months, being larger, and therefore with a larger battery (dimension of 14 x 9.5 mm, versus 16 x 8 x 3.5 mm). Both had frequency range from 138–235 MHz. The use of transmitters to track snakes were between 8 October 2019 to 16 January 2020. Three Element Folding Yagi antenna was used during the radio tracking period. Generally, the antenna can help reach radio transmitter signals up to a range of ca. 8 km. However forest terrain and vegetation can significantly affect transmission range, especially on mountainous landscapes, such as in Kubah National Park, which is characterised by a hilly topography. Additionally, a Rayleigh's test was conducted to determine the movement patterns of *T. subannulatus* where the locations was based on GPS coordinates recorded.

4.3.2 Water Bath Calibration of Transmitters

Although plotted calibration curve graphs of each unit of radio transmitter were provided at the time of purchase, an additional term of calibration using a water bath (Memmert™, WNB 7-45) was carried out to compare the readings (Figure 3.3). Each unit of radio transmitters were submerged in a temperature-controlled water bath against a calibrated thermometer. Once constant temperature was reached, pulse period was determined at 20°C, 21°C, 22°C, 23°C, 24°C, 25°C, 26°C, 27°C, 28°C, 29°C and 30°C, using TRX 2000™ Wildlife Materials, Inc. receiver. The variations observed in plotted calibration curves graph provided by manufacturer was as small as $\pm 0.001^\circ\text{C}$.

4.3.3 Transmitter Implantation Technique

Since internal attachment is required via surgical implantation techniques, the procedure was conducted by a qualified veterinarian. Isoflurane anaesthetic was administered by direct inhalation. The snake was handled with appropriate caution and placed into a transparent plastic tube of 2.0 cm diameter and 90 cm length for male snakes and 3.0 cm diameter and 100 cm length for female snakes. The snake was introduced head-first through the open end of the cylinder, the opposite end being plugged with cotton wool impregnated with isoflurane for induction of anaesthesia.

Celiotomy was executed for surgical implantation of radio transmitter. Chlorhexidine solution was used for routine aseptic preparation of the surgical site prior to the surgery. Incision at the distal third of the body length was made ca. 1.8 cm along the first and second lateral flank scale from the cloaca. Each radio transmitter was sterilized with absolute alcohol before their complete insertion, along with the antenna (Reinert & Cundall, 1982). A simple continuous pattern of 3-0 USP Polyglycolic acid suture material and one horizontal

mattress pattern of ‘seralon’ 3-0 USP were done to close the coelom incision. The incised area was wiped with iodine solution to prevent infection. After surgery, the snake was kept in captivity for 3–5 days for observations of healing before being release at the point of capture.

Placement of radio transmitter in the coelomic cavity was first introduced by Reinert and Cundall (1982) for two North American venomous snakes (*Crotalus horridus* and *Agkistrodon contortrix*). Both species share a somewhat similar shape, being short and stocky in morphology, reminiscent of *Tropidolaemus subannulatus*. The following procedure allowed maximum transmission range and no major physiological or behavioural changes in the snakes were found anatomically and during field observations.

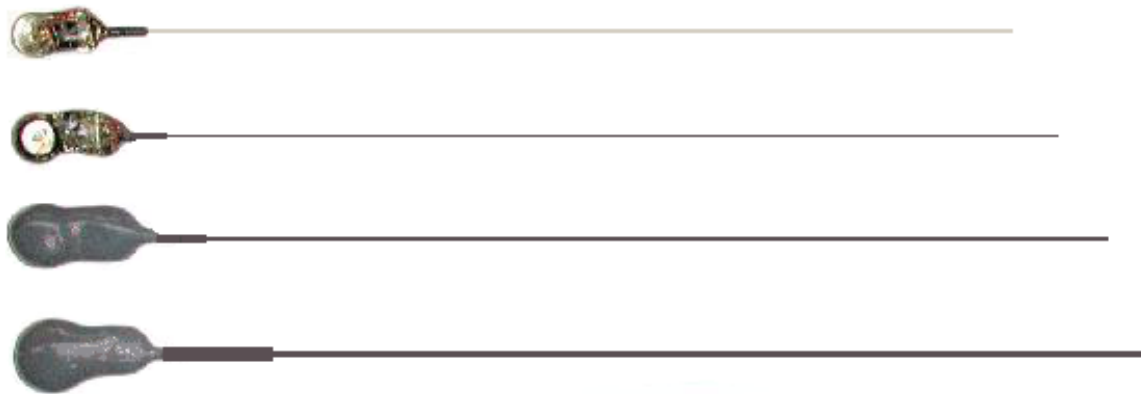


Figure 4.1: Holohil BD-2 (Holohil Systems Ltd, Canada) radio transmitter used for male *Tropidolaemus subannulatus*.



Figure 4.2: Holohil SB-2 (Holohil Systems Ltd, Canada) radio transmitter used for female *Tropidolaemus subannulatus*.



Figure 4.3: Water bath (Mettmert,WNB 7–45) used in laboratory calibration.



Figure 4.4: Female (left) and male (right) of adult *Tropidolaemus subannulatus*, demonstrating extreme sexual size dimorphism as well as dichromatism.

4.4 Results

4.4.1 Home Range Characteristics

A total of 30 location points were recorded from five individuals, consisting of two adult males and three adult females. Minimum convex polygons (MCP) were constructed using QGIS (version 3.18.3) for home range estimation, using the coordinates recorded during the radiotracking period. The locations were mapped with QGIS with each individual clustered in certain area as shown in Figure 4.5 and were revisited periodically. The 100% MCP value generated shows that the population of *T. subannulatus* under study has a home range size of 143.78 to 834.21 m². As shown in Table 4.1, most snakes show a near-identical

home range size (below 200 m²), except for a female (TROS 005) that demonstrated a home range size of 834.21 m².

Table 4.1: Summary of *Tropidolaemus subannulatus* radiotracked, radiotracking period, body mass, sex and Minimum Convex Polygon (MCP, 100%, m²), with means and standard error (SE), as recorded from October 2019 – January 2020.

Snake ID	Tracking period		Tracking Days	Morphometric		Sex	Home range 100% MCP (m²)	
	Start	End		SVL (cm)	Mass (g)			
TROS 002	10/10/2019	22/11/2019	44	57.6	91.2	Female	197.41	
TROS 005	16/10/2019	16/01/2020	93	51.6	84.0	Female	834.21	
TROS 010	20/11/2019	16/12/2019	27	64.0	259.0	Female	168.34	
TROS 004	08/10/2019	25/10/2019	18	40.0	28.0	Male	173.80	
TROS 008	15/11/2019	02/12/2019	18	39.9	23.0	Male	143.78	
					Female	Mean	8	399.99
						SE	2	217.27
					Male	Mean	5	158.79
						SE	0	15.01
					Both	Mean	7.4	303.508
						SE	1.81	132.95

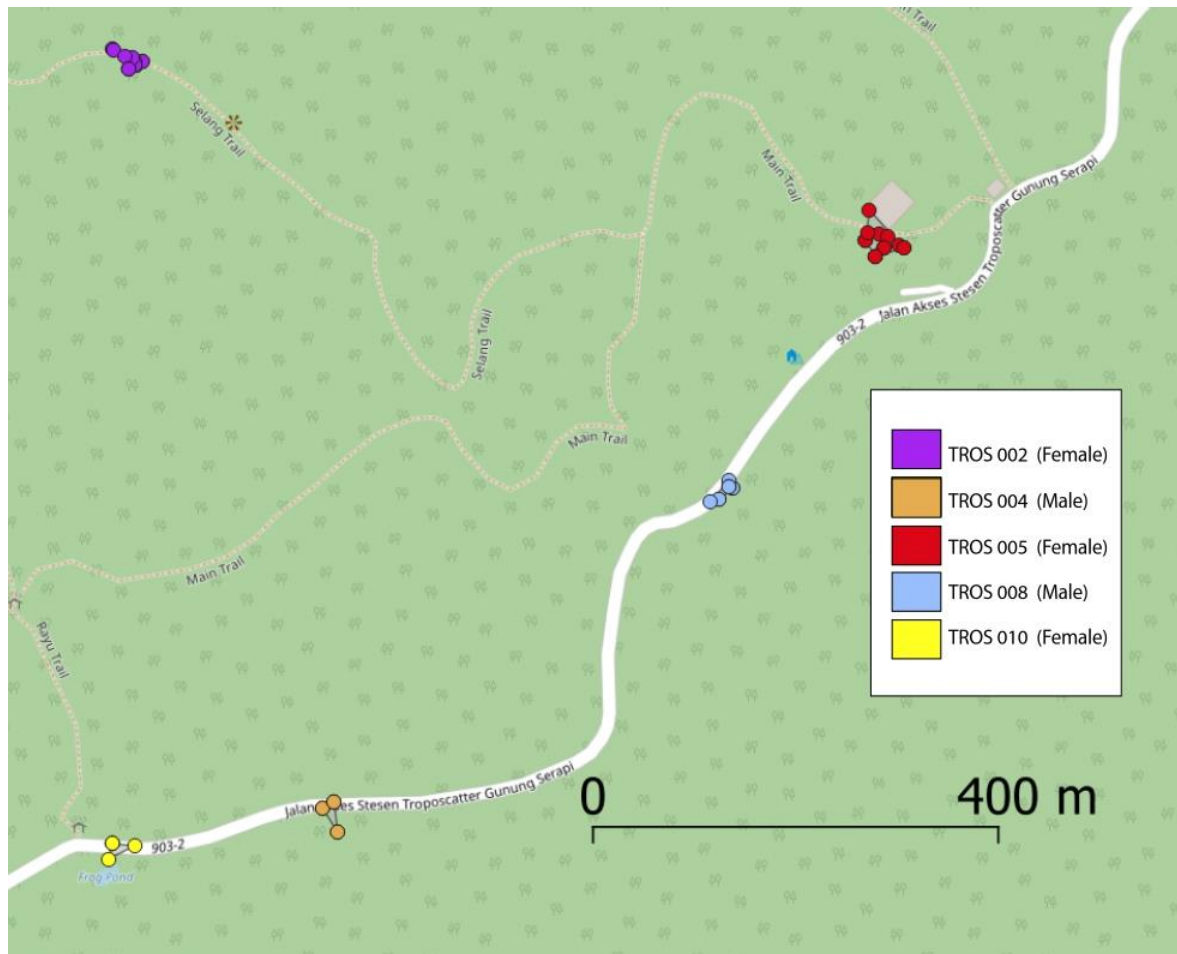


Figure 4.5: Locations of five individuals of *Tropidolaemus subannulatus* at Kubah National Park, Sarawak, East Malaysia.

4.4.2 Spatial Displacement in *Tropidolaemus subannulatus*

Each individual of *Tropidolaemus subannulatus* displayed limited movement during the study (Table 4.2). Females ($n = 3$) showed a mean horizontal movement of 27.06 m, larger than that of the males ($n = 2$), which was 11.64 m. Females had higher mean vertical movement of 16.74 m, while for males, it was 7.47 m (Table 4.2). Nonetheless, an independent-sample t-test failed to show significant differences in both horizontal and vertical movements ($p = 0.59$ and 0.33 , respectively). A Rayleigh's test revealed that two snakes in this study (a male and a female) showed no significant difference in movement,

while three others showed a significant ($p\text{-value} < 0.05$) difference (Table 4.3), suggestive of asymptote not being reached for sample size. Figure 4.6 and Figure 4.7 showed general shape of each individual movement pattern by calculating displacement from GPS waypoints. The different locations of each individual inhabit could also be the factors for the dissimilar result as none of the snake individual showed spatial overlap (Figure 4.5).

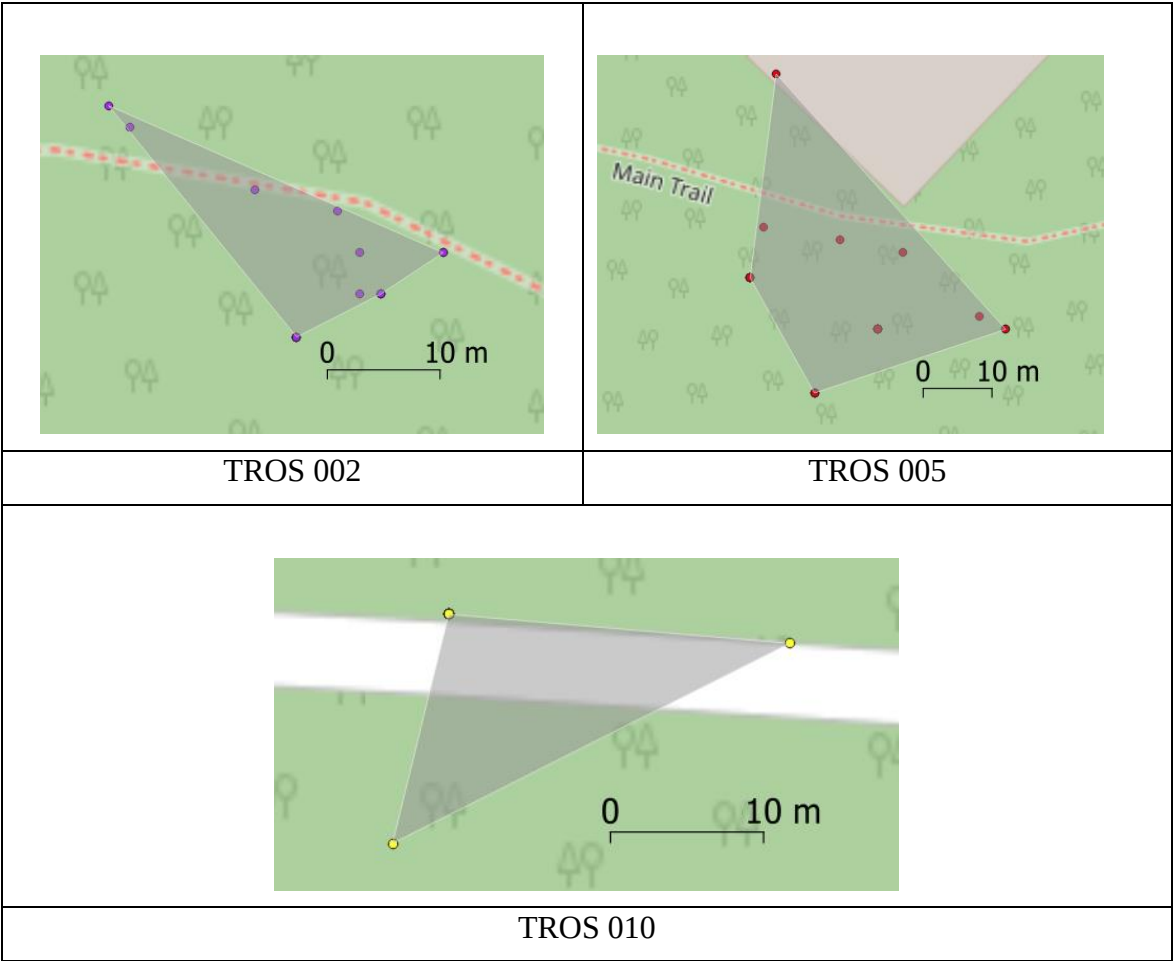


Figure 4.6: General shape of female *Tropidolaemus subannulatus* home range.

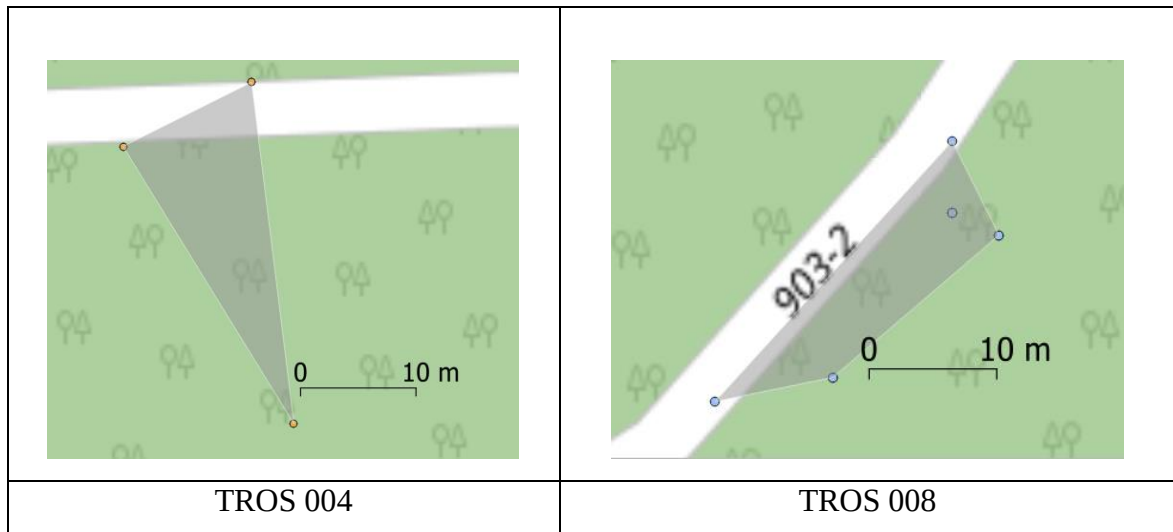


Figure 4.7: General shape of males *Tropidolaemus subannulatus* home range.

Table 4.2: Summary of *Tropidolaemus subannulatus* radiotracked, radiotracking period, tracking days, body mass, sex and movements details (horizontal and vertical displacement; mean daily displacement (MDD, m/days) with mean and standard error (SE) as recorded from October 2019 - January 2020. Abbreviations: h = horizontal; v = vertical displacements.

Snake ID	Tracking period		Tracking Days	Morphometric		Sex	Movement			
	Start	End		SVL (cm)	Mass (g)		Displacement (m)		MDD (m/days)	
							h	v	h	v
TROS 002	10/10/2019	22/11/2019	44	57.6	91.2	Female	15.13	29.07	0.34	0.66
TROS 005	16/10/2019	16/01/2020	93	51.6	84.0	Female	65.42	8.75	0.70	0.09
TROS 010	20/11/2019	16/12/2019	27	64.0	259.0	Female	0.63	12.4	0.02	0.46
TROS 004	08/10/2019	25/10/2019	18	40.0	28.0	Male	6.57	7.22	0.36	0.40
TROS 008	15/11/2019	02/12/2019	18	39.9	23.0	Male	16.71	7.71	0.93	0.43
				Female	Mean	8	27.06	16.74	0.35	0.40
					SE	2	19.63	6.25	0.20	0.17
				Male	Mean	5	11.64	7.47	0.65	0.42
					SE	0	5.07	0.25	0.29	0.02
				Both	Mean	7.4	20.89	13.03	0.47	0.41
					SE	1.81	11.51	4.11	0.16	0.09

Table 4.3: Rayleigh's test (using Biotas 2.0) for movement directionality.

Snake ID	Sex	Rayleigh's test	
TROS 002	Female	Angle Count (N)	15
		Result Statistic (R)	0.3570
		P-value	0.1480
TROS 005	Female	Angle Count (N)	23
		Result Statistic (R)	0.5920
		P-value	0.0000
TROS 010	Female	Angle Count (N)	8
		Result Statistic (R)	0.6580
		P-value	0.031
TROS 004	Male	Angle Count (N)	9
		Result Statistic (R)	0.7260
		P-value	0.0090
TROS 008	Male	Angle Count (N)	8
		Result Statistic (R)	0.4400
		P-value	0.213

4.4.3 Sexual and Individual Variation

Female snakes showed a mean Minimum Convex Polygon (MCP) value of 0.4000 m², while value for males was 0.1588 m². Nonetheless, analysis of the sexes displayed no significant difference in home range size (Independent sample t-test: $p = 0.453$, > 0.05). Further, no home ranges were found to overlap.

