



Institute of Biodiversity and Environmental Conservation

Comparative Aspects of the Ecology of Four Syntopic Species of Angle-headed Lizards, Genus *Gonocephalus* (Reptilia: Agamidae: Draconinae)

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Comparative Aspects of the Ecology of Four Syntopic Species of Angle-headed Lizards, Genus *Gonocephalus* (Reptilia: Agamidae: Draconinae)

Wong Jye Wen

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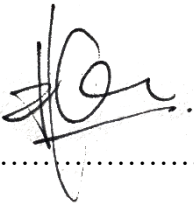
Institute of Biodiversity and Environmental Conservation

UNIVERSITI MALAYSIA SARAWAK

2023

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

Investigations on coexistence and resource partitioning among sympatric species of reptilians have been widely conducted in other parts of the world but remain poorly studied in Borneo and other parts of south-east Asia. While some generalisations of ecological aspects may be applicable to local reptilian species, species interactions may differ, depending on geographical location and environment conditions. In the present study, four *Gonocephalus* species (*G. bornensis*, *G. liogaster*, *G. doriae* and *G. grandis*) were selected for a study of their comparative biology, the rationale being their perceived ecological similarity and syntopic occurrence, to develop a better insight of the ecological phenomena of resource partitioning. Studies on ecology, specifically on home range, habitat preference, diet and thermal biology, with additional records of parasite, colouration and predation of populations at Kubah National Park, Sarawak, East Malaysia (north-western Borneo) were carried out from June 2018 to December 2019. A total of 16 lizards, representing four species, were equipped with temperature sensitive radio-transmitters, permitting the collection of data on movement and body temperature. Species of *Gonocephalus* generally occupy similar microhabitats, favouring areas with gentle to moderate slope, high canopy cover, are plastic in their usage of trees in terms of sizes or height, moderate distance to waterbodies, on tree trunk, tree branch, moderate to high humidity, moderate to high ambient temperature, low to median light intensity and low to median perch surface temperatures. All had moderate home range sizes that were similar across species and sexes. Nonetheless, species of *Gonocephalus* diverge slightly along the spatial dimension of their ecological niches by exhibiting different levels of preference towards aspects of microhabitats utilised, while the lack of interspecific home range overlaps propose that these species are occupying different parts of the forest, although a more extensive sampling that include more

individuals may be needed to confirm this. The four species were primarily shade-dwellers and have relatively low mean body temperatures. They exploit the thermal niche differently which are reflected from the spatial niche, and are likely influenced by the trophic niche. *G. bornensis* was overall a habitat generalist compared to its congeners, whereas *G. doriae* are relatively specialised. A total of 13 prey types were identified, consisting mainly of insects and other non-insect arthropod groups (earthworms and snails). However, there was insufficient evidence to conclude unequivocally that trophic resource partitioning contributed to coexistence among these species. Additionally, four nematode and three acarid species were successfully identified in these lizards. *G. doriae* serve as new host for *Orneoascaris* sp., and both *G. bornensis* and *G. liogaster* serve as new hosts for *Strongyluris* sp. Species of *Gonocephalus* displayed sexual dichromatism, where males are generally more colourful and vibrant compared to females. Individuals of the genus are able to quickly change skin colouration from dull to bright or vice versa for social interaction and thermoregulation. Furthermore, a *G. liogaster* was also found preyed upon by a *Ptyas carinata*, contributing to the list of predators of *Gonocephalus*. Overall, this study adds to the knowledge of these species and expands current understanding of resource partitioning and mechanisms of coexistence of lizard populations in Borneo's tropical rainforest, which may be beneficial for both conservation and management as well as future studies on other Bornean ectothermic species.

Keywords: Resource partitioning, coexistence, niche, lizard, Borneo

Perbandingan Aspek Ekologi Empat Spesies Sintopik Biawak Kepala Segi Besar, Genus *Gonocephalus* (Reptilia: Agamidae: Draconinae)

ABSTRAK

Kajian tentang spesis simpatrik dari segi pembahagian sumber dan perkongsian habitat masih kekurangan terutamanya di Borneo dan Asia Tenggara apabila dibandingkan dengan benua lain di dunia. Interaksi antara spesis mungkin berbeza dan bergantung kepada geografi dan kawasan sekitar. Bagi tujuan ini, empat spesis *Gonocephalus* (*G. bornensis*, *G. liogaster*, *G. doriae* dan *G. grandis*) telah dikenalpasti berdasarkan persamaan dari segi ekologi dan tindanan sintopik. Kajian telah dijalankan dari Jun 2018 sehingga Disember 2019 (18 bulan) khususnya atas julat pergerakan, keutamaan habitat, diet dan biologi haba. Tambahan pula, pembezaan dari segi warna spesis, jenis parasit dan kesan populasi dari pemangsaan di Taman Negara Kubah telah dikaji. Sebanyak 16 individu dipasangkan dengan pemancar radio sensitif suhu dimana bacaan pergerakan serta suhu badan telah dicatat. Spesis *Gonocephalus* yang dikaji secara umum memilih mikrohabitat yang serupa, dimana mereka mengutamakan kawasan yang mempunyai kecuraman cerun antara yang agak landai sehingga kecuraman yang sederhana serta kawasan penutupan kanopi yang tinggi, pokok yang berlainan saiz dan ketinggian, berdekatan dengan sumber air, di atas dahan atau batang pokok, kelembapan udara yang sederhana hingga tinggi, suhu kawasan sekitar yang sederhana hingga tinggi, kekuatan sumber cahaya yang sederhana hingga tinggi dan suhu permukaan tempat hinggap adalah rendah hingga sederhana. Semua spesis yang dikaji mempunyai jarak julat pergerakan yang sederhana tidak kira jantina. Namun, spesis *Gonocephalus* yang dikaji menyimpang sedikit dari sudut ruang dimensis relung ekologi masing-masing, dimana boleh dikatakan keempat-empat spesis ini mempunyai perbezaan dalam pengkhususan dan pemilihan habitat mereka. Kekurangan tindanan julat

pergerakan spesies yang dikaji mencadangkan bahawa mereka menduduki sudut dan bahagian yang berlainan dalam hutan yang sama. Semua spesies yang dikaji kerap memilih kawasan yang berteduh dan mempunyai purata suhu badan yang agak rendah. Spesies Gonocephalus ini berkemungkinan menggunakan pengkhususan terma secara berlainan yang barangkali dipengaruhi oleh pengkhususan ruang dan trofik. Sebanyak 13 jenis spesies mangsa telah dikenalpasti yang kebesarannya adalah serangga dan arthropod seperti cacing tanah dan siput. Namun, data yang dikumpul tidak mencukupi bagi menjelaskan hubungan pembahagian sumber trofik dan perkongsian habitat. Selain itu, empat spesies nematod dan tiga spesies akarid telah dijumpai dalam spesies yang dikaji. G. doriae yang dijadikan inang bagi Orneoascaris sp. dan G. bornensis serta G. liogaster berfungsi sebagai inang bagi Strongyluris sp. Spesies Gonocephalus menunjukkan perbezaan luaran dari segi jantina, secara umumnya jantan mempunyai lebih banyak warna dari betina. Individu dalam genus mampu menukar warna kulit dengan cepat daripada kusam kepada cerah atau sebaliknya untuk interaksi sosial dan pentermokawalaturan. Satu rekod dimana, G. liogaster telah ditemui dibaham oleh Pytas carinata, menyumbang kepada senarai pemangsa Gonocephalus. Kajian ini telah menambah pengetahuan tentang spesies ini dan meluaskan pemahaman semasa tentang pembahagian sumber dan mekanisme kewujudan Bersama populasi biawak di hutan hujan tropika Borneo.

Kata kunci: Pembahagian sumber, kewujudan bersama, niche, biawak, Borneo

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LIST OF ABBREVIATIONS

%FO	Percentage of Frequency of Occurrence
%N	percentage of abundance
%V	percentage of volume
°C	Degree Celsius
asl	Above sea level
AT	Ambient Temperature
ca.	Circa
CC	Canopy Cover
CT	Circumference of Tree
df	Degrees of freedom
DSLR	digital single-lens reflex camera
DW	Distance to Waterbody
e.g.	exempli gratia
et al.	et alia
F	Test statistic for a One-Way ANOVA
FG	Female <i>Gonocephalus</i>
g	Gram(s)
GB	<i>Gonocephalus bornensis</i>
GD	<i>Gonocephalus doriae</i>
GG	<i>Gonocephalus grandis</i>
GL	<i>Gonocephalus liogaster</i>
h	Hour
ha	Hectare

IRI	Index of Relative Importance
IUCN	International Union for Conservation of Nature
KDE	Kernel Density Estimation
km	Kilometer(s)
LI	Light Intensity
m	Meter(s)
MCP	Minimum Convex Polygon
MD	Mean Distance travelled between location
MDD	Mean Daily Displacement
MG	Male <i>Gonocephalus</i>
mm	Millimeter(s)
MSH	Melanophore Stimulating Hormone
n.d.	No Date
nMDS	Non-metric Multidimensional Scaling
No.	Number
NP	National Park
OTUs	Operational Taxonomic Units
P	P-value
PS	Perch Surface
PST	Perch Surface Temperature
PT	Gut Passage Time
r	Pearson Correlation Coefficient
R ²	Coefficient of Determination
RH	Relative Humidity
S	Slope

SD	Standard Deviation
SE	Standard Error
SVL	Snout-vent length
t	Computed t-test statistic
T _a	Ambient Temperature
T _b	Body Temperature
T _s	Perch Surface Temperature
UPGMA	Unweighted Pair Group Method with Arithmetic mean
VES	Visual Encounter Survey
VP	Vertical Position
WT	Weight

CHAPTER 1

INTRODUCTION

1.1 General Introduction

Many ecologists have examined spatial, feeding, and thermal patterns to understand how animals interact among each other and/or with their environment (e.g., MacArthur, 1958; Pianka, 1969; Ballinger et al., 1970; Pianka, 1971a; Cooke et al., 2016; Klenovšek et al., 2013). Species commonly coexist in populations with two or more closely related species (Sillero & Gomes, 2016), and in many of these studies, closely related species in the same community have shown to utilise some of their environmental resources differently, indicating the presence of niche segregation. Hutchinson (1957) regarded niche as a multidimensional space formed by axes corresponding to the environmental factors, where a species can successfully survive and reproduce. Similar species coexist through partitioning resources along certain axes of the multidimensional niche space, while competing over other axes. In other words, they differentiate themselves in one or more aspects of their ecology, which are presumably caused, maintained and/or reinforced by interspecific competition (Hutchinson, 1959; Pianka, 1973; Schoener, 1974). Hutchinson (1978) later defined these axes as “scenopoetic” axes, that included physical and chemical variables, and “bionomic” axes, which are resources that can be competed for (spatial and trophic niches). For species to coexist, some environmental variables or resources from these axes can sometimes interact and influence each another (Tracy & Christian, 1986). Additionally, closely related species were also said to exhibit character displacement to coexist in a community, whereby they acquire distinct observable functional features overtime that is believed to be developed from specialisation on different resources (Brown

& Wilson, 1956). The development of varied beak sizes in Darwin's finches in response to specialisation on different seed sizes is a representative case of character displacement and resource partitioning (Bowman, 1961). Such character displacement was suggested to be caused by phenotypic and genetic response to selective pressures that encouraged partitioning of available resources. This concept was widely accepted as a crucial factor pushing evolutionary diversification and adaptive radiation, and is believed to be widespread in nature (Brown & Wilson, 1956; Stuart & Losos, 2013; Dufour et al., 2018). Ultimately, successful partition of available resources within a community is vital not only to reduce competitive pressure, but to also increase feeding efficiency and maximise the carrying capacity of the system (Simon & Middendorf, 1976).

Habitat, food and time, representing spatial, trophic and temporal dimension respectively, were proposed to be the three main dimensions of ecological space partitioned by most lizards (Pianka, 1973). Syntopic lizard species, in theory, should partition resources along one or more of these three axes within their ecological space to limit competition (Pianka, 1973) that that can potentially lower individual fitness and, consequently, reduce population abundance (Schoener, 1983). Although widely studied, most ecological understanding of congeneric and sympatric lizard species derived from research in North (e.g., Pianka, 1986; Mattingly & Jayne, 2004; Bergeron & Blouin-Demers, 2020), central and South America (e.g., Williams, 1983; Núñez et al., 1989; Colli et al., 1992; Vrcibradic & Rocha, 1996; Vitt, 2000; Ibargüengoytía, 2005; Maia-carneiro et al., 2017). These studies were conducted in various types of habitats that established evidence indicating that sympatric congeneric lizards generally tend to vary in habitat or microhabitat use and food habits, suggesting that most lizard communities partition the spatial and trophic dimension. However, some data suggested that lizard communities are unlikely to partition in the latter

dimension (Luiselli, 2008), and temporal dimension may not be the most important of the three dimensions (Schoener, 1974; but see Rouag et al., 2007). Schoener (1974) further discussed that predators and terrestrial poikilotherms in heterogeneous environments are more likely to partition at the temporal dimension, while some provided substantiation that sympatric species with significantly different body size are likely to partition in the trophic dimension (Colli et al., 1992; Maia-Carneiro et al., 2017). Depending on the geographic location, the sequence of importance of the ecological dimensions may vary (Toft, 1985). Nevertheless, congeneric and sympatric species that overlap in geographic distribution provide an excellent opportunity to study resource partitioning and the processes of coexistence.

With a notable adaptive radiation in their evolutionary history, and over 7,144 known species from the order Squamata: suborder Sauria worldwide (Uetz, 2021), lizards have an important role in supporting global ecosystems. They are products of natural selection and have diversified to fill variety of ecological niches providing important ecosystem services. Therefore, lizards are potential model organism for the study and understanding of multiple ecological phenomena (Pianka & Vitt, 2003; Meiri, 2010). They often form part of evolutionary and ecological experiments. Nonetheless, understanding the ecology of species is a necessary condition for managing and preserving natural sites properly.

1.2 Problem Statement

Agamid lizards belonging to the genus *Gonocephalus* Kaup, 1825 are endemic to southeast Asia, west of the Wallace's line (Moody, 1980; Welch et al., 1990; Ota et al., 1992; Ananjeva & Matveyeva-Dujsebayaeva, 1996). They are arboreal and diurnal species often found in forested areas. Of the 17 known species, four species of *Gonocephalus* have been

recorded in the lowlands of Sarawak, Borneo, namely *G. liogaster*, *G. grandis*, *G. bornensis*, and *G. doriae*. These species are closely related, similar in size and are known to occupy the same macrohabitat and similar microhabitat (Das, 2006, 2010). Therefore, ecologically comparable species such as these, are anticipated to demonstrate the strongest levels of niche partitioning in overlapping distribution areas to allow coexistence. However, it is unclear how these species are able to partition their resources and to coexist. Available biological literature from previous studies on *Gonocephalus* species has focused upon on parasites (Balasingam, 1963; Singh, 1967; Mullin, 1973; Yap et al., 1974; Durette-desset, 1980; Maupin et al., 1998; Goldberg et al., 2005; Bursey et al., 2015; Okulewicz et al., 2015; Goldberg et al., 2016), morphology (Rahmi et al., 2012), and phylogenetic relationships (Ota et al., 1992). A more recent study discovered the interesting defence behaviour shown by *Gonocephalus grandis* (Shahriza, 2018). Besides these, little is known about their ecological interactions.

1.3 Objectives

The overall purpose of this research was to to determine whether the four syntopic species of *Gonocephalus* partition their resources spatially and trophically via examining their diet, habitat preference, thermal biology and home range at Kubah National Park to mitigate interspecific competition and permit coexistence. These data capacitate the examination and interpretation of the ecological relationships on a fine scale among these sympatric species. Specific objectives are stated in each chapter respectively.

CHAPTER 2

MATERIALS AND METHODS

2.1 Study Site

This study was conducted at Kubah National Park, Sarawak, Borneo (Park Headquarters at 01°36'41.7"N, 110°11'47.1"E). Kubah NP is approximately 22 km west of Kuching city, making the park one of Sarawak's most accessible parks (Figure 2.1). The park was established in 1989 to protect and preserve the area's rich flora and fauna and was opened to the public in 1995. Matang Wildlife Centre (Park Headquarters at 01°36'33.8"N, 110°09'35.3"E) is located on Kubah's west side and is part of Kubah NP.

Kubah NP covers an area of slightly over 22 square kilometers on the northwest flank and ridge of the tallest mountain in the landscape of Kuching, its summit referred to as *Gunung* (Mount) *Serapi* reaches a height of 911 m asl. Therefore, much of the park consists of steep terrain with various streams drain the flanks of the mountain. The lower elevation of the park covers approximately up to 20 m asl while the upper elevation of the park covers up to 777 m asl. *Gunung Serapi*'s summit occupied by a telecommunications tower is not included in the park whereas *Gunung Selang* (approximately 429 m asl), a lower summit on *Serapi*'s northwest ridge is included in the park. *Gunung Serapi* is built of a thick succession of sandstone, conglomerate and interbedded shale belonging to the Plateau Sandstone Formation (Hazebroek & Abang Morshidi, 2000).

The park includes five jungle trails (Main trail, Waterfall trail, Selang trail, Rayu trail, and Belian trail), and the Summit trail is a tarred road that leads to the summit of *Gunung Serapi*. The broad range of altitudes within the park contributes to a large habitat variation. Kubah NP is comprised of largely mixed dipterocarp forest (MDF), with ridge top

forest, *kerangas* forest (Bornean heath forest), riverine forest, shrub forest and secondary forest (Table 2.1), and transition between forest types is gradual. One of the main reasons for the establishment of this national park was due to its vast diversity of palm flora (Tisen, 2009). A total of 86 species of palms are recorded within the park and an additional nine species in its direct surroundings. Palms in the park are abundant both as individuals and species in lowland areas such as in *kerangas* and riverine forest but are less abundant at intermediate altitudes (140 m–350 m asl). Transitional forest between *kerangas* and MDF is particularly rich in palm species. Also, at higher altitudes, palms are abundant and at least four species prefer higher altitudes (Pearce, 1992).

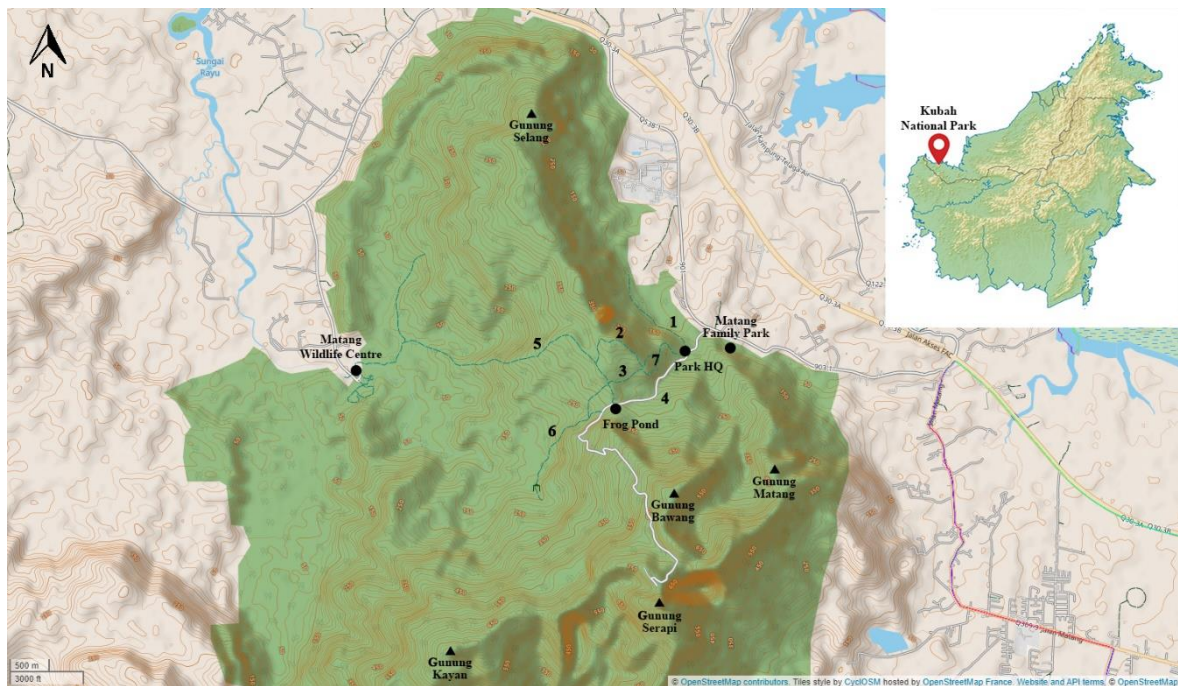


Figure 2.1: Map of Kubah National Park, in Western Sarawak, Borneo. Blue dotted lines representing existing trails; 1 = Belian trail; 2 = Selang Trail; 3 = Main Trail; 4 = Summit Trail; 5 = Rayu Trail; 6 = Waterfall Trail; 7 = Palmetum

Table 2.1: Habitat descriptions for trails in Kubah National Park, Sarawak. (Hazebroek & Abang Morshidi, 2000; Christharina & Abang, 2014; personal observations)

Trail	Forest Type	Elevation (m asl)	Plant Community
Summit	Transitional between <i>kerangas</i> and MDF	141–772	<i>Cyathea</i> sp. (tree fern), <i>Ficus</i> tree, orchids, <i>Blechnum finlaysonianum</i>
Main / Palmetum	Transitional between <i>kerangas</i> and MDF, ridge top forest	141–333	<i>Meliosma sumatrana</i> (Bulu Manok), <i>Xanthophyllum affine</i> (Nyalin), <i>Euonymus glandulosus</i> , <i>Shorea scaberrima</i> , <i>Euodia nervosa</i> , <i>Dryobalanops aromatica</i> , <i>Licuala orbicularis</i> (fan palm), <i>Daemonorops formicaria</i>
Waterfall	Mixed dipterocarp	158–306	Dipterocarp trees, <i>Ficus</i> tree, <i>Korthalsia</i> rattan palm, <i>Amorphophallus</i> sp., <i>Pandanus</i> spp., <i>Alocasia robusta</i> (Giant Aroid), <i>Durio</i> sp.
Selang	Transitional between <i>kerangas</i> and MDF, ridge top forest	233–377	<i>Johannesteijmannia altifrons</i> (crocodile tail palm), <i>Licuala orbicularis</i> (fan palm)
Rayu	Ridge top forest, MDF	21–347	<i>Bintangor</i> , <i>Dryobalanops becarii</i> , <i>Shorea inappendiculata</i> Dense herbaceous undergrowth, scarce buttresses and climbers, and single-dominant communities of trees
Belian	Shrub, secondary	78–150	<i>Eusideroxylon zwageri</i> (Belian), <i>Korthalsia</i> rattan palm, bamboo, Succession from farmland with replanting of mostly 'Engkabang', and local fruits such as <i>Artocarpus</i> spp., <i>Durio</i> spp. and <i>Musa</i> spp.

2.2 Study Species

2.2.1 Genus *Gonocephalus* Kaup, 1825

Lizards of the genus *Gonocephalus* are referred to as “angled-headed lizards” owing to their triangular-shaped cranium, which is mainly based on a well-developed canthus rostralis and a strongly raised superciliary edge (Denzer et al., 2015). Their body is laterally flattened with visible tympanum present in both sexes. Their dorsal scales are small and uniform or intermixed with larger ones. They have a strong transverse gular fold and gular sacs are present only in males (Boulenger, 1885). These medium-sized lizards have extravagant ornamentation and conspicuous phenotypes, often with males and females exhibiting sexual dimorphism (Welton et al., 2017). Species of this genus are diurnal and arboreal, and inhabit forested areas such as those primary forests, lowland forests, and montane forests (Das, 2010).

Initially, the genus *Gonocephalus* included a variety of arboreal agamid lizards from several areas such as mainland south-east Asia, the Andaman and Nicobar Islands, the Sunda Archipelago, the Philippines, New Guinea, the Bismarck Archipelago and Australia. However, at present, only those species west of the Wallace Line are considered true *Gonocephalus*. Populations from the Andaman and Nicobar Islands were assigned to the genus *Coryphophylax* Blyth, 1860, and those east of the Wallace Line are considered of the genus *Hypsilurus* Peters, 1867 (Moody, 1980; Welch et al., 1990; Ota et al., 1992; Ananjeva & Matveyeva-Dujsebayaeva, 1996). A total of 17 species are currently assigned to the genus, and five species are found in the Bornean region, namely *G. bornensis*, *G. doriae*, *G. grandis*, *G. liogaster* and *G. mjobergi* (Das, 2006). The Red List provided by the International Union for Conservation of Nature (IUCN) has assessed 17 *Gonocephalus* species (Table 2.2).

Table 2.2: IUCN Red List Assessment of the 17 *Gonocephalus* species

Species	IUCN Red List Assessment	Assessor (Year of Assessment)
<i>G. abbotti</i> Cochran, 1922	Least Concern	Grismer & Quah (2018)
<i>G. bellii</i> (Duméril & Bibron, 1837)	Least Concern	Grismer & Quah (2018)
<i>G. beyschlagi</i> Boettger, 1892	Near Threatened	Kamsi et al. (2021)
<i>G. bornensis</i> (Schlegel, 1848)	Least Concern	Iskandar & McGuire (2019)
<i>G. chamaeleontinus</i> (Laurenti, 1768)	Least Concern	Iskandar et al. (2021)
<i>G. doriae</i> (Peters, 1871)	Least Concern	McGuire & Iskandar (2018)
<i>G. grandis</i> (Gray, 1845)	Least Concern	Iskandar et al. (2021)
<i>G. interruptus</i> (Boulenger, 1885)	Data Deficient	Diesmos & Gaulke (2009)
<i>G. klossi</i> (Boulenger, 1920)	Near Threatened	Iskandar et al. (2021)
<i>G. kuhlii</i> (Schlegel, 1848)	Vulnerable	Iskandar, & Kamsi (2021)
<i>G. lacunosus</i> Manthey & Denzer, 1991	Least Concern	Kamsi et al. (2021)
<i>G. liogaster</i> (Günther, 1872)	Least Concern	Iskandar et al. (2021)
<i>G. megalepis</i> (Bleeker, 1860)	Least Concern	Kamsi et al. (2021)
<i>G. mjobergi</i> Smith, 1925	Data Deficient	McGuire & Iskandar (2018)
<i>G. pyrius</i> Harvey, Rech, Riyanto, Kurniawan & Smith, 2021	Not Evaluated	-
<i>G. semperi</i> (Peters, 1867)	Data Deficient	Gonzalez et al. (2009)
<i>G. sophiae</i> (Gray, 1845)	Data Deficient	Diesmos et al. (2009)

2.2.2 *Gonocephalus bornensis* (Schlegel, 1851)

Gonocephalus bornensis, the Bornean Angle-headed Lizard is endemic to Borneo. This species grows to an average SVL of 136 mm, which is smaller than *G. grandis* and *G. doriae*. Males of the species have nuchal crest subequal to snout length and vertebral crest distinct up to pelvic region. They have darker flanks with indistinct reticulate pattern, and iris are bluish-grey. Females have nuchal crest half of their snout length and distinct reduction of vertebral crest from the scapular region, becoming comblike along midbody to tail-base. Flanks are paler in females with distinct reticulate pattern, while iris are brown. Their gular pouch is pale with broken dark stripes. These species inhabit primary forests, up to 1,100 m asl. Their diet mostly consists of ants and spiders (Das, 2006).

2.2.3 *Gonocephalus doriae* Peters, 1871

Also known as Doria's Angle-headed Lizard, Males have continuous dorso-nuchal crest, distinctly raised and more distinct from the vertebral crest, extending beyond caudal region; dorsally red with dark and light spots or greenish to olive. Females of the species have weaker dorso-nuchal crest and indistinct on vertebral region; dorsally solid green, sometimes with dark flecks. They can grow to an average SVL of 165 mm. These lizards are endemic to the Borneo and inhabit lowland or hill forests. They are found associating with low tree trunks and shrubs. Juvenile *G. doriae* usually rests on leaves of saplings near streams and rivers. Their diet consists of mainly arthropods (Das, 2010).

2.2.4 *Gonocephalus grandis* (Gray, 1845)

Also known as the Great Angle-headed Lizard, these agamids are widely distributed across Malaysia, Singapore, Indonesia, Thailand, and extending to inhabit Laos and Vietnam (Iskandar et al., 2021). They can be found mainly in primary forest at elevations of up to

1,400 m asl. Males have high nuchal and dorsal crests that are separated while females have nuchal sail but no dorsal crest. Males have greenish-brown dorsum, through olive to nearly black; flanks are blue with yellow spots, and their dewlap is yellowish-orange to red, striped with blue. Females on the other hand, have brownish-green to black dorsum, with light V-shaped bands and blue flanks. Females also have a distinct broad postocular stripe that extends to axilla, which is followed by four dark blotches. They can grow to an average SVL of 160 mm. These lizards are usually found in riverine areas in lowland forests with closed canopy. This species is associated with tree trunks, although females and juveniles may also be found on rocky banks of streams. During the night, they would rest on leaves of saplings or the tips of twigs. Their diet consists of caterpillars, beetles, grasshoppers, ants, flies, cockroaches and spiders (Das, 2010).

2.2.5 *Gonocephalus liogaster* (Günther, 1872)

Also known as the Blue-eyed Angle-headed Lizard, it is known to inhabit Peninsular Malaysia, Sumatra and Borneo (Iskandar et al., 2021). They can grow to an average SVL of 141 mm. Males typically have bold, brown and green patterning on the upper flanks and along the back, while females tend to be darker grey and greenish, however there is great variation in colour based on age and sex. Males have bright blue iris whereas females have a brown iris. Surrounding the eye is a yellowish-orange eye ring, which is boldly coloured in males. Like *G. bornensis*, the nuchal crest and vertebral crest are continuous, and are much more pronounced in adult males. This species is known from lowland primary forest of up to 400 m elevation and peat swamp forests. They appear to be encountered more frequently near forest streams (Das, 2006).

2.2.6 *Gonocephalus mjobergi* Smith, 1925

Also known as the Mjöberg's Angle-headed Lizard, these lizards are endemic to the north-western Borneo of Gunung Murud, in the Sarawak State. They can be found mainly in montane forests at elevations of 2,134–2,250m asl, often associated with trunks of large trees (Das, 2010). The species have an average SVL of 88mm, relatively small compared to its congeners. A feature clearly distinguishing the species from all other *Gonocephalus* is the possession of enlarged dorsolateral scales forming oblique rows and an enlarged platelike scale below the tympanum which is separated from the tympanum. They also have two parallel longitudinal gular folds in the gular region (Denzler & Manthey, 2009). The dorsal crest is reduced and ridge-like. They have a pale green dorsum that is changeable to brownish-grey, with narrow reticulated grey pattern that on lower flanks encloses yellow spots. Their diet presumably consists of insects.

2.2.7 Key to Bornean species of *Gonocephalus*.

- 1 Supraciliary border strongly raised, angular posteriorly.....*doriae*

Supraciliary border not strongly raised, rounded posteriorly.....2
2. Dorsal scales equal, without large scales; females with nuchal sails, not crests.....
.....*grandis*

Dorsal scales unequal, with large scales; females with nuchal crests.....3
- 3 Dorsal crest reduced, ridge-like.....*mjobergi*

Dorsal crest distinct.....4
- 4 No enlarged scales above and below tympanum; flanks with light yellow oval spots within a network of dark reticulations; iris of males brown or light blue, surrounding skin not orange.....*bornensis*

Enlarged scales above and below tympanum; flanks with or without light rounded spots; no dark reticulations; iris of males bright blue, surrounding skin orange.....
.....*liogaster*

2.3 General Sampling Period and Methods

During the sampling period of June 2018 to December 2019, field observations on *Gonocephalus grandis*, *G. doriae*, *G. bornensis* and *G. liogaster* were carried out primarily on all existing trails in Kubah NP, and occasionally off trail surveys were conducted to cover a larger study area. Data collection in the first five months of sampling were conducted for 14 consecutive days per month, both day and night, with an average of eight hours per day, by at least two observers. Lizards were censused via Visual Encounter Survey (VES), where observers walked at a slow and standard pace while visually searching for lizards along the

path without any time-constraints to ensure the area was thoroughly examined. This is a standard technique often used by researchers, and it is useful to detect targeted lizard species in various environmental settings, including rainforest habitats (Doan, 2003; Loos et al., 2012; Lettink & Monks, 2016; Karthik & Kalaimani, 2019). Structural and thermal (six structural and four environmental) microhabitat characteristics were recorded where each reptile was seen (Table 2.3). Photographs of the lizards were also taken using a Nikon D5300 DSLR camera for further references. Individuals were captured, when possible, by hand or by noose. Measurements of individual Snout-vent length (SVL) and tail length (TL) was measured with a ruler, and weight (WT) with spring scales. Sex of the individuals were primarily determined based on secondary sexual characters of the species and/or identified by manual eversion of hemipenis (Harolow, 1996). For diet comparison purposes, stomach contents were emptied through stomach flushing as soon as the individual was caught (detailed methodology in Section 4.3). This technique is a relatively harmless method that was proposed by Legler & Sullivan, (1979), and was later adopted in many dietary studies of lizards (Powell & Russell, 1984; Christian et al., 1996; Van Leeuwen et al., 2011; Tan et al., 2020). Interesting behaviours, if any, displayed by lizards were also recorded.

Prior to release, some adults ($WT > 37$ g) were fitted with a 1.8 g BD-2 series temperature-sensitive radio transmitter (Holohil Systems Ltd. Carp, Ontario, Canada) for spatial and thermal studies (detailed methodology in Section 3.3). Radio-tracking was conducted one to two days after the devices were attached to avoid overt short-term effects resulting from immediate handling and attachment of transmitter (Kenward, 2001). Radio-tracking trips proceeded from November 2018 to December 2019, where radio telemetered lizards were tracked on alternate days, twice a day (morning/afternoon and night). Lizards were tracked to obtain a visual through triangulation method, using a Wildlife Materials, Inc.

(Carbondale, Illinois, USA) TRX-48S receiver and a hand-held 3-Element Yagi aerial. Upon locating the lizards, GPS location, structural and thermal microhabitat characteristics, and pulse rates were recorded. Disturbance was kept at minimal as to prevent possible behavioural change in the animal.

2.3.1 Challenges of Adopting Radiotelemetry

Radiotelemetry is a standard practice of addressing many important aspects of life history including space, movements and habitat use patterns of many wildlife animals (e.g., Janowski-bell & Horner, 1999; Blouin-Demers & Weatherhead, 2001; Grassman et al., 2005; Jennings et al., 2006; Höjesjö et al., 2007; Bauder et al., 2016). This method of relatively low cost compared to other telemetry methods, real-time monitoring provides exact fixes of the positions of the telemetered animals, and often allow researchers to obtain various information on the animal (Mech & Barber, 2002). In order to obtain the desired information, radiotelemetry was adopted in this study, and was accompanied by a few challenges.

Radiotelemetry can be labour-intensive and requires constant manual tracking to acquire probable estimates. As multiple lizards were tracked at the same time along different trails in Kubah NP, it was difficult to obtain more than one location or a short series of locations every few hours from each individual. One major challenge in this study was to obtain the locations of 16 individuals from four species throughout the same period of time to avoid discrepancy of data from possible seasonal changes. This was mostly not possible as some individuals maybe more difficult to locate, especially during the day when the

Table 2.3: Microhabitat habitat variables of reptile sightings to be recorded

No.	Microhabitat characteristics (Associated past studies)	Descriptions
Structural Characteristics		
1	Canopy Cover (Quartiles) (Melville & Schulte, 2001; Urbina-Cardona et al., 2006; Deepak et al., 2016; Winchell et al., 2016)	The percentage of canopy cover immediately above the perch site. Measured using Canopeo application, a multipurpose green canopy cover measurement tool developed by the Soil Physics Research Group and the App Centre.
2	Slope (°) (Urbina-Cardona et al., 2006)	The inclination of the ground where the individual was found. Measured using Clinometer application version 4.5 (1510083) on iOS.
3	Vertical position (m) (Melville & Schulte, 2001; Loos et al., 2012; Singh & Choudhury, 2016; Winchell et al., 2016)	Height of where the individual is found perching on from the ground. Measured using a measuring tape.
4	Circumference of tree (m) (Loos et al., 2012; Winchell et al., 2016)	Circumference of tree at breast height where the individual was found perching on. Measured using a measuring tape.
5	Distance to nearest water body (m) (Urbina-Cardona et al., 2006)	The distance from the individual to the nearest waterbody. Measured using a measuring tape.
6	Perch surface (Melville & Schulte, 2001; Winchell et al., 2016)	Substrate where the reptile was found perching on.
Environmental Characteristics		
1	Light intensity (lux) (Loos et al., 2012)	Perch light to lizard's location. Measured using Extech model 45170 4-in-1 humidity, temperature, airflow, and light meter.
2	Relative Humidity (% RH) (Singh & Choudhury, 2016; Urbina-Cardona et al., 2006; Winchell et al., 2016)	Humidity of the surroundings of the individual. Measured using Extech model 45170 4-in-1 humidity, temperature, airflow, and light meter.
3	Ambient Temperature (°C) (Urbina-Cardona et al., 2006; Winchell et al., 2016)	The temperature surrounding the individual. Measured using Extech model 45170 4-in-1 humidity, temperature, airflow, and light meter 5cm away from the substrate.
4	Perch surface temperature (°C) (Melville & Schulte, 2001; Winchell et al., 2016)	The temperature of the substance where the individual is perching on. Measured using thermal gun.

lizards are active. Moreover, lizards were located in different areas or trails of the park, some are far from another which require additional time to get to. The challenging landscapes of Kubah NP also hinder the tracking of these lizards. Ideally, additional personnel(s) would be effective in monitoring multiple individuals simultaneously. Hence, individuals could not be monitored simultaneously. Obtaining a visual was necessary in this study to understand the habitat preference of these lizards, however there were times where it took over an hour to locate the telemetered lizard. Therefore, when visual was not possible, the locations were estimated through triangulation. Besides that, the preliminary plan was to radio track each lizard twice a day, three times a week for 12 weeks. However, in many cases the lizards were tracked less than the desired amount of time causing unequal sampling efforts on some individuals, many of which was due to transmitter damage and battery failures. Also, some of the transmitters fell off within a few weeks of tracking. To overcome this matter, more individuals were radio tracked to compensate for those that did not achieve the desired tracking period.

The impacts of radio transmitters on these lizards were particularly of concern, given the fact that it may cause distress, irritation, or pain to the individual. The resulting data might also be inaccurate or unrepresentative of the population if the transmitter caused non-trivial changes in behaviour, survival, or reproduction (White & Garrott, 1990). Three radio-transmitter attachment methods have been tested in this study, including transmitters attached via duct tape, suture of transmitters to the dorsal crest, and harness (Section 3.3.2). The latter was adopted for this study, as the former two methods did not work well for these lizards. However, the harness used in this study was relatively rigid and caused injury to several individuals, where the harness embedded into their skin at the dorsal crest and the inner thigh (Figure 2.2). An alternative harness using a softer cotton cord was tested,

however, it did not hold on well and the transmitter was detached from the lizard in less than a week. Thereupon the initial harness material (nylon coated fishing wire fitted into a neoprene rubber tube) was continued. This potential risk was minimised through loosening the harness when required. In cases where the lizard was injured from the harness, the transmitter was removed immediately while the wound was treated with diluted chlorhexidine (wound cleaning) and a wound healing cream prescribed by a certified veterinarian. Ultimately, a better design configuration in attaching the transmitter and sourcing for more suitable materials might be beneficial to reduce these impacts.



Figure 2.2: Wound on dorsal crest and inner thigh caused by rigid harness (nylon coated fishing wire fitted into a neoprene rubber tube) to a telemetered *Gonocephalus grandis* (Tracking number 150.150)

CHAPTER 3

SPATIAL ECOLOGY AND MOVEMENT

3.1 Introduction

How spatial configuration affects population and community dynamics of organisms is an active area of research (Hart & Marshall, 2009; Cooke et al., 2016; Zainudin et al., 2017; Peshev et al., 2021), and has been used in a variety of ways, depending on ecological subdiscipline and field. It seeks to understand the processes that impact distribution and dynamics of species and how these processes unfold across space. Space influences species in multiple ways, such as how they use resources and occupy space, how and why movements, dispersals, and migrations through heterogeneous landscapes occur, as well as how organisms interact (Fletcher & Fortin, 2018). Therefore, through the integrative process of understanding perception such as population distributions (Turchin, 1991), important resources (Birchfield & Deters, 2005), dispersal strategies (Small & Rusch, 1989), social interactions (Minta, 1992), questions on patterns of spatial use could be resolved (Kenward et al., 2001).

Tropical rainforests are one of the world's most complex ecosystems (Whitmore, 1989), providing a variety of habitat for species and promoting habitat specializations (Plotkin et al., 2000). Resources in space are not uniformly dispersed and neither are species, some sites simply better than others in terms of resource availability. This generally leads to patchy environments where animals acquire resources and niches can accommodate a rich diversity of fauna (Zug et al., 2001). While animals are able to survive in different environmental conditions, their distribution and abundance are dependent on habitat structure. Organisms repeatedly rely on environmental cues to make behavioural and life-

history decisions (Schlaepfer et al., 2002). Therefore, habitat selection of lizards is highly dependent on structural characteristics of the environment (Heatwole, 1977). As Burt (1943) first described, a home range is the area traversed by the individual in its normal activities of food gathering, mating, and caring for young whereas movement is the displacement of an animal between locations, to obtain basic necessities, generally involving energy expenditure and costs of travel. Consequently, home range has been considered a significant measure of animal behavioural and resource requirements (Perry & Garland, 2002).

Syntopic species often have overlapping geographical distributions, which potentially lead to behavioural, morphological, or ecological modes of segregation. Niche differentiation at least in one dimension is though essential to ensure they are not dependent on identical resources and most importantly, to minimize interspecific competition (Pianka, 1973; Melville, 2002; Steinberg et al., 2007; Luiselli, 2008; Noble et al., 2011). Spatial niche separation is one of the main approaches of partitioning for syntopic lizards (Pianka, 1973, 1986; Toft, 1985; Luiselli, 2008), although lizards may also partition the trophic and temporal niche (Pianka, 1973)(Pianka, 1973; Fuentes, 1976; Pianka & Huey, 1978; Luiselli, 2006b; Rouag et al., 2007).

3.2 Specific Objectives

The two main objectives with relevant research questions raised in this chapter includes:

- i. To determine spatial use of four syntopic species of *Gonocephalus*.

Lizard species are known to differ in the spatial resources they exploit (see Pianka, 1973). To further understand the spatial ecology of lizards, it is vital to define general patterns of spatial use and factors that influence these spatial patterns. Hence, the question raised here is what are the sizes of activity range that each species utilizes? Does sexual variation and environmental factors affect movement rates of these lizards? Finally, do these species have specific microhabitat they prefer?

- ii. To demonstrate spatial niche differences, if any, among syntopic species of *Gonocephalus*.

Syntopic species often show overlapping geographical distributions, and thus, potentially should have modes of segregation in order to reduce interspecific competition (Pianka, 1973; Melville, 2002; Steinberg et al., 2007; Luiselli, 2007; Noble et al., 2011). Therefore, the primary question here is, whether niche partitioning occurs on a spatial scale for these syntopic species, and whether they exhibit spatial overlap? Are there within- and between-species difference in estimated home range sizes of these lizard species? Are these species spatially separated, in terms of the microhabitats they occupy? Finally, do they exhibit interspecific competition?

3.3 Specific Methodology

3.3.1 Transmitter Used

Tracking of the target species was conducted with a BD-2 series temperature-sensitive radio transmitter (Holohil Systems Ltd. Carp, Ontario, Canada). The BD-2 series are small transmitters that were designed for various application and intended for use in studies on bats, birds, reptiles, amphibians and fishes, including as glue-on, harness and tail-mount configurations. As many as eight different weight options currently exist, ranging from 0.62 g to 1.8 g. Transmitter weight is directly proportional to the battery lifespan and it is important that the transmitter attached to the subject do not weigh over 5% of the body mass, to reduce potential disturbance and hindrance to animal behaviour or health (Bertram, 1980; White & Garrott, 1990).

Since the current study utilised adult *Gonocephalus* that typically weighs at least 40 g, transmitters of 1.8 g were used. The transmitter units were $17 \times 8.5 \times 5.5$ mm (length $\times$ width $\times$ height) in dimensions. The battery lifespan of the Holohil BD-2 1.8 g is approximately 14 weeks, range from 10 to 20 weeks according to the transmitter specification from the Holohil Systems Ltd. The transmitters were encapsulated in an inert waterproof epoxy making it suitable to use in tropical rainforest weather conditions.

3.3.2 Transmitter Attachment

Numerous methods have been described and compared for attaching radio transmitters internally and externally to lizards, including ingested transmitters, transmitters attached using duct tape, suture of transmitters to the dorsal crest, transmitter collars, belts, and harnesses, and through the use of various adhesives (reviewed in Goodman et al., 2009). However, lizards as a group show a diversity of body shapes and types, and transmitter

attachment methods may need to be customised for certain species or to specific body types. *Gonocephalus* species on Borneo tend to show a deltoid cross-sectional shape, males with high dorsal crests. Three methods were tested in the current study, including transmitters attached using duct tape, sutured transmitters to the dorsal crest, and harness. Unfortunately, the first two methods of attaching the transmitters were unsuccessful, as the transmitter were found detached in under two weeks.

In this study, with some modification from Knapp and Owens' (2005) attachment method, the temperature-sensitive radio transmitters were attached externally to the lizard on the dorsal side on the left or right flank of the pelvic girdle and secured with anterior and posterior harnesses (Figure 3.3). The transmitters are positioned parallel to the lizard, with the antennae trailing alongside the lizard's tail, to minimize hindrance caused to the individuals. A 0.6 mm nylon coated fishing wire was fitted into a 1 mm neoprene rubber tube to prevent direct contact of the fishing wire and the lizard. The wire was then fitted through the transmitter and connected using a 2.2 mm single barrel crimp sleeves by sliding the wires through the crimp sleeves at opposite direction and compressing the crimp sleeves with flat-nose pliers (Figure 3.1). Excess wire was then cut off. The compressed crimp sleeve and cut wires are considerably sharp, hence a small piece of electric tape was used to tape around the area to avoid causing any injury on the lizard (Figure 3.2). This method was demonstrated in Knapp and Owens' (2005) study to be effective, as it reduced pressure on the lizard, by allowing the transmitter to move slightly with lizard movement. The procedure was easily done in the field within minutes and required minimal equipment and supplies.



Figure 3.1: Compressing crimp sleeves with a flat-nose plier after fishing wire was fitted through



Figure 3.2: Taping electric tape around the compressed crimp sleeve and cut wires



Figure 3.3: Male *Gonocephalus bornensis* fitted with temperature-sensitive radio transmitter (Holohil BD-2)

3.3.3 Microhabitat Data Collection

Lizards were tracked to obtain a visual, if possible, since triangulation may lead to large positional errors (Rettie & McLoughlin, 1999). However, triangulation was still applied to first locate the area where the lizard was last sighted, whereupon it could often be seen within a few meters, without disruption. When visual was not possible, triangulation was applied to obtain the best possible location where the target might be. Structural and thermal microhabitat characteristics were recorded where the lizard was found. Six structural and four environmental characteristics of the microhabitat for each lizard found were recorded (Table 2.1).

3.3.4 Data Analyses

Although several approaches to home-range estimation have been utilised by past workers, the two most common are the minimum convex polygon (MCP) and kernel density estimation (KDE) methods (Downs & Horner, 2008; but see Laver & Kelly, 2008; Powell & Mitchell, 2012). However, since reptiles generally do not move far and tend to consistently use the same location repeatedly and for extended periods of time, MCP is here considered to reflect accurately the maximum home range area. In similar studies for most herpetofaunas, it has been used for size comparisons between groups or across time periods (Kazmaier et al., 2002; Row & Blouin-Demers, 2006a). Despite limitations associated with this area estimator, in this study, home ranges were estimated using 100% MCP. MCP is the smallest area convex set that contains the data (Mohr, 1947; Worton, 1995). Due to its simplicity and its ease of interpretation, this approach has been useful for numerous similar studies. MCP is also a nonparametric approach and has the added benefit of not requiring independence between locations (Harris et al., 1990). Hence, the MCP analysis was adopted to provide insights into what constitutes an overall maximum range for each of the study species, while at the same time, placing each animal into a geographical context. Analyses were performed using R in R Studio, using packages ‘lubridate’ (Spinu et al., 2018), ‘sp’ (Pebesma & Bivand, 2005), ‘adehabitatHR’ (Calenge et al., 2015), ‘rgdal’ (Roger et al., 2017), and ‘maptools’ (Bivand et al., 2017) using scripts as per Leonard (2017). Spatial overlap (MCP overlap analysis) was calculated for concurrently tracked lizards using the intersect function in ArcGIS 10.7.

To evaluate overall horizontal movement, mean distance travelled between location (MD) and mean daily displacement (MDD, number of days tracked divided by distance moved) were computed. Lizard sizes, movement patterns and home range sizes of males and

female *Gonocephalus* were compared using two sample independent t-tests, activity area was log transformed to obtain a normal distribution. One-way ANOVAs were used to test for differences between the four syntopic species under study. All these comparisons were analysed with IBM SPSS software.

For microhabitat analyses, Spearman correlation coefficients were first used to determine correlations among microhabitat variables and to identify non-correlated variables. Autocorrelation was avoided by excluding variables with Spearman rho of less than or equal to -0.7 or more than or equal to 0.7 from further calculation (Loos et al., 2012). Assumptions of multivariate normality was evaluated using Kolmogorov-Smirnova and Shapiro-Wilk. Since the variables are not normally distributed, Kruskal-Wallis statistic was used to determine significant differences between species and genders. All microhabitat data were analysed with IBM SPSS software. The Morista's Similarity Index was used to analyse data on microhabitat usage, which was then subjected to a hierarchical cluster analysis using unweighted pair group method, with arithmetic mean (UPGMA) to test species association based on microhabitat attributes. Niche breadth based on microhabitat utilisation was calculated using Levin's Index (Hurlbert, 1978) and estimation of Pianka's symmetrical Niche Overlap was then analysed (Pianka, 1973). Further, habitat variables were visualised by non-metric multidimensional scaling (nMDS) based on the Bray-Curtis coefficient. The quality of the data set was assessed through the Shepard Plot and through the stress value calculation. The Shepard Plot shows how closely ordination fits real world plot dissimilarities and how well one ordination can be interpreted. The plot displayed two correlation-like statistics for goodness of fit between ordination distances and observed dissimilarity. Analysis for nMDS was performed using package 'vegan' (Oksanen et al., 2012) in R Studio.

3.4 Results

3.4.1 Home Range Analysis

A total of 25 lizards were outfitted with radio transmitters. Nine of these failed to provide adequate positional data and were removed from the analyses. This reduced the final sample size to 16, comprising four individuals for each species of *Gonocephalus* (Figure 3.4). Tracked male *Gonocephalus* in this study were not significantly larger than females based on snout-vent length (SVL) ($t = -1.366$, $df = 11$, $P = 0.199$) and weight (WT) ($t = -1.572$, $df = 14$, $P = 0.138$). There was also no significant difference between species of *Gonocephalus* in terms of SVL ($F = 2.288$, $P = 0.147$) and WT ($F = 1.248$, $P = 0.336$). Insignificance in size difference permits for assumption of variance within samples is negligible thus comparison between species of *Gonocephalus* and between gender is acceptable.

Based on the 661 location data collected from radio tracking, home range estimations for each *Gonocephalus* were generated. Home range estimates using the 100% MCP method varied from 0.079 ha (FGG2) to 1.313 ha (MGL1), mean 0.398 ha (95% confidence interval = 0.221 – 0.576 ha) across all home ranges (Table 3.1). The home range estimation revealed that male *G. liogaster* showed the largest mean home range size (0.811392 ha), while female *G. grandis* have the smallest mean home range size (0.143201 ha). Female *G. doriae* have larger MCP home range (0.726 ha) compared to the males (0.337 ha), and males of other species generally appeared to have a larger home range. However, MCP home ranges were overall not significantly different between genders ($t = -1.184$, $df = 14$, $P = 0.256$). Additionally, there were no significant difference of the means of MCP home ranges among species ($F = 1.285$, $P = 0.324$).

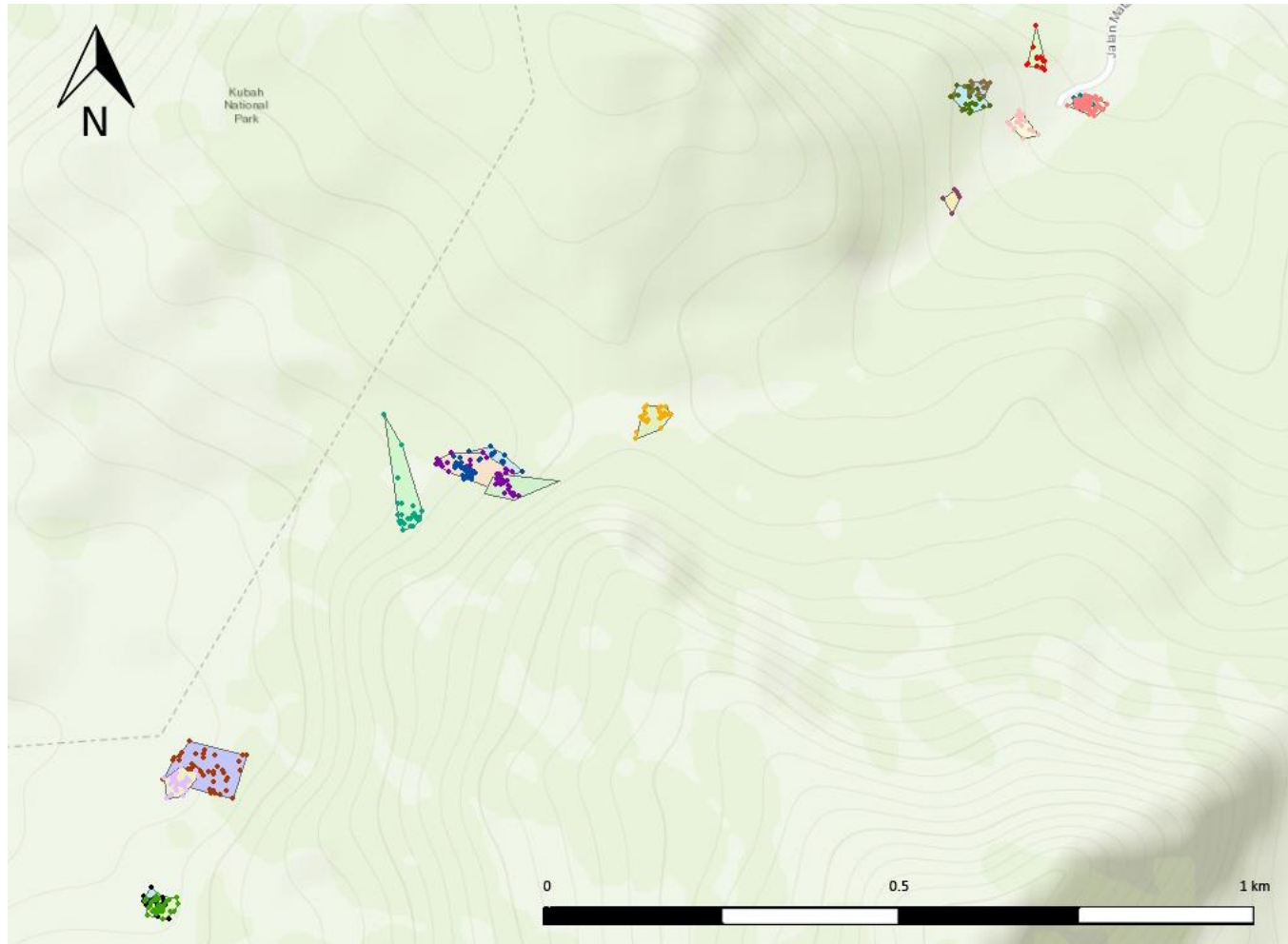


Figure 3.4: Map showing the locations of the 16 tracked individuals of *Gonocephalus*. Polygon shapes indicate the Minimum Convex Polygon (MCP, 100%, ha). ● Female *G. bornensis* (FGB)1; ● FGB2; ● Female *G. doriae* (FGD)1; ● FGD2; ● Female *G. grandis* (FGG)1; ● FGG2; ● Female *G. liogaster* (FGL)1; ● FGL2; ● Male *G. bornensis* (MGB)1; ● MGB2; ● Male *G. doriae* (MGD)1; ● MGD2; ● Male *G. grandis* (MGG)1; ● MGG2; ● Male *G. liogaster* (MGL)1; ● MGL2

Table 3.1: Summary of radio telemetered *Gonocephalus*. Species abbreviations as in Figure 3.4 caption

Individual	Tracked Duration (days)	Number of locations	mean distance between location (m)	mean daily displacement (MDD, m/day)	100% MCP (ha)	Mean 100% MCP (ha)
FGB1	83	42	8.41	0.10	0.261	0.219
FGB2	83	38	10.39	0.13	0.178	
FGD1	77	52	5.6	0.07	0.630	0.726
FGD2	77	42	13.46	0.18	0.822	
FGG1	82	49	5.97	0.07	0.207	0.143
FGG2	84	50	4.21	0.05	0.079	
FGL1	68	28	9.52	0.14	0.299	0.195
FGL2	37	14	12.18	0.33	0.09	
MGB1	70	42	11.13	0.16	0.784	0.536
MGB2	73	35	16.14	0.22	0.288	
MGD1	40	15	17.88	0.45	0.487	0.337
MGD2	77	40	7.4	0.1	0.187	
MGG1	126	78	12.4	0.1	0.197	0.219
MGG2	82	49	7.57	0.09	0.241	
MGL1	98	51	22.97	0.23	1.313	0.811
MGL2	74	36	16.24	0.22	0.31	
Mean	76.938	41.313	11.342	0.165	0.398	
SD	20.227	15.156	5.076	0.106	0.333	

Lizards exhibited considerable overlap in their respective home ranges. Of the 16 individuals tracked, six home range overlaps were observed between nine individual *Gonocephalus* (Figure 3.5). These home range overlaps were of individuals that were tracked concurrently. Of these, only one consisted of overlap between two females of the same species, and the remaining overlapping ranges were between conspecific males and

females (Table 3.2). The highest area of overlap was between the two female *G. doriae* (0.448 ha), whereas one of two pairs of *G. grandis* (FGG1 and MGG2) had the largest overlapping home range percentage (50.88%). MGD1 had home range that overlapped with the two females (FGD1 and FGD2). However, the overlap with FGD1 was minimal and was the least MCP home range overlap among all overlaps both in terms of area (0.001 ha) and percentage (0.096%). Lizards did not show any interspecific home range overlap.

Table 3.2: Home range overlap between four sympatric species of *Gonocephalus* with MCP analysis of home range overlap (ha), percentage of overlap (%) and means. Species abbreviations as in Figure 3.4 caption

Individual 1	Individual 2	Individual 1 MCP home range (ha)	Individual 2 MCP home range (ha)	Overlap MCP home range area (ha)	Overlap MCP home range percentage (%)
FGG1	MGG2	0.20696465	0.241198843	0.151125003	50.87724599
FGG2	MGG1	0.079437126	0.197283323	0.070257753	34.02927215
MGD1	FGD1	0.487121507	0.630291142	0.001078921	0.096648562
MGD1	FGD2	0.487121507	0.822409174	0.191604491	17.13927921
FGD1	FGD2	0.630291142	0.822409174	0.447822496	44.56487015
MGB2	FGB1	0.288320681	0.26107233	0.17970511	48.6099515
Mean				0.173598962	32.55287793

3.4.2 Movement Analysis

Table 3.1 show that tracked *Gonocephalus* relocated a mean of 41.313 ± 15 times, moved 11.342 ± 5.076 m along a line distance per relocation (MD), and had a mean daily displacement (MDD) straight line distance averaging at 0.165 ± 0.106 m/day, although these values vary, depending on the amount of tracking days and locations recorded. MD was significantly different between males and female *Gonocephalus* ($t = -2.310$, $df = 14$, $P = 0.037$), where males generally have a larger mean distance move. However, MDD between

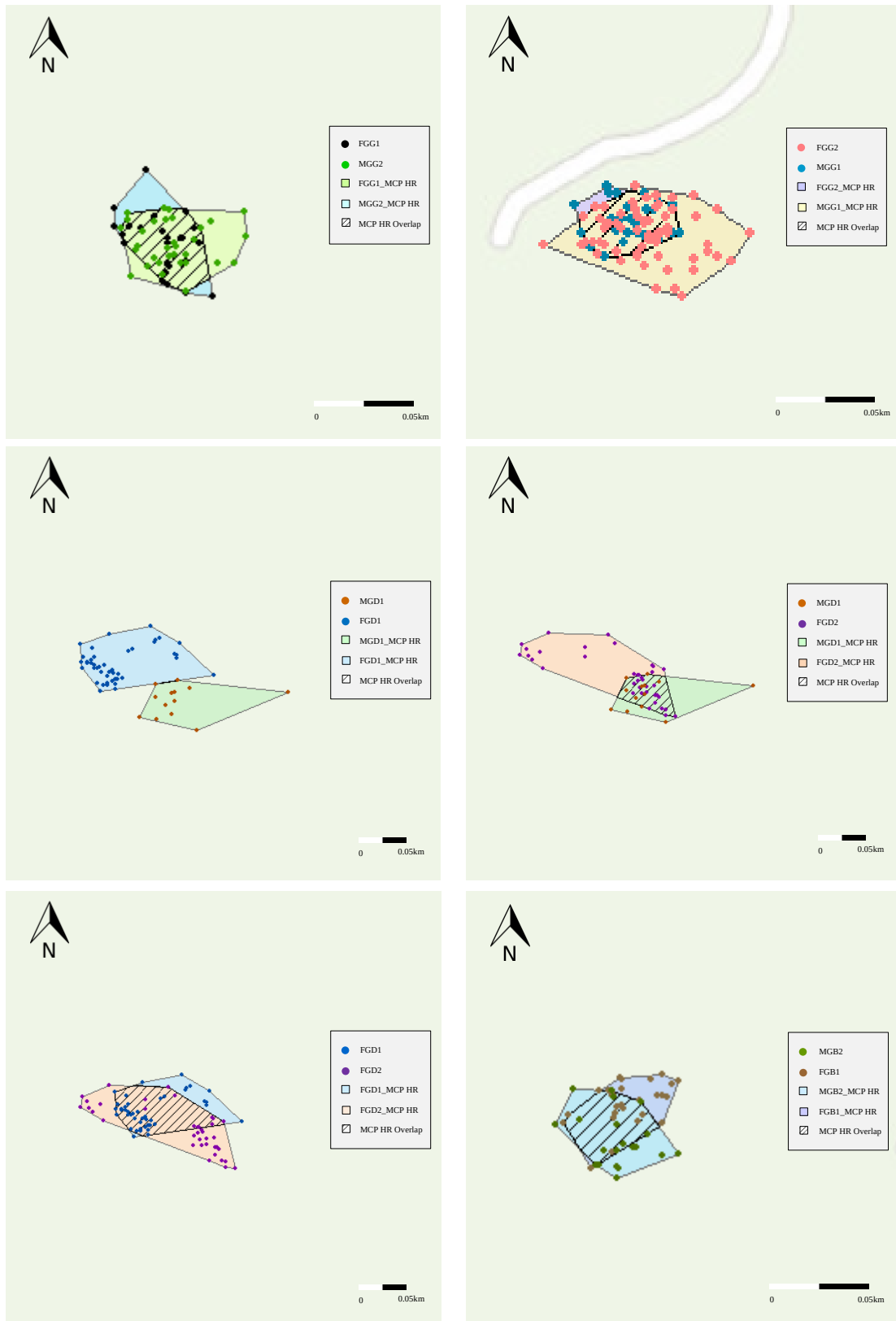


Figure 3.5: Maps showing the six overlaps of MCP home ranges. Species abbreviations as in Figure 3.4 caption

males and female *Gonocephalus* was not significantly different ($t = -1.411$, $df = 14$, $P = 0.180$). When compared between species, there was no significant difference in either MD ($F = 2.063$, $P = 0.159$) and MDD ($F = 3.246$, $P = 0.06$).

Both MD ($r = -0.354$, $P = 0.179$) and MDD ($r = -0.223$, $P = 0.407$) had no statistically significant relationship with SVL. Relationship of WT was also not significant with MD ($r = 0.172$, $P = 0.525$) MDD ($r = 0.036$, $P = 0.894$). This may be due to the insignificance difference in mass (including SVL and WT) in these telemetered lizards.

Abiotic factors were also tested for possible relationship with displacement. Results showed that distance moved had no statistically significant relationship with canopy cover ($r = 0.027$, $P = 0.482$), distance to nearest waterbody ($r = 0.032$, $P = 0.464$), relative humidity ($r = 0$, $P = 0.995$), and ambient temperature ($r = 0.071$, $P = 0.071$). However, there was a significant negative correlation between distance moved and slope with a small correlation coefficient ($r = -0.114$, $P = 0.003$). Correlations were evaluated using the guide of Evans (1996).

3.4.3 Habitat Preference Analysis

3.4.3.1 Differences in habitat distribution between species of *Gonocephalus*

Environmental variables tested demonstrated no significant correlations (Table 3.3). Correlations were evaluated using the guide of Evans (1996). The strongest was between relative humidity and ambient temperature ($r = -0.499$, $N = 713$, $p < 0.001$), and ambient temperature and perch surface temperature ($r = -0.521$, $N = 595$, $p < 0.001$). Since all variables do not have a Spearman rho of less than or equal to -0.7 or more than or equal to

0.7, therefore there was no autocorrelation and that all variables could be used for further calculation.

Table 3.3: Spearman correlation coefficients (r) among 9 microhabitat variables. (**) indicate that correlation is significant at the 0.01 level (2-tailed), (*) correlation is significant at the 0.05 level (2-tailed). CC = canopy cover (%); S = slope (°); VP = vertical position (m); CT = circumference of tree (m); DW = distance to nearest waterbody (m); LI = light intensity (lux); RH = relative humidity (% RH); AT = ambient temperature (°); PST = perch surface temperature (°)

	CC	S	VP	CT	DW	LI	RH	AT	PST
CC	1.000								
S	-.179**	1.000							
VP	.134**	0.046	1.000						
CT	-0.071	-0.010	.284**	1.000					
DW	.211**	-.281**	-0.021	-.113*	1.000				
LI	-.339**	0.007	-.241**	.190**	-0.070	1.000			
RH	.124**	-.217**	0.003	.246**	0.035	.159**	1.000		
AT	0.002	0.025	0.048	-.091*	-0.028	-.146**	-.499**	1.000	
PST	-.205**	-0.031	-.083*	-0.005	0.010	.340**	-.204**	.521**	1.000

Table 3.4 shows the summary statistics for the six structural microhabitat variables and four environmental microhabitat variables recorded for four species of radio tracked *Gonocephalus*. A total of 732 microhabitat data points were recorded from 25 individuals of *Gonocephalus* (four *G. grandis*; six *G. doriae*; eight *G. bornensis*; and seven *G. liogaster*). Kolmogorov-Smirnova and Shapiro-Wilk tests for normality show that these variables were not normally distributed ($p < 0.05$), therefore the Kruskal–Wallis statistic was used to determine whether significant differences exist in habitat utilisation of the four species. Tests show that distribution of light intensity ($P = 0.541$) and ambient temperature ($P = 0.437$) were not significantly different across all species of *Gonocephalus*. However, the distribution of canopy cover ($P < 0.001$), slope ($P < 0.001$), vertical position ($P = 0.022$),

circumference of the tree ($P < 0.001$), distance to nearest waterbody ($P < 0.001$), relative humidity ($P < 0.001$), and perch surface temperature ($P < 0.001$) was significantly different across species of *Gonocephalus*.

Paiwise comparisons of the 4 syntopic species showed that *G. liogaster* and *G. bornensis* differed significantly in terms of occupancy of sites with differences in canopy cover ($P = 0.003$), slope ($P < 0.001$), perch surface ($P < 0.001$) and relative humidity ($P < 0.001$); *G. liogaster* and *G. doriae* significantly differed in site occupied in terms of canopy cover ($P < 0.001$), slope ($P < 0.001$), perch surface ($P < 0.001$) and perch surface temperature ($P < 0.001$); *G. liogaster* and *G. grandis* was significantly different in terms of slope ($P < 0.001$), vertical position ($P = 0.039$), tree circumference ($P < 0.001$), distance to nearest waterbody ($P < 0.001$) and perch surface ($P < 0.001$); *G. bornensis* and *G. doriae* differed significantly in terms of canopy cover ($P < 0.001$), perch surface ($P < 0.001$), relative humidity ($P = 0.001$) and perch surface temperature ($P < 0.001$); *G. bornensis* and *G. grandis* was significantly different in terms of canopy cover ($P = 0.001$), tree circumference ($P < 0.001$), distance to nearest waterbody ($P < 0.001$), relative humidity ($P < 0.001$) and perch surface temperature ($P < 0.001$); as for *G. doriae* and *G. grandis*, they were significantly different in terms of canopy cover ($P < 0.001$), circumference of the tree ($P < 0.001$), distance to nearest waterbody ($P < 0.001$), perch surface ($P < 0.001$) and relative humidity ($P = 0.048$). Pairwise comparison between males and females of *Gonocephalus*, revealed that the habitat variables that were not significantly different include canopy cover ($P = 0.72$), circumference of tree ($P = 0.052$), light intensity ($P = 0.985$), relative humidity ($P = 0.195$), and ambient temperature ($P = 0.376$).

Table 3.4: Summary statistics of the 6 structural microhabitat variables and 4 environmental microhabitat variables recorded for the radio tracked *Gonocephalus* ($\bar{x} \pm SE$). CC = canopy cover (%); S = slope (°); VP = vertical position (m); CT = circumference of tree (m); DW = distance to nearest waterbody (m); PS = perch surface (0 = Tree Trunk; 1 = Tree Branch; 2 = Stem of leaf; 3 = Leaf; 4 = Wooden Plank; 5 = Ground; 6 = Vine; 7 = Rock; 8 = Buttress of tree; 9 = Tree Stump; 10 = Fallen log); LI = light intensity (lux); RH = relative humidity (%RH); AT = ambient temperature (°); PST = perch surface temperature (°). Species abbreviations as in Figure 3.4 caption

Species	n	CC	S	VP	CT	DW	PS	LI	RH	AT	PST
MGB	87	75.14± 11.67	15.02±5.86	2.38±2.61	0.27±0.41	11.54±11	0.98±1.57	1535.1± 3743.75	80.49±5.87	27.91±1.33	24.75±0.98
FGB	96	80.78± 3.94	16.04±6.14	1.64±1.51	0.2±0.34	28.39±5.99	2.18±2.51	477.75± 1309.55	75.74±9.05	28.17±1.47	25.17±1.05
MGG	127	80.84± 9.87	16.32±10.68	2.41±1.71	0.51±0.62	3.95±3.02	1.07±1.36	419.55± 506.13	81.76±8.3	28.39±2.37	24.63±1.05
FGG	100	80.48± 8.27	17.01±12.22	2.01±1.45	0.51±0.54	3.69±2.33	2±2.29	740.27± 2688.64	83.87±6.8	28.2±1.91	24.5±0.8
MGD	60	83.78± 6.56	15.13±5.86	1.99±0.69	0.21±0.37	10.67±7.12	0.31±1.19	301.48± 177.77	77.62±6.04	27.98±1.52	24.65±1.01
FGD	94	87.01± 7.06	13.2±6.64	1.84±0.64	0.22±0.3	12.1±10.88	0.27±1	517.36± 1495.07	83.71±5.42	27.92±1.43	24.22±0.77
MGL	101	84.11± 6.59	6.98±5.47	1.94±1.62	0.14±0.21	13.34±9.26	0.56±1.37	280.32± 251.55	83.12±10.6 9	28.25±1.76	24.94±0.81
FGL	67	75.49± 9.91	16.3±13.06	1.73±1.45	0.15±0.24	9.33±8.21	1.05±1.89	641.16± 1036.39	79.01±7.31	27.37±1.4	24.41±1.05
Total	732										

3.4.3.2 Similarity of Microhabitat Utilization

Despite having multiple significant differences in distribution of habitat variables, Morista's Similarity Index showed that species of *Gonocephalus* have high similarity in terms of microhabitat utilization, ranging from 0.777 between female *G. bornensis* and female *G. grandis* to 0.9872 between male and female *G. grandis* (Table 3.5). This indicated that species of *Gonocephalus* shared many of their microhabitat they occupy. However, none of the lizards in this study shared 100% of the microhabitats measured (Morista's Similarity Index = 1). For instance, given the high similarity index, the tracked female *G. grandis* were never found in areas with low to average canopy cover and perching on manmade wooden planks but male *G. grandis* were found in those areas. On the contrary, males were not found at places with low humidity, low ambient temperature, and high perch surface temperature whereas females were found at such sites.

Table 3.5: Pairwise comparison of Morista's Similarity Index of microhabitat utilization among radio-tracked *Gonocephalus* species and gender. Species abbreviations as in Figure 3.4 caption

Species	MGB	FGB	MGG	FGG	MGD	FGD	MGL	FGL
MGB	1							
FGB	0.8662	1						
MGG	0.9377	0.7874	1					
FGG	0.923	0.777	0.9872	1				
MGD	0.9287	0.8122	0.9202	0.8831	1			
FGD	0.9095	0.7914	0.9199	0.8896	0.9778	1		
MGL	0.9573	0.8607	0.9193	0.8895	0.9587	0.9572	1	
FGL	0.9659	0.8088	0.9047	0.8931	0.9061	0.8954	0.9063	1

The dendrogram of the Morista's Similarity Index (Figure 3.6) show that females of *G. bornensis* were unique compared to other species of *Gonocephalus* in terms of microhabitat utilization, being associated with the ground, far from waterbodies significantly more. Group A was further divided into 3 subclusters where subgroup C (male and female *G. grandis*) were species found strongly associated with waterbodies, and were never found far from water. They also occupied old-growth trees with large circumference more than other species; subgroup D were highly associated to trees of moderate circumference (male and female *G. doriae* and male *G. liogaster*); whereas subgroup E (female *G. liogaster* and male *G. bornensis*) were associated with low canopy areas with direct sunlight.