As shown in Figure 4.8, even though an individual female (TROS 010) weighed almost 70% more than the other two females, it did not demonstrate higher horizontal and vertical MDD value (0.46 m/days). Referring to Table 4.2, the highest horizontal MDD value was shown by female (TROS 005, 0.70) and highest vertical MDD was shown by female (TROS, 002). Both males were near-identical in mass, with one (TROS 008) showing a higher horizontal MDD (0.93 m/days) than the other (0.36), or over 60%, although vertical displacement MDD was near-identical. A male (TROS 008) displayed the highest horizontal MDD (0.93), while a female (TROS 002) displayed the highest vertical MDD (0.66).

All individuals displayed sluggish behaviour, with little movement, rarely moving from a location for days. Longest period of a snake staying at one location point was 18 days (Table 4.4).

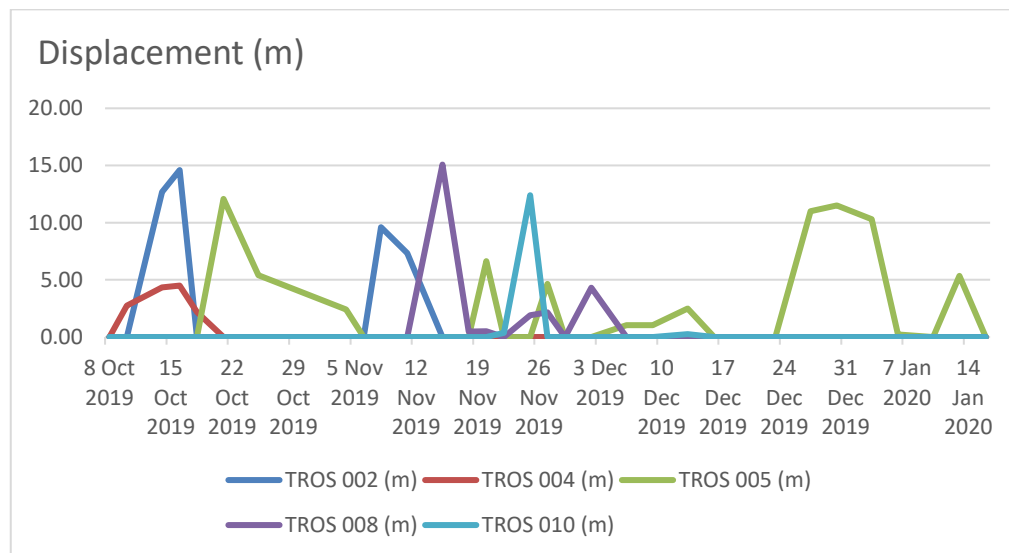


Figure 4.8: Individual variation in displacement by five individuals of *Tropidolaemus subannulatus* between location points (in metres, m).

Table 4.4: Summary of longest period stayed in one point location of *Tropidolaemus subannulatus* between October 2019 – January 2020.

Point Location	Longest Period stayed in 1 Point Location (Days)				
	TROS 002	TROS 005	TROS 010	TROS 004	TROS 008
1	2	1	1	3	1
2	5	1	5	3	1
3	4	8	1	8	3
4	9	1			1
5	2	7			1
6	2	4			
7	1	1			
8	3	18			
9	1				
10	10				

4.5 General Discussions

4.5.1 Spatial Movement of *Tropidolaemus subannulatus*

The home range size of *Tropidolaemus subannulatus*, according to 100% MCP value was computed to be 143.78–834.21 m², with mean value of 303.508 m². There was no significant difference ($p = 0.453$) between the home range size of males and females. While there are no previous studies to these results with, some comparisons can be made with other pit-vipers in Asia. Home range of green pit-vipers (*Cryptelytrops macrops*) showed mean 100% MCP value 0.18–0.41 ha, with mean value of 0.26 ha (Barnes et al., 2019). Males green pit-vipers' (*Trimeresurus macrops*) mean 100% MCP value was computed to be 0.216 ha, while females show mean 100% MCP value of 0.099 (Barnes et al., 2019). Overall, home range sizes of pit-vipers are rather small.

All locations were within the Park's existing trails, namely, the Summit Trail, the Selang Trail and the Main Trail. Three individuals were found along the Summit Trail (one female and two males), one female was found along the Selang Trail and another female on the Main Trail. The female, TROS 005, appeared to have a slightly larger home range compared to the others (834.21 m^2), while other individuals had movements restricted between 143.78 to 197.41 m^2 . This is most likely due to the amount of tracking days conducted on this particular individual. The female TROS 005 had the most tracking period of 93 days while the other snakes were tracked below 45 days. TROS 005 was also found on the Main Trail, its location with a patch of uniform lowland area, with more than 90% forest vegetation density. This species is thought to use connecting canopies to move and has never been encountered on the ground. The location of TROS 002 was at a hill with steep ridges, while the other three were on vegetation near the Summit Trail, all four seemingly at the edge of the forest.

Although no home ranges recovered from these studies overlapped among the radio-tracked individuals, two juveniles *Tropidolaemus subannulatus* were found within the home ranges of the female referred to as TROS 010. This individual was initially encountered at the Summit Trail near the Frog Pond area. Among the other females, TROS 010 was the heaviest (at 259.0 g vs. 91.2 to 84 g in the rest). Considering the differences in morphology, TROS 010 could have been a large mature female, while the other two were mid-sized adults. One of the juveniles found within the home range of TROS 010 was perched too high to be captured, the other captured and pit-tagged (ID number: 989001025002043). The tagged juvenile was released at the point of capture but was not encountered subsequently. It is plausible that the two juveniles are offsprings of TROS 010.

Movement in the target species was found to be limited. McKay (2001) showed that *T. subannulatus* in Bako National park, Sarawak moved less than 2 metres over six days. Reduced movement is known to reduce predation risk (Gerritsen & Strickler, 1977; Barnes et al., 2017). In this study, due to limited movements displayed by this sedentary species, it was also difficult to assess the true home range of the snake species. Limited tracking duration, combined with an inability to immediately replace the transmitter for continuous tracking made data asymptote hard to achieve. Two snakes that had to undergo a second surgery to replace faulty or dead transmitter batteries suffered mortality. Therefore, for this species, a transmitter replacement is not an option even though a longer tracking period was needed.

Male and female *T. subannulatus* showed no significant differences in movements, either horizontally and vertically ($p = 0.59$ and 0.33 , respectively). Nonetheless, females displayed more movement overall compared to males. A caveat here is that 40% of the tracking data had no visuals of the snake's exact location, resulting in arguably more precise horizontal location data with radiotelemetry, while those for vertical data proved more challenging. Based on field observations during tracking, the snakes spend a considerable amount of time on the same tree before moving to neighbouring trees. Although they spent significant amounts of time on the same tree, they frequently travelled up and down, and in three of five individuals returned to the same point location in certain time period.

Vertical displacement is harder to record as they travelled higher than could be observed, or were shielded by thick canopy cover, or both. Nearly 70% of female TROS 002 tracking duration data showed a perch height of over 10 m above ground, and the use of binocular helped identify locations. Limited migration potentially leads to autocorrelation between points concern (Laver & Kelly, 2008; Barnes et al., 2017). This was an issue commonly

faced during tracking of both males and females in the present study. While data show that females have higher mean displacement, there is a likelihood that females travel more looking for males, possibly resulting in male mate choice and female competition (Schlupp, 2018). It would be ideal to standardize the tracking period for all individuals which could highly help to reduce the limited data (Barnes et al, 2017). However, considering the extreme level of sexual dimorphism, transmitter battery life constrain between two models, and ethical predicament of performing multiple transmitter implant surgeries of individuals would require to be addressed to track them for a longer period of time (Strine et al., 2018).

In addition, due to the differences in battery life span, movement comparisons can be fraught with difficulties, and generally, it was difficult to draw a conclusion when comparing the movement pattern between the sexes. A study by Barnes et al. (2017) on the sexually dimorphic genus *Trimeresurus* (Orlov et al., 2002; Chanhom et al., 2011; Strine et al., 2015; Devan-Song et al., 2017) found that general conclusions regarding home range and movement of male and female snakes appear difficult. Their study explained that this is due to the males and females facing different challenges that may be reflected in behaviour, movement and spatial utilization (Madsen, 1987; Shine, 2003). Additional studies are required to evaluate statistical as well as biological independence for fixes in snakes that shows limited movement and small home range size (Barnes et al., 2017). While radio tracking made most of this study possible, some aspects of the snake's behaviour related to spatial ecology remain challenging to obtain data on.

4.5.2 Limitation of Radio Telemetry

Radio telemetry was introduced to wildlife research since the 1960s. Since then, the technology had progressed to become more practical and accessible. Especially with snakes,

radiotelemetry is undoubtedly useful to study numerous aspects of life history and ecology (Újvári and Korsós, 2000). However, it does come with its limitations.

Back at the time of the beginning of radio telemetry, the method was only possible for large animal species due to the large size of transmitters. The larger animals provide a more accurate result considering larger animal doesn't feel as much of a heavy burden being put as an extra weight on them and thus does not impair with their daily activity. Advances in technology, particularly, the miniaturisation of battery cells, have permitted a variety of transmitters, for use in a myriad of animals. The larger the size of the transmitters, the larger the life span of the battery.

In this population, *Tropidolaemus subannulatus* showed an extreme level of sexual size dimorphism. The males are the smaller of the sexes, and weight below 30 g, while females are twice that size, with weight range from 90–260 g. Consequently, males can only be tracked for a few weeks at a time, while females can be tracked for several months.

Related to the above, batteries of the transmitter can get faulty. Grigg and Beard (2001) reported that transmitter batteries are likely to grain out after a time period, and inappropriate storage condition affect temperature sensitive transmitter efficiency. This may have contributed to reduced battery life span, where the battery of the transmitter died unexpectedly earlier than the approximate life span.

While in the field, some transmitter batteries died earlier than expected. Initially there were seven individuals qualified for tracking (four females and three males). But two transmitters died before snakes were release for tracking. Three of five radio tracked snakes (TROS 002, TROS 004, TROS 010) batteries died earlier than the expected life span. While some batteries died earlier than expected in the field, others showed malfunction, also for

unknown reasons after a day or two after implantation in a snake. Of the total of seven snakes implanted for radio tracking, only five could be successfully tracked, as two had dead batteries shortly after implantation. While one individual was lost and failed to be tracked due to battery failure on the first day of tracking, the other died presumably due to trauma from a second transmitter implantation. One of the possibilities to this issue is that the magnet used to inactivate the transmitter might have been.

Another limitation is associated with the arboreal habits of *T. subannulatus*. Radio telemetry permits tracking of horizontal movements, and for the tree-living target species that was further partially or fully covered by foliage, there were no visual of nearly 40% of snakes being tracked. Especially under thick canopy cover, some individuals that perched on top of large leaves, no visual could be obtained by the observer on the ground. With no sightings high above ground and under thick canopy cover, vertical movements were hard to record or estimate.



Figure 4.9: Ventral view of an adult female *Tropidolaemus subannulatus* (TROS 005) perching on vegetation 4.15 m above ground.



Figure 4.10: Locations of five individuals of *Tropidolaemus subannulatus* at Kubah National Park, Sarawak, East Malaysia in satellite view.

4.6 General Conclusion

The home range size for *Tropidolaemus subannulatus* in this study is approximately below 200 m² in the course of this study which is relatively small for a snake of this mass, except for one individual (TROS 005) due to the extreme extended tracking period with the total home range of 834.21 m². Movement and home range between the sexes of *Tropidolaemus subannulatus* did not show significant difference. However, limited movement may have an outsized influence in home size estimation. Movement pattern demonstrates that some individuals display apparently random movement while others do not, indicating further study is required. While horizontal displacement is limited and data was easy to access, vertical movement is rather challenging to study. Due to thick canopy vegetations, visuals of snakes are difficult to obtain especially when they are high up in the canopy. Forest canopies clearly plays an important key role in this species life history as they spend long period of time and displacement high above ground. This study also shows limitations of radio tracking in wildlife studies along with other challenges faced such as transmitter battery issues.

CHAPTER 5

MICROHABITAT UTILIZATION OF *TROPIDOLAEMUS SUBANNULATUS*

5.1 Introduction

The microhabitat usage by a species is typically influenced by a complex interaction of both biotic and abiotic factors (Reinert, 1993; Lin et al., 2007). For instance, predator evasion and protection are considered the most crucial determinants of how a reptile selects its refuge sites or microhabitats (Downes & Shine, 1998; Theodoratus & Chiszar, 2000; Downes, 2001; Blouin-Demers & Weatherhead, 2002; Stapley, 2003; Lin et al., 2007), and to achieve this, many arboreal snakes would select areas with dense vegetative structures that provide cover from predators (Lillywhite & Henderson, 1993; Mullin & Cooper, 2000; Fitzgerald et al. 2002; Pringle et al., 2003; Reaney & Whiting, 2003; Shah et al., 2004; Lin et al., 2007). Additionally, the possession of camouflage colouration helps arboreal snakes to blend with surrounding vegetation, as in the focal species in this study, the Bornean Keeled Pit-viper, *Tropidolaemus subannulatus*. The green dorsum in this species presumably enables it to blend with the vegetation and avoid being spotted by potential predators. It has been argued that snakes with uniform colouration or disruptive patterns of blotches, spots, or irregular crossbands are likely to depend on crypsis, or concealment (Pough, 1976; Lillywhite, 2014).

The essential drivers of microhabitat selection are thought to be predator evasion, prey availability, thermoregulation needs and availability of refuge sites (Shah et al., 2004; Lin et al., 2007). Prey density is presumably vital for an ambush forager, such as *T. subannulatus*. Shine and Sun (2002) reported that a successful ambush site must be visited regularly by potential prey, must permit the predator to avoid detection by prey, must allow

the predator to notice target prey soon and able to see it clearly to launch an effective attack, and the site must be favourable for prey capture. Vipers had evolved to the longest and most complex fang structure to inject venom within snakes (Lillywhite, 2014), this feature providing an advantage for an arboreal viper to make a successful kill. Besides foraging and predation, thermoregulation sites are necessity for every ectotherm to carry out basic physiological functions and other activities directly affected by temperature. Hence it is natural for temperature to be a critical factor affecting microhabitat selection in reptiles (Dial, 1978; Huey et al., 1989; Webb & Shine, 1998; Kearney, 2002; Pringle et al., 2003; Lin et al., 2006). Choice of an appropriate microhabitat is particularly important for ambush-feeders, since much of their time is spent motionless at a location.

Arboreal snakes tend to be slender, with relatively low body mass compared to their ground-dwelling relatives (Lillywhite, 2014), and the habitus of arboreal snakes are supposedly adaptive for better utilisation of tree habitats (Tu et al., 2000). In the focal species, secondary sexual dimorphism includes size dimorphism (see Chapter 2), the main driver in snakes being fecundity selection and/or other ecological requirements (Shine, 1989; Tu et al., 2000). Additionally, differences in body size potentially allow the two sexes to take advantage of different microhabitats, hence reducing interspecific competition (Tu et al., 2000). Investigations on the sexually dimorphic Chinese green tree pit-viper, *Trimeresurus stejnegeri stejnegeri* reported no differences in measured parameters of habitat selection (Tu et al., 2000).

Arboreal snakes potentially face greater dangers compared to terrestrial species, since the defence of terrestrial species are solely directed to predators approaching from above, while for arboreal species, could be multi-directional (Senter, 1999; Martins et al.,

2008). Following this threat, it would make sense if arboreal snakes would choose densely vegetated sites, which would more effectively conceal them from potential danger. In addition to their cryptic camouflage colouration, it is part of their defence mechanism to stay hidden from potential threats.

5.2 Specific Objectives

Objective and questions that arise from the study of microhabitat utilization in *Tropidolaemus subannulatus* include:

To describe microhabitat selection in *Tropidolaemus subannulatus*.

1. What are the critical microhabitats utilised?
2. Are there sexual differences in microhabitat selection?

5.3 Specific Methodology

The study species are tracked via radio telemetry (see Chapter 4) and their locations marked with a Garmin™ Map60CSx Global Positioning System (GPS) hand-held unit. Microhabitat assessments, such as percentile canopy cover, tree species, distance to water bodies, density of vegetation were conducted to associate snakes to their abiotic environment. Microhabitats utilized by the species was recorded in the sexes. Relationship between tree diameter and size (here, SVL) of the snake was tested for correlation. Males and females of the target species was separately analysed for relationship between tree diameter and size for correlation. Test of correlation for vertical distance travelled (in terms of perch height) and tree diameter was also conducted separately for males and females.

5.4 Results

A total of 76 observations were recorded on habitat utilization in *Tropidolaemus subannulatus* between 8 October 2019 and 16 January 2020. The snake typically was encountered perching on vegetation, namely, ferns, saplings, live tree branches and twigs. Over 80% of the observations were of snakes associated with branches, followed by saplings (9.21%) and dead twigs (6.58%), respectively (Figure 5.1). In Figure 5.2, female *T. subannulatus*, 81.97% of the observations were recorded on tree branches, followed by saplings and twigs (8.2%) and fern (1.64%); as for the males, they were only recorded on two substrates- tree branches (86.67%), and sapling (13.33%).

When there were no visuals of the snake, radio signals suggested an upward direction of the tagged individual towards the canopies, thus assuming their body were completely shielded by vegetation, comprising leaves and branches. Large trees such as *Shorea* sp. and *Xanthophyllum* sp. can exceed 20 m in height (Figure 5.13). Sometimes being over 10 m and perching between layers of vegetation in the canopy make them hard to spot. Both males and females utilize tree branches over 80% of the time. Only one individual was found perching on a False Staghorn Fern (*Dicranopteris linearis*) (Figure 5.14). Females have been recorded to utilize ferns, saplings, tree branch and dead twigs, while males were found utilizing only tree branches and saplings. There was no significant correlation between snout-vent-length (SVL) of *T. subannulatus* with tree diameter ($P = 0.220$, $r = 0.383$) for the species (Figure 5.3). When considered separately, females showed a significant correlation ($P = 0.029$; $r = 0.858$) (Figure 5.4), while males displayed a strong relationship ($P = 0.000$, $r = 0.993$) (Figure 5.5). Vertical location of snakes (height above ground) and tree diameter show a significantly relationship ($P = 0.00$, $r = 0.690$) (Figure 5.6). Finally, females showed

a significantly correlation with vertical location and diameter of tree ($P = 0.000$; $r = 0.768$) (Figure 5.7), while for males, there was no relationship ($P = 0.220$; $r = 0.337$) (Figure 5.8).

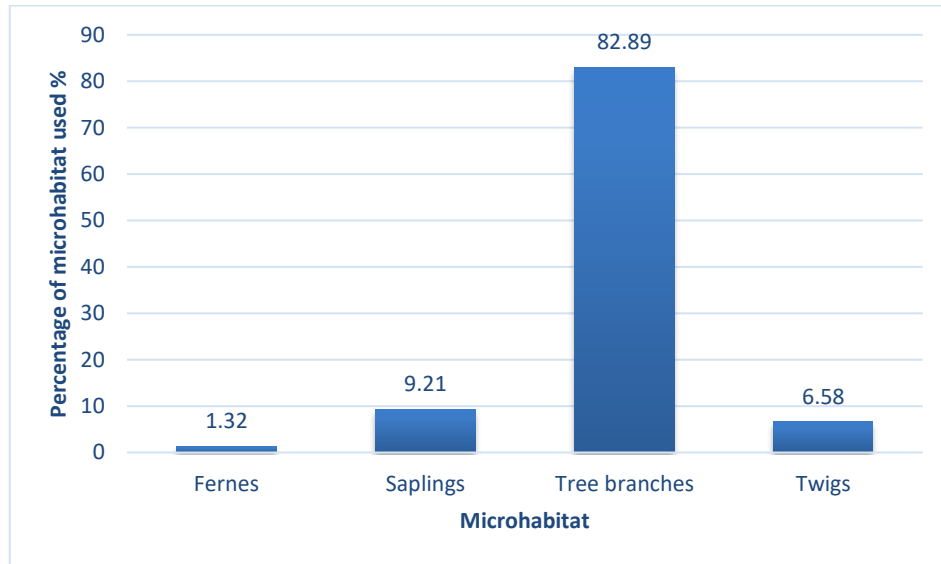


Figure 5.1: Microhabitat utilization by *Tropidolaemus subannulatus* observed in field.

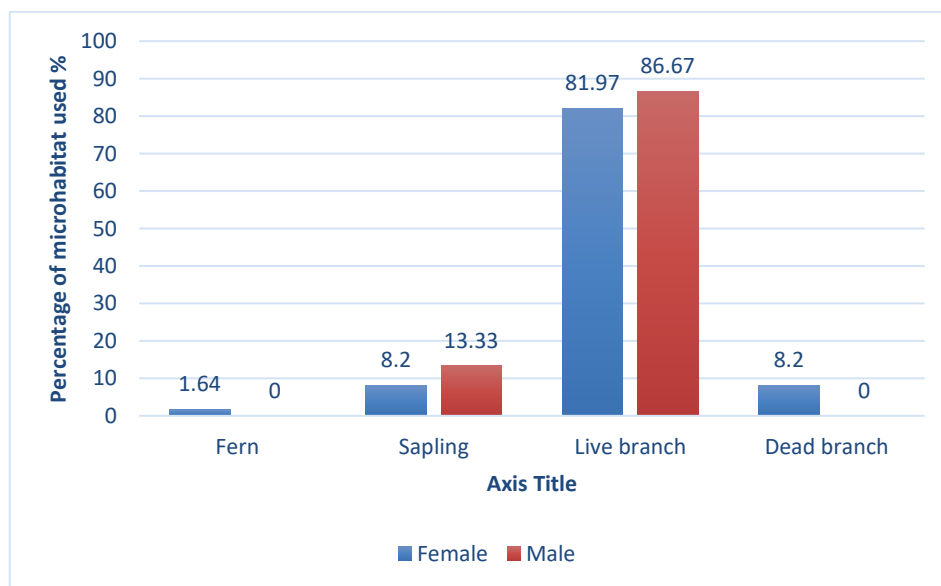


Figure 5.2: Microhabitat utilization by female and male *Tropidolaemus subannulatus* observed in field.

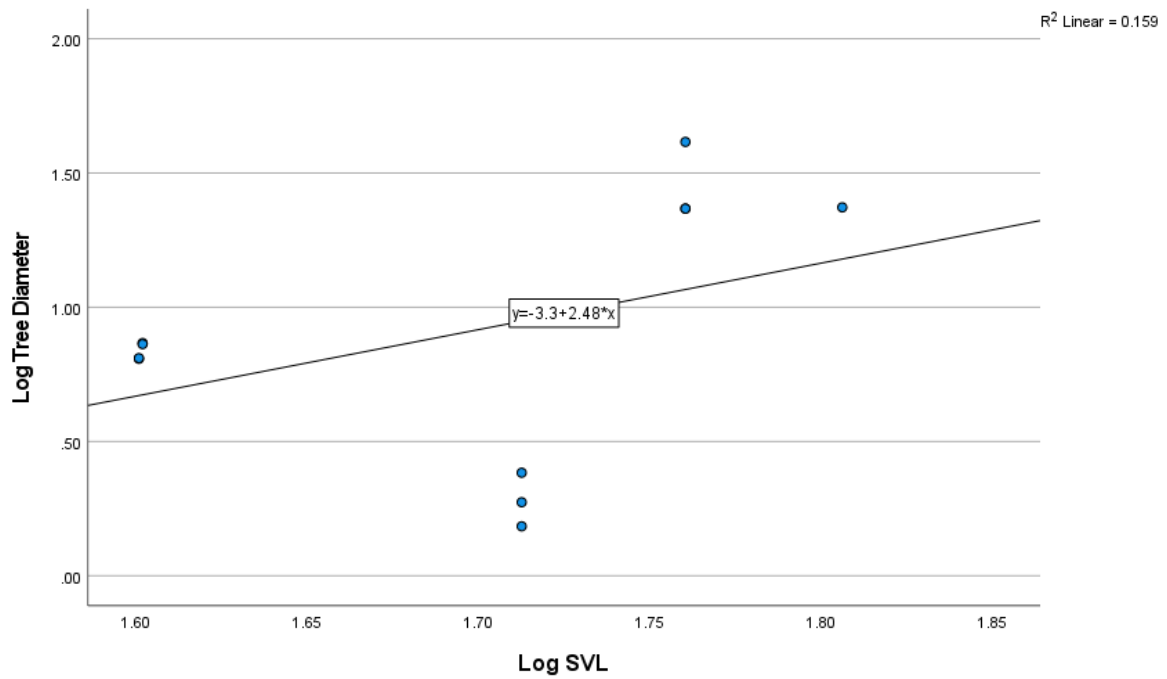


Figure 5.3: Relationship between tree diameter and SVL of *Tropidolaemus subannulatus* ($P = 0.220$, $r = 0.383$; $y = -3.3 + 2.48\text{LogSVL}$).

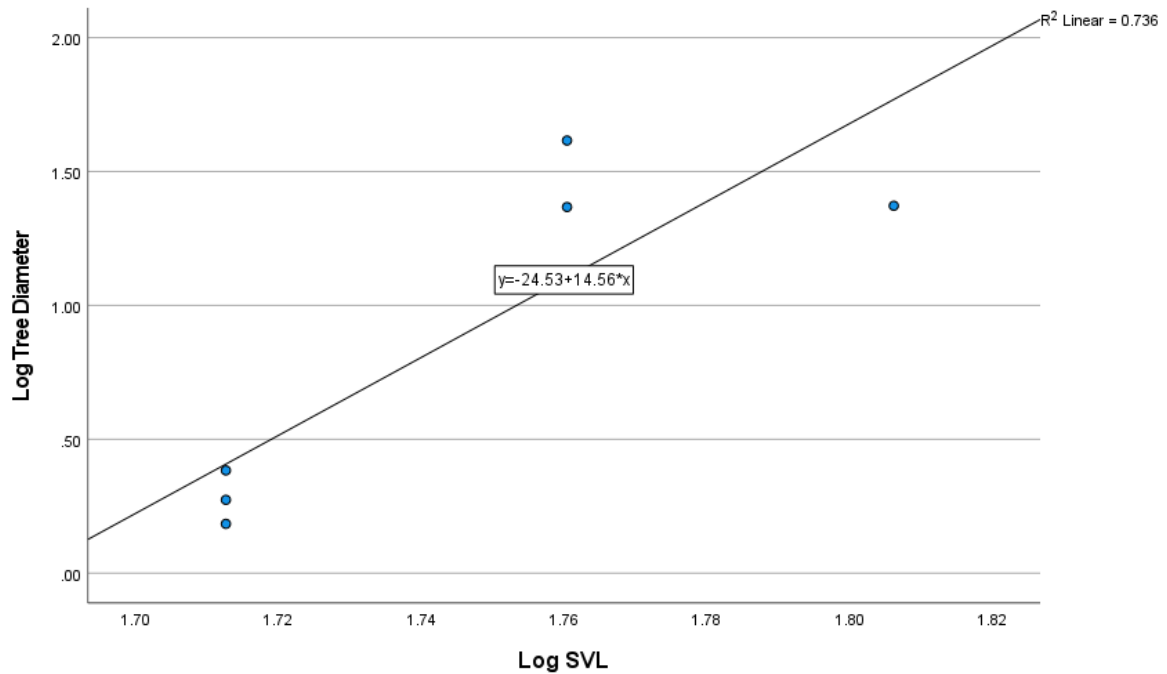


Figure 5.4: Relationship between tree diameter and SVL of female *Tropidolaemus subannulatus* ($P = 0.029$, $r = 0.858$; $y = -24.53 + 14.56\text{LogSVL}$).

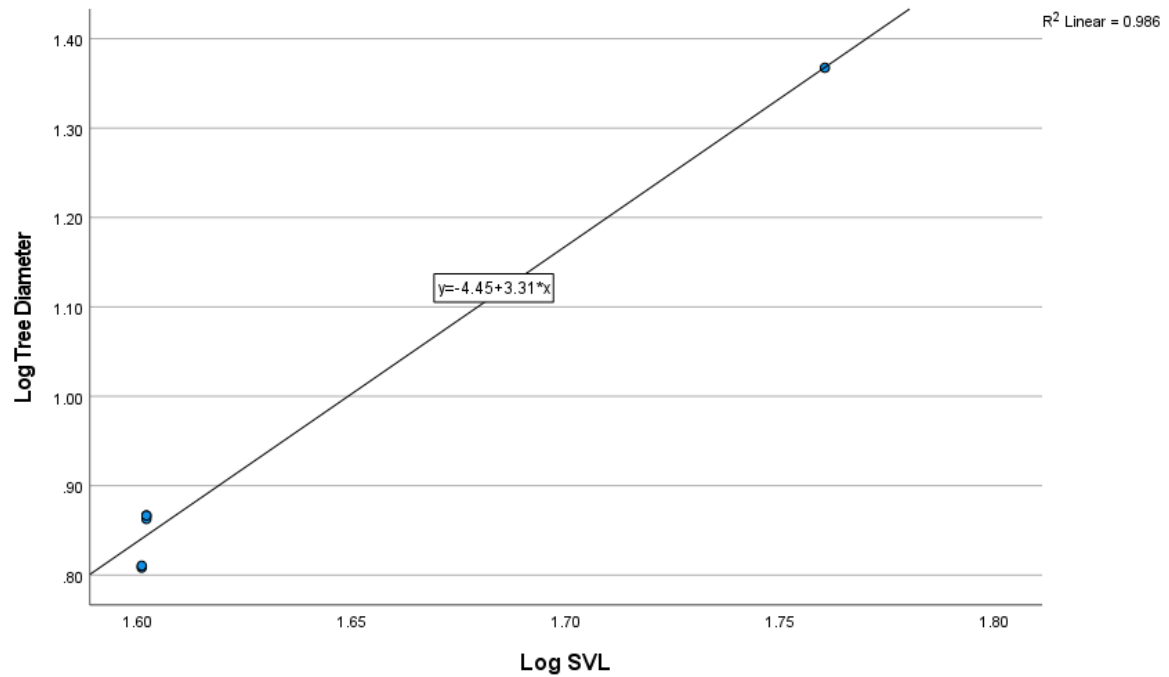


Figure 5.5: Relationship between tree diameter and SVL of male *Tropidolaemus subannulatus* ($P = 0.000$, $r = 0.993$; $y = -4.45 + 3.31\text{LogSVL}$).

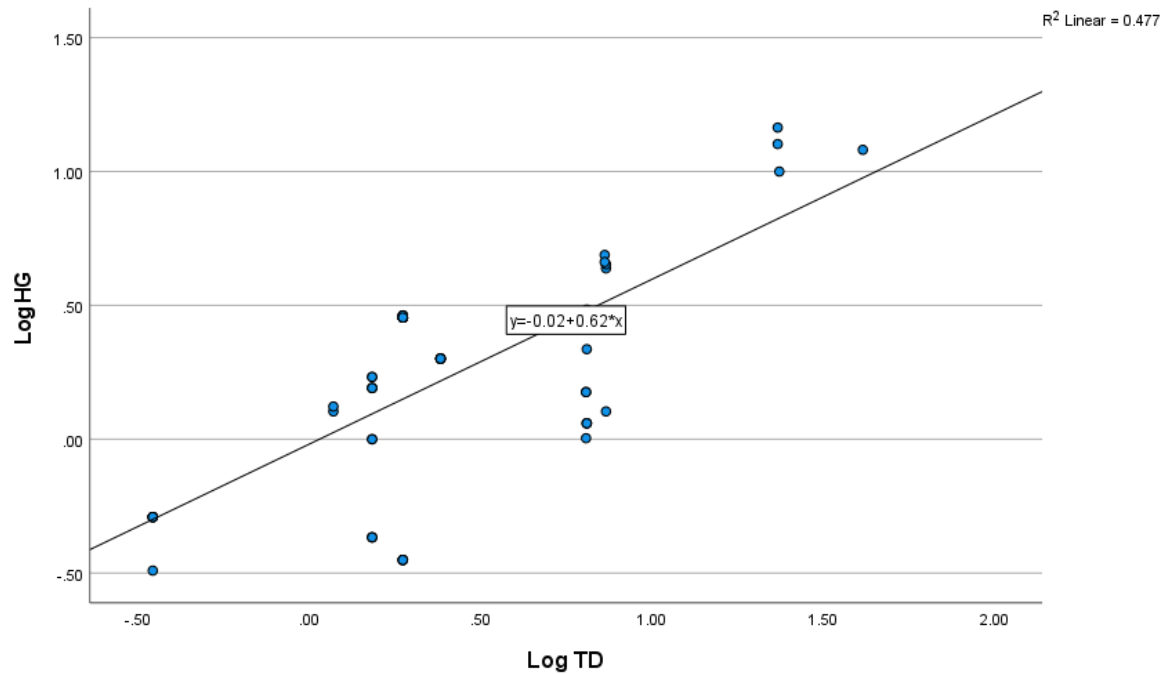


Figure 5.6: Relationship between vertical distance and tree diameter of *Tropidolaemus subannulatus* ($P = 0.000$, $r = 0.690$; $y = -0.02 + 0.62\text{LogTD}$).

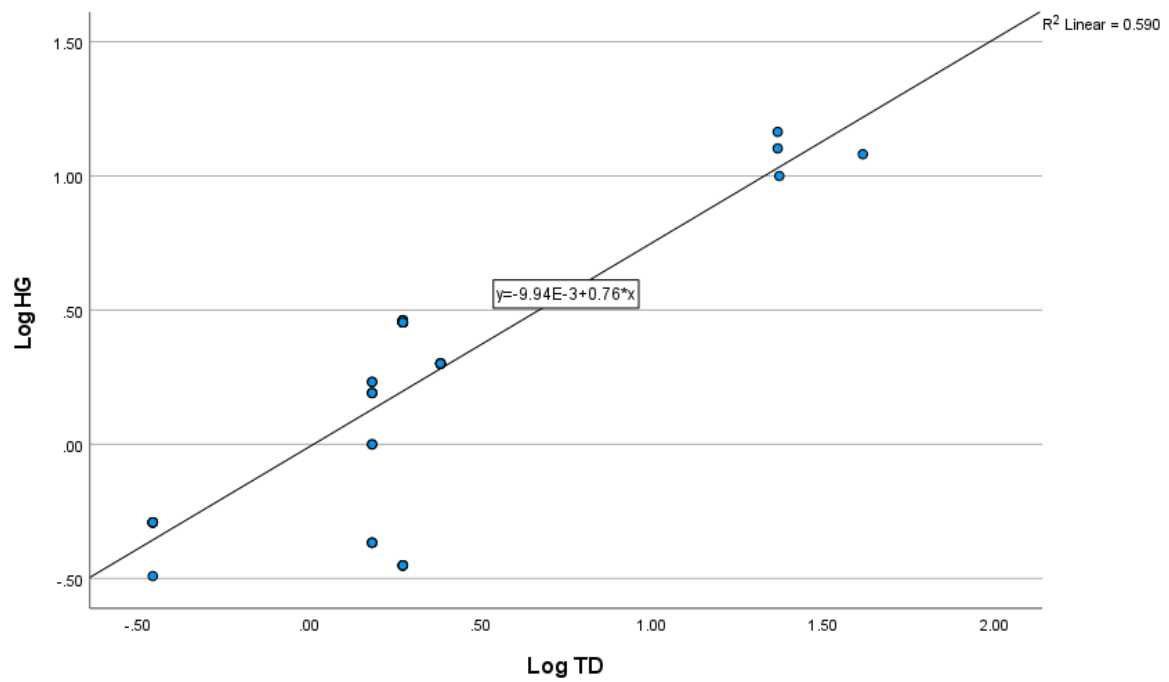


Figure 5.7: Relationship between vertical distance and tree diameter of female *Tropidolaemus subannulatus* ($P = 0.000$, $r = 0.768$; $y = -9.94e^{-3} + 0.76\text{LogTD}$).

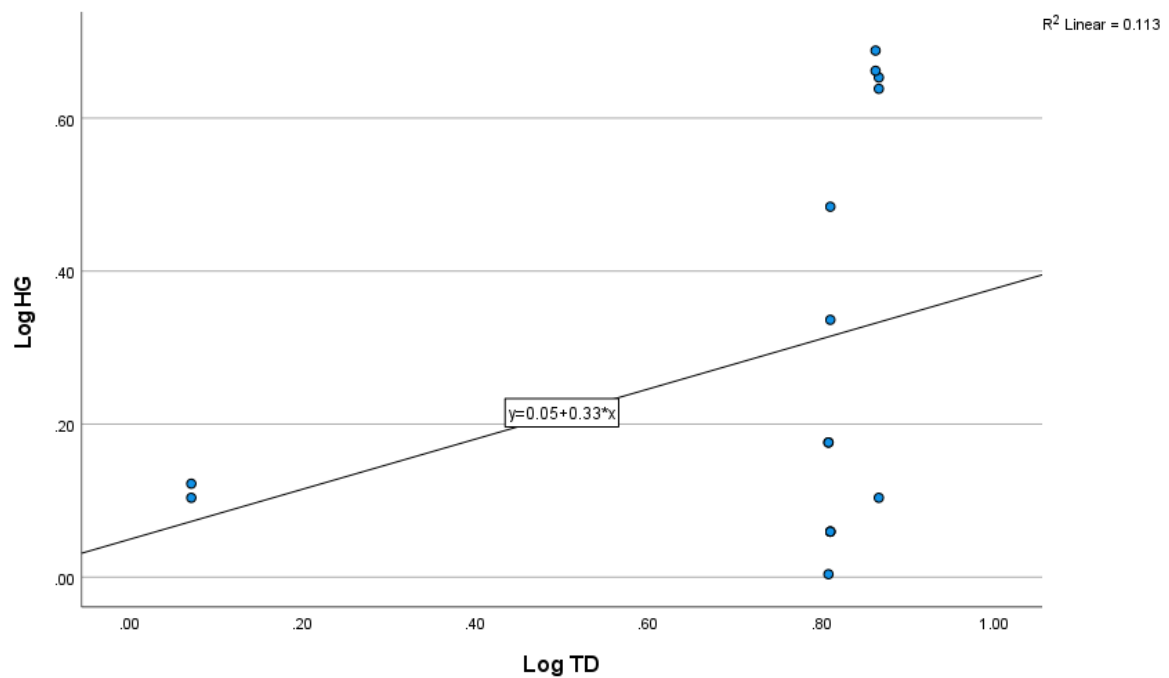


Figure 5.8: Relationship between vertical distance and tree diameter of male *Tropidolaemus subannulatus* ($P = 0.220$, $r = 0.337$; $y = 0.05 + 0.33\text{LogTD}$).