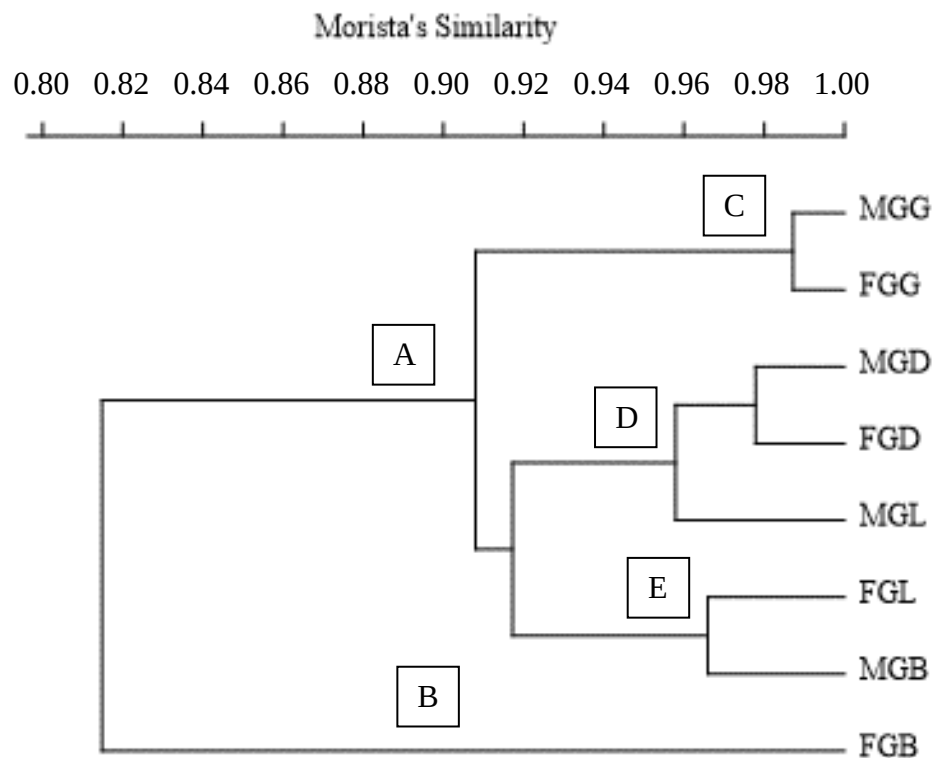


Figure 3.6: Dendrogram of Morista's Similarity Index resulting from a hierarchical cluster analysis using unweighted pair group method with arithmetic mean (UPGMA) based on sighting counts of *Gonocephalus* species associated with microhabitat. Species abbreviations as in Figure 3.4 caption

3.4.3.3 Non-metric Multidimensional Scaling Analysis (nMDS)

Figure 3.7 attempts to display the habitat preference of the radio-tracked *Gonocephalus* species in Kubah NP, based on the nMDS analysis in two dimensions. In this ordination, it highlights the similarities between samples of complex multidimensional data. Hence, the closer the species are together in the ordination space, the more similar microhabitat variable were used. In general, these *Gonocephalus* species showed a strong association with gentle to moderate slopes, high canopy cover, any tree sizes or height, near to moderate distance to water, tree trunk, tree branch, average to high humidity, moderate to high ambient temperature, low to average light intensity and low to moderate perch surface temperature, while association with low canopy cover, high perch surface temperature, wooden plank, rock, tree buttress, tree stump, and fallen log conversely were weak.

When compared to other species, males of *G. bornensis* were more tolerable of areas with low canopy cover (3.45%, n = 3), albeit still preferring high canopy covered areas (64.37%, n = 56). They also seem to prefer to perch high off the ground (50%, n = 42) on tree trunks (44.05%, n = 37) and tree branches (42.86%, n = 36), do not occupy sites on strong slope, low humidity and low ambient temperature. Females of *G. bornensis* conversely, were found to utilise the ground (21.74%, n = 20) and fallen log as substrate (4.35%, n = 4) more than its congeners and are also often found far from waterbodies (90.63%, n = 87). They were restricted to areas with high canopy cover (100%, n = 96). Males and females of *G. grandis*, seemingly occupy similar microhabitats, being associated with waterbodies (male 94.45%, n = 119; female 96%, n = 96). They also seem to prefer areas with strong slopes (male 2.36%, n = 3; female 5.05%, n = 5), low humidity (male 3.26%, n = 6; female 1.86%, n = 3), and perch on stem of leaf (male 18.82%, n = 16; female 21.88%, n = 14). Both sexes of *G. doriae* were found to be strongly associated with tree

trunks (male 90.9%, n = 50; female 89.89%, n = 80) with moderate circumference (male 67.86%, n = 38; female 68.54%, n = 61) at moderate (male 46.43%, n = 26; female 62.92%, n = 56) to high (male 46.43%, n = 26; female 30.34%, n = 27) heights, and areas with high canopy cover (male 96.67%, n = 58; female 100%, n = 94). It is also apparent in the nMDS biplot that *G. doriae* is more of a microhabitat specialist (Figure 3.7). Lastly, males of *G. liogaster* were strongly associated with gentle slopes (96.97%, n = 96), and high canopy cover (93.07%, n = 94), while females were encountered in areas with average (47.76%, n = 32) to high (50.75%, n = 34) canopy cover. Females were also found more often on trees with smaller circumference (54.1%, n = 33), whereas males preferred moderate circumference (68.8%, n = 64).

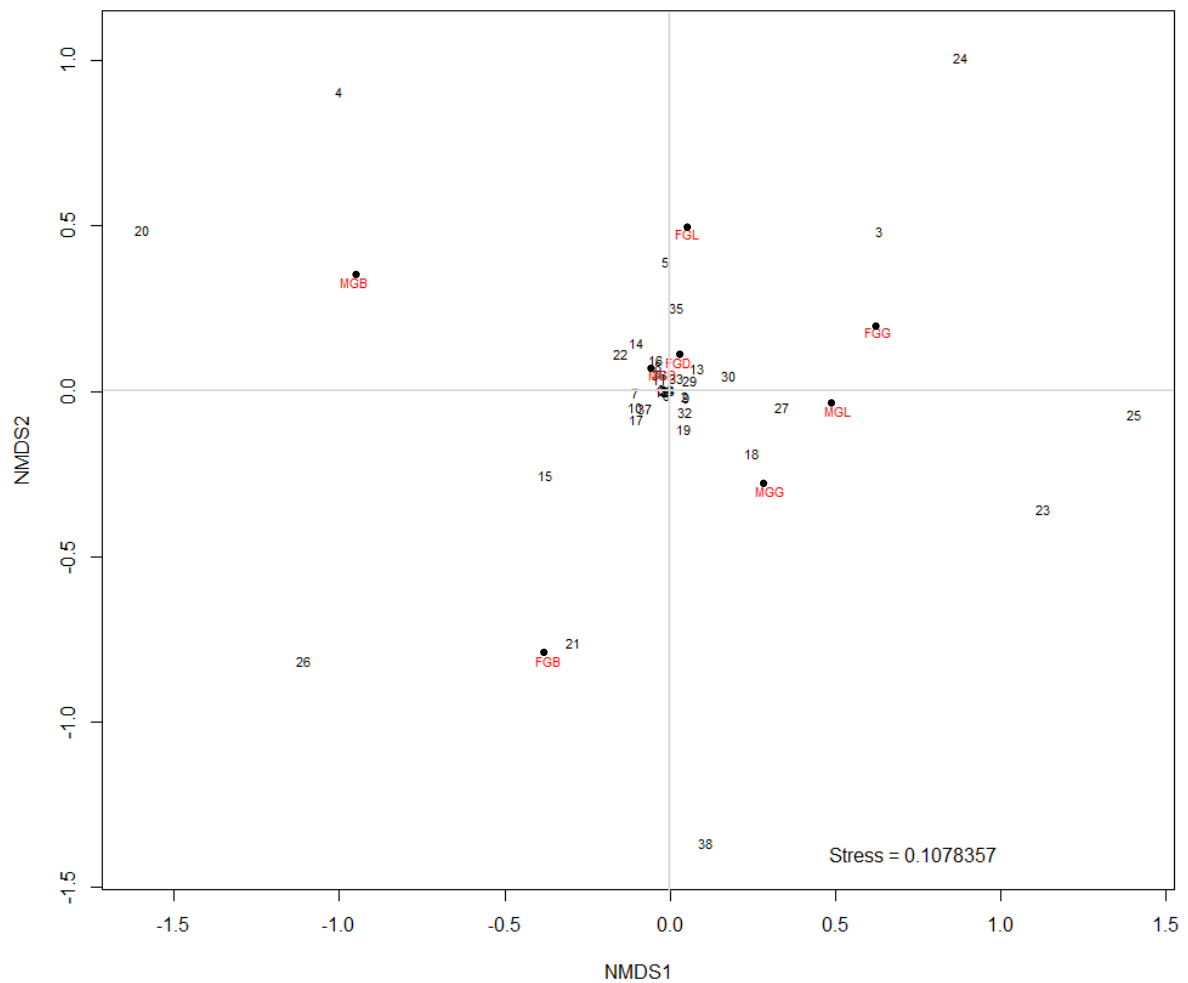


Figure 3.7: An nMDS analysis ordination biplot based on Bray-Curtis coefficient of similarities between individual number of *Gonocephalus* species and habitat variables. Numbers in the plot represents the habitat variables: 1: Gentle slope (0–20°); 2: Moderate slope (21–40°); 3: Strong slope (41–60°); 4: Low canopy cover (10–40%); 5: Average canopy cover (41–70%); 6: High canopy cover (71–100%); 7: Small circumference of tree (<0.07 m); 8: Moderate circumference of tree (0.07–0.3 m); 9: Large circumference of tree (>0.3 m); 10: Low height from ground (<1 m); 11: Moderate height from ground (1–2 m); 12: High height from ground (>2 m); 13: Near to waterbody (<10 m); 14: Moderate distance to waterbody (10–30 m); 15: Far from waterbody (>30 m); 16: Tree trunk; 17: Tree branch; 18: Stem of leaf; 19: Leaf; 20: Wooden plank; 21: Ground; 22: Vine; 23: Rock; 24: Tree buttress; 25: Tree stump; 26: Fallen log; 27: low humidity (50–66 % RH); 28: Average humidity (67–82 % RH); 29: High humidity (83–98% RH); 30: Low ambient temperature (24.0–28.9°C); 31: Moderate ambient temperature (29.0–33.9°C); 32: High ambient temperature (34.0–38.9°C); 33: Dim (1–100 lux); 34: Bright (101–1000 lux); 35: Very bright (>1000 lux); 36: Low perch surface temperature (22–24°C); 37: Moderate perch surface temperature (25–27°C); 38: High perch surface temperature (28–30°C). Dots represent the scores of species in the multivariate space (Species abbreviations as in Figure 3.4 caption)

The Shepard plot showcases the relationship between nMDS ordination distance and original observed distance (Figure 3.8). Small scatter around the line suggests that original dissimilarities are well represented in the reduced dimensions. Overall stress calculated was 0.1078357 which indicates Figure 3.7 was a useful two-dimensional diagram (Clarke, 1993).

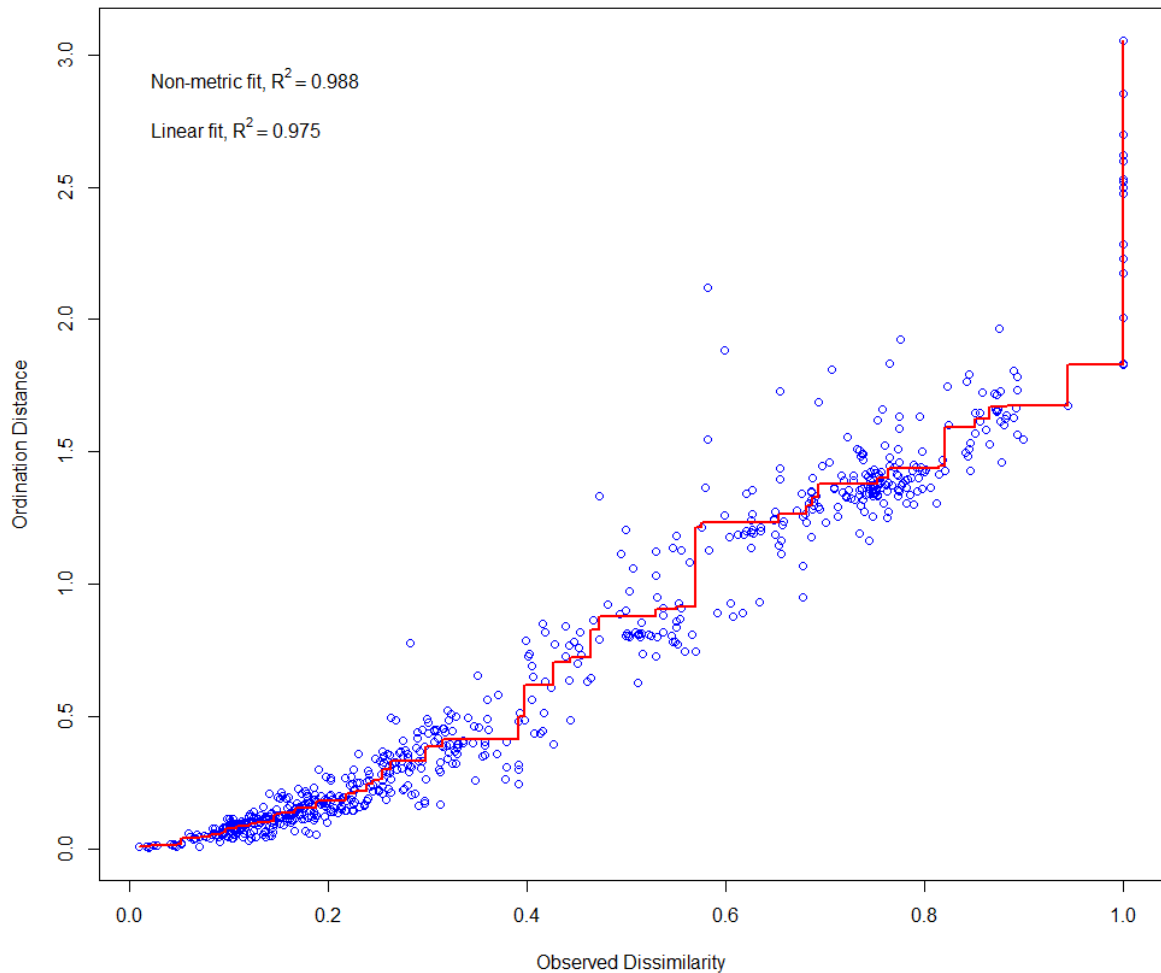


Figure 3.8: Shepard plot of nMDS ordination distance against the observed dissimilarity. Red line denotes the best-fit monotonic regression of y on x; Blue circles defines the nMDS stress

3.4.4 Niche breadth and Niche Overlap

Levin's Index show that the four species of *Gonocephalus* have similar niche breadths, ranging from 13.89 in female *G. doriae* to 17.38 in female *G. liogaster* (Table 3.6) The broad index values suggest that female *G. liogaster* is a generalist in terms of microhabitat utilisation, compared to its congeners. On the other hand, the narrow index value indicates that females of *G. doriae* have more restricted habitat requirements and are more specialised.

The Pianka's Niche Overlap Index was consistent with the Morista's Similarity Index (Table 3.6) of microhabitat utilization suggesting that species of *Gonocephalus* greatly overlapped and share many of the microhabitat. Female *G. bornensis* and female *G. grandis* overlapped the least (0.78), whereas males and females *G. doriae* overlapped the most (0.99).

Table 3.6: Levin's standardised niche breadth and Pianka's niche overlap of microhabitat utilization of telemetered *Gonocephalus*. Species abbreviations as in Figure 3.4 caption

Species	n	Niche breadth	Niche overlap							
			GB	GB	GG	GG	GD	GD	GL	GL
MGB	822	17.36	1							
FGB	863	14.04	0.87	1						
MGG	1060	14.79	0.94	0.79	1					
FGG	835	14.29	0.93	0.78	0.99	1				
MGD	540	14.11	0.93	0.81	0.92	0.88	1			
FGD	861	13.89	0.92	0.79	0.92	0.89	0.98	1		
MGL	952	15.49	0.96	0.86	0.92	0.89	0.96	0.96	1	
FGL	607	17.38	0.97	0.81	0.91	0.9	0.91	0.9	0.91	1

3.5 Discussion

Radio telemetry data reveal that adult telemetered *Gonocephalus* lizards have middling home range (mean MCP size 0.398 ha) compared to other draconines of similar size, some species shown to have large (Subba Rao & Rajabai, 1972) or smaller (J. Lin & Lu, 1982; Bandara, 2012) home ranges. These four syntopic species of *Gonocephalus* have comparable home range sizes, that was unaffected by the gender of the individual albeit most male *Gonocephalus* seems to have larger home range size, except for *G. doriae*. Though there are many factors that ultimately affects a lizard's home range size (Perry & Garland, 2002), *G. doriae* females have larger home ranges compared to those of males, conceivably due to the highly territorial nature of males, and females primarily travel further for feeding and mating (Lin & Lu, 1982; Bandara, 2012). One instance of territorial behaviour (displaying gular sac, with body lifted off perch surface from neighbouring perch) by a pair of male *G. doriae* was observed in this study (Figure 6.5). It is also commonly suggested that males establish larger home ranges with the intention of including a few females in their vicinity (Andrews, 1971; Schoener & Schoener, 1982; Stamps, 1983; Smith & Ballinger, 1995; Rocha, 1999; Perry & Garland, 2002) which explains why most males of the other three species of *Gonocephalus* have slightly larger home ranges although not apparent in this study. This phenomenon was observed in a few telemetered male individuals (MGB2, MGG2, MGD1, MGL1, MGL2) in this study where several females of the same species are found within its home range. However, not all lizards could be radio tracked, and therefore, it is uncertain whether these males in fact do have larger home range than the females.

These results also suggest that the four syntopic species of *Gonocephalus* seem to exhibit spatial separation at the study site. Although the telemetered *Gonocephalus* displayed considerable spatial overlap among their home ranges, there was no interspecific overlap.

Most of the overlaps were intersexual and some of the home ranges of these telemetered females overlapped almost half of the male home ranges. This phenomenon appears logical given that female lizards generally mate with males whose home range overlaps theirs thus increasing the rate of successful mating (Stamps, 1983; Abell, 1997). Aside from that, there was one recorded overlap between a pair of females and no male-male overlap recorded. Nevertheless, this does not imply that male-male overlap or interspecific overlap does not transpire. In addition to the previously mentioned pair of *G. doriae* males, one male *G. bornensis* was also detected within what was believed to be the edge of home range of a male *G. grandis*. Minimal spatial overlap between adult males may be indirect evidence of territorial behaviour, projecting mutual exclusion (Rocha, 1999). Like males, intersexual spatial overlaps in females may also be modest due to territorial behaviour, however with greater tolerance (Zucker, 1989; Qi et al., 2012). Intrasexual spatial overlap was also reported to increase with the increase of intersexual overlap (Aragón et al., 2004). The lack of home range overlaps in this study may be due to the small per species samples. The overlaps seen are likely suggestive and need to be confirmed with more extensive sampling. Nonetheless, this study suggests an overlap pattern where spatial overlap is more likely to happen between sexes of the same species in angle-headed lizards.

The limited movement (MD 11.342 m, MDD 0.165 m/day) displayed by the four syntopic species in this study suggests that these species tend to restrict their movements to a definite area. Although movement may have been underestimated, as these telemetered individuals were not observed continuously or monitored daily, it is apparent that the lizards exhibit high site fidelity. All these lizards have been found on the exact same perch multiple times especially at night with some individuals showing higher site fidelity than others. This pattern of site fidelity shown by these lizards was similar to those reported by Mohanty et

al. (2016). These lizards are often found relatively sedentary regardless of the time of the day, a common behaviour exhibit by sit-and-wait predators (Huey & Pianka, 1981; Cooper, 1998). Lower mobility by these lizards may be advantageous as high levels of activity and movement has been proven to increase predation risk (Gerritsen & Strickler, 1977), cost of agonistic encounters (Cooper & Vitt, 1987) and cost of maintenance at higher activity temperatures (Huey & Slatkin, 1976; Amadi et al., 2020). Regardless, *Gonocephalus* males travel a significantly greater distance between location points than do females. This may result from patrolling or conspicuously advertising their territories, as seen in many other lizard species (Baird & Timanus, 1998; Mahrt, 1998; Miles et al., 2001; Baird et al., 2012). It also heightens their chance to encounter more mating partners around them (Koenig et al., 2001). Even though males travel a greater distance between location points than females, their mean daily displacement is not significantly different than that of females. This further affirm that they do restrict their movements within an area in which was believed to be its home range. Movement was generally not affected by the microhabitat variables except slope. Most lizards prefer areas with gentler slopes as slope can easily affect the locomotor and endurance of a lizard (Pinch & Claussen, 2003; Urbina-Cardona et al., 2006).

Similar microhabitat use by these sympatric lizards was also recognised and proven through the high values of Pianka's Niche Overlap Index and Morista's Similarity Index in this study. Seemingly these lizards shared many of their microhabitat and regularly occupy habitats with gentle to moderate slope (mean $14.5 \pm 8.24^\circ$), dense canopy cover (mean $80.95 \pm 7.98\%$), any tree sizes or height (mean 0.28 ± 0.38 m circumference of tree; mean 1.96 ± 1.3 m vertical position), near to moderate distance to water (mean 11.63 ± 7.23 m), average to high humidity (mean 8.66 ± 7.44 %RH), moderate to high ambient temperature (mean $28.02 \pm 1.65^\circ$), low to average light intensity (mean 614.12 ± 1401.11 lux) and low to

moderate perch surface temperature (mean $24.66 \pm 0.94^\circ$). On the contrary, these lizards generally appeared to avoid areas with low canopy cover and high perch surface temperature. This finding was consistent with those reported by Karunarathna & Amarasinghe (2013) in that cool shaded areas with dense canopy were preferred by *Lyricephalus scutatus*, a diurnal and arboreal agamid lizard of the similar size that inhabits a similar elevation. These lizards are also often seen perching on tree trunks and tree branches while finding wooden planks, rocks, tree buttress, tree stumps and fallen logs inessential. While Ananjeva & Matveyeva-Dujsebayaeva (1996) considered *Gonocephalus* an arboreal species, observations from this research indicate that they do spend some considerable period of time on the ground during the day, as also reported by Jayasekara et al. (2019). Furthermore, they were often found perching on low shrubs and not high up the tree.

Spatial segregation is vital to reduce competition between species and permits coexistence, both from a theoretical (MacArthur & Pianka, 1966) and a practical perspective (Schoener, 1974). Spatial segregation was evidently the main factor in minimizing competition in lizard communities (Pianka, 1966; Jenssen, 1973; Saint Girons, 1975; Schoener, 1975), subsequently food resource partitioning in some cases (Pianka, 1973, 1975; Fuentes, 1976; Pianka & Huey, 1978; Mushinsky & Hebrard, 1977). Initially, the high commonalities in microhabitat selection between these species and the high niche overlap failed to provide an immediate clear niche segregation. However, this current study suggested that female *G. bornensis* have shown to be more ground dwelling and are often found far from waterbodies. Male and female *G. grandis* on the other hand were highly associated with waterbody which was consistent with the findings from Maupin et al. (1998). They are also found occupying trees with larger circumference much more than other species. Male *G. liogaster* seemed to utilise similar microhabitats as male and female *G.*

doriae and were clustered together in the dendrogram of the Morista's Similarity Index. They appeared to be highly associated to trees with moderate circumference. However, *G. liogaster* and *G. doriae* were shown to differ significantly in terms of canopy cover, slope, perch surface and perch surface temperature. Male and female *G. doriae* was strongly associated with tree trunks compared to other species similar to those reported by Das (2010) and they were most often found vertically perching. Besides, female *G. liogaster* and male *G. bornensis* also seem to prefer similar microhabitats, including low canopy areas with direct sunlight. However, they do differ significantly in terms of canopy cover, slope, perch surface and relative humidity. With regard to spatial distribution, it appears that female *G. liogaster* can be considered generalist among these species whereas female *G. doriae* are specialists. In addition, the infrequent interspecific spatial overlaps indicate that these species do exhibit resource partitioning to enable coexistence.

3.6 Conclusions

Use of space by four syntopic species of *Gonocephalus* was generally similar and all showed moderate home range sizes that did not differ significantly between sexes and species. Home range overlaps occurred between males and females of the same species and there were no interspecific overlaps which limits interspecific competition. But given the small per species samples, the lack of home range overlaps seen may be suggestive and that a more extensive sampling may be required. The data gathered in this study also indicate that these lizards share most of the microhabitat they occupy, favouring areas with gentle to moderate slope, high canopy cover, any tree sizes or height, near to moderate distance to water, tree trunk, tree branch, average to high humidity, moderate to high ambient temperature, low to average light intensity and low to moderate perch surface temperature. However, there are evidence that suggest that these lizards do exhibit subtle spatial separation, in terms of microhabitat utilisation and exhibit different levels of preference towards the microhabitat variable tested. Movement of these lizards were similar across all species of *Gonocephalus* and were fairly limited. Movement was also not affected by most abiotic factors except for slope. Males generally showed larger mean displacement than females, but restrict their movement within their respective home ranges. These observations therefore demonstrate spatial resource partitioning within the four syntopic species of *Gonocephalus* at a lowland Bornean forest.

CHAPTER 4

TROPHIC ECOLOGY

4.1 Introduction

The study of niche dynamics is fundamental for the understanding of the ecological structure among organisms in a community. To reduce interspecific competition and permit coexistence among closely related species, resources must be partitioned in such a way that each species is limited by a different factor (MacArthur, 1958). Lizards are known to partition their resources in one or more of three dimensions, temporal, spatial, and trophic (Pianka, 1986). While most lizard communities are recognised to partition resources at the spatial level (e.g., Jenssen, 1973; Pianka, 1966, 1973, 1986; Toft, 1985), some studies have suggested that the partitioning of trophic resources (Pianka, 1973; Fuentes, 1976; Pianka & Huey, 1978; Luiselli, 2006b). However, Luiselli (2008) concluded that the trophic dimension is not generally partitioned by sympatric lizards simply due to the generalist foraging strategies adopted by most lizards. Even when studies suggested otherwise, the fragmented nature of the prey removed as lizard diets often impedes the identification of prey at a finer (such as specific) level, which may have caused erroneous conclusions regarding the topic (see Luiselli, 2006, 2008). Moreover, the three said dimensions are usually corresponsive particularly when other factors are involved such as seasonal availability of food (Simon, 1975; Simon & Middendorf, 1976; Luiselli, 2006). Moreover, high dietary overlap among species does not always indicate the presence of interspecific competition for dietary resources, especially when foods are abundant (Luiselli, 2008). Nonetheless, trophic ecology remains an important scientific discipline that delves into the structure of interspecific feeding relationships.

It is generally known that diet plays a vital role within the daily life of animals, in providing energy for growth, maintenance, and fecundity (Huey & Pianka, 1981). Defining an animal's diet often offers insights into prey preferences (Tkaczenko et al., 2014), ecological roles (Chan et al., 2020), feeding behaviour (Tan et al., 2020), feeding mechanism (Dean et al., 2007), and even niche dynamics (Jara & Muñoz-Pedreros, 2017). With this background, appropriate management decisions and preservation of natural sites could then be made for the species if necessary. Trophic ecology of lizards itself is greatly influenced by both intrinsic and extrinsic factors (Pianka, 1986). Rainfall and seasonal fluctuations in availability of food resources are among the most important extrinsic factors (Pianka, 1970; Magnusson & da Silva, 1993; Rocha, 1996) whereas foraging mode, body size, sex, and ontogeny are significant intrinsic factors (Schoener, 1967; Huey & Pianka, 1981; Perry, 1996; Vitt, 2000). Lizards of the genus *Gonocephalus* reportedly feed on insects and other arthropods, including caterpillars, beetles, grasshoppers, ants, flies, cockroaches and spiders (Das, 2010). These similar-sized, lowland tropical rainforest lizards are often found living in sympatry but there are no data available on the structure of feeding relationships among these lizards.

Prey selection is the basis of trophic ecology as prey type and prey-predator size relationships often provides information on niche diversification and partitioning (Simon, 1976). Optimal foraging theory suggested that individuals ought to select food items based on net profitability (Macarthur & Pianka, 1966; Charnov, 1976). Prey types differs in quality which influences the profitability often in a way that could be predicted by certain prey characteristics such as chitin content (Zach & Falls, 1978; Jaeger & Barnard, 1981; Díaz & Carrascal, 1993) and body shape (Loop, 1974; Sherry & McDade, 1982). Soft and round arthropods such as hemipterans and spiders were considered to be an easier prey in terms of

handling in comparison to beetles and ants that are usually heavily chitinised and elongated (Díaz & Carrascal, 1993). Handling time usually also increases with prey size, hence, the majority of lizards consume prey that are much smaller than themselves and devour them whole (Pianka & Vitt, 2003). The range of prey size consumed tends to increase with lizard body mass (Brandl et al., 1994; Costa et al., 2008; Costa, 2009), with juveniles often consuming smaller prey compared to adults (Sales et al., 2011). This lies in the fact that smaller individuals are normally limited by their smaller body, head and mouth which results in a narrower range in the size of potential prey available (Peters, 1983; Vézina, 1985; Vitt, 2000). As their size increases, smaller prey may become awkward to handle and/or the energetic cost of consuming them may exceed energetic gain (Costa et al., 2008). Nevertheless, this does not necessarily denote that larger individuals exclude smaller prey from their diet as smaller prey can be more abundant (Manicom & Schwarzkopf, 2011). Larger individuals usually have greater variances of prey types and quantity (Schoener & Gorman, 1968; Scharf et al., 2000; Sales et al., 2011). Some sexually dimorphic lizards also demonstrate intersexual differences in prey size preference where females tend to consume smaller prey compared to males (Schoener & Gorman, 1968; Perry, 1996). Ultimately, the prey selection is determined by the prey abundance and availability in the environment (Arnold, 1987; Sales et al., 2011).

Two discrete foraging methods (active and ambush) have long been recognized in lizards (Pianka, 1966; Huey & Pianka, 1981; Cooper et al., 1999). While members of most lizard families typically exploit either one or the other modes of foraging, some lizards can switch between foraging tactics depending on the situation (Robinson & Cunningham, 1978; Cooper & Whiting, 2000). Insectivorous agamid lizards are widely believed to be ambush foragers or generalist predators (Pianka, 1966, 1986; Cooper, 1994; Cooper et al., 1999;

Luiselli, 2008;), often sitting and waiting for potential prey to move within range, sometimes making short forays to pursue larger prey items (Pianka, 1971b). Sit-and-wait predators frequently rely on moving or active prey that are high in density (Pianka, 1986) and are rather unselective of the different types of arthropods available in their environment (Luiselli, 2008). However, fitness are usually maximized through matching foraging decisions to environmental conditions (Dall et al., 2005). Therefore, opportunistic shifts to seasonal prey are sometimes adopted if necessary in order to target more profitable prey (e.g., Robinson & Cunningham, 1978; Rocha, 1996; Schaedla, 2004 ; Sagonas et al., 2015).

4.2 Specific Objectives

Two main objectives with relevant research questions raised in this chapter includes

- i. To determine the diet composition of four syntopic species of *Gonocephalus*;

To date, little information is available on the diet and dietary behaviour of these lizards. Hence, the question raised here is what are the dietary compositions of these lizards? Is there interspecific variation in which prey taxa or prey size are eaten and in what proportion? Which prey types are most important to these lizards?

- iii. To demonstrate niche differences, if any, among syntopic species of *Gonocephalus*.

Luiselli (2008) suggested that sympatric lizards generally do not partition the trophic dimension due to the generalist foraging strategy adopted by most lizards. Can this be applied for these syntopic species? What is the degree of dietary niche overlap between them? Is there a presence of interspecific competition for dietary resources?

4.3 Specific Methodology

4.3.1 Dietary Data Collection

Regurgitated and scat samples were collected from lizards encountered in Kubah National Park during visual encounter surveys (VES) and radio-tracking sessions. Only newly encountered individuals were captured by hand or by noose, to obtain stomach contents and/or faecal samples; individuals fitted with radio transmitters were omitted to avoid possible behavioural change that may affect an ongoing spatial study. Both regurgitated and scat samples were immediately preserved separately in vials containing 70% ethanol (Legler & Sullivan, 1979). All collected prey items were then examined under an Olympus™ SZX9 stereo microscope in the laboratory. Sclerotized parts of invertebrates such as mandibles, heads, thorax, wings and legs, were measured with a digital vernier calliper to the nearest 0.01 mm. For each stomach/faecal, total volume of each prey was measured via the water displacement method using a 1 mL insulin syringe to the nearest 0.01 mL, while the volume of larger prey items was estimated using a measuring cylinder, to the nearest 0.1 mL. Dietary items were classified into operational taxonomic units, OTUs (Sneath & Sokal, 1962) and identified to the lowest possible taxonomic level. However, most prey items could be only identified to the ordinal level due to the fragmented nature of the prey items. Prey item sizes were also estimated based on the size of fragments compared to what was published by Hill & Abang (2010). Incidental to the collection of regurgitated and scat samples, nematodes were also obtained from stomachs and faeces of some individuals. These will be reported separately in chapter 6, in a subchapter on parasites.

4.3.2 Stomach Flushing

Stomach contents were acquired from these lizards immediately after capture through stomach flushing. The technique was formally proposed by Legler & Sullivan (1979), and is a relatively innocuous method that is frequently used to study stomach content of lizards (Powell & Russell, 1984; Christian et al., 1996; Van Leeuwen et al., 2011; Tan et al., 2020; but see Luiselli et al., 2011) by obtaining the ingested food components before the completion of the digestive process. The method was carried out through the introduction of water directly into the stomach through the pharynx, using an intravenous catheter (5 mm in diameter and 110 mm in length in this study), attached to a syringe. Water was pumped into



Figure 4.1: Stomach flushing a female *Gonocephalus liogaster* after capture in Kubah National Park

the stomach slowly to force out food without injuring the lizard (Legler, 1977; Legler & Sullivan, 1979). Throughout the process, the lizard was held gently but firmly at the neck in one hand, with its mouth propped open at nearly maximum gape (typically resulted from jaw-opening threat response). Tools, such as the handle end of a dissecting forceps, were used to gently pry the jaws open.

4.3.3 Data Analyses

Diets of each species were evaluated in terms of percentage of abundance (% N), percentage of volume (% V), and percentage of frequency of occurrence (% FO). Figures for % N is the percentage of all stomach contents combined that the prey type comprised. $\% N = (n_i/N) \times 100$, where (n_i) is the number of prey of categories (i) and (N) is the total number of prey (Zaime & Gautier, 1989); Figures for % V is the percentage of all volume combined that the prey type comprised. $\% V = (v_i/v) \times 100$, where (v_i) is the volume of prey of categories (i) and (v) is the total volume of prey; Figures for % FO is the percentage of lizard stomachs in which a particular prey item was found. $\% FO = (FO_i/n) \times 100$, where (FO_i) is the number of samples containing the prey category (i) and (n) is the total number of samples. Prey types were further described according to Bigot & Bodot (1973) classification as “constant prey” ($\geq 50\%$), “common prey” ($25\% \leq \% FO < 50\%$), “accidental prey” ($10\% \leq \% FO < 25\%$), or “very accidental prey” ($< 10\%$).

For each prey group, the index of relative importance (IRI) was calculated to quantify the significance of a particular prey item in the diet. IRI is a compound index combines unique properties affecting individual measures (here including abundance, volume, and occurrence), which provides a fair view of the diet of a lizard (Tan et al., 2020). These values are merely to rank the relative importance of food types for a species; they are unsuitable to

compare between species, or between two groups of the same species. However, rank correlation coefficients can be applied to prove whether different species or groups varies in prey rankings thus showing the importance of the prey (Martin et al., 1996). The relative IRI rankings for prey categories calculated by the four species of *Gonocephalus* were compared using Spearman's rank correlation coefficient, with $\alpha = 0.05$ to determine if rankings were significantly correlated between the prey types of the four species of lizards.

Dietary niche breadth was calculated using Levins' measure of standardized niche breadth (Hurlbert, 1978). The standardize index of Levin's is a simple arithmetic ranging from 0 to 1 that suggests whether a species has a more specialised or generalised diet by measuring the uniformity of distribution of individuals among the OTUs. Dietary niche overlap on the other hand, was estimated using Pianka's symmetrical dietary niche overlap in order to predict coexistence and better understand community organization through the evaluation of overlap in utilization of the trophic niche (Pianka, 1973).

The relationship of prey size (estimated full size) and lizard SVL was visualised in scatter plots to determine presence of correlation between size of prey and predator of each species. These variables were log-transformed for linearity and coefficient of determination, R^2 was also calculated. The R^2 value is a measure of goodness of fit which reveals the percent of the variation in data values in regard of the regression line. Significance of the correlation was tested using Spearman's rank correlation coefficient, with $\alpha = 0.05$ to determine if the variables were correlated.

4.4 Results

4.4.1 Diet Composition

A total of 94 regurgitated and scat samples ($n = 24$ *G. bornensis*; $n = 21$ *G. doriae*; $n = 19$ *G. grandis*; $n = 30$ *G. liogaster*) were collected over a period of 19 months (Figure 4.2). Of these samples, 17 samples ($n = 4$ / 16.67% *G. bornensis*; $n = 5$ / 23.81% *G. doriae*; $n = 4$ / 21.05% *G. grandis*; $n = 4$ / 13.33% *G. liogaster*) contained prey items, while the remainder was empty. Among the positive samples, 21 prey comprised of 13 operational taxonomic units (OTUs) were successfully identified (Figure 4.3). The recovered diet of *G. bornensis* was composed of three OTUs, *G. doriae* was composed of five OTUs, *G. grandis* was composed of four OTUs, whereas *G. liogaster* was composed of four OTUs. The majority (84.62%) of the prey identified were insects and the remainder consist of non-insect arthropod groups (such as earthworms and snails). It is noted that the sample size collected is likely insufficient to accurately reflect the true diet composition of these lizards.