Figure 5.9: Position of male *Tropidolaemus subannulatus* found perching and sheltered by leaves above and below position.



Figure 5.10: Position of male *Tropidolaemus subannulatus* found perching and sheltered by leaves and with camouflage colouration.



Figure 5.11: Position of female *Tropidolaemus subannulatus* found perching on twigs with colours blending with vegetation.



Figure 5.12: Close up of individual in Fig. 5.11 of *Tropidolaemus subannulatus* perching on dead twigs.



Figure 5.13: *Xanthophyllum griffithii* (left) and *Shorea kunstleri* (right) trees utilized by *Tropidolaemus subannulatus*.



Figure 5.14: The fern, *Dicranopteris linearis* growing near the Frog Pond area in Kubah National Park.

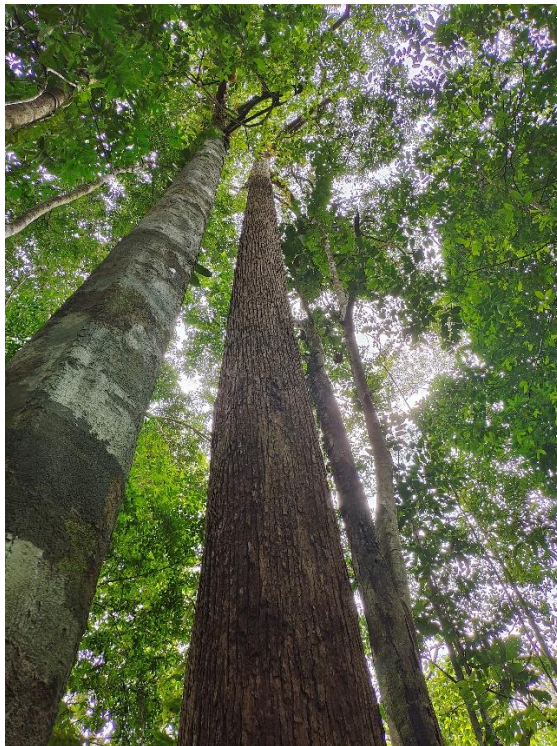
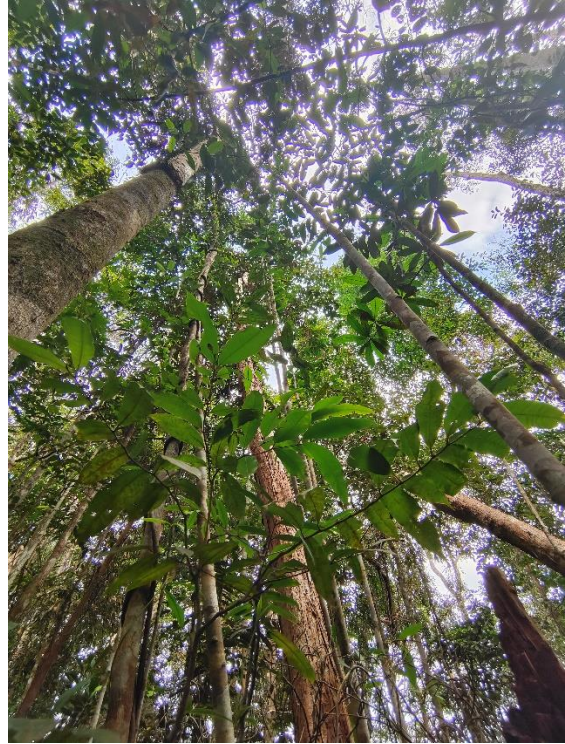


Figure 5.15: Views of canopy cover associated with *Tropidolaemus subannulatus*.

5.5 General Discussions

Most encounters of the focal species were made on branches of live trees than other microhabitats in this study. The greatest vertical limit recorded above ground for *Tropidolaemus subannulatus* was about 14 m, in this case, being at the upper level of the canopy. In one of the tracking periods, a female which was perching about 12 m on the canopy was observed to strike out at bats that were flying past at 20:18 h. Due to limited visibility at the time, it could not be determined if the strike was a threatening intention or predatory. If the latter was true, then volant mammals such as bats can be included as their potential prey. Transmitter signals were detected on canopies of tall trees such as *Xanthophyllum griffithii* and those of the genus *Shorea*. Kubah had been reported to have timber-related tree species that can grow up to 30 m tall (Mohamad Bukhori et al., 2019). Snakes may also descend and perch on shrubs and other vegetation on the lower forest strata.

Females have been recorded to utilise saplings and tree branches, and one female was found on ferns and another utilized dead twigs. Only tree branches and saplings were utilized by both sexes. This indicates that the species may utilize any vegetation. There are few comparable data from other arboreal snake species. Fitzgerald (2002) noted that the Australian Stephens' Banded Snake, *Hoplocephalus stephensii* is found on trees over 80% of the time (Fitzgerald, 2002), and is thus clearly less arboreal than *T. subannulatus*.

For such an arboreal species with limited movements and a sit-and-wait predator, refuge site is clearly a crucial requirement for concealment from prey and predators such as raptors, mammals and snake-eating snake species. Since *T. subannulatus* typically feed once every two to five months (Visser, 2015), they can stay at such sites for long periods. The longest period recorded in this study was 18 days. Retreat sites are important considering

that arboreal species are more prone to exposure to predators (Senter, 1999; Martins et al., 2008), and most radio tracked snakes were recorded from dense foliage. Arboreal snakes also require accurate neuromuscular coordination as well as the ability to sense whether the size and stability of tree branches are capable of supporting their mass during climbing (Lillywhite, 2014). Life in the canopy would require a good cantilever ability as well as utilizing volatile chemical cues. Along with their cryptic green colouration and patterns, utilizing tree branches is assumed to be advantageous in this arboreal species.

Both sexes showed a relationship between size (here, SVL) and tree diameter. It is unclear how this is associated, and whether the relatively slender bodies of males, compared to females, are responsible. In addition to the limited movement of this species, it is difficult to draw a conclusion. Shine and Sun (2002) found that the Shedao pit-viper (*Gloydius shedaoensis*) selected perched branches which were similar in diameter to the snakes that utilized them and this might help them to remain concealed from predators. The role of choosing tree diameter similar to body diameter may help in camouflage or enable support (Figure 5.11) which are displayed especially by the small and slender-bodied males in this study. Compared to the heavy-bodied females in which required to consider many factors to consider for perching. Perhaps this indicates that the morphological shape of the snake might have greater influence on the tree diameter than the length of the individual.

Males showed no significant relationship but the females had a positive relationship between vertical distance (= perching height) and tree diameter. The larger females require a greater perching support compared to the males, and thus appear to seek perches of larger diameter compared to the smaller males, consequently females often perches higher in vegetation (Henderson et al., 1998). A study by Henderson et al. (1998) on the arboreal boa (*Corallus grenadensis*) stated that as the mass increase, the snakes are in need of selecting

perches which can support their weight and bridging gaps in vegetation while still being able to have access to food. In contrast, the smaller males are not affected by this restriction. Moreover, a relatively thick-bodied Shedao pit-viper (*Gloydius shedaoensis*) constantly climbs trees and shrubs to ambush birds (Shine et al., 2002; Rudolph et al., 2004).

Females were observed to have exploit larger trees such as those of the genera *Shorea* and *Xanthophyllum* compared to males. Timber trees in Kubah are 20–75 m tall, with 50–250 cm tree diameter (Mohamad Bukhori et al., 2019). *Shorea kunstleri* is the largest tree diameter recorded being utilized by a tracked snake, at 41.31 cm diameter and over 10 m height. Alencar et al. (2017) discovered that heavier snakes are unable to move well among trees due to fragile tree branches, which made larger arboreal snakes prefer larger trees.

5.6 General Conclusion

This study indicate that *Tropidolemus subannulatus* shows a distinct association with tree branches, sometimes reaching canopies. Said microhabitat features are favourable for arboreal snakes, especially snakes with colouration mimicry whereby concealment is crucial. The focal species was found to utilize tree branches, saplings, twigs and ferns throughout the course of the study, with over 80% of the time spent on branches. Males and females displayed variation in ways of utilizing distinctive microhabitats, probably due to sexual size dimorphism. Females were found to utilize large tree of the genus *Shorea*, while males did not. Only males were found to have a relationship between body mass and tree diameter. Consequently, sexual size dimorphism can be attributed to the ability in the species to utilize different microhabitat and thus reducing potential competition for resources between the sexes.

CHAPTER 6

THERMOREGULATION STUDIES OF *TROPIDOLAEMUS SUBANNULATUS*

6.1 Review of Thermoregulation Prospects

The dependence of ectotherms on the physical environment has been the subject of intense research since the pathbreaking work of Cowles and Bogert (1944). In order to achieve an optimum body temperature, ectotherms display multiple thermal regulatory behaviours, whereby heat may be obtained via heliothermy (the act of obtaining heat via short wavelength solar radiation) and / or thigmothermy (heat conduction via direct contact with a warm substratum). Although basking is the commonly perceived behaviour of ectotherms, Garrick's (2008) generalised that thigmothermy is commonly carried out by species inhabiting forested settings, where solar radiation is hindered by tree canopy, and may not be fully limited by ambient temperatures. Factors such as metabolic rate, growth and development, as well as locomotion, being thermally dependant, optimum body temperature has significant consequences for the biology of ectotherms (Brown & Weatherhead, 2000).

Unlike endotherms, ectothermic animals have significantly lower metabolic rates, requiring lower nutrient intake (Pough, 1980; Shine et al., 2003). Cowles and Bogert (1944) showed that reptiles regulate their body temperature via selection of multiple positions in or on soil, rock or other substrate types, permitting heat gain through direct conduction, or basking, with the body entirely or partially exposed to heat sources. Increase in movements has the potential to enhance predation risk and energy loss, including movements to locate appropriate microhabitats for thermoregulatory purposes. However, reptiles do

thermoregulate by shuttling between microhabitats at no cost, as long as the favoured body temperature is within the operative environmental temperature range (Sears et al., 2016).

The background of this chapter centres around thermoregulation and thermal strategies in the target species. Such an approach is topically appropriate, in the light of current interest in global climate change, and an environmental shift has the potential to affect endotherm population viability, such as growth, survival and reproductive output (Brown & Shine, 2007). Most lowland tropical herpetofaunas have fatal thermal temperatures (= critical thermal maxima) in the range 38–42°C, while highland species have somewhat lower values (Brattstrom, 1968; Snyder & Weathers, 1975; Bickford et al., 2010). Their dependant on the thermal environment therefore makes them vulnerable to environmental change, and in case of extreme climatic changes, can lead to extirpation.

Borneo has a tropical climate, being warm and humid year round, where temperature variance is significantly low compared to temperate regions. With the majority of the world's herpetofauna (and indeed a majority of ectotherms) concentrating in the world's tropics, the effect of climate change on populations remains largely unknown and may have catastrophic consequences if unchecked. In this study, the Bornean Keeled Pit-viper, *Tropidolaemus subannulatus*, a widespread and familiar venomous snake from the lowlands of the island, was studied for over a four months period, to understand the effect of ambient and local temperatures on the thermoregulation strategies in the species.

iButton data loggers and temperature sensitive radio transmitters have been routinely used in recent years to measure reptile body temperatures, by implanting or harnessing these devices in free-ranging animals. Researchers are able to record the body temperature of reptiles without the need to handle them. Also, handling a venomous snake multiple times in order to take the body temperature on field is potentially dangerous, impractical, and

sometimes, leads to inaccurate data. Thermal data are valuable to gain a better understanding of a species such as the one focussed on the present study, with its limited movement and also showing site-fidelity, remaining at a location for days or even weeks. In summary, a comprehensive understanding of its thermal requirements is crucial to understanding the natural history as well as conservation requirements of an ectothermic species.

6.2 Specific Objectives

The specific study objectives and research questions of this study were:

To determine the thermal range of *Tropidolaemus subannulatus*.

- Is the species a thermoregulator or thermoconformer?
- Are core body and surface temperatures correlated?
- Does ambient and substrate temperatures influence core body and surface temperatures?

6.3 Specific Methodology

6.3.1 Thermal Data Methodology

Ambient temperatures (T_a) were taken with EXTECHTM 4-in-1 Environmental Meter model 45170 (Extech Instruments, Massachusetts). A thermal gun, FlukeTM 62 MAX Infrared Thermometer (Fluke Europe B.V., the Netherlands) was used to record the readings of substrate temperatures (T_s) and body surface temperatures (T_{bs}). T_s and T_{bs} reading was taken over a '1-inch' spot at distance of ca. 25 cm from the subject. Readings such as ambient temperature and humidity were taken at more than 50 cm above the ground just below the snake with 4-in-1 Environmental Meter. For the internal body temperature (T_b), temperature sensitive transmitters model Holohil BD-2 and Holohil SB-2 (Holohil Systems Ltd, Canada) were used. Base graph was provided upon receiving the radio transmitter purchase The

average value of time taken to complete 11 pings were recorded and then the readings of temperature were calculated according to the equation obtained from each individual transmitter calibration (Figure 6.1). The transmitter was calibrated using the water bath calibration method (see Chapter 4).

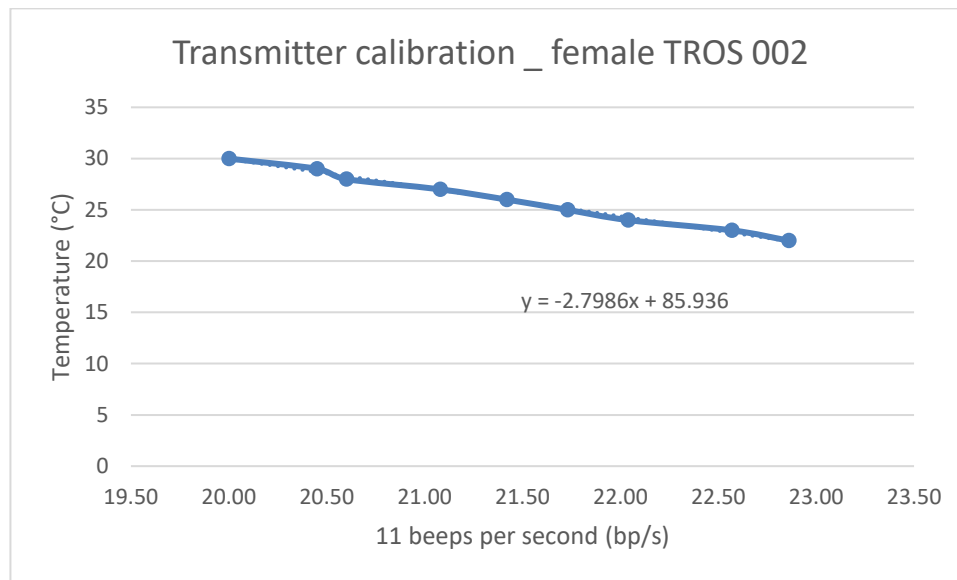


Figure 6.1: Graph showing details of transmitter calibration using the water bath technique, showing the relationship between 11 pings per second (bp/s) and temperature (°C) of radio transmitter 151.501, with the equation obtained.

6.3.2 Data Analyses

Regression analyses were conducted to determine relationships between variables, and correlations were done depending on the normality of the data. A paired sample t-test was done to determine whether there are any significant difference between core body temperature and surface body temperature. The tests were done using IBM SPSS Statistics software (version 28.0.0.0). Data were transformed to log value for linearity.

6.4 Results

6.4.1 Body Temperature in *Tropidolaemus subannulatus*

Mean snout-vent length (SVL) for females was 57.73 ($\pm$ SE 3.58) cm, while the corresponding figure for males was 39.95 ($\pm$ SE 0.05) cm; mean weight of females was 144.73 ($\pm$ SE 57.17) g, vs. 25.5 ($\pm$ SE 2.50) g for males (Table 6.1). Mean minimum body temperature was 22.97°C ($\pm$ SE 0.11) and mean maximum body temperature is 30.56°C ($\pm$ SE 0.78). Mean minimum body temperature of females was 23.01°C ($\pm$ SE 0.19), while for males was 22.91°C ($\pm$ SE 0.12). Mean body temperature between the two sexes showed no significant difference ($P = 0.285$, 95% confidence interval). Mean maximum body temperature for female and male was 31.76°C ($\pm$ SE 0.25) and 30.56°C ($\pm$ SE 0.76), respectively. Females showed mean body temperature of 26.50°C ($\pm$ SE 0.66) and males 25.26°C ($\pm$ SE 0.25). Temperature range can be seen in Figure 6.2. To identify the influence of thermal preference to body mass, mean body size (here, SVL measurement) was used. A Pearson correlation test reveal no relationship between body size and mean body temperature ($P = 0.584$, Pearson correlation, r : 0.333) (Figure 6.3). A paired sample t-test (P -value < 0.001), show a significant difference between core body temperature and surface body temperature. Correlation test shows P -value < 0.001 and Pearson correlation value, r of 0.707. This suggests that body surface temperature is strongly correlated with body temperature.

Table 6.1: Summary of *Tropidolaemus subannulatus* radio tracked, including morphometric data, sex and minimum and maximum body temperatures (°C), with means and standard errors (SE).