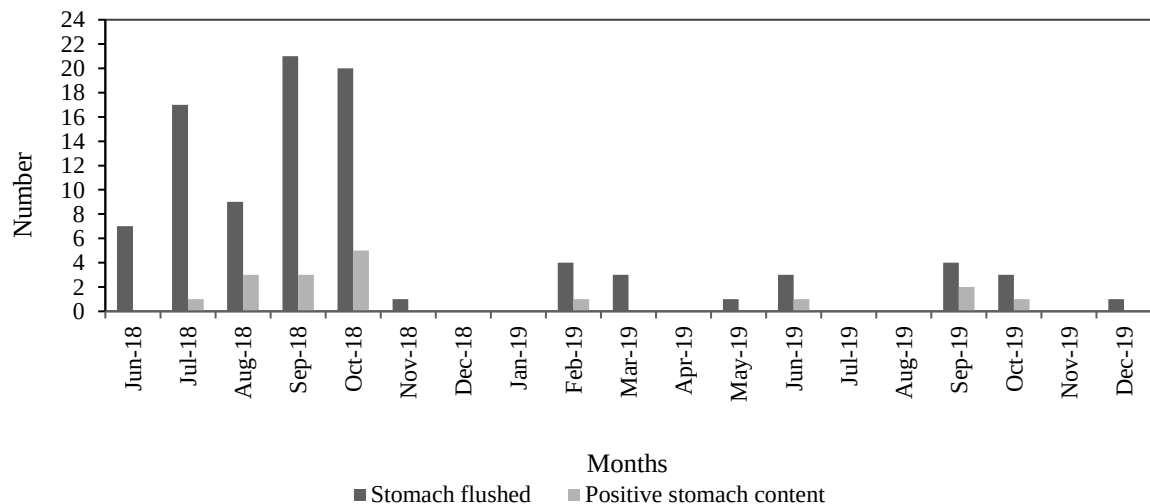


Figure 4.2: Bar chart showing the total amount of stomachs flushed and positive regurgitated and scat samples that were collected from June 2018 to December 2019

Table 4.1 shows the dietary composition of the four syntopic species of *Gonocephalus* collected in this study and evaluated in terms of percentage of abundance (% N), percentage of volume (% V) and percentage of frequency of occurrence (% FO). Results of the Spearman's rank correlations between different measures (% N, % V and % FO) taken for each species are shown in Table 4.2. Typically, the different measures produced similar rankings of the importance of prey taxa. However, in the case of *G. grandis* percentage of frequency of occurrence did not correlate significantly with either percentage of abundance or percentage of volume. The mean number of prey consumed per individual did not differ between the four species ($F = 0.604$, $P = 0.624$). Between the categories (OTUs), prey consumed was also not significantly different numerically ($F = 0.685$, $P = 0.755$) and volumetrically ($F = 0.994$, $P = 0.472$). In addition, this study show a relatively low % FO (<10%) in almost all OTU categories, suggesting that all these prey were considered as “very accidental prey” based on Bigot and Bodot's (1973) classification. The highest % FO recorded was cockroach (Blattidae) in *G. grandis* (10.53%) but was also considered as an “accidental prey”. Indications are that there was no “constant” ($\geq 50\%$) or “common” ($25\% \leq \% \text{FO} < 50\%$) prey that was identified for these lizards. Additionally, IRI rankings were not significantly correlated between the prey types of the four species of lizards suggesting a difference in their relative use of prey type (Table 4.3). As it appears that beetles (Coleoptera) were ranked highly for *G. bornensis*, earthworm (Megascolecidae) was highest for *G. doriae*, assassin bug (Reduviidae) was ranked greatest for *G. grandis*, whereas grasshopper (Acrididae) was most important for *G. liogaster*.

Table 4.1: Dietary composition the four syntopic species of *Gonocephalus*. OTUs = operational taxonomic units; n = abundance; v = volume (mL); FO = frequency of occurrence; IRI = index of relative importance; all percentages in parentheses

Phylum	OTU		G. bornensis (n = 4)	G. doriae (n = 5)	G. grandis (n = 4)	G. liogaster (n = 4)
Arthropoda	Acrididae	n (%)	-	-	-	1 (25)
		Vol (%)	-	-	-	0.04 (80)
		FO (%)	-	-	-	1 (3.33)
		IRI	-	-	-	350
	Blattidae	n (%)	-	-	2 (40)	-
		Vol (%)	-	-	-	-
		FO (%)	-	-	2 (10.53)	-
		IRI	-	-	421.053	-
	Coleoptera	n (%)	2 (50)	-	1 (20)	-
		Vol (%)	0.01 (100)	-	-	-
		FO (%)	2 (8.33)	-	1 (5.26)	-
		IRI	1250	-	105.263	-
	Diptera	n (%)	-	-	-	1 (25)
		Vol (%)	-	-	-	0.01 (20)
		FO (%)	-	-	-	1 (3.33)
		IRI	-	-	-	150
	Formicidae	n (%)	-	3 (37.5)	1 (20)	1 (25)
		Vol (%)	-	0.03 (0.74)	<0.01	<0.01
		FO (%)	-	2 (9.52)	1 (5.26)	1 (3.33)
		IRI	-	364.163	105.263	83.333
	Hemiptera	n (%)	-	1 (12.5)	-	-
		Vol (%)	-	<0.01	-	-
		FO (%)	-	1 (4.76)	-	-
		IRI	-	59.524	-	-
	Lepidoptera	n (%)	1 (25)	-	-	-
		Vol (%)	<0.01	-	-	-
		FO (%)	1 (4.17)	-	-	-
		IRI	104.167	-	-	-
	Lycidae	n (%)	-	1 (12.5)	-	-
		Vol (%)	-	<0.01	-	-
		FO (%)	-	1 (4.76)	-	-
		IRI	-	59.524	-	-
	Phasmatodea	n (%)	-	-	-	1 (25)
		Vol (%)	-	-	-	<0.01
		FO (%)	-	-	-	1 (3.33)
		IRI	-	-	-	83.333
	Reduviidae	n (%)	-	-	1 (20)	-

Table 4.1: continued

		Vol (%)	-	-	0.01 (100)	-
		FO (%)	-	-	1 (5.26)	-
		IRI	-	-	631.579	-
	Termitidae	n (%)	-	2 (25)	-	-
		Vol (%)	-	0.04 (0.98)	-	-
		FO (%)	-	1 (4.76)	-	-
		IRI	-	123.728	-	-
Mollusca	Gastropoda	n (%)	1 (25)	-	-	-
		Vol (%)	<0.01	-	-	-
		FO (%)	1 (4.17)	-	-	-
		IRI	104.167	-	-	-
Annelida	Megascolecidae	n (%)	-	1 (12.5)	-	-
		Vol (%)	-	4 (98.28)	-	-
		FO (%)	-	1 (4.76)	-	-
		IRI	-	527.524	-	-

Table 4.2: Results of Spearman rank correlation coefficients (r_s) comparing percentage of abundance (% N), percentage of volume (% V) and percentage of frequency of occurrence (% FO) as indices of prey importance for species of *Gonocephalus*. (**) indicate that correlation is significant at the 0.01 level (2-tailed), (*) correlation is significant at the 0.05 level (2-tailed)

Species	% N × % V	% N × % FO	% V × % FO
<i>G. bornensis</i>	$r_{s(13)} = 0.628$, P = 0.022*	$r_{s(13)} = 1^{**}$	$r_{s(13)} = 0.628$, P = 0.022*
<i>G. doriae</i>	$r_{s(13)} = 0.751$, P = 0.003**	$r_{s(13)} = 0.989$, P = 0**	$r_{s(13)} = 0.708$, P = 0.007**
<i>G. grandis</i>	$r_{s(13)} = 0.380$, P = 0.2	$r_{s(13)} = 1^{**}$	$r_{s(13)} = 0.380$, P = 0.2
<i>G. liogaster</i>	$r_{s(13)} = 0.637$, P = 0.019*	$r_{s(13)} = 1^{**}$	$r_{s(13)} = 0.637$, P = 0.019*

Table 4.3: Results of Spearman rank correlation coefficients (r_s) comparing index of relative importance (IRI) rankings for prey types of four species of *Gonocephalus*

Species	<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
<i>G. bornensis</i>	1			
<i>G. doriae</i>	$r_{s(13)} = -0.415$, P = 0.159	1		
<i>G. grandis</i>	$r_{s(13)} = 0.021$, P = 0.947	$r_{s(13)} = -0.182$, P = 0.551	1	
<i>G. liogaster</i>	$r_{s(13)} = -0.356$, P = 0.233	$r_{s(13)} = -0.182$, P = 0.551	$r_{s(13)} = -0.179$, P = 0.558	1



Figure 4.3: Prey items collected from regurgitated and scat samples of species of *Gonocephalus*. 1st row left to right: leg of cockroach (Blattidae) $\times 18.75$, whole ant (Formicidae) $\times 9.45$, leg of trilobite beetle (Lycidae) $\times 18.75$. 2nd row left to right: ead of trap jaw ant (Formicidae) $\times 37.5$, leg joint of beetle (Coleoptera) $\times 75$, urticating hair of a butterfly or moth caterpillar (Lepidoptera) $\times 18.75$. 3rd row left to right: coxa and femur of ant (Formicidae) $\times 30$, head with pronotum and leg of grasshopper (Acrididae) $\times 18.75$, termite alates wings (Termitidae) $\times 9.45$. 4th row left to right: assassin bug wing (Reduviidae) $\times 18.75$, whole snail (Gastropoda) $\times 30$, whole earthworm (Megascolecidae)

4.4.2 Niche Breadth and Niche Overlap

Levin's Index, in terms of prey composition obtained from this study show that species of *Gonocephalus* have similar niche breadths ranging from 0.139 in *G. bornensis* to 0.292 in *G. doriae* (Table 4.4). *G. doriae* having the most diverse food spectrum appeared to be generalist forager compared to the other species followed by *G. liogaster*. However, the narrow breadth of these species could well be due to the small sample sizes.

For the estimation of Pianka's symmetrical dietary niche overlap, results suggest that the trophic niches of these species barely overlapped and shared little to no prey items (Table 4.4). The highest overlap was between *G. doriae* and *G. liogaster* (35%), while two other pairs had no overlaps at all seemingly implying that these pairs exhibit niche partitioning on a trophic level.

Table 4.4: Levin's standardised niche breadth and Pianka's symmetrical niche overlap based on prey composition in *Gonocephalus*

Species	n	Niche breadth	Niche overlap			
			<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
<i>G. bornensis</i>	4	0.139	1			
<i>G. doriae</i>	6	0.292	0	1		
<i>G. grandis</i>	5	0.214	0.308607	0.267261	1	
<i>G. liogaster</i>	4	0.25	0	0.353553	0.188982	1

4.4.3 Predator-prey Body Size Relationships

The body sizes and weights of lizards with regurgitated and scat samples in this study ranges from 81–144 mm SVL and 16–76 g respectively, generally sub adults and adults of these species. Diet samples for smaller individuals were not present due to the intravenous catheter used for stomach flushing was too large to fit through a juvenile's pharynx without causing discomfort or injury to the individual. Both size ($F = 1.645$, $P = 0.227$) and weight ($F = 0.119$, $P = 0.947$) were not significantly different between the species of *Gonocephalus*. The negative correlation between mean predator size and niche breadth was also insignificant ($r = -0.6$, $N = 4$, $p = 0.4$).

Identifiable prey ($n = 21$) collected from these samples are mostly fragmented (90.5%). Therefore, the full size of these fragmented prey items were estimated referencing Hill & Abang, (2010). The prey items obtained had estimated full size that ranges from 1.6–315 mm. Results revealed that the mean estimated prey sizes between the four species was not significantly different ($F = 0.5$, $P = 0.688$), suggesting that these species feed on similar sized prey.

Figure 4.4 shows the relationship of prey estimated full size and lizard SVL. The scatter plots for *G. bornensis* (A), *G. grandis* (C) and *G. liogaster* (D) displayed a positive relationship. Although the trend seems to imply that larger individuals feed on larger preys, but these relationships were not statistically significant (*G. bornensis*: $r = 0.316$, $N = 4$, $p = 0.684$; *G. grandis*: $r = 0.289$, $N = 5$, $p = 0.637$; *G. liogaster*: $r = 0.6$, $N = 4$, $p = 0.4$), suggesting that prey size are independent of lizard size for these three species. On the contrary, *G. doriae* in scatter plot (B) showed an opposite trend but was statistically significant ($r = -0.745$, $N = 8$, $p = 0.034$) indicating that smaller individuals prefer larger prey.

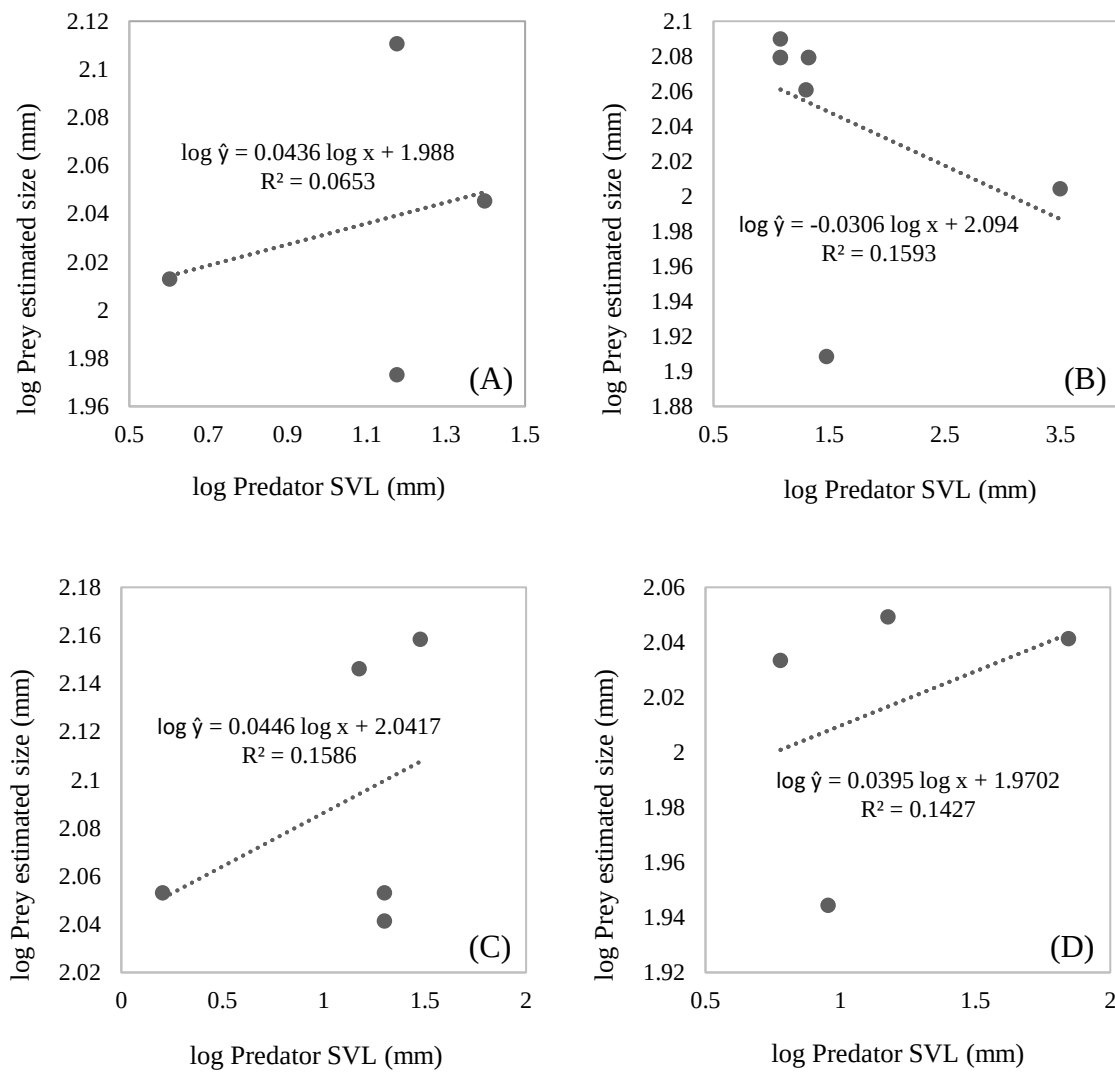


Figure 4.4: Scatter plots showing log prey estimated full size against log predator snout-to-vent length, SVL. (A) *Gonocephalus bornensis* as predator; (B) *Gonocephalus doriae* as predator; (C) *Gonocephalus grandis* as predator; (D) *Gonocephalus liogaster* as predator

4.4.4 In-situ Feeding Observations

During the period of field data collection, three individuals of *Gonocephalus* were observed feeding on three separate occasions. The observations included an adult female *G. bornensis* masticating on a *Dinomyrmex gigas*, Formicidae (as observation 1, Figure 4.5); an adult female *G. doriae* fitted with a radio transmitter (tracking number 150.649)

successfully preyed on a large earthworm, Megascolecidae (as observation 2); and an adult male *G. liogaster* fitted with a radio transmitter (tracking number 150.970) feeding from an ant trail, Formicidae (as observation 3). Although not included in the dietary analyses, prey consumed during these observations did not add to the prey types recorded in the regurgitated and scat samples.

On all three occasions, a similar pattern was observed where these lizards would climb down from a tree to forage on the forest floor and then climb up another tree to feed or after feeding. All feeding observation was made during the day (1330 h, 1229 h, and 0912 h respectively) and these lizards fed on prey that crossed path with them while they were on the move. Handling time was relatively short and almost instant for observation 3 but was slightly longer in the first two observations which may be due to the size of the prey.



Figure 4.5: An adult female *G. bornensis* masticating a *Dinomyrmex gigas* (giant forest ant) on 12 August 2018, at 1330 h

4.5 Discussion

The dietary constituents of the four syntopic species of *Gonocephalus* examined in this study consisted of mainly arthropods, suggesting that these species are insectivorous, as in most agamids (Huey & Pianka, 1981). All prey recorded in this study had low occurrence and were different in value as prey type for each species of lizard. Beetles (Coleoptera) were shown to be relatively most important for *G. bornensis*, earthworm (Megascolecidae) for *G. doriae*, assassin bug (Reduviidae) for *G. grandis*, whereas grasshopper (Acrididae) for *G. liogaster*. It is uncertain that there is in fact a difference in the relative importance of each prey type in the diet among the four species, considering these prey were still categorised as “very accidental prey” in the results. This could possibly be explained by a type II statistical error as a result of the small positive regurgitated and scat sample size. While this study did not yield reliable insights on the most important prey for each of these species, ants (Formicidae) were arguably a common prey as it was the only category of food shared among all four lizards. Ants are fairly common and indisputably an important prey in many other agamids (Capel-Williams & Pratten, 1978; Znari & El Mouden, 1997; Heideman, 2002; Tan et al., 2020) for the simplest reason that they are abundant and can be captured easily. However, it is apparent that these lizards are not entirely myrmecophagous but like many agamid lizards, for which ants are a common component of their diet (Tan et al., 2020). This may be due to the fact that ants are usually small, contain much undigestible chitin and low in caloric value compared to other arthropods. If they were to adopt a specialised ant-eating diet, a large number is to be consumed daily in order to compensate the energy used for handling (Pianka 1986; Withers & Dickman, 1995). According to Hart et al. (2002), foods eaten by many individuals but in small amounts or small volumes might show a high

frequency of occurrence, but it may not be highly significant in the diet. Hence, ants can be considered as a common prey but not necessarily of most important to these lizards.

It was also evident that earthworms and snails were part of their diet similarly reported in some agamids (Subba Rao & Rajabai, 1972; Schaedla, 2004; Tan et al., 2020) and many other lizard species in different biomes (Avery, 1966; Vitt et al., 1996; Spencer et al., 1998; ; Vitt et al., 1998; Brown et al., 2012; Picelli et al., 2019). Earthworms inhabit various horizons of the soil including on top of the soil in the surface litter of the forest (Reynolds, 1994) which the iridescent terrestrial earthworm (Megascolecidae) is often seen at the study site. When disturbed, they can sometimes jump into the air attempting to escape as per Reynolds's (1994) description. However, they can still be considered an easy prey that provides valuable source of protein with no hard or keratinized parts (Strüssmann et al., 2013). Land snails (Gastropoda) on the other hand have shells that seemed to require higher energy for handling, but they can also provide high energy and nutrients, including calcium (Graveland & van Gijzen, 1994). According to Schilthuizen et al. (2003), land snails have a lower abundance in non-limestone forests. Therefore, it may be appropriate to assume that snails are not as an important prey for these lizard species compared to the other arthropods. In this study, only *G. doriae* was recorded feeding on earthworms in two separate occasions, whereas a small snail was found in the stomach of a *G. bornensis*, there was not enough evidence to prove that whether the other species of *Gonocephalus* will also feed on these two prey types.

No vegetation matter was observed in these lizard diets, which suggests that they are principally insectivorous rather than herbivorous. Herbivory in lizards specifically from the families of Agamidae, Gerrhosauridae, Iguanidae, and Scincidae are common in larger individuals (over 300 g). The theory being that, insectivory diet is insufficient to sustain the

energy needs of these larger individuals (Sadek, 1981; Troyer, 1984), and therefore they had to rely on vegetation which is readily available in most habitats and requires comparatively low energy expenditure for acquisition (Pough, 1973). Plant material is a less digestible food option and may cause substantially slower growth which may not be suitable for smaller individuals which require higher energy in proportion to their mass (Pough, 1973; Schluter, 1984). Herbivory in smaller individuals can also developed as a response of seasonal scarcity of insects or during colder months in areas where there are seasonal changes (Znari & El Mouden, 1997). Since the largest individual captured only weighs 76 g and the climate in Sarawak remains fairly stable throughout the year, it is therefore sensible that these *Gonocephalus* species do not require plant matter to sustain energy needs.

The four syntopic species of *Gonocephalus* showed a relatively narrow niche breadth in this study which suggest that these lizards are somewhat specific feeders. Feeding on a low variety of prey is possible, but improbable as most lizard species worldwide are known to be generalist foragers (Luiselli, 2008). What is happening here can be explained by insufficient data collected, therefore this study may not provide a good representation of the true diet composition of these lizards. Given a larger sample size, the outcome will possibly reveal a wider niche breadth for each species. Nevertheless, the 13 operational taxonomic units (OTUs) that were successfully identified as prey for these species seemingly resembles other diurnal and arboreal agamid lizards of the similar size that inhabits a similar elevation such as *Acanthosaura*, *Bronchocela cristatella*, *Calotes*, *Lyriocephalus scutatus*, and *Lophocalotes achlios* (Cox et al., 1998; Das, 2010; Karunarathna & Amarasinghe, 2013; Harvey et al., 2018), suggesting a comparable feeding pattern perhaps. It is feasible that these *Gonocephalus* lizards might also feed on other prey types such as mosquitoes, small butterflies, moths, spiders, centipedes, millipedes, and dragon flies in addition to the findings

in this study, making them rather opportunistic feeders. Tropical rain forest is always recognised for their vast diversity of arthropods (Stork, 1991) which mostly, if not all are potential food items for insectivorous lizards. On that account, these *Gonocephalus* lizards are probably not restricted by food shortages and can afford to adapt the optimal strategy by selectively target prey offering the maximum net energy gain (Stephens & Krebs, 1986; Manicom & Schwarzkopf, 2011). The insignificant association between body size and niche breadth in predators obtained from this study is most likely also resulted from an optimal foraging behaviour as suggested by Costa et al. (2008). However, optimal foraging is probably just an optional strategy (Díaz & Carrascal, 1993) as these lizards evidently consume any suitable sized arthropods that cross path with them, employing the sit-and-wait strategy and generally spend relatively little time actively foraging which are behaviours typically displayed by opportunistic feeders or food generalists (Pianka, 1971; Huey & Pianka, 1981; Luiselli, 2008). The in-situ feeding observations from this study are in agreement with the commonly held view that agamid lizards are sit-and-wait predators whereby they rely on visual cues (Huey & Pianka, 1981; Cooper, 1998) to make short but quick bouts to ambush preys in order to minimise energy expend (Pough, 1973; Brown & Nagy, 2007). Although these lizards have been observed to pursue a prey, the engagements were never more than a meter away. From the samples collected in this study, many prey captured can be classified as evasive or active prey that typically jump or fly to escape which is also in conformity with the findings on other ambush predators (Huey & Pianka, 1981; Pianka, 1986; Tan et al., 2020).

Additionally, the narrow niche overlap recovered between species pairs may be an error based on sample size constraints. It is strongly believed that these species might have had a higher overlap rate at the trophic niche than what was reported in the results of this

study. Opportunistic feeders as explained previously are usually relatively unselective of the prey available in their environment. Knowing that these sympatric lizards do share most of the microhabitat they occupy and activity time, they will have access to the same range of arthropod prey which can in turn increase the dietary niche overlap. Luiselli (2008) also mentioned in his study that lizard communities are unlikely to partition available food resources. Many other studies on trophic partitioning by coexisting lizards also agreed with this theory where sympatric lizards shares a similar diet composition resulting in a high dietary overlap (e.g., Capula & Luiselli, 1994; Hofer et al., 2003; Kuo et al., 2007; Sutherland, 2011; Maia-carneiro et al., 2017), albeit some studies have shown otherwise (Bombi & Bologna, 2002; Kuranova et al., 2005; Luiselli, 2007). Regardless, high dietary overlap does not necessarily indicate that there are competition between the overlapping species (Luiselli, 2008). Possible reasons for the lack of partitioning in the trophic level that allowed niche overlap and coexistence could be due to partitioning at other ecological niche dimension (temporal and spatial) and high food abundance (Kuo et al., 2007; Mamou et al., 2016).

This study further demonstrates that prey size was not significantly correlated with predator body size, and that larger individuals of these lizards do not necessarily feed on larger prey items. Results for *G. doriae* suggest a negative correlation that appear to suggest that smaller individuals feed on larger prey. This may be due to a single earthworm (largest prey item collected) that was found in the stomach of an insignificantly smaller *G. doriae*, though larger individuals can also easily feed on these earthworms. Thus, it is believed that the insufficient sample size might have also impacted the results of these predator–prey body size relationships. Studies often suggest that prey size should be positively correlated with predator body size (Brandl et al., 1994; Costa et al., 2008; Costa, 2009). Larger predators

were frequently shown to forage optimally by avoiding smaller prey because energetic cost of consuming smaller prey often exceeds energetic gain (Costa et al., 2008; Costa, 2009). However, profitability is not necessarily dependent on prey size but more so on prey type (Díaz & Carrascal, 1993). Nevertheless, results suggest that these lizards seem to consume largely on small sized preys, and occasionally on large arthropods. This perhaps was another way to minimize energy expenditure as handling time usually increases linearly with prey mass (Díaz & Carrascal, 1993). This is especially true in regards of these lizards as they usually chew on larger preys prior to swallowing. In other respects, this feeding behaviour may also be the case whereby predator includes larger preys into its diet as it grows but minimum prey size remains constant or increases at a much slighter slope (e.g., Sales et al., 2011). Unfortunately, results collected was insufficient to explore the presence of ontogenetic shifts in diet of these lizards to prove the said feeding behaviour. Regardless, these general feeders presumably feed on a wide range of prey sizes independent of their body size and there also seems to be no segregation in prey size consumed among the lizards.

4.6 Conclusions

Little literature has been available on the diet of *Gonocephalus* species. This study serves as the first assessment to record the diet of these lizards and presents a general idea on their feeding behaviour. *Gonocephalus* species were recorded to consume from 13 operational taxonomic units in this study including earthworm and snails that was not recorded previously. Although this study failed to determine any predilection for a certain prey, ants were considered as a common prey shared among these lizards. They displayed behaviours of an opportunistic feeder and assumed to also sometimes adopt the optimal feeding behaviour. Although only anecdotal information is available, indications are that the diversity of prey is believed to be in proportion relative to the availability in the environment. Additionally, there was no association between predator and prey body sizes in this genus. It is expected that the four species will largely overlap along the trophic axes of ecological space than what was reported. Even though findings detected dietary differences among these lizards, there was insufficient evidence to indicate presence of dietary partitioning among these congeneric lizards.

CHAPTER 5

THERMAL ECOLOGY

5.1 Introduction

Thermal resources are known to substantially influence life processes by altering physical properties and chemical rates related to metabolism. Factors such as topographical features, habitat heterogeneity, seasons and climate change often interact to produce complex patterns that affect environment temperature (Díaz et al., 2006; Deutsch et al., 2008; Sears et al., 2011; Graae et al., 2012). Thermal properties of a habitat is an indispensable resource especially for ectotherms (Magnuson et al., 1979; Hertz, 1992a). As a result, thermal studies have long been recognised as a fundamental aspect of ectotherm ecology. Lizards, as ectotherms, are known to rely on immediate environment temperature for their normal physiological and biochemical processes (Stevenson, 1985; Folguera et al., 2011; Zeng et al., 2013), which thus affects their behavioural and physiological capacity such as movement, habitat selection, reproduction and prey handling (Precht et al., 1973; Huey & Stevenson, 1979; Díaz, 1994; Angilletta et al., 2002).

Thermoregulation in lizards was initially assumed to be cost effective and that most lizards thermoregulate carefully (Bogert, 1959) and that the evolution of body temperatures is conservative within taxa (Bogert, 1949; Brattstrom, 1965). Huey and Slatkin (1976), however revealed their idea of benefits and costs of thermoregulation which propounded that thermoregulatory can be impractical in some lizards. Documentation of thermoconformity (Hertz, 1974; Huey, 1974; Huey & Webster, 1975; Herczeg et al., 2003; Basson et al., 2017), lack of careful thermoregulation (Soulé, 1963; Huey, 1974; Huey & Webster, 1975; Christian & Weavers, 1996), inter- and intraspecific body temperature differences (Soulé,

1963; Brattstrom, 1965; Pianka, 1969; Tosini & Avery, 1993; Labra et al., 2009) in lizards have challenged the original concept of physiological homeostasis in the lineage. Most lizards are relatively adept at regulating their body temperatures (T_b) within a specific range of tolerance often referred to as “set-point range” (Barber & Crawford, 1977; Hertz et al., 1993) as long as heat sources are available (Cowles & Bogert, 1944; Barber & Crawford, 1977; Bowker, 1984; Raske et al., 2012). Some lizards have set-point range that varies with season (Patterson & Davies, 1978; Sievert & Hutchison, 1989; Van Damme et al., 1986), sex and age (Patterson & Davies, 1978; Van Damme et al., 1986), physiological state (Barber & Crawford, 1977), hydric conditions (Rozen-Rechels et al., 2021), and food availability (Huey & Slatkin, 1976; Brown & Griffin, 2005). Lizards with different distributions, temporal activity patterns, and habitat utilisation also exhibit different thermal preferences and tolerances (Qu et al., 2011). This is achieved via adoption of different thermal strategies which often depend on the balance between their costs and benefits (Huey & Slatkin, 1976; Blouin-Demers & Nadeau, 2005), as excessive thermoregulation can sometimes reduce fitness (Soulé, 1963).

While most lizards are known to thermoregulate behaviourally by adjusting their activity periods (Hertz, 1992b; Adolph & Porter, 1993; Díaz & Cabezas-Díaz, 2004; Meiri et al., 2013; Ortega & Pérez-Mellado, 2016), shifting discriminately within the complex thermal structure of their microhabitats (‘thermotaxis’; Cowles & Bogert, 1944; Bauwens et al., 1996; Díaz & Cabezas-Díaz, 2004; Sagonas et al., 2017), or postural changes in body orientation (Bauwens et al., 1996; Aguado & Braña, 2014; Black & Tattersall, 2017; Rangel-Patiño et al., 2020). Nonetheless, not all lizards thermoregulate in the same way. Many species, especially in the tropics, apparently do not regulate their temperatures carefully (Ruibal & Philibosian, 1970; Hertz, 1974; Christian & Weavers, 1996), as thermoregulation

can be difficult or expensive in such environments (Huey, 1974). The canopy in tropical forests often shades the understory and only sparse patches of sunspots are available as basking sites, hence, a majority of tropical lizards tend to absorb heat mainly through convection (Bakken, 1992). Many have also developed the capacity to be active over a range of temperatures even at relatively low T_b that are close to their surroundings (Inger, 1959; Ruibal, 1961; Hertz, 1974). Additionally, some lizards are able to change colour (darker or lighter) rapidly to thermoregulate through regulating the absorptance of solar energy in both UV-visible (300–700 nm) and near-infrared (NIR; 700–2600 nm) wavelengths (Walton & Bennett, 1993; Langkilde & Boronow, 2012; Smith et al., 2016; Jayasekara et al., 2018). Several studies have also looked into the biochemical and physiological mechanisms that control thermal responses in lizards such as regulating blood flow and heat rates during heating and cooling (Bartholomew & Tucker, 1963; Morgareidge & White, 1969; Baker et al., 1972; Dzialowski & O'Connor, 2001).

Variance in thermal preferences and thermoregulatory behaviours among species and in some taxonomic groups have led us to believe that species may undergo thermal niche partitioning (e.g., Labra et al., 2009; Hertz et al., 2013). Indeed, much research suggests that if species are limited in space or time, they can compete for thermoregulatory opportunities (Ruibal, 1961; Roughgarden et al., 1981; Tracy & Christian, 1986; Buckley & Roughgarden, 2005; Paterson & Blouin-Demers, 2017). Some authors have suggested that sympatric reptiles differing in thermal preferences generally inhabit different thermal habitats with evidence of competition for and partitioning of thermal resources based on structural habitat (Ruibal, 1961; Schoener, 1970; Scheers & Van Damme, 2002; Singh et al., 2002; Row & Blouin-Demers, 2006; Sears & Angilletta, 2015; Li et al., 2017). However, Paterson & Blouin-Demers (2017) pointed out that because thermal resources cannot be consumed and

depleted by organisms in most circumstances, the competitive mechanism unlikely to be exploitative. Rather, interference competition for thermal resources may result in partitioning (Mushinsky et al., 1980; Paterson & Blouin-Demers, 2017). Nevertheless, documentation of lizard diel thermal biology is necessary for understanding their life history processes, as it can reveal much information of a species' such as their thermal preferences, thermal range, activity times and the degree of overlaps with syntopic congeners.

5.2 Specific Objectives

The three main objectives, with relevant research questions raised in this chapter, include:

- i. To describe the thermal biology of four syntopic species of *Gonocephalus*;

Different species have different preferred or ecritic body temperatures (Ruibal, 1961). Hence, what are the thermal preferences, thermal ranges, and active body temperatures of the four species? Do these species exhibit interspecific or sexual variation in their thermal biology?

- ii. To determine the factors affecting the thermal biology of *Gonocephalus*;

Since temperature is a major determinant of a lizard's spatial and trophic niche (Pianka, 1973), what are the factors that affect the thermal biology used by these species. Is body temperature correlated to ambient and substrate temperatures? Does humidity of the surroundings affect them as well? What other factors influence their thermal biology?

- iii. To determine thermal regulation strategies used by *Gonocephalus*.

Huey & Slatkin (1976) suggested that lizards thermoregulate differently, where some thermoregulate actively and others might not, depending on the cost and benefits of thermoregulating in its environment. To further understand the thermoregulation of these

lizards, it is vital to understand the behaviours of these lizards in order to identify the source of heat gain. Also, do these lizards exhibit the same thermoregulation strategy?

5.3 Specific Methodology

5.3.1 Thermal Data Collection

Thermal data were recorded from lizards encountered in Kubah National Park during visual encounter surveys (VES) and radio-tracking trips. Two non-invasive methods were used to measure the body temperature, T_b of these lizards and their perch surface, T_s . These temperature readings were taken repeatedly thrice to compute a mean value for the measurements. Ambient temperature, T_a was measured using a 4-in-1 humidity, temperature, airflow, and light meter (Extech model 45170, Nashua, New Hampshire, USA).

5.3.2 Non-invasive Methods to Measure Body Temperature

The use of a thermocouple to measure cloacal temperature is a conventional and well-established method for estimating T_b in reptiles. However, there are several drawbacks to this approach. Because the animal must first be trapped and handled, followed by the insertion of a thermocouple into the cloaca, such process may cause the animal's respiration rate to increase (Langkilde & Shine, 2006) and may further initiate a stress response involving elevated plasma corticosterone (Moore et al., 1991; Langkilde et al., 2005; Langkilde & Shine, 2006) which can potentially result in an unrepresentative T_b measurement. Hence, two non-invasive methods were used to measure the body temperature, T_b in this study.

Body surface temperature, T_b and perch surface temperature, T_s were recorded using a handheld infrared laser thermometer (Fluke 62 MAX) (Figure 5.1). The unit measures

temperatures from -30°C to 500°C with an accuracy of +1.5°C or +1.5% of reading, whichever is greater (Fluke Corporation, 2012). Infrared thermometers determine surface temperature through measuring the amount of infrared energy radiated by the target's surface and have been proven to accurately measure T_b in ectotherms such as amphibians and reptiles (Christian et al., 1998; Rowley & Alford, 2007; Chukwuka et al., 2019). An important factor to consider when using an infrared thermometer is the measure distance between the device and the subject (Taylor et al., 2020). When temperature is taken far from the subject, the accuracy of the reading can become dubious, as there will be more atmospheric interference (Faye et al., 2016). Moreover, infrared thermometer measures temperature of an area also known as a spot. The Fluke 62 MAX had a 10:1 distance to spot ratio which means it measures a 1-inch spot at distance of 10 inches (Fluke Corporation, 2012). The spot radius increases with distance and the laser emitted from the device only act as guide for users to pinpoint the target for more accurate readings (Figure 5.2).

The second method include the external attachment of thermal sensitive radio-transmitters on the lizards to obtain their T_b . While most studies surgically implanted the transmitters to obtain core body temperature of the study subject (e.g., Rismiller & Heldmaier, 1982; Seebacher et al., 2005; Rock & Cree, 2008), transmitters were attached externally to the lizard at the dorsal side on the left or right flank of the pelvic girdle in this study, given the light body mass of these lizards. Handling was kept to a minimum when transmitters were attached, thus reducing stress on the animal and avoiding unnecessary mortality. Furthermore, many studies have demonstrated the reliability of using skin temperature as a proxy for measuring body temperature in lizards (Bartholomew & Tucker, 1963; Berg et al., 2015; Barroso et al., 2016). The BD-2 series temperature-sensitive radio transmitter from Holohil Systems Ltd. (Carp, Ontario, Canada) was used in this study (refer

to Sections 3.3.1 and 3.3.2 for details of transmitter and attachment method). The transmitter allowed estimates of the T_b of the lizard by counting the pulse rate (time taken to complete 10 pulses) and correlating it to the calibration curves of each transmitter. Any increment or decrement in temperature results in a corresponding increase or decrease in pulse rate that differs among individual transmitters. Hence, each transmitter was calibrated before the attachment in a water bath.

These non-invasive methods present an ethically valid approach to the study of thermal biology in animals which reduces stress, preserving natural behaviours, and most importantly diminishing the chance of altering the animals' T_b . Additionally, these methods can ease the process of data collection, as researchers can rapidly record T_b without having to catch the animal multiple times.

5.3.3 Data Analyses

All T_b recorded using the two non-invasive methods were tested using t-tests to test for statistically significant differences. T_b of the four species measured using the two methods were also compared using one-way ANOVAs. Since the temperature recorded were not equal for the four species, and violated the assumption of homogeneity of variances, the Welch's t-test was conducted to further support the significance of the one-way ANOVAs. In case where significant difference was present, a Games-Howell post hoc test was conducted to compare all possible combinations of group differences. This also applies analogously to all following comparisons between females and males T_b , day and night T_b , active and sedentary T_b , and with environmental variables. A multiple regression analysis was used to evaluate the combined influence of T_a , T_s , and RH on T_b . All data were log-transformed for linearity and analyses were performed in IBM SPSS software.



Figure 5.1: Measuring surface body temperature, T_b and perch surface temperature, T_s using a handheld infrared laser thermometer (Fluke 62 MAX)



Figure 5.2: The single red laser emitted from the handheld infrared laser thermometer pinpoints the target for accurate temperature readings. Picture shows an adult female *Gonocephalus bornensis*

5.4 Results

5.4.1 Body Temperature, T_b of *Gonocephalus*

The mean for all field T_b recorded for the four species of *Gonocephalus* was 24.7°C ($\pm$ SD 1.1; $\pm$ SE 0.03; $n = 820$) when measured with the handheld infrared laser thermometer and 26.1°C ($\pm$ SD 1.3; $\pm$ SE 0.04; $n = 714$) when measured using temperature-sensitive radio transmitter. T_b ranged from 19.4°C to 34.9°C for the sample. Figure 5.3 and Table 5.2 show the T_b of the four species of *Gonocephalus* measured via the two non-invasive methods. T_b recorded from the two non-invasive methods were shown to differ significantly in this study ($t = 20.520$, $df = 1291.703$, $P < 0.001$). T_b measured using temperature-sensitive radio transmitter showed significant difference ($F = 16.747$, $P < 0.001$) between several pairs of *Gonocephalus* (Table 5.1), however, when measured using the handheld infrared laser thermometer T_b was not significantly different interspecifically ($F = 1.089$, $P = 0.354$).

Additionally, T_b measured using temperature-sensitive radio transmitter showed no significant difference between females and males ($t = 0.646$, $df = 686.732$, $P = 0.518$). Within each species, *G. grandis* ($t = -1.936$, $df = 218.077$, $P = 0.054$), *G. bornensis* ($t = 0.821$, $df = 149.158$, $P = 0.413$) and *G. liogaster* ($t = 0.987$, $df = 161$, $P = 0.325$) also did not show significant difference intersexually, however, T_b was significantly different ($t = 3.048$, $df = 82.443$, $P = 0.003$) between females and males of *G. doriae*. When handheld infrared laser thermometer was used, female, male and juveniles showed no significant difference ($F = 0.382$, $P = 0.683$) in T_b , even within each respective species (*G. grandis*: $F = 0.511$, $P = 0.603$; *G. doriae*: $F = 0.104$, $P = 0.902$; *G. bornensis*: $F = 0.116$, $P = 0.891$; *G. liogaster*: $F = 0.82$, $P = 0.922$). Effect of SVL ($r = 0.035$, $N = 156$, $p = 0.669$) and mass ($r = 0.059$, $N = 160$, $p = 0.46$) on T_b was also not relevant in this study.

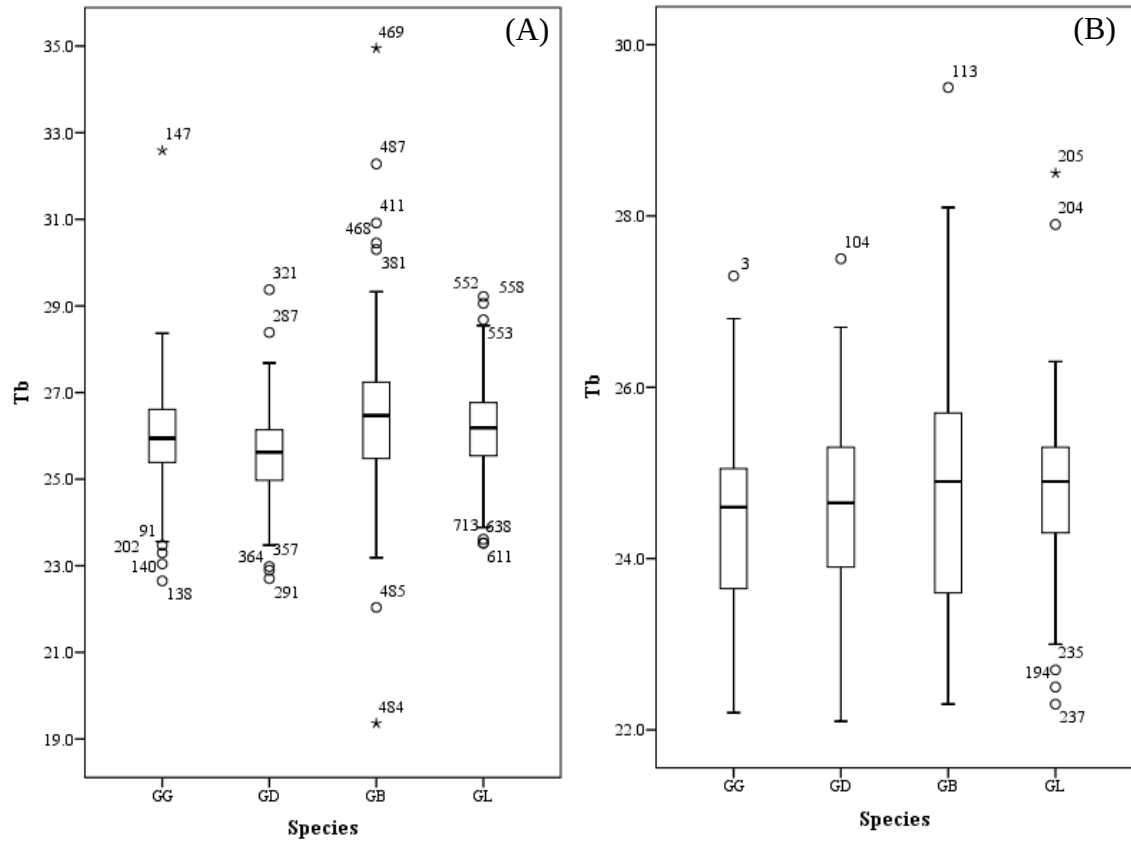


Figure 5.3: Boxplots used to visualise differences between T_b in the four species of *Gonocephalus*. (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. GG: *Gonocephalus grandis*; GD: *Gonocephalus doriae*; GB: *Gonocephalus bornensis*; GL: *Gonocephalus liogaster*; Thick line in the middle represents median; Top and bottom box lines show first and third quartiles; Whiskers show the maximum and minimum values; (°) defines outliers; (*) denotes extremes

Table 5.1: Games-Howell post hoc comparisons of mean body temperature, T_b between species of *Gonocephalus*. (*) mean difference is significant at the 0.05 level

	<i>G. grandis</i>	<i>G. doriae</i>	<i>G. bornensis</i>	<i>G. liogaster</i>
<i>G. grandis</i>	-			
<i>G. doriae</i>	<0.001*	-		
<i>G. bornensis</i>	0.004*	<0.001*	-	
<i>G. liogaster</i>	0.465	<0.001*	0.119	-

Table 5.2: Body temperature, T_b of four species of *Gonocephalus* measured via two non-invasive methods. n = total individual; N = total individual of species; SD = standard deviation; SE = standard error; Juv = juvenile

		<i>G. grandis</i>			<i>G. doriae</i>			<i>G. bornensis</i>			<i>G. liogaster</i>		
		Female	Male	Juv	Female	Male	Juv	Female	Male	Juv	Female	Male	Juv
T _b measured via infrared laser thermometer	n	17	28	11	23	17	10	31	37	7	33	19	8
	N	56			50			75			60		
	Mean (°C)	24.7	24.5	24.2	24.5	24.6	24.7	24.9	24.9	24.6	24.9	24.8	24.8
	N mean (°C)	24.5			24.6			24.8			24.8		
	SD	1.1			1.1			1.5			1.1		
	SE	0.1			0.2			0.2			0.1		
	Minimum (°C)	22.2	22.8	22.4	22.1	22.1	23.2	22.3	22.6	22.6	22.3	22.5	23.3
	Maximum (°C)	27.3	26.8	25.4	27.5	26.6	26.7	29.5	27.6	26.5	28.5	25.8	26.2
T _b measured via temperature-sensitive radio transmitter	n	100	125	NA	92	54	NA	95	84	NA	66	97	NA
	N	225			146			179			163		
	Mean (°C)	25.8	26.2	NA	25.7	25.4	NA	25.9	26.8	NA	26.3	26.1	NA
	N mean (°C)	26.0			25.5			26.5			26.2		
	SD	1.1			1.0			1.7			1.1		
	SE	0.1			0.1			0.1			0.1		
	Minimum (°C)	23.5	22.7	NA	22.7	22.9	NA	23.2	19.4	NA	23.5	23.5	NA
	Maximum (°C)	28.3	32.6	NA	28.4	29.4	NA	30.9	34.9	NA	29.2	28.4	NA

5.4.2 Relationship of T_b and Ambient Temperature, T_a

The mean value of field T_a was 27.8°C ($\pm$ SD 1.8; $\pm$ SE 0.06; $n = 934$) measured using a 4-in-1 humidity, temperature, airflow, and light meter. T_a recorded ranges from 20°C to 37.5°C. Day temperature readings averaged 27.7°C ($\pm$ SD 1.2; $\pm$ SE 0.06; $n = 441$) while night-time temperature was slightly higher, averaging 27.9°C ($\pm$ SD 2.2; $\pm$ SE 0.1; $n = 493$). However, there was no significant difference between day and night temperatures ($t = -1.751$, $df = 798.84$, $P = 0.08$).

T_a was positively correlated to T_b of these lizards (A: $r = 0.319$, $N = 696$, $p < 0.001$; B: $r = 0.741$, $N = 238$, $p < 0.001$) where both correlations were positive suggesting that T_b of these lizards increases with T_a (Figure 5.4). Figure 5.5 shows the regression of $\log T_b$ of each *Gonocephalus* on $\log T_a$. The regressions are highly significant for all species of *Gonocephalus* in both non-invasive methods of measuring T_b (Table 5.3). From this, it seemed that T_b of *G. liogaster* ($R^2 = 0.2227$) is most closely correlated to T_a compared to the other species of *Gonocephalus* when T_b was measured using temperature-sensitive radio transmitters. However, when T_b was measured using the infrared laser thermometer, T_b of *G. doriae* ($R^2 = 0.6723$) is most closely correlated to T_a .

Generally, these lizards have lower T_b than the associated T_a and T_b were never equal to T_a in both non-invasive methods of measuring T_b (Table 5.4). On average, T_b recorded were 1.98°C ($\pm$ SD 1.89; $\pm$ SE 0.07; $n = 696$) lower than T_a when measured using temperature-sensitive radio transmitters, whereas T_b recorded was 2.38°C ($\pm$ SD 0.98; $\pm$ SE 0.06; $n = 238$) lower than T_a when measured using the infrared laser thermometer.

Table 5.5 shows a summary of the day and night T_b of the species of *Gonocephalus* recorded from the two non-invasive methods. Although day and night T_a were fairly similar, T_b of these lizards were significantly higher during the day (measured via infrared laser

thermometer: $t = 6.28$, $df = 121.999$, $P < 0.001$; measured via temperature-sensitive radio transmitter: $t = 8.324$, $df = 687.882$, $P < 0.001$). Within each species, day T_b of *G. grandis* ($t = 3.069$, $df = 53$, $P = 0.003$), *G. bornensis* ($t = 4.691$, $df = 71$, $P < 0.001$), and *G. liogaster* ($t = 3.913$, $df = 25.372$, $P = 0.001$) was significantly different from night T_b when measured via infrared laser thermometer, only *G. doriae* showed no significant day and night difference in T_b ($t = 0.232$, $df = 48$, $P = 0.817$). However, when T_b was taken using the temperature-sensitive radio transmitter, all species showed significant different day and night T_b (*G. grandis*: $t = 6.779$, $df = 214.997$, $P < 0.001$; *G. doriae*: $t = 2.886$, $df = 136.206$, $P = 0.005$; *G. bornensis*: $t = 4.108$, $df = 157.736$, $P < 0.001$; *G. liogaster*: $t = 3.605$, $df = 158$, $P < 0.001$)

Table 5.3: Pearson correlation coefficients (r) for the relation of log body temperature, T_b and log ambient temperature, T_a by species of *Gonocephalus* using two non-invasive methods to measure T_b . N = number of pairs of data; p = p-value

	<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
T_b measured via temperature-sensitive radio transmitter	$r = 0.23$, $N = 177$, $p = 0.002$	$r = 0.373$, $N = 142$, $p < 0.001$	$r = 0.337$, $N = 217$, $p < 0.001$	$r = 0.472$, $N = 160$, $p < 0.001$
T_b measured via infrared laser thermometer	$r = 0.704$, $N = 73$, $p < 0.001$	$r = 0.820$, $N = 50$, $p < 0.001$	$r = 0.760$, $N = 55$, $p < 0.001$	$r = 0.743$, $N = 60$, $p < 0.001$

Table 5.4: Differences between body temperature, T_b and ambient temperature, T_a ($T_b - T_a$) of the four species of *Gonocephalus* measured via two non-invasive methods. < 0 = difference less than zero; $= 0$ = difference equals zero; > 0 = difference more than zero; percentages in parentheses

	$T_b - T_a$	<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
T_b measured via temperature-sensitive radio transmitter	< 0 , n (%)	153 (86.441)	136 (95.775)	212 (97.696)	147 (91.875)
	$= 0$, n (%)	0 (0)	0 (0)	0 (0)	0 (0)
	> 0 , n (%)	24 (13.559)	6 (4.225)	5 (2.304)	13 (8.125)
T_b measured via infrared laser thermometer	< 0 , n (%)	72 (98.63)	50 (100)	55 (100)	60 (100)
	$= 0$, n (%)	0 (0)	0 (0)	0 (0)	0 (0)
	> 0 , n (%)	1 (1.37)	0 (0)	0 (0)	0 (0)

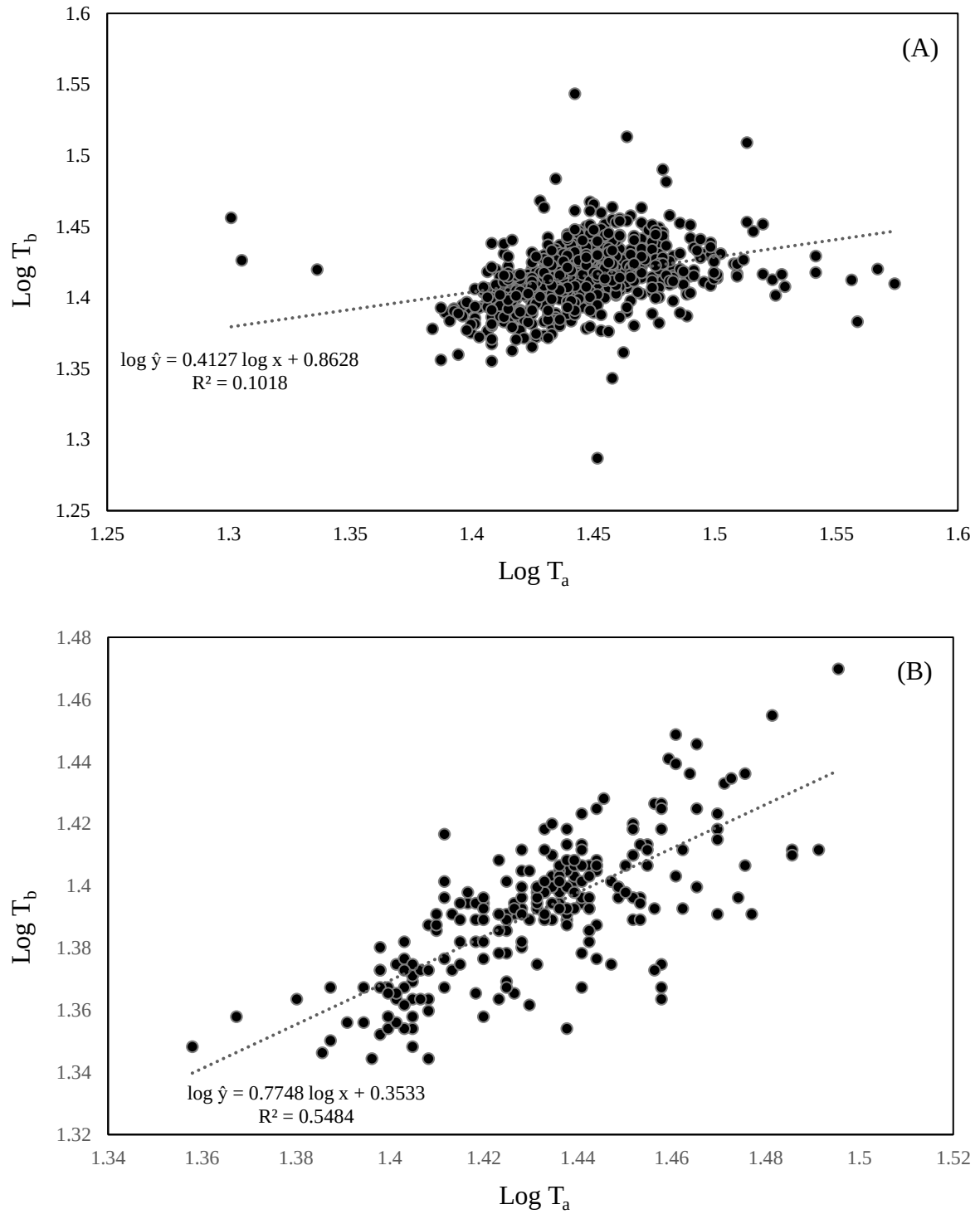


Figure 5.4: Regression of log body temperature, T_b of *Gonocephalus* on log ambient temperature, T_a . (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. R^2 = Coefficient of determination

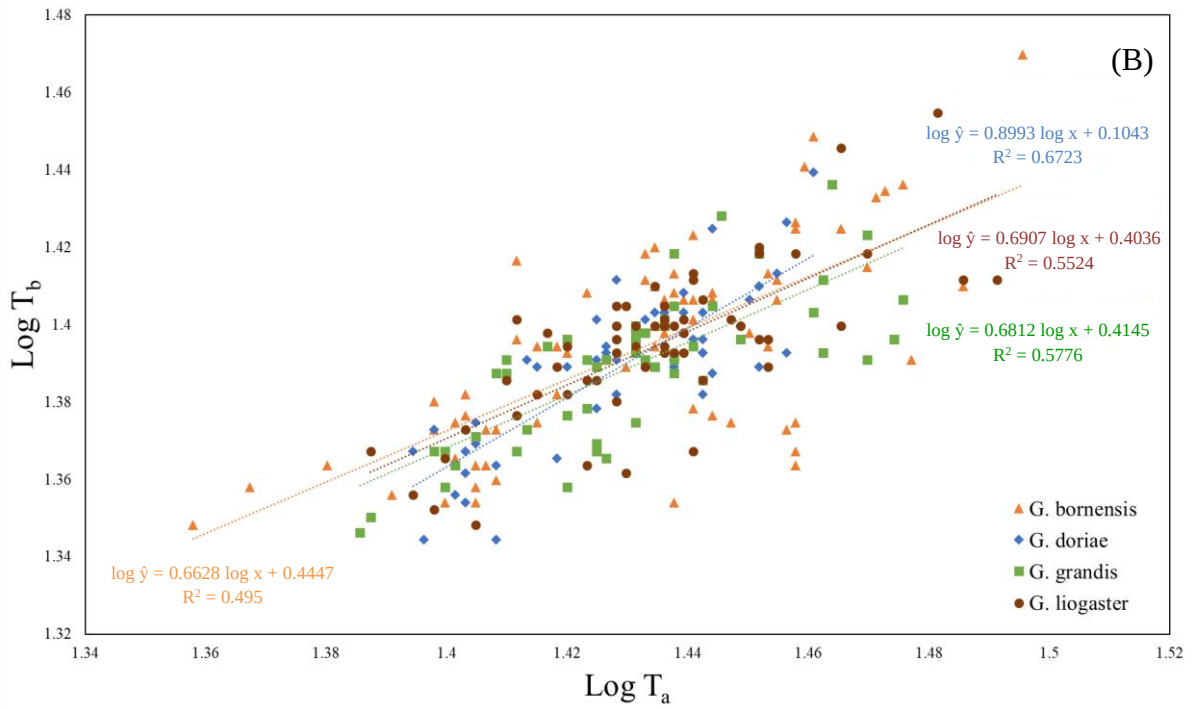
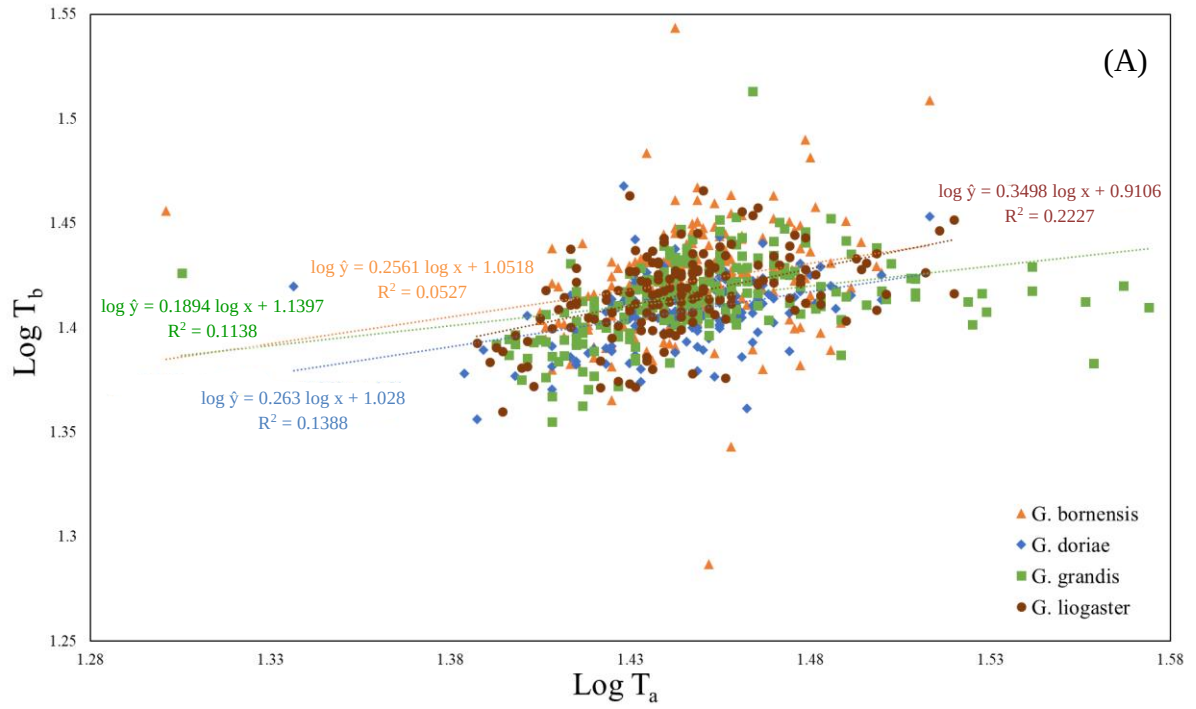


Figure 5.5: Regression of log body temperature, T_b of each *Gonocephalus* on log ambient temperature, T_a . (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. R^2 = Coefficient of determination

Table 5.5: Day and night body temperature, T_b of the four species of *Gonocephalus* measured via two non-invasive methods. n = total individual; N = total individual of species; SD = standard deviation; SE = standard error

		<i>G. grandis</i>		<i>G. doriae</i>		<i>G. bornensis</i>		<i>G. liogaster</i>	
		Day	Night	Day	Night	Day	Night	Day	Night
T _b measured via infrared laser thermometer	n	10	45	13	37	30	43	16	44
	N	55		50		73		60	
	Mean (°C)	25.4	24.3	24.6	24.6	25.7	24.2	25.7	24.5
	N mean (°C)	24.5		24.6		24.8		24.8	
	SD	1.1		1.1		1.5		1.1	
	SE	0.1		0.2		0.2		0.1	
	Minimum (°C)	23.8	22.2	23	22.1	23.1	22.3	24.5	22.3
	Maximum (°C)	27.3	26.2	25.8	27.5	29.5	26.6	28.5	26.3
T _b measured via temperature-sensitive radio transmitter	n	119	98	77	65	94	83	82	78
	N	217		142		177		160	
	Mean (°C)	26.4	25.5	25.8	25.3	27.0	26.0	26.4	25.8
	N mean (°C)	26.0		25.6		26.5		26.1	
	SD	1.1		1.0		1.7		1.2	
	SE	0.1		0.1		0.1		0.1	
	Minimum (°C)	22.7	23.0	23.5	22.7	19.4	23.2	23.5	22.9
	Maximum (°C)	32.6	27.4	29.4	28.4	34.9	28.6	29.2	28.3

5.4.3 Relationship of T_b and Substrate Temperature, T_s

Associated T_s varied from 22.1°C to 30.0°C with an average of 24.7°C ($\pm$ SD 1.1; $\pm$ SE 0.04; $n = 839$). Figure 5.5 illustrates the regressions of T_b on T_s for both non-invasive methods of measuring T_b (A: $r = 0.676$, $N = 600$, $p < 0.001$; B: $r = 0.992$, $N = 238$, $p < 0.001$). The regressions are highly significant for both, suggesting that T_b of these lizards are likely to be influenced by T_s . The slope of regression in Figure 5.6 (B) is steeper than that of Figure 5.6 (A) and the R^2 is higher, indicating that T_b measured via the infrared laser thermometer is more closely coupled to T_s . This can be further visualised by looking into the differences between T_b and T_s (Table 5.7), when T_b was measured via the infrared laser thermometer varied, it from -1.6 °C to 0.7 °C. On average, T_b was only 0.02°C above T_s ($\pm$ SD 0.2; $\pm$ SE 0.01; $n = 239$). A total of 180 (75.63%) of these recorded T_b were equal to T_s , while 49 (20.59%) had higher T_b readings and only nine (3.78%) T_b were lower than T_s . However, when T_b was recorded with temperature-sensitive radio transmitters, differences between T_b and T_s were greater. The differences varied from -5.8°C to 8.8°C and T_b was on an average 1.4°C higher than T_s ($\pm$ SD 0.96; $\pm$ SE 0.04; $n = 600$). A total of 564 (94%) of the recorded T_b had higher readings than T_s and the remaining 36 (6%) were lower. There were no equal T_b and T_s recorded when T_b was measured via temperature-sensitive radio transmitters.

Figure 5.7 shows the regression of $\log T_b$ of each *Gonocephalus* on $\log T_s$. The regressions are highly significant for all four species of *Gonocephalus* in both non-invasive methods of measuring T_b (Table 5.6). From this, it seemed that T_b of *G. doriae* is most closely correlated to T_s compared to its congeners, when T_b was measured using temperature-sensitive radio transmitters. However, when T_b was measured using the infrared

laser thermometer, the regressions of all species appeared fairly similar, in that T_b of all four species were highly correlated to T_s .

Generally, these lizards have higher T_b than the associated T_s when T_b were measured via temperature-sensitive radio transmitters. Especially in *G. grandis*, 98.6% of the T_b recorded were higher than T_s . Amongst all its congeneric species, *G. doriae* showed the highest percentage (10.8%) of readings with lower T_b than the T_s . However, when T_b was measured using the infrared laser thermometer, most of the lizards had the same T_b and T_s reading.

Table 5.6: Pearson correlation coefficients (r) for the relation of log body temperature, T_b and log substrate temperature, T_s by each species of *Gonocephalus* using two non-invasive methods to measure T_b . N = number of pairs of data; p = p-value

	<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
T_b measured via temperature-sensitive radio transmitter	$r = 0.645$, $N = 170$, $p < 0.001$	$r = 0.385$, $N = 139$, $p < 0.001$	$r = 0.873$, $N = 139$, $p < 0.001$	$r = 0.712$, $N = 152$, $p < 0.001$
T_b measured via infrared laser thermometer	$r = 0.988$, $N = 73$, $p < 0.001$	$r = 0.993$, $N = 50$, $p < 0.001$	$r = 0.994$, $N = 55$, $p < 0.001$	$r = 0.998$, $N = 60$, $p < 0.001$

Table 5.7: Differences between body temperature, T_b and substrate temperature, T_s ($T_b - T_s$) of four species of *Gonocephalus* measured via two non-invasive methods. N = total individual of species; SD = standard deviation; < 0 = difference less than zero; = 0 = difference equals zero; > 0 = difference more than zero; percentages in parentheses

		<i>G. bornensis</i>	<i>G. doriae</i>	<i>G. grandis</i>	<i>G. liogaster</i>
T _b measured via temperature-sensitive radio transmitter	N	170	139	139	152
	Mean (°C)	1.518666	1.193381	1.363069	1.326962
	Minimum (°C)	-5.83957	-2.53349	-1.36487	-0.92134
	Maximum (°C)	8.849871	4.875297	2.795514	3.804957
	SD	1.219127	1.046414	0.566025	0.789472
	< 0, n (%)	9 (5.3)	15 (10.8)	2 (1.4)	10 (6.6)
	= 0, n (%)	0	0	0	0
	> 0, n (%)	161 (94.7)	124 (89.2)	137 (98.6)	142 (93.4)
T _b measured via infrared laser thermometer	N	73	50	55	60
	Mean (°C)	0.031507	0.042	-0.01091	0.033333
	Minimum (°C)	-1.6	-0.1	-0.9	-0.1
	Maximum (°C)	0.5	0.7	0.1	0.4
	SD	0.229054	0.141551	0.125717	0.0837
	< 0, n (%)	4 (5.5)	1 (2)	2 (3.6)	2 (3.3)
	= 0, n (%)	48 (65.8)	39 (78)	49 (89.1)	44 (73.3)
	> 0, n (%)	21 (28.8)	10(20)	4 (7.3)	14 (23.3)

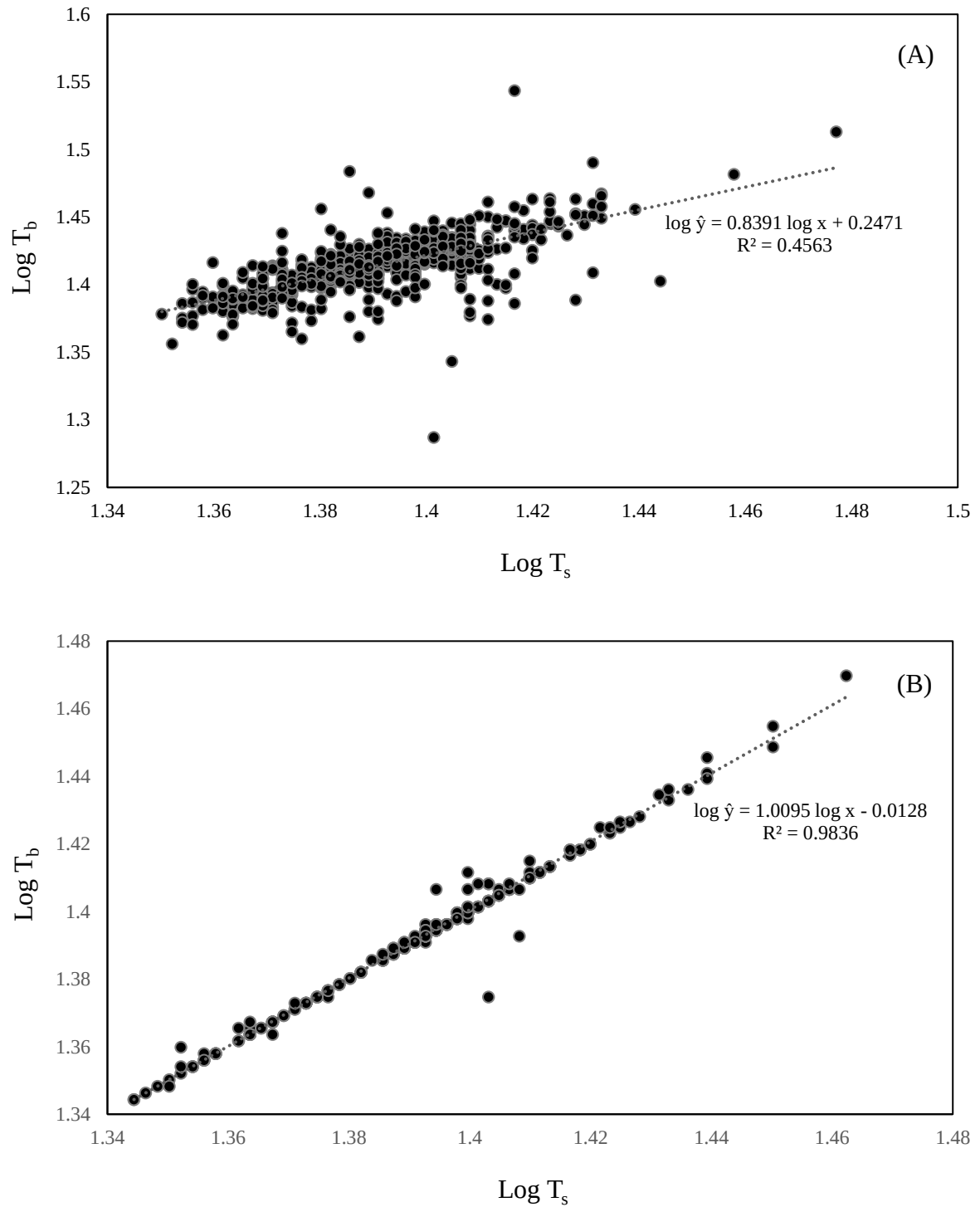


Figure 5.6: Regression of log body temperature, T_b of *Gonocephalus* on log substrate temperature, T_s . (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. R^2 = Coefficient of determination

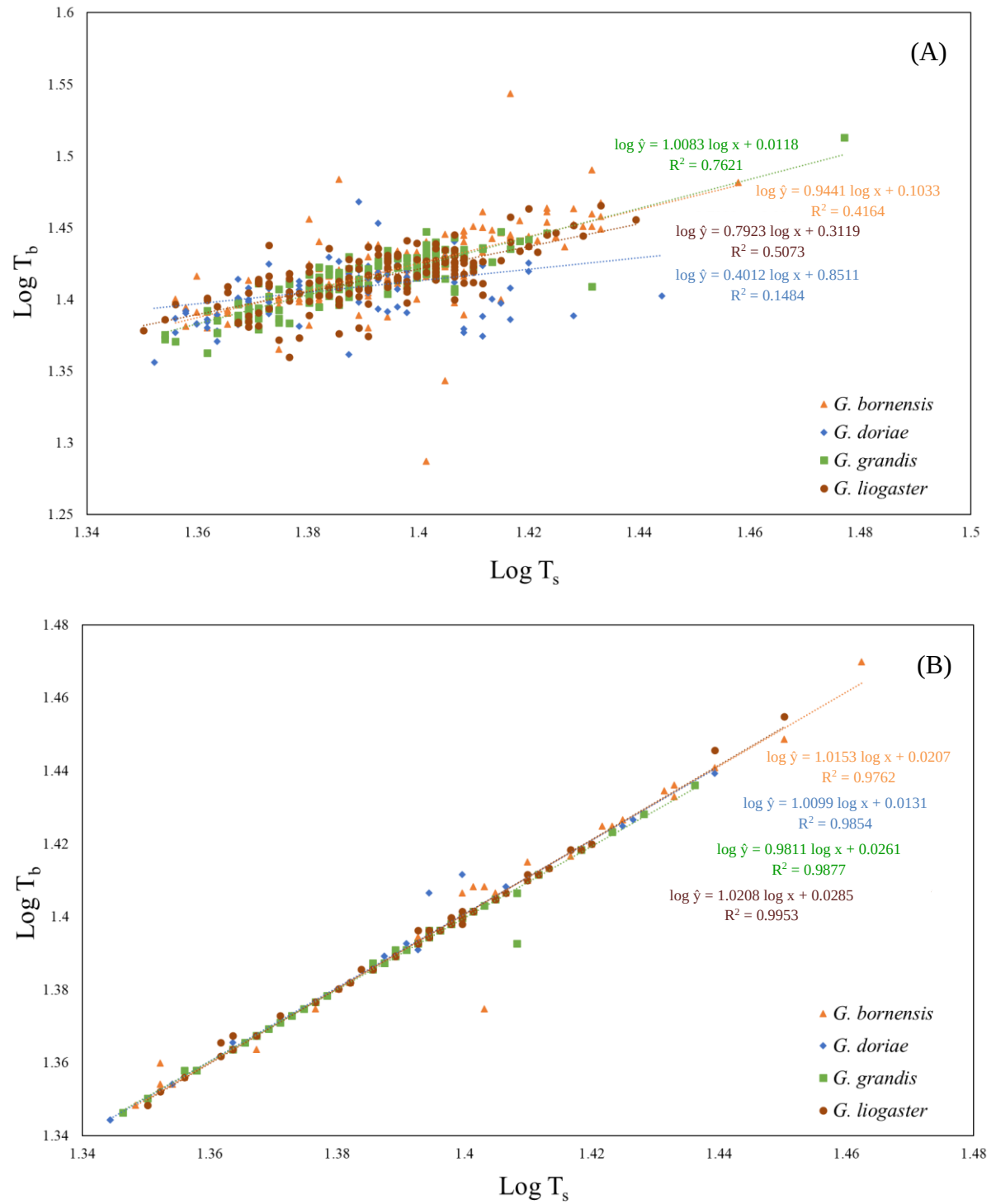


Figure 5.7: Regression of log body temperature, T_b of each *Gonocephalus* on log substrate temperature, T_s . (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. R^2 = Coefficient of determination

5.4.4 Relationship of T_b and State of Activity

In this study, state of activity was regarded as either sedentary or active when lizard was initially encountered. Lizards were considered sedentary when it shows no sign of movement such as perching or sleeping whilst when lizards showed any intensity of movement such as running, walking, and foraging were considered as active.