Morphometric						
Snake ID		SVL (cm)	Mass (g)	Min T_b (°C)	Max T_b (°C)	Mean (°C)
TROS 002		57.6	91.2	22.79	31.28	26.65
TROS 005		51.6	84.0	23.38	31.84	27.56
TROS 010		64.0	259.0	22.86	32.15	25.30
TROS 004		40.0	28.0	23.03	28.02	25.51
TROS 008		39.9	23.0	22.79	29.53	25.01
Female	Mean	57.73	144.73	23.01	31.76	26.50
	SE	3.58	57.17	0.19	0.25	0.66
Male	Mean	39.95	25.5	22.91	28.78	25.26
	SE	0.05	2.50	0.12	0.76	0.25
Both	Mean			22.97	30.56	26.01
	SE			0.11	0.78	0.48

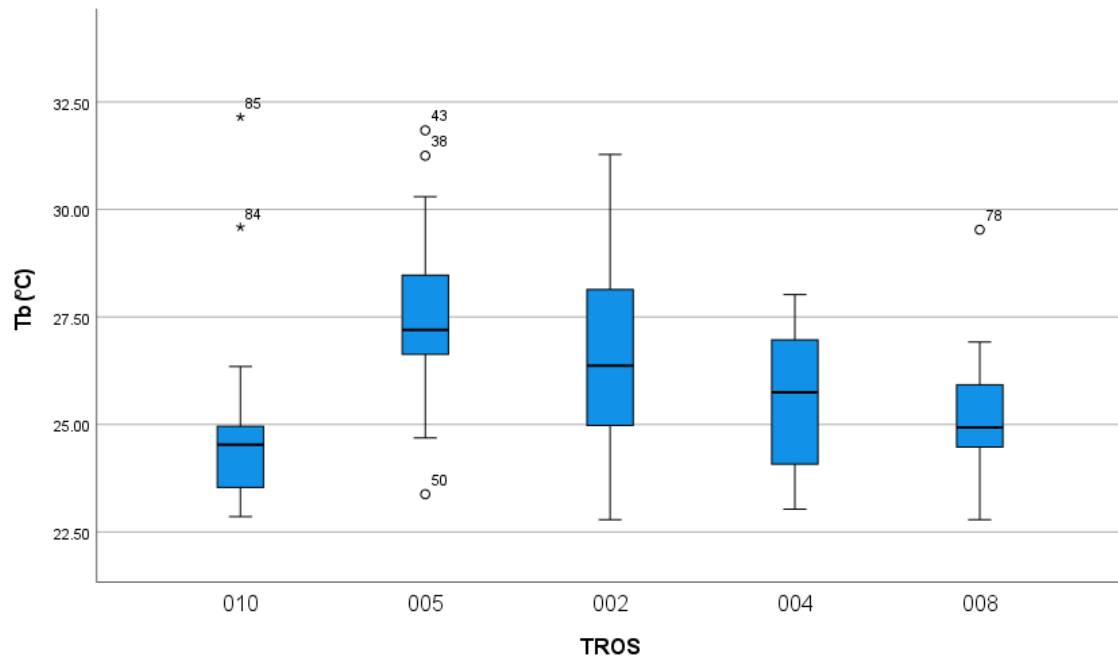


Figure 6.2: Boxplot showing differences in body temperature among *Tropidolaemus subannulatus* individuals. The middle line within the box represents median; top and bottom box lines represent first and third quartiles; whiskers at each end shows the maximum and minimum values; (°) defines outliers; (*) denotes extremes.

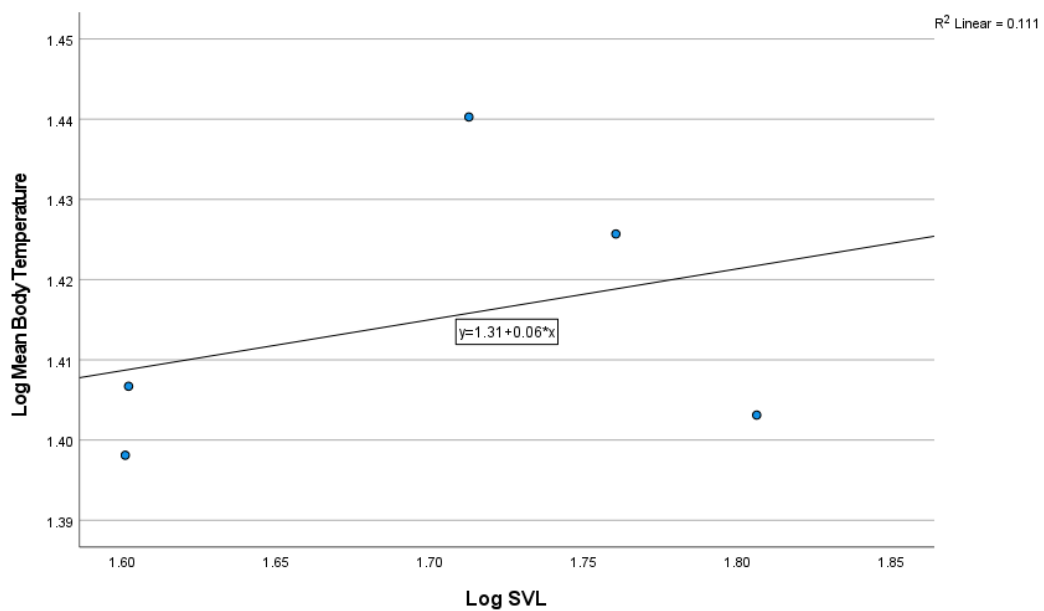


Figure 6.3: Relationship between body size (SVL) and mean body temperature of *Tropidolaemus subannulatus* in log form displayed no relationship (P-value = 0.655, Pearson correlation, $r = 0.274$, and regression equation $y = 1.31 + 0.06 \text{ Log SVL}$).

6.4.2 Relationship Between Body Temperature to Ambient Temperature

Tracking data were collected between 0900 h and 2200 h within the sampling period of October 2019 to January 2020. There was a significant relationship between ambient and core body temperatures ($P = 0.038$, $r = 0.209$) (Figure 6.4). Surface body temperature and ambient temperature also showed a significant relationship ($P = 0.027$, $r = 0.298$) (Figure 6.5). These demonstrate that heliothermy *per se* is not a major thermoregulatory mechanism in the species.

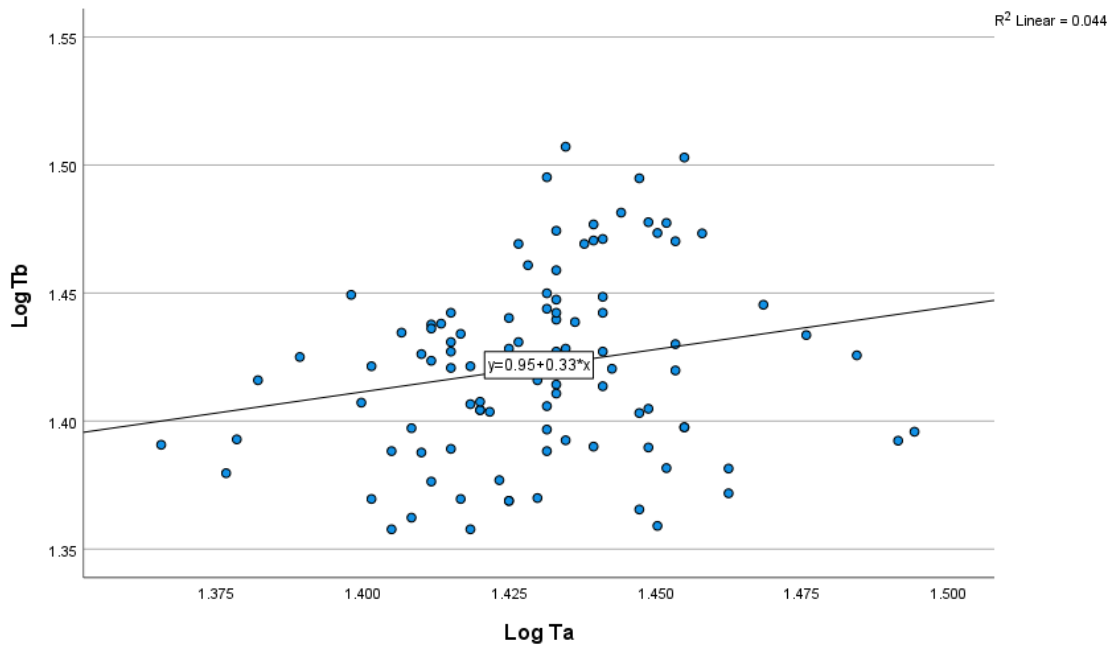


Figure 6.4: Relationship between core body temperature and ambient temperature of *Tropidolaemus subannulatus* displays significant relationship ($P = 0.038$, $r = 0.209$; $y = 0.95 + 0.33 \text{LogTa}$) on log paper.

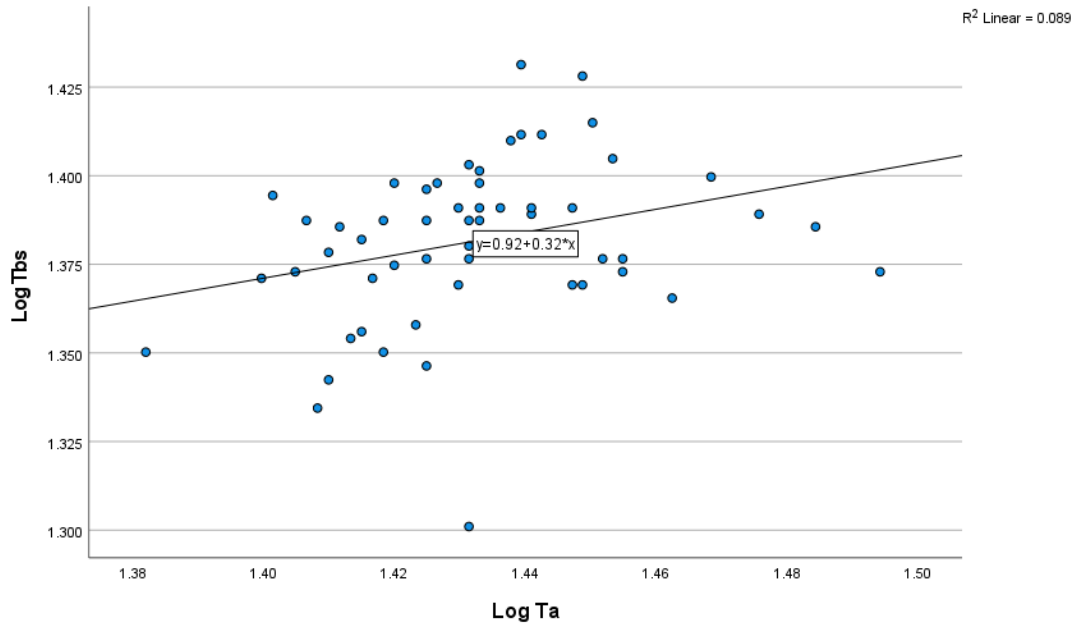


Figure 6.5: Relationship between surface body temperature and ambient temperature of *Tropidolaemus subannulatus* shows significant relationship ($P = 0.027$, $r = 0.298$; $y = 0.92 + 0.33 \text{LogTa}$) on log paper.

6.4.3 Relationship Between Body Temperature to Substrate Temperature

In order to determine whether the target species relies on thigmothermy, data of substratum temperature were taken. The relationships between core body temperature and substrate temperature shows a significant relationship ($P < 0.01$, $r = 0.671$) (Figure 6.6), as did surface body temperature and substrate temperature ($P < 0.001$, $r = 0.993$) (Figure 6.7). These relationships demonstrate the role of thigmothermy in the species as pit-viper absorbs heat via substrate.

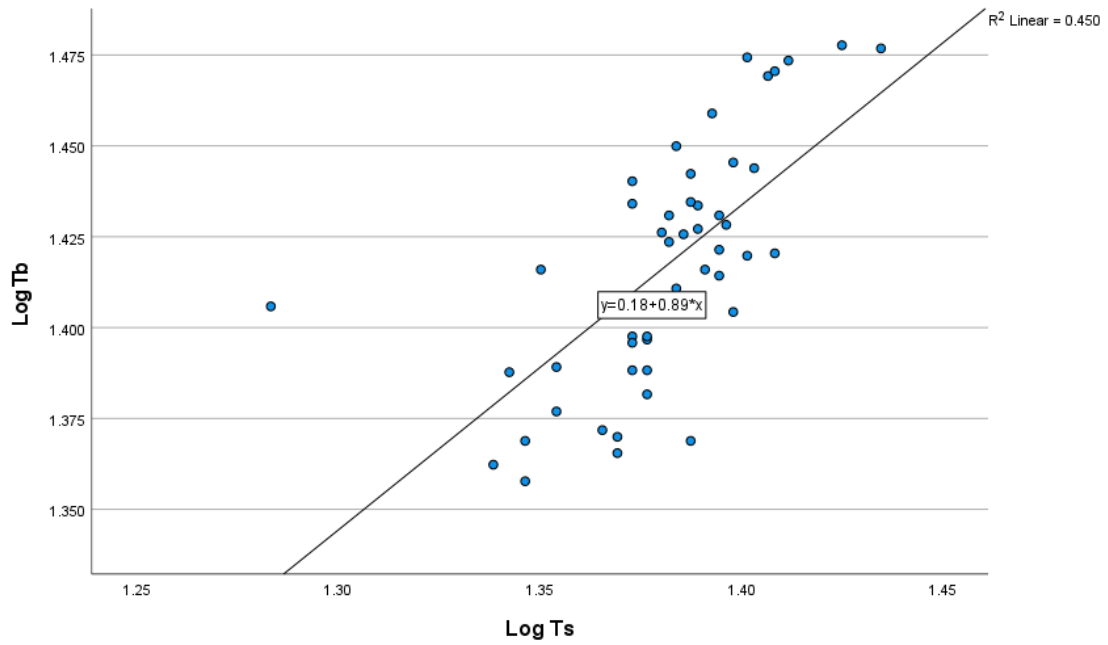


Figure 6.6: Relationship between core body temperature and substrate temperature of *Tropidolaemus subannulatus* displays significant relationship ($P < 0.001$, $r = 0.671$; $y = 0.18 + 0.89\text{LogTs}$) on log paper.

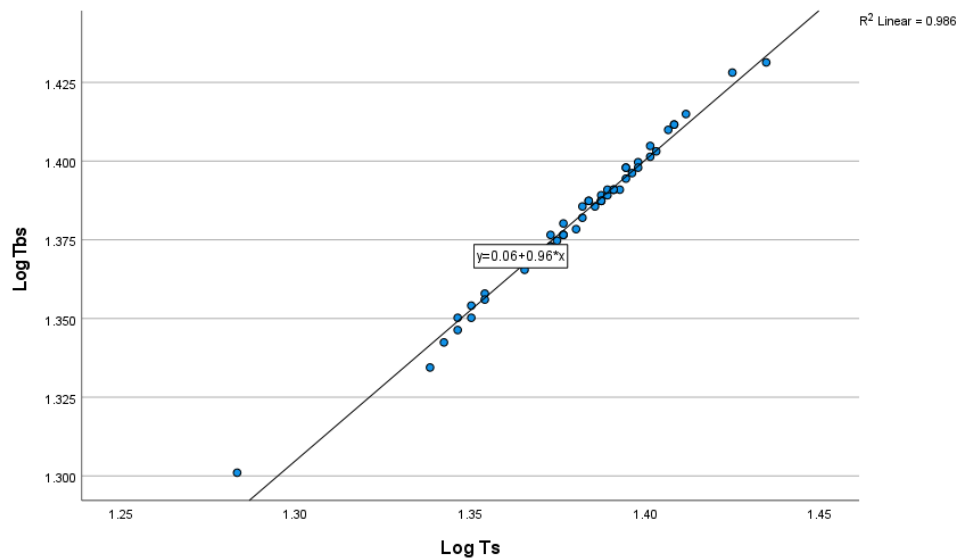


Figure 6.7: Relationship between surface body temperature and substrate temperature of *Tropidolaemus subannulatus* ($P < 0.001$, $r = 0.993$; regression equation $y = 0.06 + 0.96\text{LogTs}$) on log paper.

6.4.4 Relationship Between Body Temperature to Relative Humidity

To determine if humidity bears a relationship with body temperature, readings of relative humidity were taken. The range of percentage of relative humidity in the air recorded was 66.1–95.5% RH, with a mean of 88.12% RH. There was no statistical relationship ($P = 0.105$, $r = 0.165$; $P = 0.207$, $r = 0.178$) for either core or surface body temperatures in the target species (Figure 6.8 and Figure 6.9).

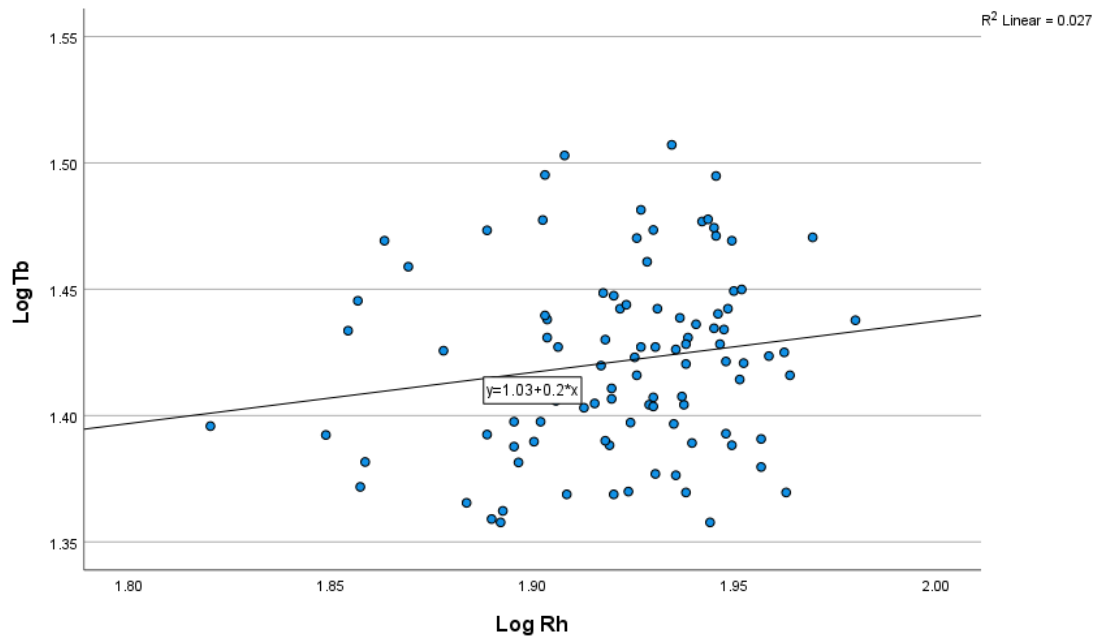


Figure 6.8: Relationship between core body temperature and relative humidity of *Tropidolaemus subannulatus* shows no significant statistic ($P = 0.105$, $r = 0.165$; $y = 1.03 + 0.20 \text{LogRH}$).

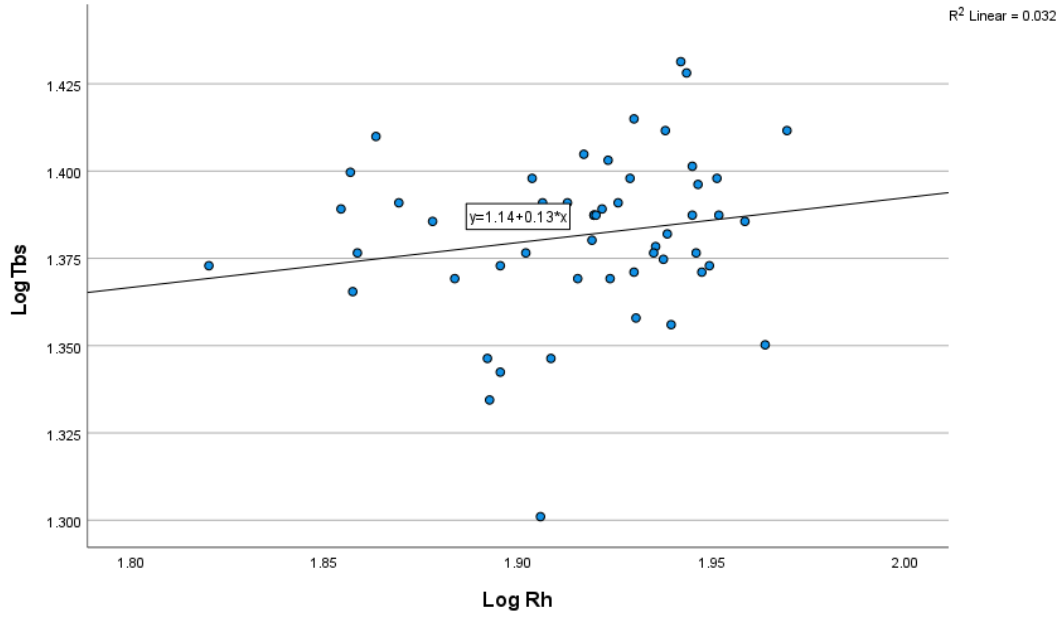


Figure 6.9: Relationship between body temperature and relative humidity of *Tropidolaemus subannulatus* shows no significant statistic ($P = 0.207$, $r = 0.178$; $y = 1.14 + 0.13 \text{LogRH}$).