Disregarding the time of the day, many of the lizards encountered were sedentary ($n = 1430$; 94.62%). Besides one individual that jumped off its perch even before it was approached, there were no lizards that were active at night. This come as no surprise as they have been previously classified as diurnal species (Das, 2010). Nevertheless, only 5.38% of the observed lizards were active during the day. Table 5.10 shows a summary of sedentary and active body temperature, T_b of the four species of *Gonocephalus* measured via two non-invasive methods. Active lizards during the day had an average T_b of 26.9°C ($\pm$ SD 1.2; $\pm$ SE 0.19; $n = 43$) measured via temperature-sensitive radio transmitters and 25.65°C ($\pm$ SD 1.3; $\pm$ SE 0.23; $n = 30$) measured via the infrared laser thermometer. Sedentary lizards during the day had an average T_b of 26.5°C ($\pm$ SD 1.4; $\pm$ SE 0.09; $n = 248$) measured via temperature-sensitive radio transmitters and 25.3°C ($\pm$ SD 1.2; $\pm$ SE 0.19; $n = 39$) measured via the infrared laser thermometer. Whereas sedentary lizards during the night had an average T_b of 25.6°C ($\pm$ SD 1.06; $\pm$ SE 0.06; $n = 314$) measured via temperature-sensitive radio transmitters and 24°C ($\pm$ SD 1.1; $\pm$ SE 0.085; $n = 169$) measured via the infrared laser thermometer. Active lizards generally had significantly higher T_b than sedentary lizards (measured via temperature-sensitive radio transmitter: $t = 4.848$, $df = 50.603$, $P < 0.001$; measured via infrared laser thermometer: $t = 4.627$, $df = 37.986$, $P < 0.001$) and sedentary lizards showed significantly higher T_b during the day compared to night (measured via temperature-sensitive radio transmitter: $t = 7.849$, $df = 456.657$, $P < 0.001$).

When compared among the four species of *Gonocephalus*, mean active T_b during the day was not significantly different ($F = 0.272$, $P = 0.845$) but mean sedentary T_b was significantly different between some species both by day ($F = 10.644$, $P < 0.001$) and at night ($F = 12.805$, $P < 0.001$). Table 5.8 and Table 5.9 show the Games-Howell post hoc comparisons of day and night sedentary mean T_b between species of *Gonocephalus*, respectively. All active and sedentary mean T_b in both day and night was not significantly different between sexes (Active: $t = 0.976$, $df = 39.864$, $P = 0.335$; Day sedentary: $t = -0.672$, $df = 225.78$, $P = 0.502$; Night sedentary: $t = -1.082$, $df = 311.380$, $P = 0.280$).

Table 5.8: Games-Howell post hoc comparisons of day sedentary mean body temperature, T_b between species of *Gonocephalus*. (*) mean difference is significant at the 0.05 level

	<i>G. grandis</i>	<i>G. doriae</i>	<i>G. bornensis</i>	<i>G. liogaster</i>
<i>G. grandis</i>	-			
<i>G. doriae</i>	0.001*	-		
<i>G. bornensis</i>	0.84	<0.001*	-	
<i>G. liogaster</i>	0.34	0.002*	0.045*	-

Table 5.9: Games-Howell post hoc comparisons of night sedentary mean body temperature, T_b between species of *Gonocephalus*. (*) mean difference is significant at the 0.05 level

	<i>G. grandis</i>	<i>G. doriae</i>	<i>G. bornensis</i>	<i>G. liogaster</i>
<i>G. grandis</i>	-			
<i>G. doriae</i>	0.139	-		
<i>G. bornensis</i>	0.002*	<0.001*	-	
<i>G. liogaster</i>	0.014*	<0.001*	0.932	-

Table 5.10: Sedentary and active body temperature, T_b of the four species of *Gonocephalus* measured via two non-invasive methods. n = total individual; N = total individual of species; SD = standard deviation; SE = standard error

		<i>G. grandis</i>		<i>G. doriae</i>		<i>G. bornensis</i>		<i>G. liogaster</i>	
		Sedentary	Active	Sedentary	Active	Sedentary	Active	Sedentary	Active
T _b measured via infrared laser thermometer	n	56	19	48	2	51	5	56	6
	N	75		50		56		62	
	Mean (°C)	24.5	25.9	24.6	24.5	24.4	25.3	24.7	25.7
	N mean (°C)	24.8		24.6		24.5		24.8	
	SD	1.5		1.1		1.1		1.1	
	SE	0.2		0.2		0.1		0.1	
	Minimum (°C)	22.3	23.7	22.1	24.5	22.2	24.4	22.3	24.8
	Maximum (°C)	28.1	29.5	27.5	24.5	26.8	27.3	28.5	27.9
T _b measured via temperature-sensitive radio transmitter	n	163	9	136	6	120	26	152	4
	N	172		142		146		156	
	Mean (°C)	26.5	26.9	25.4	26.8	25.8	26.8	26.1	27.4
	N mean (°C)	26.5		25.5		26.0		26.2	
	SD	1.7		1.1		1.1		1.1	
	SE	0.1		0.1		0.1		0.1	
	Minimum (°C)	19.4	24.9	22.7	26.1	23.0	25.7	23.5	26.2
	Maximum (°C)	34.9	32.3	28.4	29.4	32.6	28.0	29.1	29.2

5.4.5 Relationship of T_b and Relative Humidity, RH

The mean for all field RH recorded was 83% ($\pm$ SD 7.565; $\pm$ SE 0.245; $n = 956$) measured within recorded ranges from 52.8% to 98.4%. Daily readings averaged 83.44% ($\pm$ SD 6.05; $\pm$ SE 0.287; $n = 445$), while night temperature was recorded to be somewhat lower, averaging at 82.52% ($\pm$ SD 8.719; $\pm$ SE 0.391; $n = 497$). Correlation suggested that there was a significant difference between day and night ($t = 1.901$, $df = 886.485$, $P < 0.001$). Active and sedentary lizards also showed significance difference in RH preference ($t = 5.388$, $df = 104.147$, $P < 0.001$) with active lizards preferring an average of 86.4% ($\pm$ SD 5.469; $\pm$ SE 0.636; $n = 74$) whilst sedentary lizards preferred an average of 82.7% ($\pm$ SD 7.763; $\pm$ SE 0.282; $n = 758$). Between species of *Gonocephalus*, significant difference in the context of RH preference was observed ($F = 0.7.426$, $P < 0.001$), the difference detected between *G. bornensis* and its congeners (Table 5.11). Figure 5.8 illustrate the regressions of RH on T_b for both non-invasive methods of measuring T_b . The regressions are significant for both (A: $r = -0.155$, $N = 696$, $p < 0.001$; B: $r = -0.166$, $N = 238$, $p = 0.01$), suggesting that T_b of these lizards are likely to be influenced by RH. Figure 5.8 (A) showed a positive correlation indicating that T_b increases with RH whereas Figure 5.8 (B) showed the contrary.

Table 5.11: Games-Howell post hoc comparisons of relative humidity, RH between species of *Gonocephalus*. (*) mean difference is significant at the 0.05 level

	<i>G. grandis</i>	<i>G. doriae</i>	<i>G. bornensis</i>	<i>G. liogaster</i>
<i>G. grandis</i>	-			
<i>G. doriae</i>	0.586	-		
<i>G. bornensis</i>	<0.001*	0.014*	-	
<i>G. liogaster</i>	0.826	0.98	0.004*	-

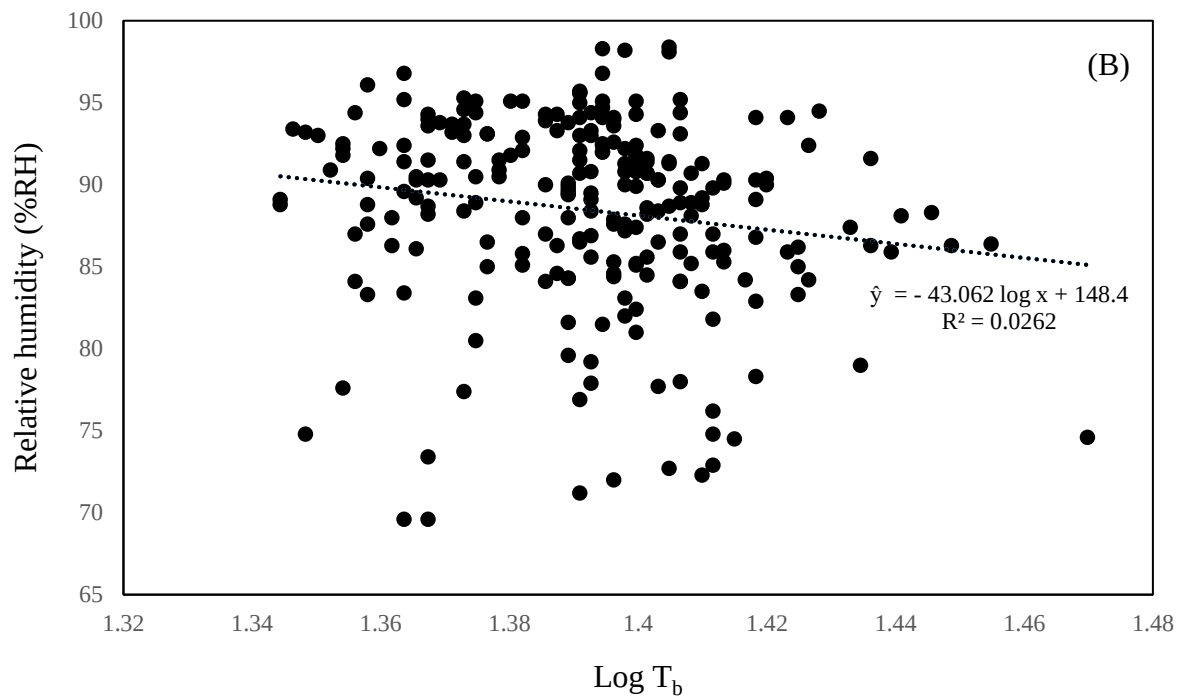
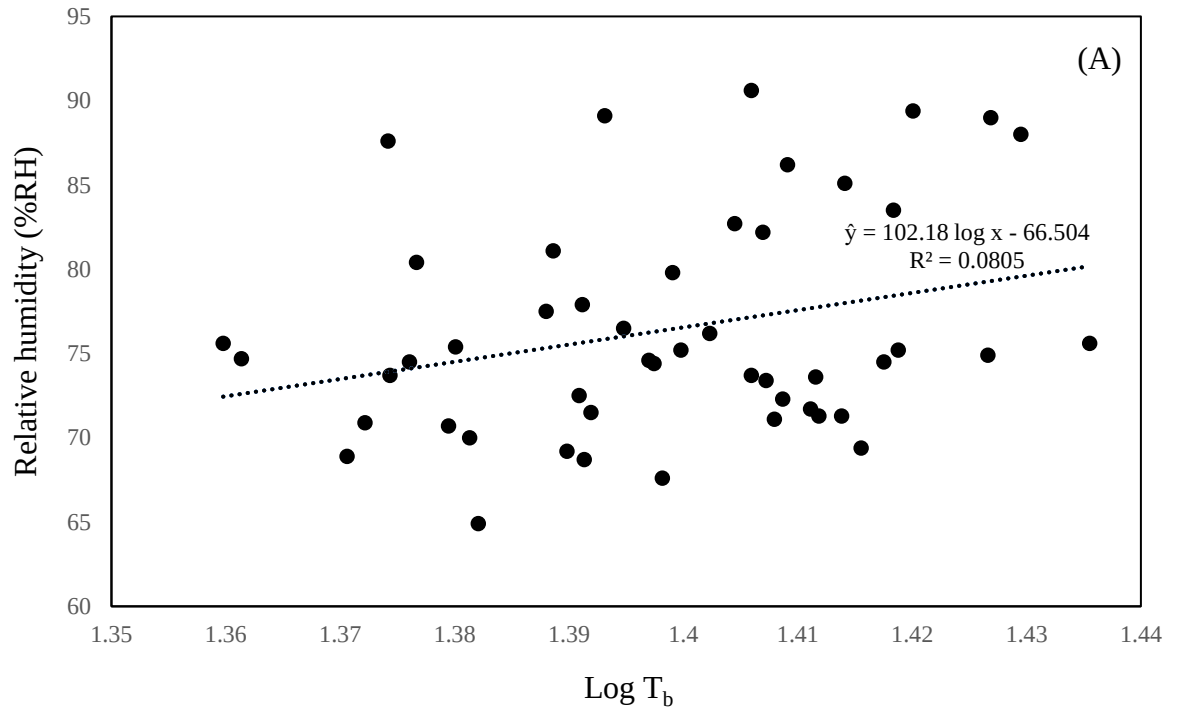


Figure 5.8: Regression of relative humidity, %RH on log body temperature, T_b of *Gonocephalus*. (A) T_b measured via temperature-sensitive radio transmitter (B) T_b measured via infrared laser thermometer. R^2 = Coefficient of determination

5.4.6 Multiple Regression

Multiple regression resulted in the equation: $\widehat{T_b} = 0.266 + (-0.000298) RH + (-0.0933) \log T_a + 0.94 \log T_s$ ($r^2 = 0.528$, $p < 0.001$), suggesting that the additive effect of all three environmental variables interacted significantly, influencing the T_b of these lizards. However, when multiple regression analysis was conducted only between T_b , T_a and T_s , the regression resulted in the equation: $\widehat{T_b} = 0.186 + (-0.0438) \log T_a + 0.94 \log T_s$ ($r^2 = 0.521$, $p < 0.001$) and that T_b was affected mainly by T_s ($t = 22.502$; $p < 0.001$) and not so much of the T_a ($t = -1.55$; $p = 0.121$).

For each species, the relationships between T_b , T_a and T_s were also tested separately and the four multiple-regression equations that best explained T_b were highly significant (Table 5.12). Generally, the lizards' T_b was affected mainly by T_s ($t_{GD} = 6.976$; $t_{GG} = 18.537$; $t_{GL} = 11.4$; $p < 0.001$) except for *G. bornensis* where both T_a ($t = -3.0423$; $p = 0.0027$) and T_s ($t = 10.848$; $p < 0.001$) had a combine influence on its T_b .

Table 5.12: Multivariable regression equations used to predict body temperatures in each species of *Gonocephalus*

Species	Equation	r^2	p
<i>Gonocephalus bornensis</i>	$\widehat{T_b} = 0.242 + (-0.266) \log T_a + 1.121 \log T_s$	0.446	< 0.001
<i>Gonocephalus doriae</i>	$\widehat{T_b} = 0.43 + 0.104 \log T_a + 0.595 \log T_s$	0.383	< 0.001
<i>Gonocephalus grandis</i>	$\widehat{T_b} = 0.0132 + (-0.0132) \log T_a + 1.021 \log T_s$	0.768	< 0.001
<i>Gonocephalus liogaster</i>	$\widehat{T_b} = 0.324 + 0.01067 \log T_a + 0.774 \log T_s$	0.578	< 0.001

5.5 Discussion

Two non-invasive methods used in this study to measure body temperature, T_b of *Gonocephalus* lizards yield significantly different readings. The resulting temperature measured via the infrared laser thermometer were significantly lower in comparison to readings from the thermal sensitive radio-transmitters even when measurements were taken of the same individual at the same time. The most unusual aspect is that the T_b recorded had similar and mostly the same (75.63%) reading as the recorded perch surface temperature, T_s . The low discrepancies may have been due to handling error while using the device, in particular shooting distance error. Shooting distance tend to cause errors and understates surface temperatures (Faye et al., 2016; Chukwuka et al., 2019). It is believed that readings of T_b recorded from the handheld infrared laser thermometer may have been fallacious and does not reflect the lizards' actual T_b . Extra caution in the distance of measurement should have been taken to ensure an accurate reading of the lizard's T_b . Henceforth, further discussion on T_b will be based on readings obtained from the thermal sensitive radio-transmitters.

The mean T_b values were similar between *G. liogaster* and *G. grandis* as well as between *G. liogaster* and *G. bornensis* but were mostly significantly different from each other, suggestive of differences in thermal preference amongst these syntopic species. Previous studies reported predominantly higher T_b values recorded from other tropical lizards (Inger, 1959; Ruibal, 1961; Fitch, 1968; Hertz, 1974; Shine & Lambeck, 1989; Dharani & Mahaulpatha, 2015; Jayasekara et al., 2018; Karthik & Kalaimani, 2019) but comparable to some rainforest lizards that inhabit shaded parts of the forest (Inger, 1959; Rocha, 1991; Vitt & Avila-Pires, 1998). Thermal preference and tolerance can vary based on habitat use, temporal activity pattern, and geographic distribution between lizard species

(Ruibal, 1961; Rand, 1964; Huey, 1974; Huey et al., 1989; Andrews, 1998; Feder et al., 2000; Melville & Schulte, 2001; Qu et al., 2011b; Meiri et al., 2013; Gómez Alés et al., 2017), as well as between lizards of the same population that differ in physiological, or developmental conditions (Mathies & Andrews, 1997; Le Galliard et al., 2003; Lin et al., 2008; Qu et al., 2011a). Qu et al. (2011b) reported that lizards using open habitats with direct sun exposure typically select higher T_b and are better able to withstand high T_b than lizards using shaded habitats. Even though a few individuals of *G. liogaster* and *G. bornensis* have been seen basking in sunspots, *Gonocephalus* generally rarely exposed themselves to direct sunlight and preferred areas with high canopy cover and low to average light intensity (see Chapter 3), similar to some tropical rainforest species (Inger, 1959; Ruibal, 1961; Vitt et al., 2001, 2002, 2003). As a result, it stands to reason that they have a lower mean T_b than other heliothermic tropical species that bask. Apart from that, these species also have T_b that are usually below those of T_a , consistent with Ruibal's (1961) findings on *Anolis allogus* and *A. lucius*. Inger (1959) included two T_b records from *G. liogaster* in his study which falls within the T_b range reported in this study, and both T_b recorded were also lower than that of the T_a stated. Ruibal (1961) explained in his study that this phenomenon may be due to an imbalance between heat gain by conduction from air and heat lost by evaporation through respiratory as well as conduction to the substratum. Since shaded areas are often devoid of radiant heat capable of raising perch surface temperatures over those of the surrounding air, most perches are probably constantly colder than that of the air as well and that the lizards would probably gain heat from the air instead of its perch. Nonetheless, these species do gain heat conceivably through conduction from their surrounding environment as depicted from the positive correlation between T_b and T_a as well as between T_b and T_s . These correlations, as well as the multiple regression analysis, however, suggest these lizards' T_b is more closely coupled to substrate than to air temperatures, and that substrate temperatures have a greater

influence on their T_b . T_b was mostly greater than T_s , implying that these lizards were able to increase their T_b through some behavioural or perhaps physiological means. In view of the foregoing considerations, although these *Gonocephalus* species have comparatively low T_b , they are not entirely passive thermally (Hertz, 1974) and may be non-heliothermic or rather facultative non-heliotherms whereby they bask whenever opportunities arise.

Among these *Gonocephalus* species, *G. doriae* was found to associate the strongest with high canopy covered areas which may be one of the reasons why they had the lowest mean T_b and significantly differed from all others. Given that these four syntopic species inhabit fairly similar environmental conditions and are of similar size (except for adult male *G. grandis*), another possible reason to why they adopt such low T_b may also be due to the overall lighter skin pigments in *G. doriae* compared to the other species (see Chapter 6.2 for colour descriptions). *G. doriae* generally retains the same colouration throughout the day, however, the other three species of *Gonocephalus* observed in this study tend to shift to a darker or duller colouration during the day. A few studies have demonstrated colour shifts (darker or lighter) in lizards which enable them to thermoregulate through regulating the absorptance of solar energy in both UV-visible (300–700 nm) and near-infrared (NIR; 700–2600 nm) wavelengths (Walton & Bennett, 1993; Langkilde & Boronow, 2012; Smith et al., 2016; Jayasekara et al., 2018). Given the possibility that *Gonocephalus* are non-heliotherms, such thermal gain is probably attributable to exposure to indirect solar radiation. Though many melanistic ectotherms typically absorb more total energy than lighter ectotherms, Norris, (1967) reported otherwise for some desert lizard.

The four syntopic species of *Gonocephalus* in this study have shown to differ in thermal ranges with *G. liogaster* showing the narrowest range followed by *G. doriae*, *G. grandis* and lastly *G. bornensis*. *G. liogaster* and *G. doriae* are within a fairly narrow thermal

range, comparable to most tropical lizards (Hertz, 1974; Vitt & Zani, 1996; Dharani & Mahaulpatha, 2015), *G. grandis* on the other hand, showed a more comparable thermal range to some other tropical lizards (Ruibal, 1961; Vitt & Avila-Pires, 1998; Vitt et al., 1998), while *G. bornensis* demonstrated the broadest thermal range, seemingly eurythermal, that were more similar to *Eutropis rudis* (Inger, 1959). Given the fact that physiological functions are highly temperature-dependent and most are optimal within a small range of T_b (Angilletta et al., 2002), it is vital that species are able to do so. Many species were known to utilise behavioural adjustments to carefully thermoregulate in order to achieve such narrow thermal range (Hertz, 1992b; Adolph & Porter, 1993; Díaz & Cabezas-Díaz, 2004; Meiri et al., 2013; Ortega & Pérez-Mellado, 2016; Sagonas et al., 2017; Rangel-Patiño et al., 2020). Hertz (1974), showed otherwise in *Anolis polylepis*, a species that maintains a T_b that was constantly higher than the T_a passively rather than relying on behavioural thermoregulation. Such T_b was predicted to highly correlate with T_a and maintain through a combination of exposure to indirect solar radiation, casual facultative basking, and transit through sunlit areas, probably common in many non-heliotherms or tropical forest lizard species where careful thermoregulation is not possible (Huey & Webster, 1975). Soulé, (1963) then stresses that the variance of T_b depends on the heterogeneity of the study site, thus in areas with homogenous thermal environment, such as in Borneo, the animal would not show as great of a thermal variance as those living in the desert. This is true in this study, as all temperature recorded were within the range of T_a and these species also had T_b correlated to T_a . The broad thermal range exhibit by *G. bornensis* could have been resulted from an individual eurythermy, as those extreme temperatures recorded was only from one individual and was not tolerated by other individual in the population (Huey & Webster, 1975).

Huey and Pianka (2007) provided evidence that gender differences in field thermal biology are rare in desert lizards and speculated that gender differences in closed tropical forest will most likely be minimal as well judging by the poor thermal heterogeneity in space and time. While some studies have corroborated this prediction (e.g., Hertz, 1974; Lee, 1980; Hatano et al., 2001; Gómez Alés et al., 2017), many also have reported gender thermal differences in lizards that usually arise from reproductive state differences (e.g., Beuchat, 1986; Rock et al., 2000) and behavioural differences (e.g., Patterson & Davies, 1978; Forsman & Shine, 1995; Smith & Ballinger, 1995; Woolrich-Pina et al., 2012; Ortega et al., 2016). In this study, males and females of *Gonocephalus* did not differ significantly in mean T_b which is consistent with Huey and Pianka's (2007) prediction, but males and females of *G. doriae* did differ. The intersexual thermal difference in this species possibly indicates some gender related physiological or behavioural variations among the sexes (Smith & Ballinger, 1995; Singh et al., 2002). Although T_a was not significantly different for both, males preferred significantly higher T_s than females which suggest that males could be selecting warmer perches than females. Yet females of *G. doriae* showed significantly higher mean T_b . While many studies have reported lower T_b in gravid females (Beuchat, 1988; Mathies & Andrews, 1997; Le Galliard et al., 2003; Díaz et al., 2006), such T_b shift is most likely to accommodate the thermal requirements of eggs or embryo development during gestation. Since *Gonocephalus* generally have lower T_b than most species, an increase in T_b in gravid females would be rational. Female adaptive reproduction behaviours such as increase basking have also been regarded as the determinant of thermal variations in some lizards (Shine, 1980; Schwarzkopf & Shine, 1991; Rock et al., 2000). Unfortunately, the reproductive condition of the lizards was not examined in this study to draw such conclusion. Gillis (1991) on the other hand proposed that such differences could reflect variation in activity levels between the sexes whereby males are more actively moving while females are

more stationary. Females that are sedentary may be gaining more heat through conduction than active males that are constantly shifting around. A possible event considering in this study, *Gonocephalus* males were found travelling a significantly greater distance between location points than females and *G. doriae* males also showed greater mean daily displacement compared to females (see Chapter 3.4.2). However, results derived from active lizards having higher T_b contradicts this. Another possible reason for such thermal variation could be due to dietary differences between the sexes. Although diet collection in this study was insufficient to provide a meaningful quantitative conclusion to state any firm conclusion on the trophic ecology of these lizards and were only collected from newly encountered individuals instead of the telemetered lizards, most diet collected from *G. doriae* were from females. Could this be an indication that the females observed in this study are feeding more than males? An Earthworm (family: Megascolecidae) was found in one of the females and another was observed being preyed by another telemetered female *G. doriae* (see Chapter 4). Earthworms are rich in protein, essential amino acids and essential fatty acids, making them an ideal source of food supplement for animals and even humans (Madhusudan et al., 2017; Sun & Jiang, 2017). These dietary lipids may influence body temperature selection in ectotherms by altering their body lipid composition (Geiser & Learmonth, 1994). A high saturated fatty acid diet causes an increase in T_b (Geiser & Learmonth, 1994), while a high polyunsaturated fatty acid diet causes a decrease (Geiser et al., 1992). Feeding can lead to an increase in T_b as a result of increased metabolizable energy intake during digestion; conversely, starved lizards tend to select lower T_b in order to save energy (Witten & Heatwole, 1978; Huey et al., 2001; Brown & Griffin, 2005). Such thermal variation however may not be continuous over a 24-hour period.

Body temperature of activity is regularly associated to foraging behaviour (e.g., Bowker, 1984; Bowker et al., 1986; Hatano et al., 2001), since lizards with different foraging habits exhibit daily activity patterns that require different metabolic rates (Huey & Pianka, 1981; Brown & Nagy, 2007). Given that the majority of agamid lizards are sit-and-wait predators (Huey & Pianka, 1981; Cooper, 1998), it is unsurprising that these lizards are mostly stationary regardless of the time of day and maintained a relatively low T_b . Inger and Greenberg (1966) mentioned that diurnal lizards may be most active at higher temperatures and lower humidities, as supported by Nicholson et al. (2005) and Blair (2009). Hence, it may be worthy to also mention that relative humidity was slightly but significantly higher during the day which may be an additional reason why most lizards found were not active. However, these lizards were recorded to be active at higher humidity. Hall and Root (1930) suggested that reptiles will generally show little response to variations in humidity, this is especially true in areas such as Borneo where the environmental conditions remain relative constant throughout the year. Therefore, it is believed that the slight difference in humidity recorded between active and sedentary lizards although significant might have little to no effect on their activity pattern. Those that are physically active during the day naturally have significantly greater T_b than those that are sedentary, a common trend discovered in other lizards as well (Bowker et al., 1986; Crowley, 1987; Lorenzon et al., 1999). By maintaining a higher T_b while active, these animals are able to optimise their physiological performance (Huey & Slatkin, 1976; Amadi et al., 2020). In spite of this, mean T_b of active lizards in this study were lower than other tropical lizards previously studied (Inger, 1959; Ruibal, 1961; Fitch, 1968; Hertz, 1974; Shine & Lambeck, 1989; Dharani & Mahaulpatha, 2015; Jayasekara et al., 2018; Karthik & Kalaimani, 2019). Similar to thermal preference and tolerance, habitat use, temporal activity pattern, season and geographic distribution also influences their field active T_b (Ruibal, 1961; Huey, 1974; Huey et al., 1989; Andrews, 1998;

Hertz, 1992a, 1992b; Feder et al., 2000; Hatano et al., 2001; Melville & Schulte, 2001; Qu et al., 2011b; Meiri et al., 2013; Gómez Alés et al., 2017). The low T_b in *Gonocephalus* reported in this study conforms with macrophysiological studies that have revealed that some tropical lineages, especially those non-heliotherms, are typically active at low T_b and are not tolerant of high temperatures albeit inhabiting year-round warm areas (Huey et al., 2009). Inger (1959) also reported comparable active T_b adopted by the rainforest scincid lizard, *Sphenomorphus sabanus* when environmental temperatures are low. The interspecific similarities in mean active T_b may reflect a similar thermoregulatory behaviour and temporal activity pattern among these *Gonocephalus* species. On the other hand, mean sedentary T_b was considerably different in both day and night. Although lizards remained sedentary during the day, their day T_b were significantly higher than night T_b . A logical explanation to this may be due to exposure to indirect solar radiation during the day where the lizards could gain heat even when inactive (Hertz, 1974), aside from heat gain through conduction from their surroundings (Ruibal, 1961). *G. doriae* possesses a significantly different day mean sedentary T_b than the other three species, potentially by reason of the aforementioned justifications noted on their lower preferred T_b . *G. grandis* also seems to adopt a significantly lower T_b at night similar to *G. doriae* but their day mean sedentary T_b were more closely coupled with *G. bornensis* and *G. liogaster*. *G. bornensis* and *G. liogaster* seemed to have higher sedentary T_b during the day, but the former retains a significantly higher T_b . These varying sedentary temperatures is potentially resulted from the slight difference in microhabitats they occupy (Chapter 3). Mean sedentary T_b seemed to mirror the trend of canopy cover preferred by these lizards, with *G. doriae* preferring the highest canopy covered areas followed by *G. grandis*, *G. liogaster* and lastly *G. bornensis*. Although, all are predominantly shade dwelling species, *G. liogaster*, *G. bornensis*, and *G. grandis* were found in areas of forest edges. These areas have slightly sparser canopy covers that allowed

some sunlight to filter down the forest floor which in turn creates more basking opportunities and exposure to indirect solar radiation during the day. Additionally, females of *G. bornensis* were often found stationary on the ground possibly sitting and waiting for prey, a behaviour that may also allow them to gain heat from the forest floor (Vitt et al., 2001), thus enabling a maintenance of a higher mean sedentary T_b during the day. On the other hand, the lowered mean sedentary T_b in *G. grandis* during the night may be related to their preference to stream areas. Pohlman et al. (2009) mentioned that forest edges which includes perennial streams have lower air temperatures compared with the forest interior at nightfall.

5.6 Conclusions

The four syntopic species of *Gonocephalus* studied are predominantly shade dwellers having relatively low mean body temperature and moderate thermal range that are correlated to both ambient and substrate temperatures. They typically maintained their body temperatures below those of the ambient temperature but above those of the substrate temperature. Body temperatures are likely influenced primarily by passive convection from indirect solar radiation, casual facultative basking, and transit through filtered sunlight, instead of careful thermoregulation from making behavioural adjustments. Therefore, these species are believed to be non-heliothermic or rather facultative non-heliotherms. Additionally, difference in interspecific thermal preferences may be attributed to the difference in microhabitat they occupy, especially canopy cover. *G. doriae* was most distinct of all species studied, having the lowest mean body temperature and intersexual thermal variations that may be by virtue of trophic differences, while *G. bornensis* had maximum fitness at higher body temperatures compared with the other studied species. It should be noted that colouration might also have contributed to the interspecific thermal differences among these lizards. These supposing sit-and-wait predators were mostly sedentary throughout the day but when active, they possess similar temperature preference, indicating a similar thermoregulatory behaviour and temporal activity pattern among these species. They were able to be active at low temperatures that was not obviously affected by humidity of its surroundings.

CHAPTER 6

MISCELLANEOUS ASPECTS OF FIELD BIOLOGY

6.1 Parasites

6.1.1 Introduction

Parasitoid organisms are highly diversified and representatives can be found in many different phyla (Poulin & Morand, 2000). Reptiles in the wild are almost always infected and infested by a wide variety of endo- and ectoparasites (Jacobson, 2007). However, there are fewer known species of amphibian and reptile parasites than there are for species of fishes, birds and mammals (Poulin & Morand, 2000). Platyhelminths (trematodes and cestodes), acanthocephalans, nematodes, pentastomids, protozoans, and arachnids (acari) are typical parasites of reptiles. Nematodes and protozoa are among the most frequented endoparasites found in reptiles, probably owing to their direct life cycles (Machin, 2015; Hazreen, 2017). Species of *Gonocephalus* has been reported to be parasitised by a long list of endoparasites, including some nematodes, platyhelminths and protozoa. Table 6.1 shows a list of parasites previously found in some of the Peninsular Malaysia and Bornean *Gonocephalus* species. There is a single record of infestation on *Gonocephalus* by an ectoparasite *Amblyomma helvolum*, a tick that typically infests snakes and lizards in Asia and Australia, recorded in *Gonocephalus sophiae* from the Philippines (Auffenberg, 1988).

6.1.1.1 Platyhelminths

Two classes of platyhelminths are often found in reptiles namely Trematoda (flukes) and Cestoda (tapeworms) (Crusz & Sanmugasunderam, 1973b; Kennedy et al., 1982; Crusz & Daundasekera, 1988; Dobson et al., 2008; Rataj et al., 2011; Okulewicz et al., 2015; Goldberg et al., 2015; Goldberg et al., 2017).

Trematodes, also known as flukes, depending on the species can widely parasitise its host. Eggs were reported within the intestine, liver, brain, spleen, kidney, heart, lung, pancreas, testes, and bladder of host, while adult flukes occupy heart, blood vessels, lungs, wall of the stomach and intestine (Glazebrook et al., 1989; Johnson et al., 1998; Machin, 2015; Choe et al., 2020). Detection of eggs can usually be found in scat samples of infected hosts. Dispersion of trematodes are usually through ingestion of infected intermediate host. Trematodes have an indirect life cycle, requiring an intermediate host and a definitive host in order to complete its life cycle (Kennedy et al., 1987; Wolke et al., 1982; Johnson et al., 1998). Reptiles can serve as definitive host for these parasites (Diaz-Figueroa & Mitchell, 2005). Often, trematodes are not regarded to be significant parasites in reptiles. Species of the genera *Spirorchis* and *Styphlodora*, on the other hand, are pathogenic and can cause significant health issues such as lethargy, diarrhoea, starvation, dehydration, fluid imbalance, hemiplegia, ulcerative lesions, hemorrhage, necrosis, bacteremia in turtles and snakes (Wolke et al., 1982; Johnson et al., 1998; Choe et al., 2020).

Cestodes, also known as tapeworms, lack a digestive system and therefore reside in large and small intestines of vertebrates for better absorption of nutrients (Diaz-Figueroa & Mitchell, 2005; AL-Mayali & Anah, 2018; Robert et al., 2020). Cestode are typically not host specific but like trematodes, require one or two intermediate host to complete its life cycle (Conn, 1985; Diaz-Figueroa & Mitchell, 2005). Reptiles may serve as the definitive, paratenic, or intermediate hosts for a wide variety of cestodes. Although most species of tapeworms are generally nonpathogenic in wild reptiles, some snake and lizard host showed symptoms such as intestinal necrosis, epithelial loss, round cell infiltrate within tunica muscularis, weight loss, edema, hemorrhage, ulceration of the intestinal mucosa that could potentially turn lethal (Diaz-Figueroa & Mitchell, 2005).