6.5 General Discussions

It has been argued that ectotherms thrive under a set of optimum temperatures that ensure normal physiological functions. *Tropidolaemus subannulatus* displays a mean minimum and maximum body temperature of 22.97°C and 30.56°C, with a mean of 26.01°C. As a tropical species, it is perhaps unsurprising that the demonstrated thermal range is smaller compared to that of the Central Asian blunt-nosed viper (*Macrovipera lebetina turanica*) in a multi-seasonal habitat (17–34°C; Cherlin & Shepilov, 2014), and more similar, although less tropical Malayan pit-viper (*Calloselasma rhodostoma*) (24.5–32.4°C; Daltry et al., 1998). Body mass showed no relationship to body temperature, suggesting a lack of ontogenetic effect on thermal biology. Ergo despite the sexual dimorphism in size between the sexes in the target species, there were no significant differences in thermal range. The large thermal range further explains how daily environmental temperature fluctuations

(7.59°C) can be tolerated, without the need to make significant movements tied to thermal requirements.

Ambient temperature plays important key role in many reptile life histories, such as for sex determination and is also associated with breeding phenology. Cornejo-Páramo et al. (2020) reported that ambient temperature is vital, affecting many reptiles during the breeding season, apart from helping interpret the impact of sex determination system on geographic distribution. For example, Janzen's (1994) study of the Painted turtles (*Chrysemys pica*) showed that the annual cohort sex ratio at hatchling stage was an effect of local fluctuations in ambient temperature. Oviparous species are more vulnerable to temperature change, since eggs tend to be vulnerable to environmental temperature fluctuations with minimal ability to thermoregulate (Telemeco et al., 2016; Cordero et al., 2018; Singh et al., 2020). This is thus a significant abiotic factor for ectotherms as it can cause lifelong consequences (Singh et al., 2020). Mori (2021) reported that gravid females were recorded to have higher body temperature than males and non-gravid females at given air temperature. Since none of the tracked females are gravid during the period of this study, a more and longer research period is needed to determine this.

Unlike in the temperate zone, reptiles of the tropics may be less linked to ambient temperature considering forest in the tropics are dense over large areas, offering thermal gradients. Thus, reptiles in temperate zone constantly face the challenge of ambient temperature constrain and basking opportunities (Brown & Shine, 2002). Many studies on such case were done on temperate zone ectotherms where small diurnal reptiles that inhabit deserts with high range in ambient temperatures to commit their time and effort of thermoregulation in order to maintain stable body temperatures (Cowles & Bogert, 1944; Cogger, 1974; Avery, 1982; Shine & Madsen, 1995). In this study, ambient temperature

appear to have significant influence on body temperature, but is weakly correlated where core body temperature and surface body temperature (Figure 6.4 and Figure 6.5). Being arboreal and largely shielded by canopy cover, the target species may be sheltered from solar exposure. As ambient temperature is shown to be not significant via-a-vis thermoregulation, it can be said that heliothermy is not the primary thermal strategy, especially as the target species can perch on dense vegetation for day or weeks and show limited movement.

Heliothermic reptiles tend to be diurnal, and typically regulate body temperature by basking and shifting into multiple positions or posture to maximise heat absorption (Cowles & Bogert, 1944). However, other species may demonstrate different strategies of heat gain, such as thigmothermy, which is relatively more significant for nocturnal reptiles that have no access to solar radiation (Garrrick, 2008). This strategy is adopted by sit-and-wait species with limited movements, such as *T. subannulatus*. Both core body and surface body temperatures show significant relationships with substratum temperature as displayed in Figure 6.6 and Figure 6.7. Substrate temperature have a higher influence towards body temperature (core body temperature: $P < 0.01$, $r = 0.671$; surface body temperature $P < 0.001$, $r = 0.993$) than ambient temperature (core body temperature: $P = 0.038$, $r = 0.209$; surface body temperature: $P = 0.027$, $r = 0.298$). Thus, the adaption of thigmothermy strategy may involve choosing of microhabitat within the appropriate thermal range.

Humidity plays a vital role in the physiological needs of organism. The occurrence of *Calloselasma rhodostoma* to specific microhabitats is strongly correlated to relative humidity which was hypothesized probably due to increase in feeding success or their susceptibility towards dehydration (Daltry et al., 1998). For snakes in temperate regions, relative humidity plays a significant factor for survival. For instance, hibernating snakes reside in den microsites with wide range in ambient humidity regimes to survive the winter

(Costanzo, 1988). Study on the insular pit-viper (*Gloydius shedaoensis*) from north-eastern China have shown that relative humidity may be one of the drivers of snake activity times and choice of foraging sites (Daltry et al., 1998; Sun et al., 2001).

Borneo is known for its hot and humid climate. Relative humidity is high year-round, and this study shows that *Tropidolaemus subannulatus* is not affected by ambient relative humidity since there was no significant relationship (core body temperature: $P = 0.105$, $r = 0.165$; surface body temperature: $P = 0.207$, $r = 0.178$). One female was found perched on the same spot for 18 days, regardless of the weather which included rain events. This indicates large thermal tolerance and the lack of behavioural control in *T. subannulatus*.

Tropidolaemus subannulatus spends its life on the canopy and other arboreal habitats in Kubah National Park, with a varying denseness of vegetation. As vegetation density should be negatively correlated to temperature and may be associated with the vertical movement of the species in a search for the optimal microhabitat to achieve desired optimal temperature.

6.6 General Conclusion

It is critical have a good understanding of the thermal requirements of reptiles. Their wide range of thermal tolerance shows the wide temperature variation and flexibility for physiological requirement. There was a significant relationship between ambient temperature with core body temperature and surface body temperature. Substrate temperature have significant relationship with core body temperature and surface body temperature with stronger correlation compared to ambient temperature. Apart from occasional change in posture, *Tropidolaemus subannulatus* can remain motionless for days or weeks, and is assumed to be a thermoconformer considering their strong correlation with substrate temperature. Reduced movement and shift of body position indicate that the species

does not display much behavioural control of thermoregulation. Microhabitat selection strictly occurs under canopy cover, for multiple reasons such as thermoregulatory behaviour, protection from predation or selection of an ambush site to prey. Therefore canopy cover and vegetation are a significant feature for thermoregulatory behaviour in the species. Further detailed data on habitat selection would yield detailed information on the mechanism of thermoregulation in the species.

CHAPTER 7

PREY HANDLING BEHAVIOUR OF *TROPIDOLAEMUS SUBANNULATUS*

7.1 General Review

Being limbless, options available for prey immobilisation by snakes are either constriction or envenomation. Striking is a distinctive technique used by snakes as an act of defensive or predatory mechanism, although a defensive strike is made out of warning without actual contact or inflicting a bite (Lillywhite, 2014). On the other hand, a predatory strike is apparently more calculated and carefully executed. A successful strike requires the capability to cover spatial distance between the snake itself and the target, ensuring the target has no time to respond and avoid the strike, and the snake must be accurate enough to create physical contact with the target (Young, 2010). Snake can strike at speeds beyond the capacity of the human eye to track, and it has been reported that a snake lunge can take under half a second, from resting position, erection of fangs, injection of venom and return to initial stance (Kardong, 1986; Kardong & Bels, 1998; LaDuc, 2002). Most snakes practicing ambush tend to be heavy-bodied, such as boids (members of the family Boidae, comprising boas) and viperids (Viperidae, or vipers) (Young, 2010).

Among venomous species, envenomation strategy tends to be different, depending on the nature of prey. Larger prey tends to be envenomated and immediately released, since large prey may be dangerous, considering mammalian prey can actively struggle. On the other hand, snakes typically maintain a grasp on smaller prey types, and continue to hold them in the mouth firmly prior to swallowing, which takes place after the prey ceases to struggle (Lillywhite, 2014). Snakes typically transport their prey via asynchronous ratcheting movements of their upper jaws in which the jaws from left or right side of the

head, alternately moving over the prey (Gans, 1961; Cundall, 1987; Kley & Brainerd, 1999), suggesting that the lower jaws have little direct role in prey transportation, but they do act as a control of the prey position in the mouth and to press it against teeth of the overlying palatine and pterygoid bones.

Although *Tropidolaemus subannulatus* is known to feed on birds and small mammals (Stuebing et al., 2014), data regarding their predatory behaviour are lacking in the literature. Their sexual dimorphism goes beyond colour and pattern, as they also display significant differences in morphology. Adult males are particularly slender, while females are heavy-bodied. Further, female can grow up to 1 meter in length, whereas males are under half that size. *Tropidolaemus subannulatus*, like other members of its subfamily (Crotalinae) are thought to identify prey through specialized infrared (thermal) receptors, apart from being aided by other senses, such as vision and chemoreceptors (de Cock Buning, 1983; Shine & Sun, 2002). Prey size tend to increase with the predator body size. The study by Shine & Sun (2002) on *Gloydius shedaoensis* demonstrates that the minimum and maximum prey size increase with snake body size and suggest that small snakes may be limited to feed on small birds either due to a physical inability to ingest larger prey related to gape-limitation, a preference for smaller birds, or due to ecological or behavioural factors that reduce encounter rate with larger birds.

Understanding details of the feeding behaviour of *Tropidolaemus subannulatus* is critical for a more complete understanding of its the life history, including its ecological requirements.

7.2 Specific Objectives

The two specific objectives of this chapter dealing with mechanism of prey capture in *Tropidolaemus subannulatus* include:

- To prepare an ethogram of the predatory behaviour.
- To provide a temporal classification of predatory behaviour.

7.3 Specific Methodology

A lab setting as shown in Figure 7.1 was established, where a transparent glass tank measuring 90 cm x 45 cm x 45 cm was used. A 5 cm x 5 cm printed grid was placed on a frontal plane and at the bottom of the tank, to facilitate the estimation of distance and for scale. A video recorder SonyTM HDR-XR350 with 24 Mbps shooting rates was mounted onto a tripod (Manfrotto 055YPro Pro Tripod, with Pro Ball Head 468 MH054MO-Q5) and placed in front of the setting to record all behavioural activities. Prey used was the ‘newborns of the *Rattus norvegicus*, which were placed 20 cm away from the head of the snake. Some prey were capable of moving in the tank until it got close enough to receive a strike by the snakes. These results were captured with high-speed digital videography. In order to analyse their behaviour, snakes acquired from the field were placed in the tank. The snakes were not fed at least one week prior to the experiment. A total of eight predatory behaviour (Table 6.1) were recorded for the feeding behaviour analysis, with four successful feeding experiment. A total of six adult females, three males and six juveniles were used in these observations of feeding behaviour. Only four females successfully feed while none of the others did. The ambient temperature at the lab settings has a mean of 26°C. Video records of their predatory behaviour were compared, where their common behavioural steps were documented. The MTS video of feeding behaviour captured was analysed with Lightworks

(version 2021.1). A prey behaviour ethogram was constructed to interpret standard predatory behaviour. Distinctive behavioural acts, such as tongue flicks before strike, and of mandibular retractions and gapes after feeding, were recorded. Time was also recorded to analyse the amount of duration taken place for each prey handling behaviour with mean and standard error analysis.

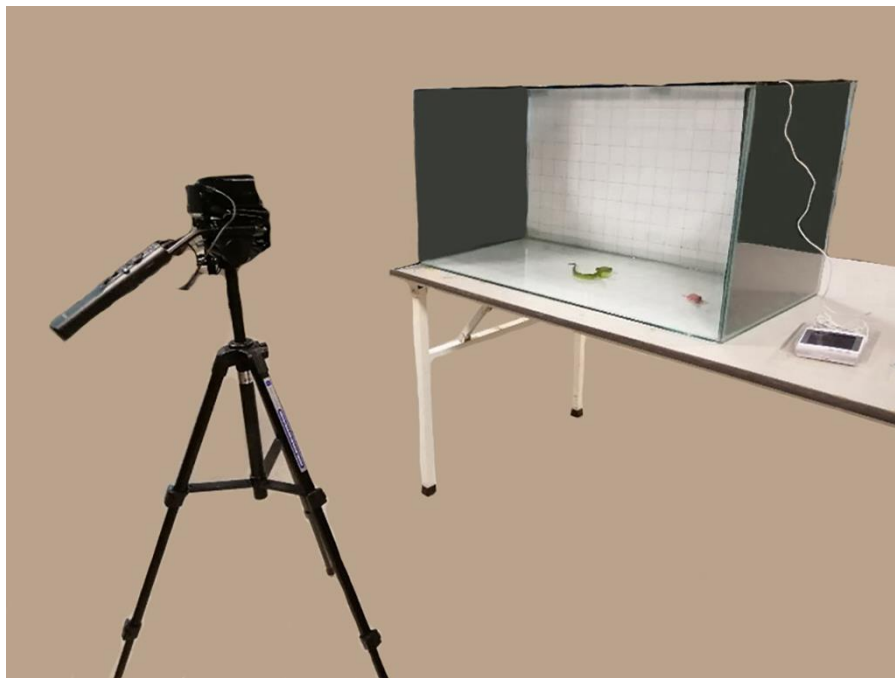


Figure 7.1: Lab setting on prey handling experiment. A SonyTM HDR-XR350 video recorder, mounted onto a tripod was placed in front of the setting to record all behavioural activities.

7.4 Results

7.4.1 Snake Response and Behaviour

In all 15 experiments, seven snakes shifted their heads towards the direction of prey at the moment of introduction of the prey to the tank. Only four (of 15; 26%) snake individuals successfully completed the process of striking, killing and ingestion, while the rest appeared uninterested and ignored the prey, with no kill nor envenomation or strike

behaviour observed. The snakes that failed to show a response to the prey remained motionless, without any attempt to investigate the prey being introduced. One individual that investigated the prey offered recorded the tongue flick behaviour, but returned to its original perch without displaying further action relevant to predation.

Little variation in behaviour among individuals that took an interest in and subsequently ingested the prey were recorded. Three subsequent phases were identified in the predatory behaviour leading to a successful feed, as shown in Table 7.1. The first is the pre-capture phase, which started with the snake noticing the prey. The second began with a strike at prey until the entire ingestion event took place. The final is the post feeding phase, starting after prey has been completely swallowed, followed by jaw adjustment (or ‘the yawn’) after the feed. Thereafter, snakes typically remained motionless (three of four individuals), except for one which became active and moved around the tank in an apparent bid to escape.

7.4.1.1 Pre-capture Phase

Pre-capture phase involved the snake detecting and approaching the prey. Detection is here defined as when the snake clearly noticed the prey, with its head turned towards it. When the prey was transferred into the tank for the experiment, the state of detection is thought to occur when the respective snake shifted the head towards the direction of the prey and seemingly observed the target to be. This action is interpreted as the snake acknowledging and taking an interest in the prey. The next step being approach, the snake will slowly align its head towards the prey (Figure 7.2).

7.4.1.2 Feeding Phase

Three behavioural displays were recorded during this phase, namely prey capture, prey evaluation, and prey ingestion (Table 7.1). Prey capture is the process whereby the

snakes move their heads toward the prey. A mean period of 186.58 seconds was taken for the snake begin to strike once its head is approximately 10 cm away from the prey and presumably proceed to envenomate the victim. The prey will either be released immediately upon presumed envenomation or continued to be retained in the mouth. The next subphase is prey evaluation, where the snake presumably waits to make sure that the prey is dead, before starting the process of ingestion. During this subphase, snakes tend to stay motionless. The final act is that of swallowing, where the snake starts to transport the prey into the oesophagus. In *Tropidolaemus subannulatus*, the swallowing mechanism displayed is via asynchronous ratcheting movements of their fangs, in which the left or right fangs alternately push the prey inwards.

7.4.1.3 Post-feeding Phase

Post-feeding phase involves muscle recovery. Once a prey has been successfully swallowed, the snake readjusts the jaw via a characteristic gape (or ‘yawn’), whereby it opens the mouth wide. This behaviour is accompanied by multiple tongue flicks. Snakes exhibit gape display and tongue flicks frequently for 5–15 minutes. All four feeding snakes lifted the front part of the body above ground, presumably to aid with peristalsis.

7.4.2 Temporal Analysis of Prey Handling Behaviour

Data for all temporal analyses are in Table 7.2. Pre-capture phase showed the shortest of the prey handling time (range 17.09–495.01 sec; mean = 186.58 sec; $\pm$ SE 109.28). Figure 7.6 shows feeding and post-feeding phase demonstrated a near equal mean prey handling time of 822.62 sec (range 433.08–1336.22 sec; $\pm$ SE 191.48) and 708.39 sec (range 392.16–1079.06 sec; $\pm$ SE 175.07), respectively. The ingestion process itself did not take as long as prey evaluation. Ingestion time period ranged 259.19–1313.10 sec (mean = 580.39 sec; $\pm$ SE

247.43). In general, the pre-capture phase only took about 10.9% of the handling time, while the feeding phase took 47.9% and post-feeding phase, about 41.2%.

Table 7.1: Nomenclature for predatory ethogram of *Tropidolaemus subannulatus* utilised in the current study. Modified from Danaisawadi et al. (2016).

Predatory phase	Functional category	Behavioural display	Description
Pre-capture (186.58 sec)	Detection	Head shift	Head tilts towards direction of prey
		Eye fix	Stares at prey
	Approach	Approach	Head moves towards prey
Feeding (822.62 sec)	Capture	Strike	Strikes at prey and either let go immediately after envenomation or prey continued to be held in the mouth
	Prey evaluation (Dead or alive)	Wait	Stays motionless
	Swallow	Upper jaw retraction	Transports prey body into oesophagus
Post-feeding (708.39 sec)	Muscular recovery	Gape	Opens mouth widely
		Tongue flick	Protrudes and withdraws tongue

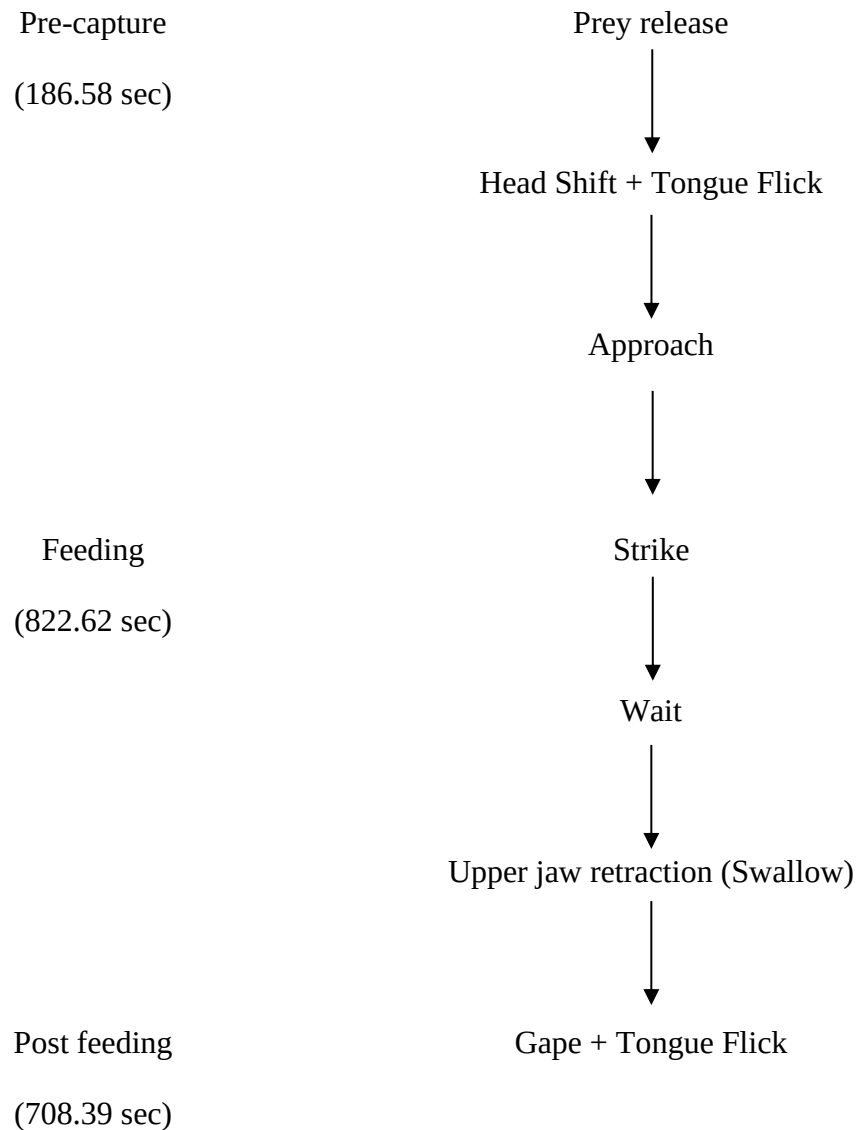


Figure 7.2: Flow chart of predatory behaviour observed in *Tropidolaemus subannulatus*.



Figure 7.3: *Tropidolaemus subannulatus* swallowing prey, using left fang to push prey towards oesophagus.



Figure 7.4: *Tropidolaemus subannulatus* swallowing using right fang to push prey towards oesophagus.

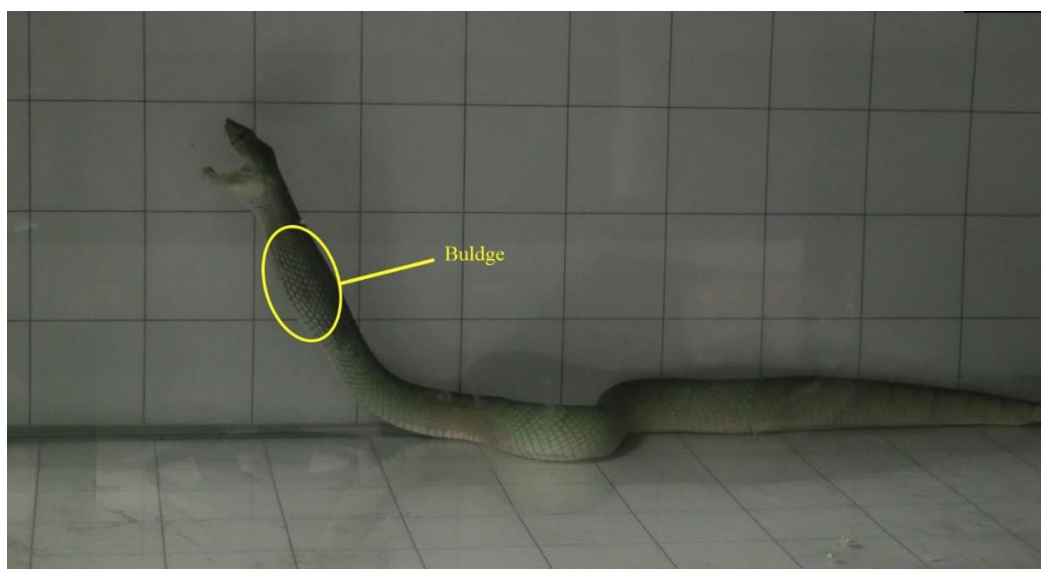


Figure 7.5: *Tropidolaemus subannulatus* showing gape behaviour while lifting its front body part to aid in peristalsis to push down the food bolus (displayed in image as a bulge).

Table 7.2: Mean and standard error of time length (seconds) of predatory phase in four females of *Tropidolaemus subannulatus*.

Individual	Predatory phase		
	Pre-capture	Feeding	Post feeding
TROS 001	47.12	852.07	427.3
TROS 003	17.09	433.08	1079.06
TROS 006	187.10	1336.22	935.03
TROS 009	495.01	669.12	392.16
Mean	186.58	822.62	708.39
SE	109.28	191.48	175.07

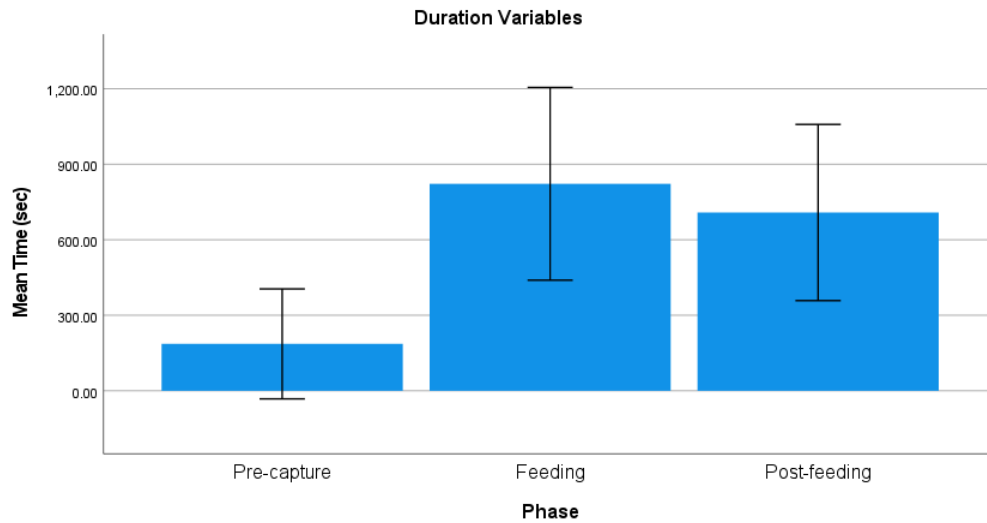


Figure 7.6: Mean time prey handling variables in *Tropidolaemus subannulatus* with standard deviation.

7.5 General Discussions

The present behavioural analysis reveals that individual snakes show slightly different feeding behaviour, with several common components. A total of four of 15 feeding behaviour experiments were made with different individuals. A majority of the 11 individuals that did not feed, displayed no interest in the prey, ignoring the prey even when close to them, occasionally even with direct physical contact. Snakes are known to exhibit variable feeding behaviours, depending on prey types of prey and circumstances of encountered in other studies (e.g., Mori, 1991; Mehta, 2003; Danaisawadi et al., 2016). A heavy-bodied viperids, such as Puff adders (*Bitis arietans*) are reported to be capable of achieving mean strike velocities and accelerations of 2.6 and 72 m/sec², respectively (Young, 2010). Visser (2015) reported that the feeding frequency in *Tropidolaemus subannulatus* can vary between 2–5 months, based on observations in captivity. Therefore, it is possible that individuals in the current experiment may have fed in the wild prior to being caught and tested for feeding behaviour experiment. Additionally, one of these individuals killed its prey

but did not attempt to ingest. There are multiple possibilities which can cause this, such as that the snake perhaps perceiving the prey as a threat, size of the prey were deemed undesirable, the prey presented was not their diet preference, or the snake was simply not hungry,

During the pre-capture phase, three of four individuals displayed 5-6 tongue flicks before prey strike. All snakes in the experiment did not change position but waited till the prey moved into the direction of the snake's head, the strike initiated when the prey was about 10 cm away from the snake's head. Cundall (2002) discovered that up to 47% of strikes by rattlesnakes (*Crotalus*) result in neither fang penetrating the prey, and that increase in distance of strike increases the probability of missed fang contact or penetration. The presumed consequence is vipers preparing for predatory strike when prey is in an extremely close range.

Feeding phase is one of the lengthiest and presumably important phases for the focal species. Upon striking and presumably envenoming the prey, they either let the prey go immediately (one of four observations) or held it in the mouth (three of four observations). Lillywhite (2014) noted that snakes usually retain a grasp on smaller prey and persist in holding it in the mouth firmly, till the prey stops struggling, before proceeding with ingestion. Typically, snakes are likely to release large mammals right away from a bite following envenomation, as larger prey have the potential to struggle and even fight back and cause harm. However, in the present case, the new-borns of *Rattus norvegicus* offered during the experiment was subequal to or smaller than bird or mammal potentially consumed in the wild. Being ambush-feeders, arboreal vipers may not release large prey from their bite all the time, at least not when high above the ground. Regardless of time taken in prey processing prior to ingestion, swallowing does not start immediately. It is assumed that the snake wants to ensure that prey is dead for a safe feed, as it was observed that in some

instances, the prey displayed muscle twitching several minutes after being envenomated and following collapse. The time interval between prey mortality and ingestion also varied between individuals. Two individuals started ingesting prey under 5 minutes after envenoming, while two began ingestion about 120 minutes after envenoming. Lillywhite (2014) stated studies by Greenbaum et al. (2003) and Chiszar et al. (2008) that viperids are capable of recognizing envenomated prey. Their studies also revealed that envenomated rodent can move a significant number of distances before succumbing to venom. Thus, taking that into consideration which indicates in this prey handling behaviour study that the snake was probably waiting for the prey to die from the venom and planned to trail it.

Post-feeding phase began once prey had been successfully swallowed completely, which involves muscle recovery (gape) and tongue flick. It had been recorded that the anterior and posterior excursions of the palate and maxillary bones in vipers surpass those in other non-viper clades (Lillywhite, 2014). There were little to none tongue flicks observed before feeding. This author attributed the lack of this behaviour to a somewhat furtive behaviour, as it waits to ambush their prey. The tongue flicking enables the snake to transfer molecular particles from the environment to vomeronasal organ which is located in the roof of the snake's mouth (Halpern & Kubie, 1980; Kahmann, 1932; Chiszar et al., 1982). After swallowing the prey, gape is observed and accompanied by high rates of tongue flicks which can last for between 5-15 minutes after swallowing the prey. Chiszar and Radcliffe (1976) suggested that the tongue flicks may allow the snake to detect other possible prey which might occur in the vicinity. Alternately, the snake may be on generally alert for possible threats from predator after swallowing its prey. With a recently swallowed prey, the presence of a predator or any form of danger could result in the snake being forced to regurgitate its food in order to escape.

The handling time of prey during the pre-capture phase appear to be the shortest among the three phases. Feeding and post feeding period took a relatively long time to complete. It is crucial for snakes to confirm that their prey is dead before consuming it, especially if the prey is a small mammal, since they can struggle and caused injury to the snake, which can also increase energetic costs of predation. A failed killing can result in energy wasted, in which the effect can be significant for sedentary species, such as the pit-vipers.

Depending on the amount of venom concentration or output, and the size of prey, the envenomation process can potentially yield different prey-killing duration. As mentioned before, snakes usually maintain a grasp on smaller prey while larger prey are strike and released. Venom is intended to immobilise and digest prey (Thomas & Pough, 1979; Mackessy, 1988; Hayes, 1991; Daltry et al., 1996). Prey types, such as new-born *Rattus norvegicus* are relatively small which weight about 10 g. One of the feeding females with approximately 40 cm SVL had been recorded to envenom and release the small defenceless prey. Studies had shown that the strength of venom can be age-dependant (Chippaux et al., 1991) or show significant geographical variation as a result of diet (Daltry et al., 1996). It was found that coagulant activity in venoms is related to age as decreasing in coagulant activity increased with snake age (Bonilla et al., 1973; Kamiguti & Hanada, 1985; Gutierrez et al., 1990; Chippaux et al., 1991). This may lead to an extra precautionary step to immediately release prey, even though prey size is small. Further studies are required on this species to understand the behaviour.

7.6 General Conclusion

These observations were made *ex-situ* with a sample of four adult female *T. subannulatus*. provide new information on foraging behaviour of a common venomous

snake. The species displayed eight common predatory behaviour (head shift, eye fix, approach, strike, wait, upper retraction, gape and tongue flick) in three different phases, namely pre-capture, feeding, and post-feeding phases during experiments with feeding with new-born *Rattus norvegicus*. In the pre-capture phase, which is the temporally the shortest, there are head shift, eye fix and head move towards prey. During the long feeding phase, actions involve strike, wait to ensure prey death, and swallowing of prey. Post-feeding phase is a process of muscular recovery, followed by high-rate tongue flick that can last for about 15 minutes. The feeding behaviour of *T. subannulatus* is almost similar to that of the constricting rat snake, *Coelognathus helena* hatchlings where the prey house mouse (*Mus musculus*) is killed via constriction and assessed it dead or alive prior to swallowing (Mehta, 2003). Unlike snail-eating snake *Pareas carinatus*, this species directly extracts and swallow the prey (snail) regardless of the prey condition (Danaïswadi et al., 2016). Considering none of males and juveniles succeeded in the feeding experiment, further research is required with more prey choice. Danaïswadi et al. (2016) study on *P. carinatus* displayed different feeding temporal pattern based on different prey type. Understanding the foraging and prey-handling behaviour are important and has the potential to provide deeper understanding on evolutionary fitness, as well as the biotic and abiotic factors which interacts with the focal species.

CHAPTER 8

GENERAL CONCLUSION, LIMITATION, AND RECOMMENDATION

Knowledge of an organism's life history is the first step towards its conservation and management. The capability of having the right goals and strategies is key to successful in such activities. Ectotherms are arguably the most vulnerable organisms in the planet, on account of global warming, and although some species are capable of tolerating high thermal range, a majority are not. Microhabitats plays a vital key role for the survival of these species as they are extensively utilized. What they need to survive could differ in different life stage as had been mentioned before. A minor shift of biotic and abiotic factors in the environment could either benefit them, pose no changes or harm them instead.

An active foraging predator would naturally require a large home range, thus theoretically speaking, ambush predator would have a smaller home range. Nonetheless, a different stage of life history, such as the breeding season, would motivate an ambush predator to forage for a mate. The current study reveal that *Tropidolaemus subannulatus* have a relatively small home range and it appears that the sexes have no significant differences in spatial use in terms of area despite the presence of sexual size dimorphism. Individuals studied did show some unique behaviours, such as in movement pattern. Since some movements appear random and some not, asymptote could not be achieved in the present study. Conducting a sound comparative study with this species is challenging. It is suggested that more samples and a longer study period be allocated to obtain reliable answers on the biology of the species.

Their preference of perching on tree branches makes their study a challenge when high above ground. Although this tells us the significance of trees and canopies as their main

microhabitats, these snakes are practically out of sight. Their need to feed infrequently permits the occupancy of refugial sites for long periods. On account of its limited movement, it would be appropriate if studies are conducted for longer periods, preferably years. This would be interesting to research on and see how snakes react to different seasons, particularly in tropical Borneo, the dry and wet months.

Two females which were recaptured and underwent a second radio transmitter implantation surgery failed to recover post-surgery. Assuming the snake did not eat upon the first release and tracking, that might contribute to the stressful situation since they did not have enough resources to recover. If this is the case, then studying males *T. subannulatus* could be more challenging. Smaller individual necessitates smaller transmitter, which leads to smaller battery capacity. However, radio transmitter technology has been steadily advancing since its first introduction, and it is hoped that new technology will permit smaller and lighter transmitters, with long-lasting batteries, in the near future, that can facilitate such studies.

While on the topic of advanced telemetry, radio-sensitive transmitters have allowed researchers to record both body surface temperature and core body temperature of an animal remotely. Implanting transmitter into the coelomic cavity of *T. subannulatus* have shown that the species possesses a wide thermal range. This is to be expected for an ambush predator with restricted movement.

The *ex-situ* experiments show how the species waits till the prey gets extremely close before launching a strike. Since only four individuals have a successful feeding, it is recommended that future studies provide more prey types as well as sizes.

Many basic questions remain unanswered. For instance, the information regarding dietary cycle, reproductive phenology, and other aspects of life history of the target species. The eyes don't see what the mind doesn't know. Knowledge being the foundation of achievement, more research needs to be done on the biology of the Bornean Keeled Pit-viper, to better understand a familiar component of the island's biological diversity.

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APPENDICES

Appendix A: Morphometric measurements (cm) and body mass (g) of *Tropidolaemus subannulatus*.

ID	Sex	Life stage	Weight (g)	Head width (cm)	Max jaw width (cm)	SVL (cm)	ToL (cm)	Pit tag / Transmitter
TROS 001	Male	Adult	18.0	1.69	18.5	37	44	234281
TROS 002	Female	Adult	91.20	2.97	3.00	57.6	67.8	232462
TROS 003	-	Juvenile	8.0	1.39	1.34	25.5	30.3	989001025002764
TROS 004	Male	Adult	28.0	2.00	1.69	40.0	47.6	234282
TROS 005	Female	Adult	84.0	2.90	2.7	51.6	60.3	232461 / 232457
TROS 006	Male	Adult	26.0	1.46	1.19	40.3	47.9	989001025002706
TROS 007	Male	Adult	22.0	1.67	1.56	35.5	43.4	234284
TROS 008	Male	Adult	23.0	1.85	1.74	39.9	47.4	234283 / 989001025002771
TROS 009	Female	Adult	120.0	3.34	3.07	61.0	72.1	232459
TROS 010	Female	Adult	259.0	3.93	3.44	64.0	76.3	232460
TROS 011	Female	Juvenile	30.0	1.89	1.85	42.8	51.2	989001025002737
TROS 012	Female	Juvenile	45.0	2.40	2.05	52.0	73.3	989001025002945
TROS 013	Female	Juvenile	30.0	1.84	1.72	34.2	47.1	989001025002898
TROS 014	Male	Adult	25.0	1.84	1.74	39.6	47.1	989001025002943
TROS 015	Male	Adult	27.0	1.85	18.2	39.2	46.3	247901
TROS 016	Male	Juvenile	14.0	1.60	1.41	29.8	35.7	989001025002943

TROS 017	-	Juvenile	19.0	-	-	39.0	46.1	247901
TROS 018	Male	Juvenile	-	-	-	28.0	33.4	-
TROS 019	Female	Juvenile	14.0	-	-	30.5	36.7	-
TROS 020	Male	Juvenile	8.0	1.31	1.18	26.8	32.0	989001025002727
TROS 021	-	Juvenile	8.0	1.44	1.19	24	29	989001025002685

Appendix B: GPS coordinates of location of *Tropidolaemus subannulatus*, equipped with radio transmitters.