6.1.1.2 Acanthocephalans

Acanthocephala, also known as thorny-headed worms, are found in many reptiles (Crusz & Ching, 1975; Lim & Shabrina, 1998; Dobson et al., 2008; Rataj et al., 2011; Wicaksono et al., 2020). Adults lack of mouth parts and alimentary tracts, and are reported to infest the intestines so that they are able to absorb nutrients that have been digested by the host (Ribas & Casanova, 2006). These parasites have indirect life cycles, typically relying on various arthropods as their intermediate host and sometimes a paratenic host (Carmichael & Moore, 1991; Bollache et al., 2001; McCormick & Nickol, 2004; Ribas & Casanova, 2006). Reptiles can act as the paratenic or definitive host (Diaz-Figueroa & Mitchell, 2005; Rataj et al., 2011). In such instances, cystacanths may be detected in the mesenteries or implanted in the intestinal wall (Wilson & Carpenter, 1996). The eggs are released into the environment along with the host's faeces and when consumed by a suitable intermediate host, development begins and they remain as an infective cystacanth until the intermediate hosts are preyed by the definitive host (Nicholas, 1967; Ribas & Casanova, 2006). Intermediate hosts were reported to experience behavioural changes (Moore, 1984; Carmichael & Moore, 1991), colour changes (Camp & Huizinga, 1979), and reduction of reproductive success (Bollache et al., 2001). The attachment proboscis is equipped with many chitinized hooks that are able to cause significant damage to the definitive host's intestinal wall (Martin et al., 1983).

6.1.1.3 Nematodes

Nematodes are commonly known as round worms and are reported in all groups of reptiles (Crusz & Sanmugasunderam, 1973a; Crusz & Daundasekera, 1988; Lim & Shabrina, 1998; Dobson et al., 2008; Rataj et al., 2011; Robert et al., 2020). Adults typically inhabit tubular organs, free-living in body cavities, subcutaneously, lungs and nasal passages in reptiles. Some of these parasites are also found attaching firmly to the gastric mucosa in

stomach (e.g., Adeoye & Ogunbanwo, 2007; Goldberg et al., 2015; Goldberg et al., 2016). Transmission occurs sometimes by fomites, but most commonly via faecal ingestion (Hazreen, 2017). A number of nematodes are potentially pathogenic, while some may be beneficial to the host, but most nematode parasites show no visible symptoms or signs (Diaz-Figueroa & Mitchell, 2005; Davies, 2008; Machin, 2015). Nematodes found in *Gonocephalus* were previously recorded from the orders Ascaridida, Spirurida (suborder Spirurina) and Strongylida (Mullin, 1973; Durette-desset, 1980; Goldberg et al., 2005; Bursey et al., 2015; Okulewicz et al., 2015; Goldberg et al., 2016), but other studies have reported nematodes from orders such as the Rhabditida, Oxyurida, and Enoplida, from other reptiles (Adeoye & Ogunbanwo, 2007; Rataj et al., 2011; Machin, 2015).

Order Ascaridida consists of monoxenous species where development is restricted to a single host species (Superfamily Cosmocercoidea and Heterakoidea), hetroxenous species where development involves several host species (Ascaridoidea, Seuratoidea and Subuluroidea) and auto-infective species where reinfection with larvae produced by parasitic worms already in the body (Atracitidae). Cucullanids and members of Ascaridoidea typically rely on vertebrate intermediate hosts and sometimes paratenic hosts whereas other hetroxenous species (except Cucullanids) may rely on arthropod intermediate hosts to complete their life cycle. Reptiles have been reported to serve as paratenic host for some species of Ascaridida (Bursey et al., 2016; Goldberg et al., 2016). Order Spirurida (suborder Spirurina) consists of species with indirect life cycle, relying on arthropods as their intermediate host (Anderson, 2000; Diaz-Figueroa & Mitchell, 2005) and sometimes paratenic hosts (Diaz-Figueroa & Mitchell, 2005). Reptiles have been reported to serve as paratenic host for some species of Spirurida (Goldberg et al., 2015). The order Strongylida, on the other hand, consist of some hematophagous species and are generally monoxenous

species (Diaz-Figueroa & Mitchell, 2005). The order Rhabditida comprises species that have a direct life cycle and a heterogonic (free-living) phase (Diaz-Figueroa & Mitchell, 2005). The order Oxyurida consists of microphagous species that are monoxenous and typically infest the posterior gut of many vertebrates as well as arthropods (e.g., Goldberg et al., 2015). Transmission and development of these parasites are consistent in both invertebrate and vertebrate host (Anderson, 2000). Lastly, the order Enoplida, specifically *Capillaria* species from the Trichuridae family are the only parasites known to infect reptiles (Wolf et al., 2014; Machin, 2015). These types of parasites are also monoxenous (Anderson, 2000).

6.1.1.4 Pentastomids

Pentastomes, also known as tongue-worms, are relatively large parasites found in a wide variety of reptiles, most commonly in snakes and lizards (e.g., Riley & Self, 1980; Lim & Shabrina, 1998; Goldberg et al., 2010; Rataj et al., 2011; Wolf et al., 2014). Site of infestation are reported primarily in the lungs for adults and young adults (Riley, 1986; Rataj et al., 2011). Most pentastomes adopt indirect life cycles, whereby it encysts and moults into infective nymph in the lower digestive tract of intermediate hosts (insects, frogs, lizards, and mammals) that will then be preyed by another intermediate host or the definitive host (Ali & Riley, 1983; Riley & Self, 1980; Paré, 2008). Around 90% of pentastome species rely on reptiles as their definitive host (Riley, 1986), and that more than one species of pentastomes infesting a single definitive host is possible (Almeida et al., 2007). Pentastomes are hematophagous but anemia in hosts is yet to be discovered. Deaths related to pentastomes are typically from pneumonia or bacterial infections (Riley, 1986; Paré, 2008).

6.1.1.5 Protozoa

Reptiles are infected by a wide range of Protozoa (e.g., Maupin et al., 1998; Diaz-Figueroa & Mitchell, 2005; Rataj et al., 2011; Wolf et al., 2014; Okulewicz et al., 2015) that

are usually non-pathogenic (Diaz-Figueroa & Mitchell, 2005; Scullion & Scullion, 2009). Types of protozoa in reptiles includes those of amoebas, flagellates, coccidians, haemosporidians, and ciliates. Infections are typically dispersed by fomites, through mechanical vector, or through consumption of contaminated food and water (Scullion & Scullion, 2009).

Amoebas such as *Entamoeba invadens* are perhaps the most serious protozoal pathogen of snakes, lizards, and giant tortoises (Kojimoto et al., 2001; Brewer et al., 2008). Although some reptiles may not be seriously affected, many can become carriers (Divers, 2020). These parasites invade blood vessels, lungs, spleen, pancreas, liver, kidneys, large intestine and subdermal tissues (Kojimoto et al., 2001), and have a direct life cycle where excystation takes place in the intestines, resulting in eight trophozoites per cyst. Trophozoites proliferate and further infiltrate the gut mucosa, and finally encyst into the infectious form, which will then be excreted in the faeces (Geiman & Ratcliffe, 1936). Symptoms may include anorexia, dehydration, vomiting, mucoidal or hemorrhagic diarrhea, thickened intestines and gas accumulation causing swelling of the abdomen and cloacal protrusion which often causes death (Geiman & Ratcliffe, 1936; Kojimoto et al., 2001; Scullion & Scullion, 2009).

Some of the common flagellated protozoa include species of *Trichomonas*, *Giardia*, *Hexamita*, *Leptomonas*, and *Monocercomonas*. They are found associated with tissue changes in the small intestine, and generally gastrointestinal tract, cloaca, kidneys, bile duct, coelomic cavity, and blood vessels due to renal rupture (Jakob & Wesemeier, 1995; Juan-Sallés et al., 2014); Wilson & Carpenter, 1996). Similar to amoebas, they also have a direct life cycle. Diseases associated to flagellates include urinary diseases, bacterial or viral infections, and inflammation in other organs, including the gallbladder, lung, ureters, and

oviduct, (Jakob & Wesemeier, 1995; Richter et al., 2008; Scullion & Scullion, 2009; Juan-Sallés et al., 2014).

Many Coccidial protozoa are found in reptiles such as species of *Eimeria*, *Isospora*, *Caryospora*, and *Cryptosporidium* (Greiner, 2003). They are obligate intracellular parasites that are typically host specific (Greiner, 2003; Diaz-Figueroa & Mitchell, 2005; Machin, 2015). Coccidian protozoans typically infect intestinal tracts of animals, but depending on the species, predilection sites may differ and some can also be found in the stomach, kidney, bile ducts and gall bladder of reptiles (Xiao et al., 2004; Holz, 2017; Divers, 2020). The severity of illness varies according on the kind of coccidia and the host infected, and most species of coccidia found in reptiles are regard as non- pathogenic. Due to their direct life cycle, they can multiply rapidly, especially in immunocompromised reptiles. Oocysts are often resilient and can persist in a dessicated state for weeks (Divers, 2020). Diseases related to coccidians include those of cryptosporidiosis in snakes (Brownstein et al., 1977; Carmel & Groves, 1993) and lizards (Koudela & Modrý, 1998) and intranuclear coccidiosis (Jacobson et al., 1994; Greiner, 2003; Garner et al., 2006). Most of the infection from coccidian protozoa causes sloughing of the intestinal lining, hyperplasia of the epithelium and enterocytes, and inflammatory cells in the mucosa (Greiner, 2003).

Plasmodium from the suborder Haemospororina is most commonly found infecting reptiles, especially snakes and lizards (e.g., Telford, 1982; Wilson & Carpenter, 1996; Diaz-Figueroa & Mitchell, 2005; Matta et al., 2018). While the majority of *Plasmodium* species exclusively infect immature erythrocytes, *P. azurophilum*, which is found in anole lizards, infects both immature leukocytes and erythrocytes (Schall, 1990). They show an indirect life cycle, whereby sporogony occur in insect host (mosquito), while schizogony and gamogony occur in reptile. Schizogony typically occur in the blood cells of the host in species of

Plasmodium. Malaria is a disease commonly resulted from the subsequent destruction of the host's red blood cells by *Plasmodium*. Heavy infestations with some *Plasmodium* species can induce severe haemolytic anaemia and even mortality, whereas other species can cause enlargement of spleen (Diaz-Figueroa & Mitchell, 2005).

Ciliates (*Nyctotherus* and *Balantidium*) are more often found in herbivorous reptiles as commensals, typically in the gastrointestinal tracts, and are believed to facilitate host digestion (Wilson & Carpenter, 1996; Diaz-Figueroa & Mitchell, 2005; Scullion & Scullion, 2009; Rataj et al., 2011; Machin, 2015). Like many other protozoans, they have direct life cycle which require a single one host and replicate through conjugation (Schuster & Ramirez-Avila, 2008; Scullion & Scullion, 2009). *Balantidium coli* is the only known species of ciliates that can be potentially pathogenic resulting in colitis.

6.1.1.6 Arachnids (subclass Acarida)

Many reptiles are found parasitised by ticks and mites (e.g., Lim & Shabrina, 1998; Bannert et al., 2000; Prawasti et al., 2013; Hazreen, 2017; Mendoza-Roldan et al., 2020). They occupy a variety of niches and can colonize different areas of the host's body such as connective tissue under the scales, head, eye, ear, axillae, thigh, tail, toes, cloaca, or even the respiratory system depending on their size and ability (e.g., Mauri & De Alzuet, 1985; Bauer et al., 1990; Bannert et al., 2000; Bertrand & Modrý, 2004; Castro et al., 2019; Mendoza-Roldan et al., 2020). Squamate reptiles undergo periodic skin-shedding which often removes ectoparasites from their skin surface, hence, large infestations are often rare in these animals (Davies, 2008). Dispersion of ticks and mites are usually through physical contact (e.g., mating or fighting), or are sometimes picked up from surrounding substrates (Rivera et al., 2003; Prawasti et al., 2013). Dispersion of these parasites also rely highly on the density of the host population (Hazreen, 2017). In addition, these parasites are incapable of flight or

long-distance travel, hence, sometimes they would also disperse through phoresy (Houck & OConnor, 1991). Many mites only attached to its host when feeding while most ticks feed on a different host during each parasitic stage, either from the same host species (1-host ticks) or different host species (3-host ticks) each time (Dame & Fasulo, 2002). Although many lizard species are able to withstand high infestation load with no apparent negative impact (Moritz et al., 1991; Rocha et al., 2008; Mendoza-Roldan et al., 2019), heavy infestation in other reptiles can cause harmful side-effects such as reduce biological fitness through movement impairment (Main & Bull, 2000; Garrido & Pérez-Mellado, 2014), dehydration, lethargy, growth impairment (Wozniak and DeNardo, 2000), anaemia and dysecdysis impairment (DeNardo and Wozniak, 1997; Davies, 2008).

6.1.2 Specific Objective

The main objective of this subchapter is to identify parasite species of the four species of *Gonocephalus* at Kubah National Park. All parasites recorded from this genus were of species found from other areas (Balasingam, 1963; Singh, 1967; Mullin, 1973; Yap et al., 1974; Durette-desset, 1980; Maupin et al., 1998; Goldberg et al., 2005; Bursey et al., 2015; Okulewicz et al., 2015; Goldberg et al., 2016), and no records of parasites are known for *G. bornensis* and *G. doriae*. Hence, one of the goals was to ascertain parasites associated with these species?

Table 6.1: Host list for the seven species of *Gonocephalus* found in Peninsular Malaysia and Borneo. References in parentheses: 1, Goldberg et al. (2016); 2, Goldberg et al. (2005); 3, Bursey et al. (2015); 4, Maupin et al. (1998); 5, Singh (1967); 6, Durette-desset (1980); 7, Mullin (1973); 8, Yap et al. (1974); 9, Okulewicz et al. (2015); 10, Balasingam (1963)

Parasite			<i>Gonocephalus</i> Host						
Phylum	Family	Species	<i>G. grandis</i>	<i>G. bornensis</i>	<i>G. liogaster</i>	<i>G. abbotti</i>	<i>G. bellii</i>	<i>G. chamaeleon tinus</i>	<i>G. robinsoni</i>
Nematoda	Ascarididae	<i>Orneoascaris sandoshami</i>	(1)	-	(3)	(1, 2)	(1)	-	-
		Ascarididae gen. sp. (Larval)	-	-	-	-	-	(1)	-
		Ascaridid sp. (female)	-	-	-	-	-	(9)	-
	Cosmocercidae	<i>Cosmocercoides malayensis</i>	-	-	(3)	-	(1)	-	(1)
	Heterakidae	<i>Meteterakis singaporensis</i>	(1)	-	(3)	(1)	(1)	(1)	-
		<i>Meteterakis cophotis</i>	-	-	-	-	-	(9)	-
		<i>Strongyluris calotis</i>	(10)	-	-	-	(1)	-	(1)
	Kathlandiidae	<i>Falcaustra malaysiia</i>	-	-	-	(1)	(1)	-	-
	Molineoidea	<i>Oswaldocruzia</i> sp.	-	-	-	-	-	(9)	-
	Physalopteridae	<i>Abbreviata borneensis</i>	(1)	-	-	-	(1)	-	-
		Physalopteridae gen. sp. (Larval)	-	-	-	-	-	(1)	-
	Spiocercidae	Physocephalus sp. (Larval)	(1)	-	(3)	-	(1)	-	-
	Trichostrongyloidea	<i>Typhlopsia quentini</i>	(6)	-	-	-	-	-	-
	Filarioidea	<i>Gonofilaria rudnicki</i>	-	(7)	-	(2)	-	-	-
Platyhelminthes	Cyclophyllidea	Cysticercus (Larval)	(1)	-	-	-	-	-	-
	Linstowiidae	<i>Oochoristica javaensis</i>	-	-	-	-	-	(1)	-
	Mesocoeliidae	<i>Mesocoelium gonocephali</i>	(5)	-	-	-	-	-	-
Protozoa	Plasmodiidae	<i>Plasmodium</i> sp.	(8)	-	-	-	-	-	-
	Eimeriidae	<i>Isospora caryophila</i> (coccidian)	(4)	-	-	-	-	-	-
	Eimeriidae	<i>Isospora gonocephali</i> (coccidian)	(4)	-	-	-	-	-	-
	Eimeriidae	<i>Eimeria cameronensis</i> (coccidian)	(4)	-	-	-	-	-	-

6.1.3 Specific Methodology

Parasite samples were obtained simultaneously with a dietary study from lizards encountered in Kubah National Park during visual encounter surveys (VES) and radio-tracking trips (see Chapter 4.3.1). Stomach flushing was primarily used to obtain endoparasites; more details of methods are in Chapter 4.3.2. Lizards caught were also carefully examined for ectoparasites. Both endo- and ectoparasites found in these lizards were immediately preserved in vials containing 70% ethanol (Legler & Sullivan, 1979). A female *Gonocephalus grandis* (SVL 123 mm) with obvious signs of dermal infection was euthanised, the body cavity opened via a longitudinal incision. The oesophagus, stomach, and large intestine were removed, separated, slit open carefully with scissors and examined for helminths under an Olympus™ SZX9 stereo microscope. The dissected lizard was then stored in 70% ethanol.

Nematodes were first soaked in lactophenol in order to clear the specimens. They were then placed on a glass slide in a few drops of lactophenol and placed under a cover slip. All collected parasites were examined under a Nikon Eclipse 80i microscope. Photomicrographs of all parasites were taken with Nikon DS-5Mc 5.0-megapixel microscope camera attached to the camera port of the microscope and viewed in the NIS-Elements imaging software. Measurements were taken in micrometre (μm). Nematodes were identified to the lowest possible taxonomic level following Anderson et al. (2009), Gibbons (2010), and by comparisons to their respective original descriptions.

6.1.4 Results

A total of 38 nematodes were retrieved from stomachs of 22 ($n = 93$, 23.7%) individuals of *Gonocephalus* through stomach flushing, and three acarids were found

attached to three separate individuals at different parts of the lizards (Figure 6.2). From a dissected female *G. grandis*, two nematodes were found in the stomach, five in the large intestine, many encysted larvae were found attached to the interior wall of the skin (Figure 6.1 H), and the liver was heavily infested by tapeworm cysts (Figure 6.1 K). Four nematode species were identified, while others were of females and larvae that remain unidentified (Table 6.2). Of the identified nematode species, *G. doriae* serve as new host for *Orneoascaris* sp., and both *G. bornensis* and *G. liogaster* serve as new hosts for *Strongyluris* sp.

Table 6.2: Number of parasites (n) and site of infection found in *Gonocephalus* host from this study

Parasite	<i>Gonocephalus</i> Host	n	Site of Infection
Nematoda			
<i>Meteterakis</i> sp.	<i>G. grandis</i>	5	Stomach
<i>Abbreviata borneensis</i>	<i>G. grandis</i>	2	Stomach
<i>Orneoascaris</i> sp.	<i>G. doriae</i>	1	Stomach
	<i>G. liogaster</i>	4	Stomach
<i>Strongyluris</i> sp.	<i>G. bornensis</i>	1	Stomach
	<i>G. liogaster</i>	1	Stomach
Female species 1	<i>G. liogaster</i>	1	Stomach
	<i>G. bornensis</i>	4	Stomach
Female species 2	<i>G. liogaster</i>	2	Stomach
	<i>G. bornensis</i>	1	Stomach
Female species 3	<i>G. liogaster</i>	2	Stomach
Female species 4	<i>G. liogaster</i>	3	Stomach
	<i>G. bornensis</i>	1	Stomach
Larvae	<i>G. bornensis</i>	1	Stomach
	<i>G. liogaster</i>	4	Stomach
	<i>G. grandis</i>	-	Interior wall of skin (cyst)
Cestoda			
Encysted larvae	<i>G. grandis</i>	-	Liver
Acarida			
<i>Amblyomma</i> sp. (Larvae)	<i>G. doriae</i>	1	Gular Sac
species 1 (mite)	<i>G. grandis</i>	1	Head (parietal region)
<i>Amblyomma</i> sp.	<i>G. bornensis</i>	1	Neck

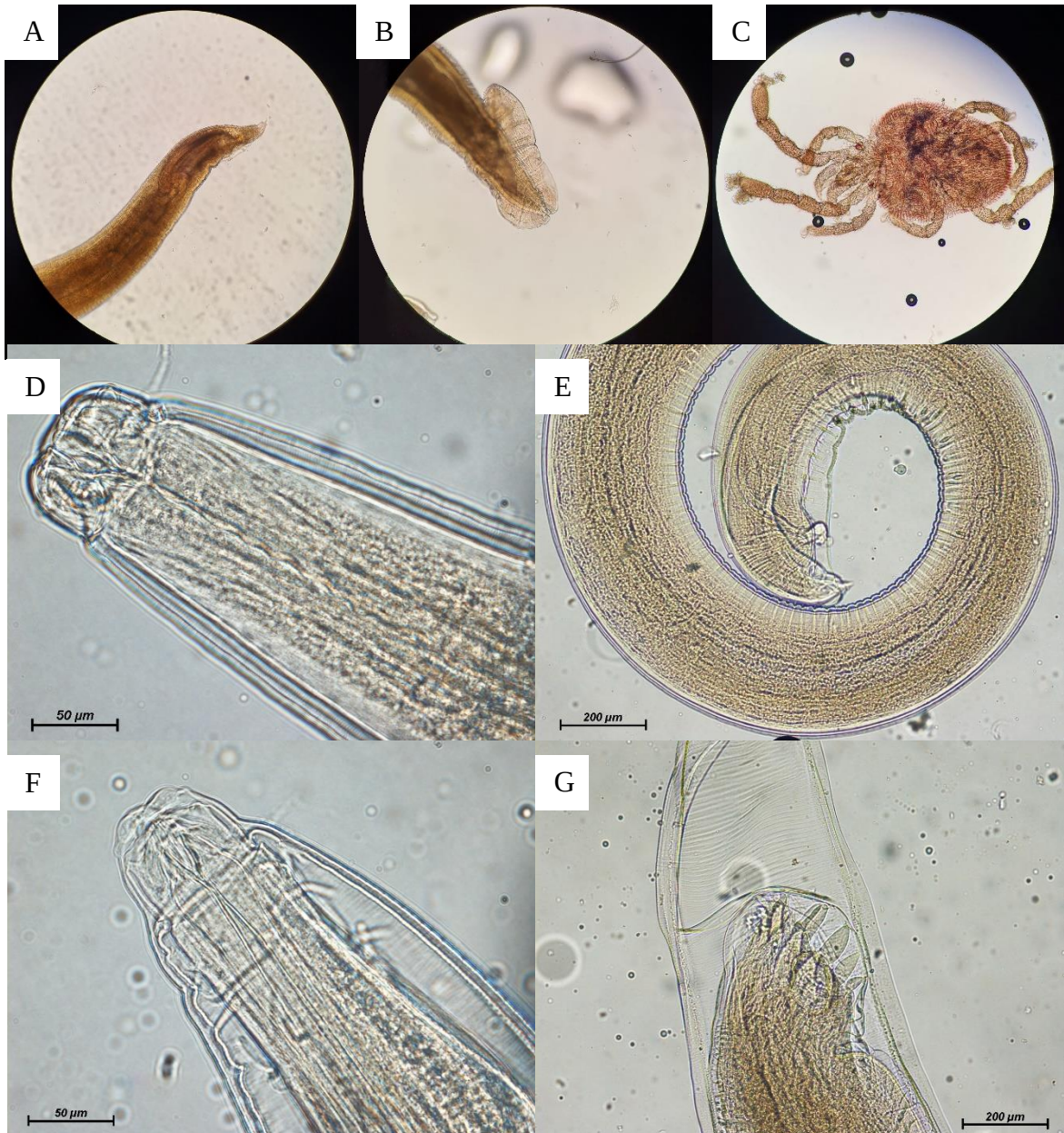


Figure 6.1: Parasites collected from species of *Gonocephalus*. (A) Lateral view of posterior end of male *Meteterakis* sp. showing spicule, 10×/0.25; (B) Dorsal view of posterior end of male *Abbreviata borneensis* showing copulatory bursa, 10×/0.25; (C) species 1 (mite), 10×/0.25; (D) Lateral view of anterior end of male *Orneoascaris* sp., 10×/0.25; (E) Lateral view of posterior end of male *Orneoascaris* sp., 10×/0.25; (F) Lateral view of anterior end of male *Strongyluris* sp., 10×/0.25; (G) Lateral view of posterior end of male *Strongyluris* sp. showing copulatory bursa, 10×/0.25; (H) Interior skin wall of *G. grandis* (SWM067) showing cyst; (I) Interior skin wall showing dissected cyst exposing coiled nematode larvae; (J) Lateral view of unidentified nematode larvae from interior skin wall, 40×/0.75; (K, L) Liver of *G. grandis* (SWM067) showing dissected cysts containing tapeworm larvae; (M) Lateral view of tapeworm larvae, 10×/0.25U*7i

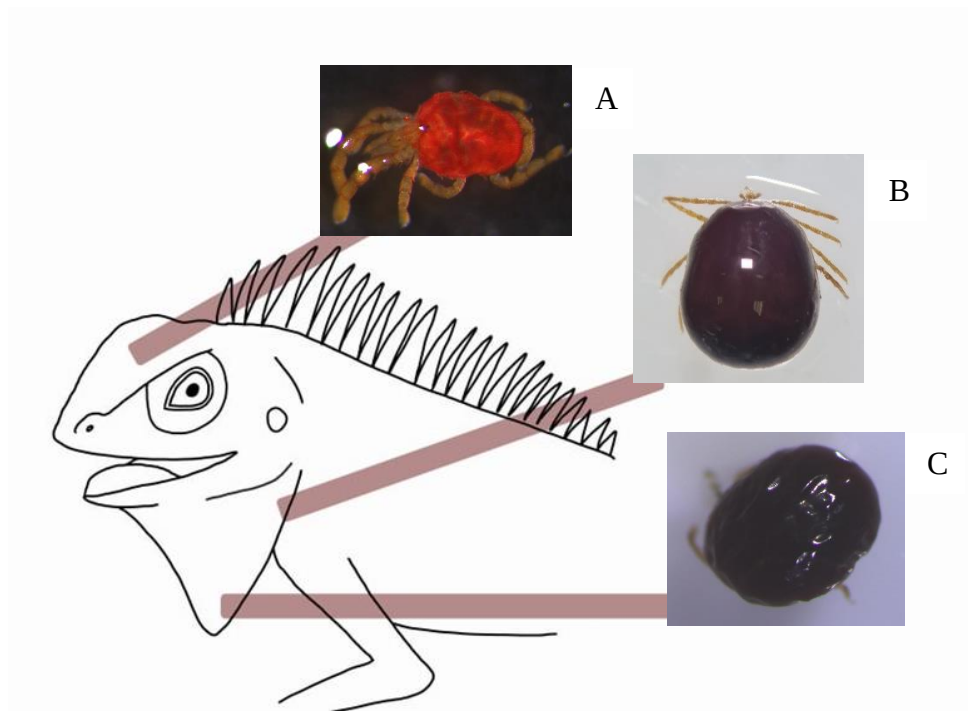
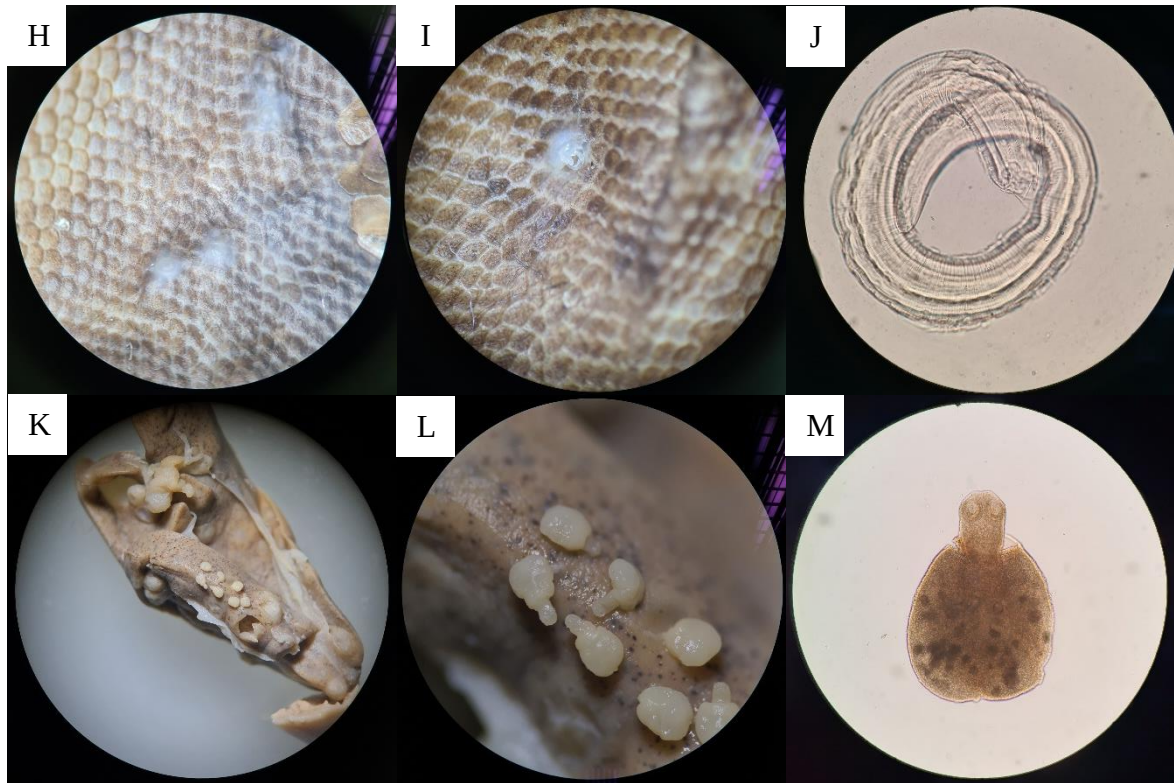


Figure 6.2: Site of infection on *Gonocephalus* by three species of acarids. (A) species 1 (mite) attach to parietal region of head; (B) species 2 (tick) attach to neck; (C) *Amblyomma* sp. attach to gular sac

6.2 Colouration

6.2.1 Introduction

Reptiles display a broad range of body colouration and patterns, from monochromatic to striking vivid colouration and from plain looking to complex patterns. Numerous reptile species are known to exhibit intra- and interspecific colour and pattern polymorphism as well as sexual dichromatism (e.g., Hover, 1985; Wolf & Werner, 1994; Macedonia et al., 2004; Kuriyama et al., 2013; Rossi et al., 2019) which depends on the relative importance of selective pressures (sexual selection and natural selection; Andersson, 1994; Stuart-Fox & Ord, 2004). Body colour is said to be the visible expression of the animal's internal condition, hence why reptiles are also known to exhibit colour changes gradually or rapidly depending on their reproductive stage, seasons, and other extrinsic factors (Bagnara & Hadley, 1973; Cooper & Greenberg, 1992; Stuart-Fox & Ord, 2004; Weiss, 2006; Langkilde & Boronow, 2012; Smith et al., 2016; Jayasekara et al., 2018). The ability of these animals to produce such wide variety of colouration and patterns have always been an important topic in evolutionary biology. Static structural combination of pigment cells (xanthophores, erythrophores, iridophores, and melanophores) in the dermis ultimately determine the colour and pattern seen on reptiles (Taylor & Hadley, 1970; Bagnara & Hadley, 1973; Morrison, 1995; Kuriyama et al., 2006; Kuriyama et al., 2013; Kuriyama et al., 2020). Yellows, oranges, and reds are produced by xanthophores and erythrophores through the selective absorption of short wavelength light by pterinosomes containing pteridine and carotenoid vesicles in cells. Blacks and browns are produced by the light-absorbing melanophores whereby its density often results in the overall skin lightness or darkness. Iridophores, on the other hand, are light-reflecting cells that have platelets composed of crystalline purines and pteridines, producing structural colours through thin-

layer interference and the scatter or diffraction of light from stacks of reflecting platelets (Bagnara & Hadley, 1973). Studies have suggested that these pigment cells are not solely for the production of colour and patterns, but can also provide some physiological functions such as rapid colour changing that aid in camouflage and possibly passive thermal protection (Teyssier et al., 2015).

Various functions have been reported on the evolution of colour pattern and melanism in reptiles. Perhaps the most distinguished role of these colour traits is for social signalling. Colour signals have evolved to be easily recognisable by intended recipients in which behavioural choices are influenced (Cooper & Burns, 1987; Osorio & Vorobyev, 2008). With colours, species are able to recognise conspecifics for intrasexual interactions (Ord et al., 2015; Smith et al., 2016; Bruinje et al., 2019) and sexual selections (LeBas & Marshall, 2000; Kamath, 2016), while supporting reproductive isolation among sympatric species (Cooper & Greenberg, 1992). In most species with sexual dichromatism, the gender with lower parental investment, usually males, are often more vibrantly coloured than females which are important for social signalling (Ferguson, 1966; Cooper & Greenberg, 1992; Amdekar & Thaker, 2019; Rossi et al., 2019; but see Weiss, 2006; Ord et al., 2015) and some added benefits (Langkilde & Boronow, 2012; Jayasekara et al., 2018). Many lizards are also able to change their colouration rapidly to become more conspicuous during times of courtship or intrasexual interactions (Zug et al., 2010; Pal et al., 2011; Batabyal & Thaker, 2017). Colour variation in some of these social interactions are reported to associate with stress hormones (Greenberg, 2002; Lewis et al., 2017). Vivid colourations are common, but not definitively, in body regions that can be viewed easily by conspecifics during bouts of display such as the ventral, flank and dewlap, and are otherwise concealed as to reduce

predation risk (Hover, 1985; Cooper & Greenberg, 1992; Stuart-Fox et al., 2004; Ord et al., 2015; Rossi et al., 2019).

Another important role of colouration and pattern in reptiles is for protection. Some reptiles are generally dull in body colour, they are generally perceived cryptic to avoid detection by visual predators (Stuart-Fox et al., 2004), while others display aposematic coloration that are vibrant which serve as signalling features, such as to advertise unprofitability to predators (Pough, 1988; Cooper & Greenberg, 1992; Castilla et al., 1999). Some species have been able to also divert predatory attacks to less lethal autotomous body parts that are brightly coloured (Wilkinson, 2003; Watson et al., 2012). Whereas in some special cases, lizards' vivid colouration (patagial colouration of *Draco* sp.) mimics that of its surroundings (falling leaves) for better camouflage and further reduce predation risk (Klomp et al., 2014).

Additionally, body colours can improve regulation of body temperature and protect from harmful stimuli such as UV radiation (Walton & Bennett, 1993; Langkilde & Boronow, 2012; Smith et al., 2016; Jayasekara et al., 2018). This is especially important for poikilotherms, as reflectance has a significant effect on the warming rates of animals exposed to insolation (Porter & Norris, 1969). Skin colour is influenced by the position of the melanosomes within the melanophores that are regulated by melanophore stimulating hormone (MSH) and other hormones such as norepinephrine (Taylor & Hadley, 1970). These hormone productions are sensitive to heat which then aggregate or disperse melanosomes resulting in darkening or lightening of the skin (Bagnara & Hadley, 1973). Although the heating rates caused by colour change were minimal, it has a significant effect on the total time spent above a certain body temperature or on basking duration (Clusella Trullas et al., 2007). Individuals with darker skin generally benefit more at low temperature

circumstances since they heat up faster in comparison to lighter individuals at a given solar radiation level (Langkilde & Boronow, 2012). Nevertheless, bright colours may only be displayed after the animal gain sufficiently heat, owing to both physiological constraints and because higher body temperatures enable individuals to behaviourally adapt for greater conspicuousness (Olsson et al., 2013).

6.2.2 Specific Methodology

To describe sexual dichromatism in the four species of *Gonocephalus*, descriptions were prepared by examination of photographs of live animals and matching with the colour swatches of Smithe (1975; 1981).

6.2.3 Sexual Dichromatism in the Four Species of *Gonocephalus*

Following colour descriptions are made according to individuals observed throughout the study. Colour comparisons were made based on photographs of live animals and matching with the colour swatches of Smithe (1975; 1981).

6.2.3.1 *Gonocephalus bornensis* (Schlegel, 1848)

Male colour description: Dorsum Fuscus (Colour No. 21) to Vandyke Brown (Colour No. 221), with a network of Clay Colour (Colour No. 123B) markings; a dark nuchal-gular collar encircling throat; sides of head Clay Colour (Colour No. 123B); flanks with Clay Colour (Colour No. 123B) oval areas, each with a pale yellow-green centre; lower jaw cream-coloured with dark brown longitudinal stripes, those near throat converging; tympanum unpatterned cream-coloured; nuchal and body crest brown and yellow, darker basally; dewlap grey to cream-coloured, with dark, broken stripes; labials with indistinct

darker bars; brown radiating lines from orbit of eye; iris bluish-grey, pupil black; limbs brown with dark bands; venter grey or cream; and tail brownish-cream with brown-black bands.

Female colour description: Dorsum buff (Colour No. 124), with a network of raw umber (Colour No. 23) markings, comprising five dark transverse bands; a dark nuchal-gular collar encircling throat; sides of head and flanks with buff with dark green to Pistachio (Colour No. 161) oval areas, each with a pale yellow-green centre; lower jaw yellow or cream-coloured with dark brown longitudinal stripes, those near throat converging; tympanum unpatterned green or cream-coloured; nuchal and body crest brown and yellow, darker basally; dewlap cream-coloured, with dark, broken stripes; labials with brown bars; brown radiating lines from orbit of eye; iris of brown or light blue, edged with yellow, pupil black; limbs green or brown with dark bands; venter yellow or cream, with buff (Colour No. 124) transverse bands entering from the flanks; and tail yellow-cream with buff (Colour No. 124) bands.

6.2.3.2 *Gonocephalus grandis* (Gray, 1845)

Male colour description: Dorsum, including head, scales of crest and the top two-thirds of torso and upper surfaces of limbs Greenish Olive (Colour No. 49), lower third of body Buff-Yellow (Colour No. 53), with large Turquoise Blue (Colour No. 65) areas; a small Buff-Yellow (Colour No. 53) spot in centre of tympanum; gular sac Chamois (Colour No. 123D), with Turquoise Blue (Colour No. 65) stripes that coalesce at apically; limbs with slightly darker bands; iris brown, with a pale yellow edge.