No.	ID	Date	Coordinates
1	TROS 002	10-Oct-19	N 01°36.820', E 110°11.341'
2	TROS 002	14-Oct-19	N 01°36.820', E 110°11.341'
3	TROS 002	14-Oct-19	N 01°36.820', E 110°11.341'
4	TROS 002	16-Oct-19	N 01°36.822', E 110°11.344'
5	TROS 002	18-Oct-19	N 01°36.822', E 110°11.344'
6	TROS 002	21-Oct-19	N 01°36.822', E 110°11.340'
8	TROS 002	04-Nov-19	N 01°36.820', E 110°11.340'
9	TROS 002	06-Nov-19	N 01°36.829', E 110°11.328'
10	TROS 002	08-Nov-19	N 01°36.828', E 110°11.329'
11	TROS 002	08-Nov-19	N 01°36.824', E 110°11.339'
12	TROS 002	11-Nov-19	N 01°36.825', E 110°11.335'
13	TROS 002	11-Nov-19	N 01°36.818', E 110°11.337'
14	TROS 002	15-Nov-19	N 01°36.818', E 110°11.337'
15	TROS 002	15-Nov-19	N 01°36.818', E 110°11.337'
16	TROS 002	18-Nov-19	N 01°36.818', E 110°11.337'
17	TROS 002	20-Nov-19	N 01°36.818', E 110°11.337'
18	TROS 004	08-Oct-19	N 01°36.425', E 110°11.440'
19	TROS 004	10-Oct-19	N 01°36.425', E 110°11.440'
20	TROS 004	10-Oct-19	N 01°36.425', E 110°11.440'
21	TROS 004	14-Oct-19	N 01°36.428', E 110°11.446'
22	TROS 004	14-Oct-19	N 01°36.428', E 110°11.446'
23	TROS 004	16-Oct-19	N 01°36.428', E 110°11.446'
24	TROS 004	16-Oct-19	N 01°36.428', E 110°11.446'
25	TROS 004	18-Oct-19	N 01°36.412', E 110°11.448'
26	TROS 004	21-Oct-19	N 01°36.412', E 110°11.448'
27	TROS 004	25-Oct-19	N 01°36.412', E 110°11.448'

28	TROS 005	21-Oct-19	N 01°36.730', E 110°11.736'
29	TROS 005	25-Oct-19	N 01°36.743', E 110°11.731'
30	TROS 005	04-Nov-19	N 01°36.727', E 110°11.729'
31	TROS 005	06-Nov-19	N 01°36.727', E 110°11.729'
32	TROS 005	08-Nov-19	N 01°36.727', E 110°11.729'
33	TROS 005	08-Nov-19	N 01°36.727', E 110°11.729'
34	TROS 005	11-Nov-19	N 01°36.727', E 110°11.729'
35	TROS 005	11-Nov-19	N 01°36.727', E 110°11.729'
36	TROS 005	25-Nov-19	N 01°36.731', E 110°11.730'
37	TROS 005	27-Nov-19	N 01°36.723', E 110°11.739'
38	TROS 005	27-Nov-19	N 01°36.723', E 110°11.739'
39	TROS 005	29-Nov-19	N 01°36.723', E 110°11.739'
40	TROS 005	02-Dec-19	N 01°36.723', E 110°11.739'
41	TROS 005	02-Dec-19	N 01°36.723', E 110°11.739'
42	TROS 005	06-Dec-19	N 01°36.729', E 110°11.741'
43	TROS 005	09-Dec-19	N 01°36.723', E 110°11.739'
44	TROS 005	09-Dec-19	N 01°36.723', E 110°11.739'
45	TROS 005	13-Dec-19	N 01°36.718', E 110°11.734'
46	TROS 005	13-Dec-19	N 01°36.718', E 110°11.734'
47	TROS 005	16-Dec-19	N 01°36.718', E 110°11.734'
48	TROS 005	16-Dec-19	N 01°36.718', E 110°11.734'
49	TROS 005	27-Dec-19	N 01°36.724', E 110°11.747'
50	TROS 005	30-Dec-19	N 01°36.723', E 110°11.749'
51	TROS 005	30-Dec-19	N 01°36.723', E 110°11.749'
52	TROS 008	15-Nov-19	N 01°36.595', E 110°11.658'
53	TROS 008	15-Nov-19	N 01°36.595', E 110°11.658'
54	TROS 008	18-Nov-19	N 01°36.599', E 110°11.656'
55	TROS 008	20-Nov-19	N 01°36.596', E 110°11.656'
56	TROS 008	20-Nov-19	N 01°36.596', E 110°11.656'
57	TROS 008	22-Nov-19	N 01°36.596', E 110°11.656'
58	TROS 008	25-Nov-19	N 01°36.589', E 110°11.651'
59	TROS 008	27-Nov-19	N 01°36.589', E 110°11.651'
60	TROS 008	02-Dec-19	N 01°36.588', E 110°11.646'
61	TROS 010	20-Nov-19	N 01°36.405', E 110°11.340'
62	TROS 010	22-Nov-19	N 01°36.406', E 110°11.328'
63	TROS 010	27-Nov-19	N 01°36.406', E 110°11.328'
64	TROS 010	29-Nov-19	N 01°36.406', E 110°11.328'
65	TROS 010	02-Dec-19	N 01°36.406', E 110°11.328'
66	TROS 010	02-Dec-19	N 01°36.406', E 110°11.328'
67	TROS 010	06-Dec-19	N 01°36.406', E 110°11.328'
68	TROS 010	06-Dec-19	N 01°36.406', E 110°11.328'
69	TROS 010	13-Dec-19	N 01°36.398', E 110°11.326'

Appendix C: Data on abiotic factors related to spatial biology of *Tropidolaemus subannulatus* (microhabitat preferences and canopy cover).

Microhabitat preference	Male	Female
Fern	-	1
Sapling	2	5
Tree branch	13	50
Dead twigs	-	5

Appendix D: Data on relationship between vertical displacement (height above ground) versus tree diameter in females of *Tropidolaemus subannulatus*.

Height above ground (m)	Circ of tree (cm)	SVL (cm)	Tree Diameter	Log HG	Log TD
12.670	73.2	57.6	23.31210191	1.102777	1.367581
14.600	73.2	57.6	23.31210191	1.164353	1.367581
12.057	129.7	57.6	41.30573248	1.081239	1.61601
0.323	1.1	57.6	0.350318471	-0.4908	-0.45554
0.512	1.1	57.6	0.350318471	-0.29073	-0.45554
0.512	1.1	57.6	0.350318471	-0.29073	-0.45554
0.512	1.1	57.6	0.350318471	-0.29073	-0.45554
0.512	1.1	57.6	0.350318471	-0.29073	-0.45554
0.512	1.1	57.6	0.350318471	-0.29073	-0.45554
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.000	7.6	51.6	2.420382166	0.30103	0.383884
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.900	5.9	51.6	1.878980892	0.462398	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922

2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
2.900	5.9	51.6	1.878980892	0.462398	0.273922
2.900	5.9	51.6	1.878980892	0.462398	0.273922
2.850	5.9	51.6	1.878980892	0.454845	0.273922
0.354	5.9	51.6	1.878980892	-0.451	0.273922
0.354	5.9	51.6	1.878980892	-0.451	0.273922
0.354	5.9	51.6	1.878980892	-0.451	0.273922
0.354	5.9	51.6	1.878980892	-0.451	0.273922
1.000	4.8	51.6	1.52866242	0	0.184312
1.000	4.8	51.6	1.52866242	0	0.184312
1.708	4.8	51.6	1.52866242	0.232488	0.184312
1.708	4.8	51.6	1.52866242	0.232488	0.184312
1.554	4.8	51.6	1.52866242	0.191451	0.184312
1.554	4.8	51.6	1.52866242	0.191451	0.184312
1.554	4.8	51.6	1.52866242	0.191451	0.184312
0.430	4.8	51.6	1.52866242	-0.36653	0.184312
0.430	4.8	51.6	1.52866242	-0.36653	0.184312
0.430	4.8	51.6	1.52866242	-0.36653	0.184312
10.000	74	64	23.56687898	1	1.372302

Appendix E: Data on relationship between vertical displacement (height above ground) versus tree diameter in males of *Tropidolaemus subannulatus*.

Height above ground (m)	Circ of tree (cm)	SVL (cm)	Tree Diameter	Log HG	Log TD
1.270	3.7	40	1.178343949	0.103804	0.071272
1.325	3.7	40	1.178343949	0.122216	0.071272
1.270	23.1	40	7.356687898	0.103804	0.866682
4.350	23.1	40	7.356687898	0.638489	0.866682
4.500	23.1	40	7.356687898	0.653213	0.866682
4.880	22.9	40	7.292993631	0.68842	0.862906
4.592	22.9	40	7.292993631	0.662002	0.862906
1.500	20.2	39.9	6.433121019	0.176091	0.808422
1.500	20.2	39.9	6.433121019	0.176091	0.808422
1.009	20.2	39.9	6.433121019	0.003891	0.808422
1.147	20.3	39.9	6.464968153	0.059563	0.810566
1.147	20.3	39.9	6.464968153	0.059563	0.810566
1.147	20.3	39.9	6.464968153	0.059563	0.810566
3.050	20.3	39.9	6.464968153	0.4843	0.810566
2.170	20.3	39.9	6.464968153	0.33646	0.810566

Appendix F: Data on relationship between snout-vent-length (SVL) versus tree diameter in females of *Tropidolaemus subannulatus*.

Circ of tree (cm)	Dia of tree	SVL (cm)	Log Tree Diameter	Log SVL
73.2	23.31	57.6	1.36758	1.760422
129.7	41.31	57.6	1.61601	1.760422
7.6	2.42	51.6	0.38388	1.71265
5.9	1.88	51.6	0.27392	1.71265
4.8	1.53	51.6	0.18431	1.71265
74	23.57	64.0	1.3723	1.80618

Appendix G: Data on relationship between snout-vent-length (SVL) versus tree diameter in males of *Tropidolaemus subannulatus*.

Circ of tree (cm)	Dia of tree	SVL (cm)	Log Tree Diameter	Log SVL
23.1	7.36	40	0.86668	1.60206
22.9	7.29	40	0.86291	1.60206
20.2	6.43	39.9	0.80842	1.600973
20.3	6.46	39.9	0.81057	1.600973
73.2	23.31	57.6	1.36758	1.760422
23.1	7.36	40	0.86668	1.60206

Appendix H: Ambient, substrate, body surface and core body temperatures of free-ranging *Tropidolaemus subannulatus*.

No.	Freq / Tros	Ts (°C)	Ta (°C)	Tbs (°C)	Tb (°C)	Log Ts	Log Ta	Log Tbs	Log Tb
1	501	22.00	25.70	22.00	24.42	1.342423	1.40993	1.34	1.39
2		NA	27.60	NA	28.09	NA	1.44091	NA	1.45
3		23.40	28.10	23.40	25.4	1.369216	1.44871	1.37	1.40
4		19.20	27.00	20.00	25.46	1.283301	1.43136	1.30	1.41
5		NA	25.90	NA	27.42	NA	1.4133	NA	1.44
6		NA	26.80	NA	28.9	NA	1.42813	NA	1.46
7		NA	27.00	NA	31.28	NA	1.43136	NA	1.50
8		NA	28.30	NA	30.02	NA	1.45179	NA	1.48
9		NA	27.30	NA	26.49	NA	1.43616	NA	1.42
10		NA	28.70	NA	29.74	NA	1.45788	NA	1.47
11		22.20	26.20	22.20	22.79	1.346353	1.4183	1.35	1.36
12		24.80	27.10	25.00	25.96	1.394452	1.43297	1.40	1.41

13		23.60	28.50	23.60	24.98	1.372912	1.45484	1.37	1.40
14		25.60	27.70	25.80	26.33	1.40824	1.44248	1.41	1.42
15		23.80	27.00	24.00	24.45	1.376577	1.43136	1.38	1.39
16		23.40	26.90	23.40	23.44	1.369216	1.42975	1.37	1.37
17		NA	NA	NA	26.41	NA	NA	NA	1.42
18		NA	25.00	NA	28.14	NA	1.39794	NA	1.45
19	660	22.20	26.60	22.20	23.38	1.346353	1.42488	1.35	1.37
20		24.20	27.10	24.40	25.75	1.383815	1.43297	1.39	1.41
21		21.80	25.60	21.60	23.03	1.338456	1.40824	1.33	1.36
22		NA	27.10	NA	28.02	NA	1.43297	NA	1.45
23		23.80	28.30	23.80	24.08	1.376577	1.45179	1.38	1.38
24		NA	27.10	NA	27.52	NA	1.43297	NA	1.44
25		23.60	31.20	23.60	24.88	1.372912	1.49415	1.37	1.40
26		24.80	26.70	25.00	26.97	1.394452	1.42651	1.40	1.43
27		NA	27.60	NA	25.92	NA	1.44091	NA	1.41
28	341	25.00	29.40	25.10	27.89	1.39794	1.46835	1.40	1.45
29		25.50	27.40	25.70	29.46	1.40654	1.43775	1.41	1.47
30		27.20	27.50	27.00	29.98	1.434569	1.43933	1.43	1.48
31		25.20	27.10	25.20	29.81	1.401401	1.43297	1.40	1.47
32		26.60	28.10	26.80	30.04	1.424882	1.44871	1.43	1.48
33		23.60	26.60	23.80	27.56	1.372912	1.42488	1.38	1.44
34		25.80	28.20	26.00	29.75	1.41162	1.45025	1.41	1.47
35		22.40	24.10	22.40	26.06	1.350248	1.38202	1.35	1.42
36		25.60	27.50	25.80	29.55	1.40824	1.43933	1.41	1.47
37		24.20	27.00	24.40	28.18	1.383815	1.43136	1.39	1.45
38		NA	28.00	NA	31.25	NA	1.44716	NA	1.49
39		NA	25.80	NA	27.40	NA	1.41162	NA	1.44
40		NA	25.80	NA	27.30	NA	1.41162	NA	1.44
41		NA	26.20	NA	26.39	NA	1.4183	NA	1.42
42		NA	27.80	NA	30.30	NA	1.44404	NA	1.48
43		NA	28.50	NA	31.84	NA	1.45484	NA	1.50
44		NA	27.10	NA	27.69	NA	1.43297	NA	1.44
45		23.60	26.10	23.50	27.17	1.372912	1.41664	1.37	1.43
46		NA	26.00	NA	27.69	NA	1.41497	NA	1.44
47		24.40	27.60	24.50	27.69	1.38739	1.44091	1.39	1.44
48		24.10	26.00	24.10	26.97	1.382017	1.41497	1.38	1.43
49		24.00	25.70	23.90	26.68	1.380211	1.40993	1.38	1.43
50		24.40	26.60	24.40	23.38	1.38739	1.42488	1.39	1.37
51		NA	27.20	NA	24.69	NA	1.43457	NA	1.39
52		24.50	29.90	24.50	27.14	1.389166	1.47567	1.39	1.43
53		NA	26.00	NA	26.74	NA	1.41497	NA	1.43
54		25.30	27.00	25.30	27.79	1.403121	1.43136	1.40	1.44
55		24.70	27.10	24.60	28.77	1.392697	1.43297	1.39	1.46
56		24.40	25.50	24.40	27.20	1.38739	1.40654	1.39	1.43

57		NA	26.70	NA	29.46	NA	1.42651	NA	1.47
58		NA	27.30	NA	27.46	NA	1.43616	NA	1.44
59		NA	27.20	NA	26.81	NA	1.43457	NA	1.43
60		24.10	25.80	24.30	26.52	1.382017	1.41162	1.39	1.42
61		NA	24.50	NA	26.61	NA	1.38917	NA	1.43
62		23.50	25.10	23.50	25.54	1.371068	1.39967	1.37	1.41
63		24.90	26.60	24.90	26.81	1.396199	1.42488	1.40	1.43
64		24.50	27.60	24.60	26.74	1.389166	1.44091	1.39	1.43
65		23.70	26.30	23.70	25.37	1.374748	1.41996	1.37	1.40
66		24.30	30.50	24.30	26.65	1.385606	1.4843	1.39	1.43
67		24.80	25.20	24.80	26.39	1.394452	1.4014	1.39	1.42
68		NA	27.10	NA	26.74	NA	1.43297	NA	1.43
69		24.60	26.90	24.60	26.06	1.390935	1.42975	1.39	1.42
70		25.00	26.30	25.00	25.37	1.39794	1.41996	1.40	1.40
71	700	25.20	28.40	25.40	26.29	1.401401	1.45332	1.40	1.42
72		22.60	26.50	22.80	23.82	1.354108	1.42325	1.36	1.38
73		23.60	25.40	23.60	24.45	1.372912	1.40483	1.37	1.39
74		23.80	27.00	23.80	24.93	1.376577	1.43136	1.38	1.40
75		23.80	28.50	23.80	24.98	1.376577	1.45484	1.38	1.40
76		22.60	26.00	22.70	24.5	1.354108	1.41497	1.36	1.39
77		NA	28.40	NA	26.92	NA	1.45332	NA	1.43
78		NA	28.40	NA	29.53	NA	1.45332	NA	1.47
79		NA	27.50	NA	24.55	NA	1.43933	NA	1.39
80		NA	26.30	NA	25.56	NA	1.41996	NA	1.41
81		NA	25.40	NA	22.79	NA	1.40483	NA	1.36
82	300	23.40	28.00	23.40	23.2	1.369216	1.44716	1.37	1.37
83		NA	26.40	NA	25.33	NA	1.4216	NA	1.40
84		NA	27.60	NA	29.59	NA	1.44091	NA	1.47
85		NA	27.20	NA	32.15	NA	1.43457	NA	1.51
86		NA	31.00	NA	24.68	NA	1.49136	NA	1.39
87		NA	26.00	NA	26.35	NA	1.41497	NA	1.42
88		NA	28.20	NA	22.86	NA	1.45025	NA	1.36
89		NA	23.20	NA	24.59	NA	1.36549	NA	1.39
90		NA	29.00	NA	24.07	NA	1.4624	NA	1.38
91		NA	23.90	NA	24.71	NA	1.3784	NA	1.39
92		NA	26.10	NA	23.42	NA	1.41664	NA	1.37
93		NA	23.80	NA	23.97	NA	1.37658	NA	1.38
94		NA	25.80	NA	23.79	NA	1.41162	NA	1.38
95		NA	25.60	NA	24.96	NA	1.40824	NA	1.40
96		23.20	29.00	23.20	23.54	1.365488	1.4624	1.37	1.37
97		NA	25.20	NA	23.42	NA	1.4014	NA	1.37
98		NA	28.10	NA	24.53	NA	1.44871	NA	1.39

Appendix H: Journal Publications

1. **Martin, V.** & Das, I. (2022) Prey-handling in the Bornean Keeled Pit-viper *Tropidolaemus subannulatus*. *Malayan Nature Journal*, 74(2), 337–346.
2. Das, I. & **Martin, V.** (2022) Herpetology 2024: Which snake? World Congress of Herpetology Newsletter 3(2):14-21.
3. **Martin, V.** & I. Das. (2023) Bornean Keeled Pit-viper. In: Bako National Park. Biodiversity between land and the sea. pp:111–113. M.A. Jayasilan, M.K. Suaidi & I. Das (Eds.). UNIMAS Publisher, Kota Samarahan and Natural History Publications (Borneo), Kota Kinabalu.