Female colour description: Dorsum Greenish Olive (Colour No. 49), with an Olive-Brown (Colour No. 28) broad postocular stripe extends across top of tympanum and meets

the scapular region and turns upwards to join the vertebral region; supralabial region Pale Horn Colour (Colour No. 92); vertebral region with regular darker bands, subequal to intervening paler regions, that extend to the tail; lower half of flanks with oval Straw Yellow (Colour No. 56) marks; venter pale; dorsal surfaces of limbs Pale Horn Colour (Colour No. 92) with distinct Olive-Brown (Colour No. 28) bands; pupil brown with a narrow yellow ring.

6.2.3.3 *Gonocephalus doriae* Peters, 1871

Male colour description: Head and body Lime Green (Colour No. 159), the flanks with scattered spots, occupying a single scale, of Raw Umber (Colour No. 23), as well as Dusky Brown (Colour No. 19) larger, irregular patches along upper flanks, the largest on axillary region; upper surfaces of limbs Lime Green (Colour No. 159), with faint grey areas; belly Cream Colour (Colour No. 54), with Warm Buff (Colour No. 118) bars on lower flanks, covering 4-5 scales; anterior third of tail Lime Green (Colour No. 159), with Dark Brownish Olive (Colour No. 129) bands, each band covering 3-4 scales; midtail Salmon Colour (Colour No. 106) with wider dark bands, 5-6 scales thick. Pupil black; iris Ferruginous (Colour No. 41), with a paler inner ring; Throat Cream Colour (Colour No. 54), with faint, grey stripes, more distinct medially, where it shows Flesh Colour (Colour No. 5); scales on vertebral region as dorsum, with scattered grey scales.

Female colour description: Dorsum Lime Green (Colour No. 159), with extensive Blackish Neutral Gray (Colour No. 82) pattern, comprising a series of larger, irregular inverted 'C'-shaped and subtriangular marks on axillary region, as well as along the top two-thirds of the flanks; dorsal spine comprising Lime Green (Colour No. 159) scales, the median ones with darker intervening areas; several Spectrum Yellow (Colour No. 55) transverse bars across the lower-most part of flanks; two short, Blackish Neutral Gray (Colour No. 82)

postocular stripes extend to around posterior of head, beyond level of tympanum; gular sac Pistachio (Colour No. 161), each scale with a darker interscale area; supralabials and infralabials, as well as the leading edge of gular sac Pale Horn Colour (Colour. No. 92); dorsal surface of limbs Lime Green (Colour No. 159), with dark bars indistinct or absent; belly Lime Green (Colour No. 159); tail Lime Green (Colour No. 159), with subdued Blackish Neutral Gray (Colour No. 82) bars; iris brown with a narrow yellow ring.

6.2.3.4 *Gonocephalus liogaster* (Günther, 1872)

Male colour description: Dorsum and forehead Hair Brown (Colour No. 119A) or Greenish-Olive (Colour No. 49), with rounded pale spots on flanks; tail Fuscous (Colour No. 21) with Buff-Yellow (Colour No. 53) subequal cross-bars; gular sac of males Drab-Gray (Colour No. 119D), with Hair Brown (Colour No. 119A) blotches or longitudinal lines; sides of head Drab (Colour No. 27), orbital region Olive Brown (Colour No. 28); pupil black; iris True Blue (Colour No. 168A); skin surrounding orbit Spectrum Orange (Colour No. 17).

Female colour description: Dorsum and forehead Lime Green (Colour No. 59), darkening to Sepia (Colour No. 119), with Greenish Olive (Colour No. 49) to Pale Pinkish Buff (Colour No. 121D) areas; flanks with darker reticulations and isolated, rounded Buff-Yellow (Colour No. 53) scales; pupil black; iris Sky Blue (Colour No. 66) or Cinnamon Drab (Colour No. 219C), eye colour variation may be a result of ontogeny; two or three rows of Straw yellow (Colour No. 56) scales between upperlabials and orbit; throat Pale Pinkish Buff (Colour No. 121D), with Sepai (Colour No. 119) longitudinal stripes; nucho-dorsal scales are mostly Olive (Colour No. 50), and occasionally, Pale Horn Colour (Colour No. 92); tail Greenish Olive (Colour No. 49) with subequal cross-bands of Lime Green (Colour No. 59).

6.2.4 Discussion

Species of *Gonocephalus* displayed sexual dichromatism, with males being more colourful and vibrant compared to their female counterparts, as reported in many other agamid lizards (Stuart-Fox & Ord, 2004; Pal et al., 2011; Ord et al., 2015). Most of the vivid colourations and patterns are focused in areas of body, such as lower half of flanks or gular sacs in most of these species, most likely to increase visibility by conspecifics while still be able to conceal from visual predators (Hover, 1985; Cooper & Greenberg, 1992; Stuart-Fox et al., 2004; Ord et al., 2015; Rossi et al., 2019). Additionally, these species are apparently able to change the colour of their skin readily from dull to bright. Night colourations are bright, however during the day, many individuals appeared to be dull and dark, except for *G. doriae* that generally retains a similar colouration throughout the day. Dull colouration displayed by these species during the day, suggest passive thermoregulation from exposure to indirect solar radiation (Walton & Bennett, 1993; Langkilde & Boronow, 2012; Smith et al., 2016; Jayasekara et al., 2018). This is further confirmed by individuals that appeared darker when exposed to direct sunlight in comparison to those perching in shaded areas (Figure 6.4). Furthermore, species of *Gonocephalus* in this study responded to handling stress by adopting darker colouration at most instances (Figure 6.5), which differed from those reported by Lewis et al., (2017) and Amdekar and Thaker (2019).

A number of lizards are capable of swiftly changing their skin colours to enhance their appearance during courtship or intrasexual exchanges (Zug et al., 2010; Pal et al., 2011; Batabyal & Thaker, 2017). The same applies to species of *Gonocephalus*, or at least *G. doriae*. Males of *G. doriae* were seen displaying different colourations on multiple occasions, and it is believed to be associated to social interactions within the species. Some adult males were found partially (Figure 6.7 B) or fully (Figure 6.7 C) Salmon coloured

(Colour No. 106) during the day, and the colour intensity reduces at night. Although the breeding season of these lizards is not documented, the vibrant colouration mentioned in matured males is only seen throughout July to December, possibly representing breeding season of the species. Intrasexual interaction between a pair of male *G. doriae* was observed during this study, where both individuals attempt to dominate each other with visual displays such as colouration and posture (Figure 6.3). Such dyadic contests are common in highly visual, territorial lizard species as to reduce costly fights (Hover, 1985; Olsson, 1994; Sinervo & Lively, 1996; Healey et al., 2007). The changes in body colouration during aggression is due to a physiological stress response where stress hormones, such as corticosterone are produced and affects the pigment cells in the dermis (Greenberg, 2002).

Female *G. bornensis* observed in the study area demonstrated colour polymorphism. Those that are located at lower elevations (< 233 m asl) in the Palmetum and Belian trail of the study site seemed to have umber (Colour No. 23) markings, transverse bands as described in Chapter 6.2.3.1. They have an overall lighter reddish-brown appearance (Figure 6.6) which differed from individuals observed from higher elevations (Waterfall Trail, parts of Main Trail, Selang Trail, Rayu Trail and Summit Trail; > 233 m asl), that displayed brownish or darker colouration (Figure 6.4 A). Colour polymorphism in lizards are widespread across different species, commonly reported in areas of display during social interactions (throat, head or ventral; but see Chapple, 2005; Chapple et al., 2008), and one or both sexes may be polymorphic (Stuart-Fox et al., 2020). While such polymorphism is often reported in male lizards, some observations have also concurrently reported colour polymorphism displayed by females (e.g., Svensson et al., 2001; Sacchi et al., 2007; Tobler et al., 2011; Blouin-Demers et al., 2013). However, colour polymorphism exhibit in only females on the other hand were not reported. Males of *G. bornensis* observed in this study showed no obvious

colour polymorphism as was apparent in the females. Studies have reported different reproductive strategies (r- and K-strategies) associated with behavioural and physiological traits exhibited by different female morphs in some species (Zucker & Boecklen, 1990; Sinervo et al., 2000; Vercken et al., 2007; Galeotti et al., 2013). Further investigation is required to understand this discrepancy in colouration.



Figure 6.3: A pair of adult male *Gonocephalus doriae* displaying conspicuous colouration during competition



Figure 6.4: Adult Female *Gonocephalus bornensis* day colouration. (A) Colouration in shade; (B) Colouration under direct sunlight

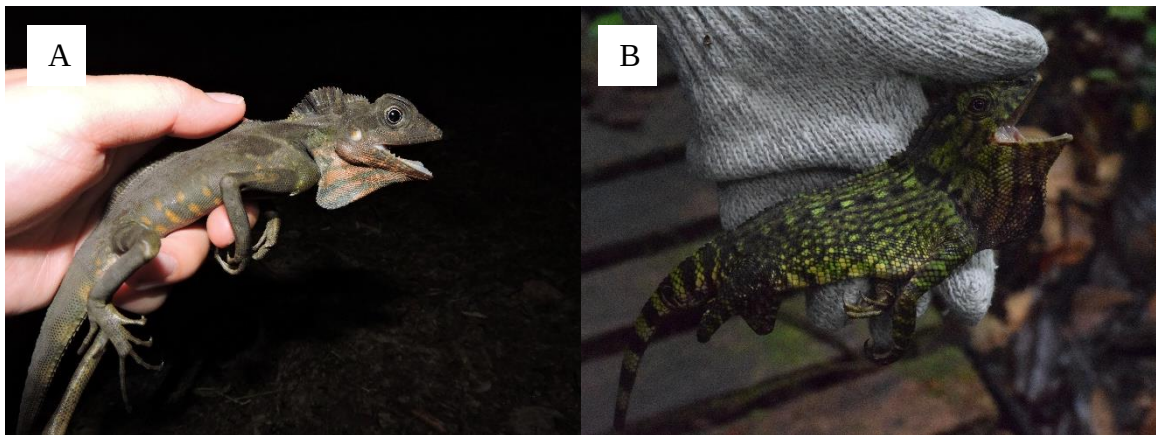


Figure 6.5: Stress colouration resulted from handling. (A) Adult Male *Gonocephalus grandis*; (B) Adult Female *Gonocephalus doriae*



Figure 6.6: Adult female *Gonocephalus bornensis* observed in Palmetum trail at Kubah National Park showed umber (Colour No. 23) markings and transverse bands



Figure 6.7: Dynamic physiological colour change in adult male *G. doriae*. (A) Natural colouration; (B) Partially breeding colouration; (C) Colouration associated to courtship or intrasexual interactions

6.3 Predation

Knowledge on evolutionary and behavioural ecology are enriched by the study of predator–prey interactions, as physiological, anatomical, and behavioural adaptations in both predators and prey are often associated with such relationships (e.g., Amo et al., 2004; Schaedla, 2004; Labra & Hoare, 2015; Mohanty et al., 2016; Bateman et al., 2017; Ruxton et al., 2019). *Gonocephalus liogaster* is often found perching on tree trunks during the day and sleep clinging onto slender tree branches with their heads directed towards the trunk at night. Such sleeping behaviour is regularly observed in many arboreal lizards as to enhance detecting and subsequently avoiding nocturnal predators (Mohanty et al., 2016). Regardless, lizards with such strategies are often mentioned as prey of snakes (McCleary & Ichtiarani, 2015; Mohanty et al., 2016; Luu et al., 2019). Within the genus, *G. chamaeleontinus* has been reported as prey of the cat snake, *Boiga drapiezii* (Cegalerba & Szwemberg, n.d.) in Sumatra, Indonesia.

In this study, a telemetered *Gonocephalus liogaster* (Holohil BD-2; frequency 150.150) was discovered to be preyed upon by a Keeled Rat Snake, *Ptyas carinata* (Günther, 1858) after being tracked for five weeks. The adult female *G. liogaster* (SVL = 110 mm; TL = 258 mm; WT = 50 g) was fitted with a temperature-sensitive radio transmitter on 18 October 2019 and was released to its original position where it was found on 19 October 2019. Tracking started on 21 October 2019 and a total of 16 positions were obtained from both day and night. The individual was fairly inactive most of the time and typically stayed within a small home range with minimal distance moved between observations. It was even sometimes found perching on the same tree at the same position during the day and at night. On one occasion, however, the individual was found ca. 45 m from its previous location, across the paved road of the Summit Trail where it was observed to be laying eggs on the

ground (25 October 2019). The individual was then found back at its original vicinity on the next sighting.

On 29 November 2019 at 1046 h, radio signals from the transmitter that was fitted on the individual were detected 87 m north-east (01.61128°N, 110.1952°E, 117 m elevation) from the previous location, where it was found one-day prior. The signals lead to an adult (ca. 2.5 m) *P. carinata* (Figure 6.8 A) that was lodged deep within a root mass of an uprooted tree, ca. 3 m off the tarred Summit Trail, it was undeterred by the disturbance caused from the discovery. The snake was identified from its distinct caudal pattern of pale spots and a reticulate pattern (Stuebing et al., 2014). On 2 December 2019, at 1115 h, the snake was found using the signal from the radio transmitter 109 m southeast (01.61051°N, 110.1958°E, 172 m elevation) from the previous location. The signals originated from a deep fissure of a rocky stream bank (Figure 6.8 B), under dense undergrowth. Upon discovery, the snake became alerted and moved deeper within the rocks. On 6 December 2020 at 1033 h, radio signals came from a location 89 m north-north-east (01.61128°N, 110.1961°E, 159 m elevation) from the previous point, however, there was no visuals of the snake, and the transmitter was found hanging ca. 1.4 m above ground on a vine (Figure 6.8 C). The site had a thick layer (ca. 7 cm) of leaf litter on the ground with minimal undergrowth. The transmitter found had faeces adhering to it, again proving that the *G. liogaster* was preyed upon by *P. carinata* and that the transmitter was excreted by the snake after digestion. While the anterior harness that was used to secure the transmitter to the pelvic girdle of the lizard was snapped, the transmitter itself was undamaged during the passage through the gut of the snake.

Presuming that the *P. carinata* has preyed on the *G. liogaster* after the last sighting of the lizard (on 27 November 2019, 1832 h) and defaecated on the same day the transmitter was found, it is suggested that that snake had a maximum throughput period of ca. eight and

a half days from consuming the lizard. The snake moved 285 m during this period and the mean displacement per day was 33.53 m with a mean elevation of 170.8 ± 9 m. The gut passage time, PT assumed for this predator was comparable with other terrestrial colubrid snakes, which typically range from 3.5 to 11.6 days (Skoczylas, 1978; Lillywhite et al., 2002). The individual of *P. carinata* was estimated to be ca. 2.5 m in total length, and weigh ca. 3 kg, The *G. liogaster* would be consider an average-sized meal for the individual of *P. carinata* which was estimated to be ca. 2.5 m in total length, and weigh ca. 3 kg. The known diet of *P. carinata* included those of large frogs and small mammals (Konopik et al., 2014), while other species from the genus feeds on a variety of prey, including frogs, toads, lizards, rats, bats, and even snakes (Saha & Chaudhuri, 2017). PT values are generally affected by various factors such as the texture and quality of food, meal size, feeding frequency, temperature, activity, gut morphology, as well as nutritional and physiological status of the animal (Lillywhite et al., 2002). Since tracking was not conducted continuously, the displacement and mean displacement per day could have been underestimated, while PT value may be overestimated.

This observation contributed to the list of predators of *Gonocephalus* while simultaneously revealed some biological knowledge regarding the *P. carinata* including movements, microhabitat use and diet.



Figure 6.8: Microhabitats associated with radio signals related to predation on *Gonocephalus liogaster* by *Ptyas carinata*. (A) Within the root mass of an uprooted tree, showing the caudal region of the snake; (B) Inside a rock fissure along a stream bank, also showing the caudal region of the snake; and (C) the excreted transmitter hanging on a vine associated with saplings

CHAPTER 7

GENERAL CONCLUSION AND RECOMMENDATIONS

Lizards often coexist in assemblages with two or more closely related species, and tend to partition available resources in their environment to reduce competitive pressure. Resource or niche partitioning by lizards typically happen in one or more of the three main dimensions (spatial, trophic and temporal) with some being more influential than others depending on the environmental conditions and other factors. Not all species partition their resources to the same degree, and although this ecological phenomenon have been well documented for a variety of lizards worldwide. Such investigations are at its infancy in the lowland tropical rainforests of Borneo. Species of *Gonocephalus* in the lowlands of Kubah National Park, Sarawak, Borneo occur in sympatry and share many of their ecological attributes, making them excellent subjects for the study of resource partitioning and processes of coexistence in this region. These species are similar in size but display different body colourations and patterns which is believed to be a form of character displacement resulted from selection that aid in species recognition and reduce competition.

This study demonstrates that the four syntopic species, although subtle, diverge along the spatial dimension of their ecological niches by exhibiting differences in preference towards aspects of their microhabitat use, such as canopy cover, tree diameter, distance to waterbody and perch surface. Home range overlaps occur only between males and females of the same species, suggest that the species are able to separate themselves by using different parts of the forest. *G. bornensis* is a habitat generalist compared to its congeners, widely occupying many parts of the forest, whereas *G. doriae* are relatively specialised with the microhabitat they utilise. Evidence to indicate presence of partitioning in the trophic

dimension among these congeneric lizards was unsatisfactory, however, it is believed that dietary partitioning is probably unlikely given the opportunistic nature of these lizards. The difference in interspecific thermal preferences shown by these ectotherms is noted to correlate strongly with canopy cover of the spatial niche, and are probably also influenced by their trophic niche. Hence, thermal niche could also be partitioned by these lizards.

This study contributes to the ecological knowledge of these species and lay a foundation for the understanding of resource partitioning and the processes of coexistence of lizard populations in the tropical rainforests of Borneo which may be useful for a variety of purposes, from conservation and management to understanding the natural history of other Bornean ectothermic species. There remains much to learn concerning the community ecology of squamate reptiles in the region, and future studies can employ additional microhabitat data such as plant community associated with the species for refining conclusions regarding spatial ecology, as well as explore activity patterns to better understand the temporal dimension. Collection of dietary samples should be amplified and include sampling of potential prey species for providing a more comprehensive analysis of the trophic niche. Additionally, in-depth investigation on life history traits such as sexual maturity, morphology and reproduction may also be beneficial to the understanding of coexistence in sympatric species.

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APPENDICES

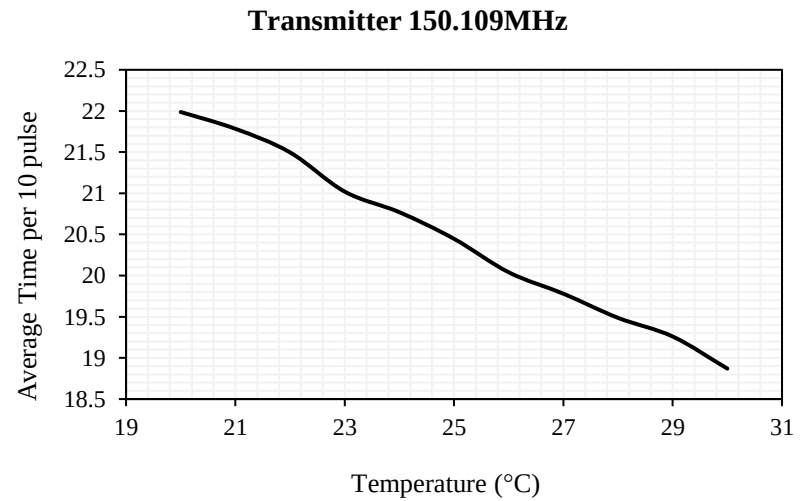
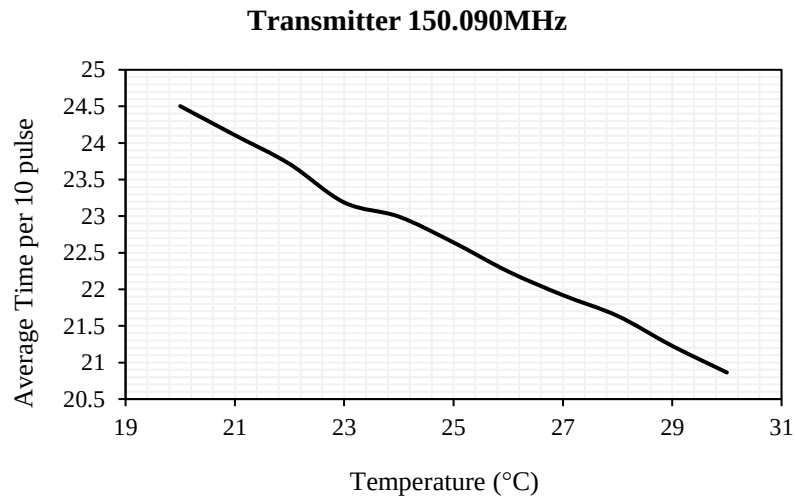
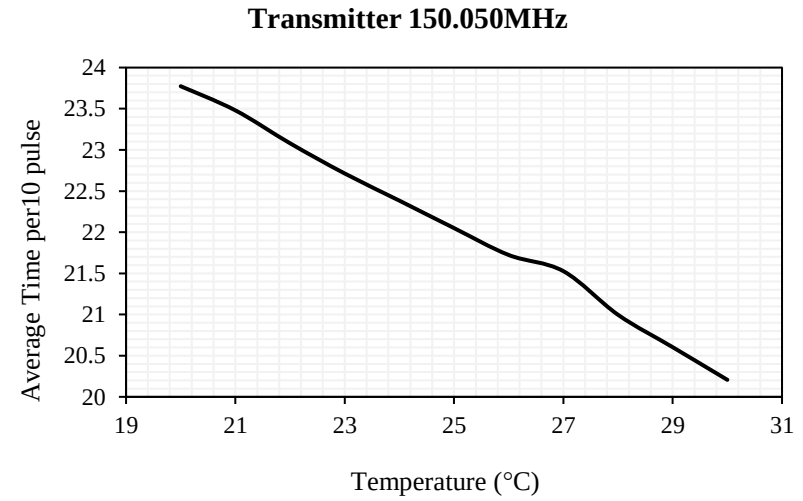
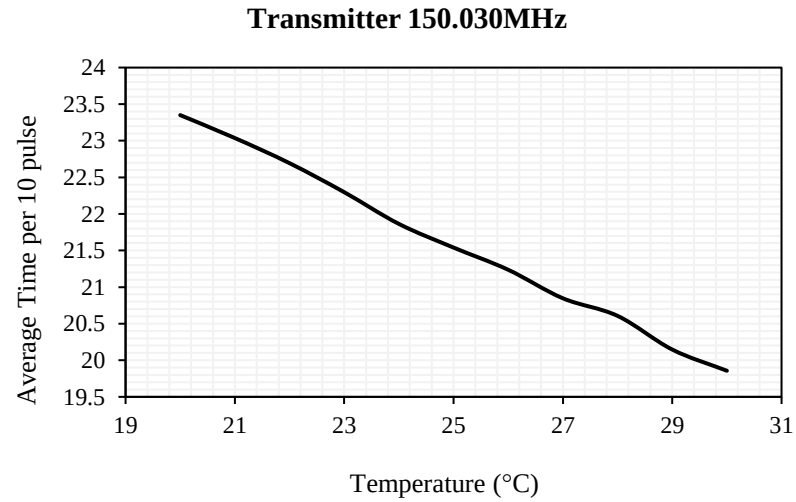
Appendix 1: Journal Publication

Wong, J. W., & Das, I. (2021). Predation on *Gonocephalus liogaster* (Günther, 1872) (Agamidae) by *Ptyas carinata* (Günther, 1858) (Colubridae) in Sarawak, Borneo. *Herpetology Notes*, 14, 349–351.

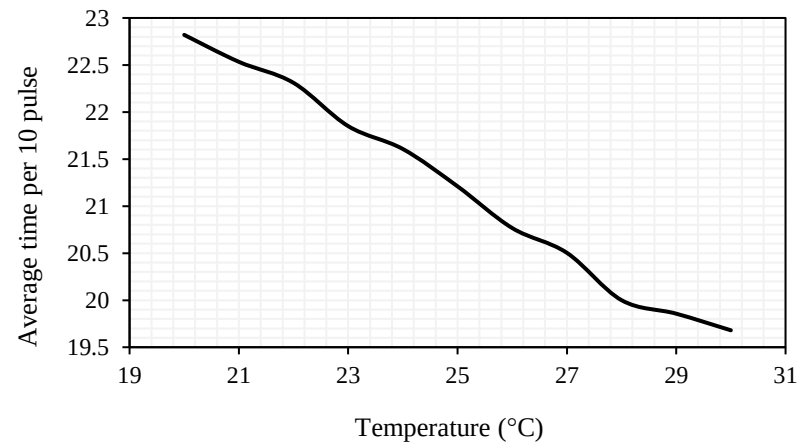
Appendix 2: Calibration of 16 units of BD-2 series temperature-sensitive radio transmitter (Holohil Systems Ltd. Carp, Ontario, Canada).

No.	Serial No.	Transmitter Frequency (MHz)	Temperature (°C)	20	21	22	23	24	25	26	27	28	29	30
1	232441	150.030	Average Time per 10 pulse	23.35	23.04	22.69	22.30	21.86	21.54	21.24	20.85	20.61	20.15	19.86
2	232442	150.050		23.77	23.48	23.08	22.71	22.38	22.05	21.72	21.53	21.00	20.60	20.21
3	232443	150.090		24.50	24.11	23.71	23.19	22.99	22.64	22.24	21.92	21.64	21.23	20.86
4	232444	150.109		21.99	21.78	21.50	21.02	20.77	20.45	20.04	19.78	19.49	19.26	18.87
5	232445	150.150		22.82	22.53	22.31	21.85	21.61	21.21	20.77	20.50	20.00	19.86	19.68
6	232446	150.230		23.83	23.34	23.17	22.68	22.19	22.12	21.63	21.32	21.00	20.59	20.24
7	232447	150.350		23.59	23.08	22.74	22.44	22.04	21.83	21.61	21.19	20.87	20.50	20.10
8	232448	150.370		22.71	22.50	22.09	21.91	21.50	21.14	20.74	20.49	20.15	19.92	19.56
9	232449	150.649		24.64	24.21	23.83	23.53	23.27	22.78	22.44	22.09	21.72	21.22	20.86
10	232450	150.689		23.54	23.42	22.91	22.67	22.38	22.01	21.54	21.20	20.84	20.45	20.08
11	232451	150.709		23.65	23.36	23.02	22.47	22.18	21.83	21.46	21.32	20.82	20.57	20.25
12	232452	150.870		23.32	23.11	22.67	22.36	21.87	21.67	21.34	20.83	20.53	20.21	20.02
13	232453	150.890		23.94	23.55	23.15	22.87	22.38	21.99	21.59	21.18	20.82	20.42	20.05
14	232454	150.910		22.17	21.96	21.47	21.20	20.89	20.68	20.16	19.90	19.63	19.27	18.88
15	232455	150.970		24.05	23.83	23.37	22.94	22.73	22.30	21.79	21.59	21.24	20.85	20.43
16	232456	150.990		24.64	24.33	23.65	23.40	23.11	22.66	22.23	21.94	21.47	21.18	20.83

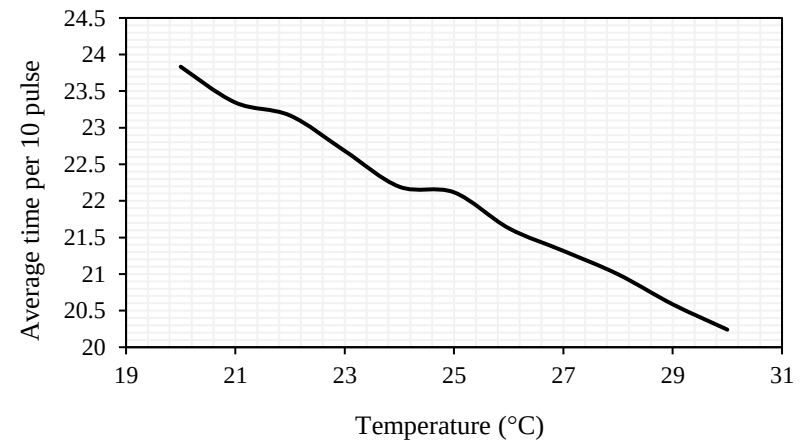
Appendix 3: Calibration curves of the 16 units of BD-2 series temperature-sensitive radio transmitter used.



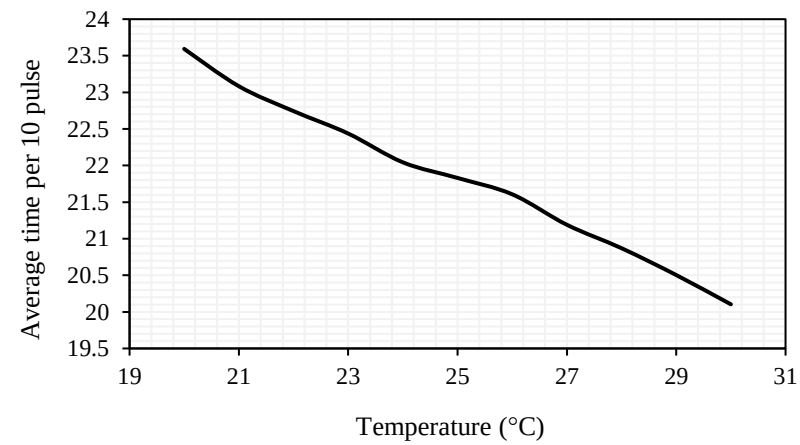
Transmitter 150.150MHz



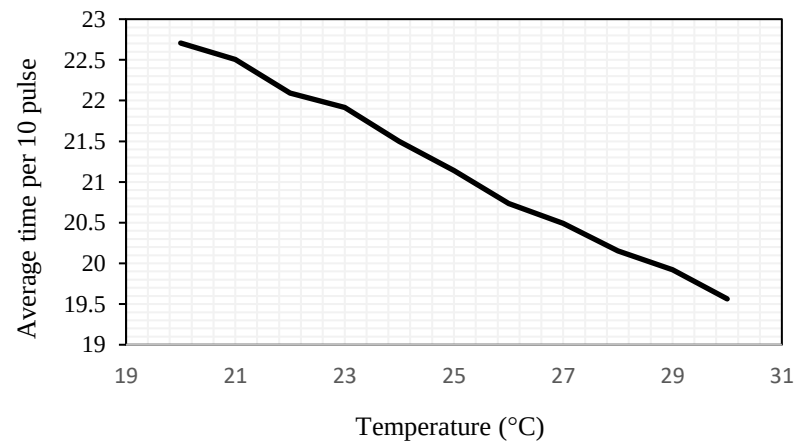
Transmitter 150.230MHz



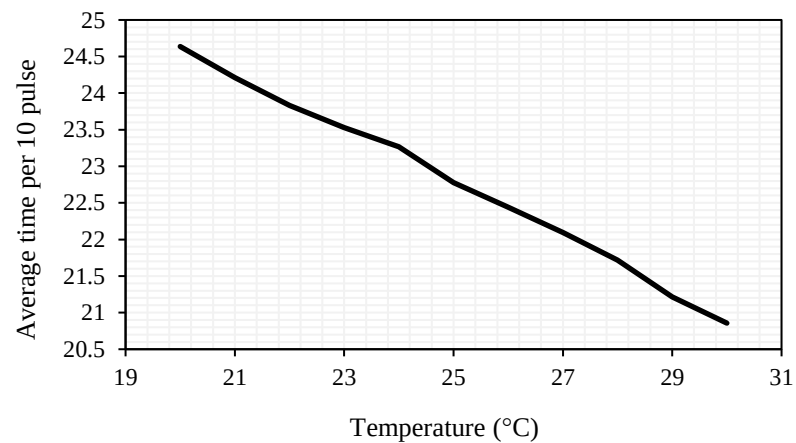
Transmitter 150.350MHz



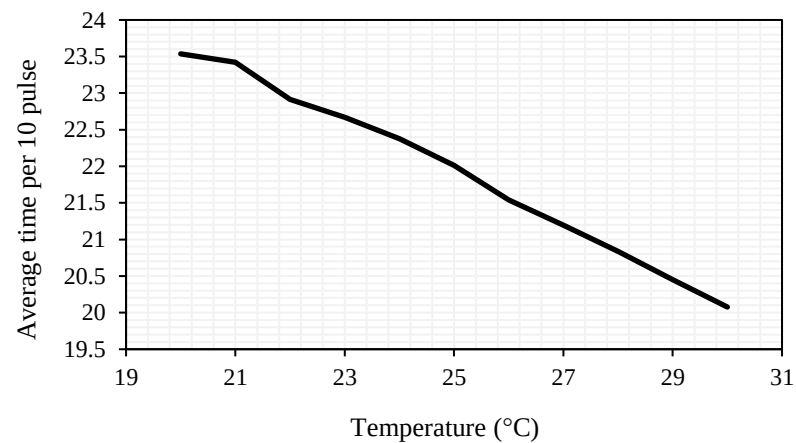
Transmitter 150.370MHz



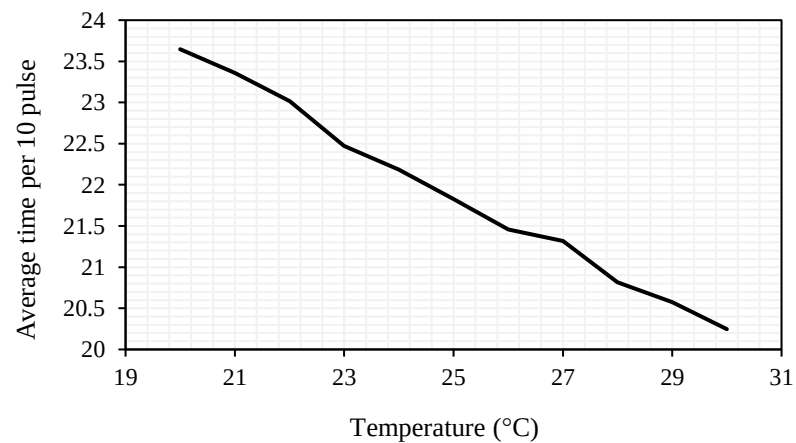
Transmitter 150.649MHz



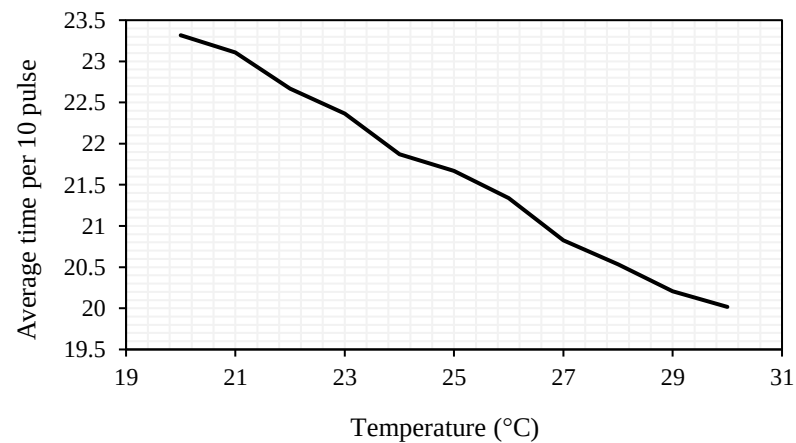
Transmitter 150.689MHz



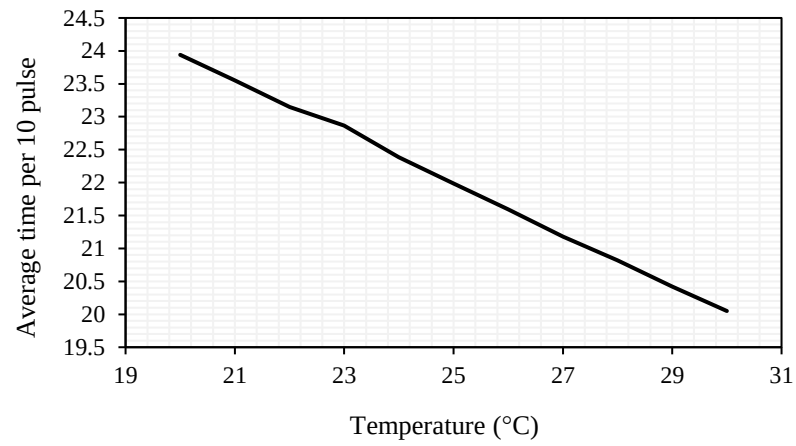
Transmitter 150.709MHz



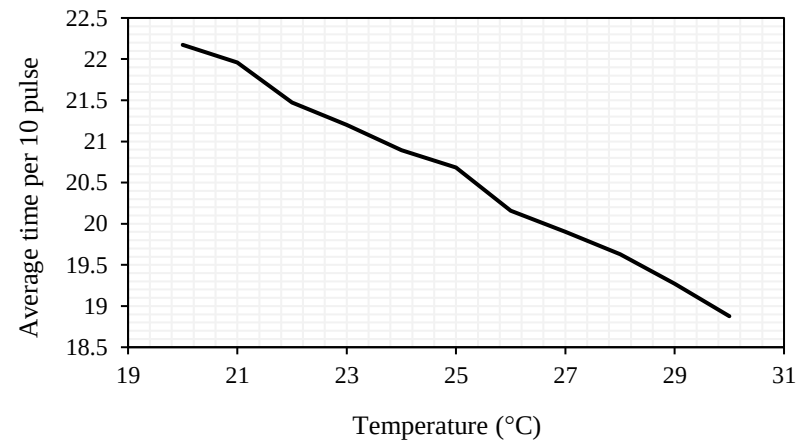
Transmitter 150.870MHz



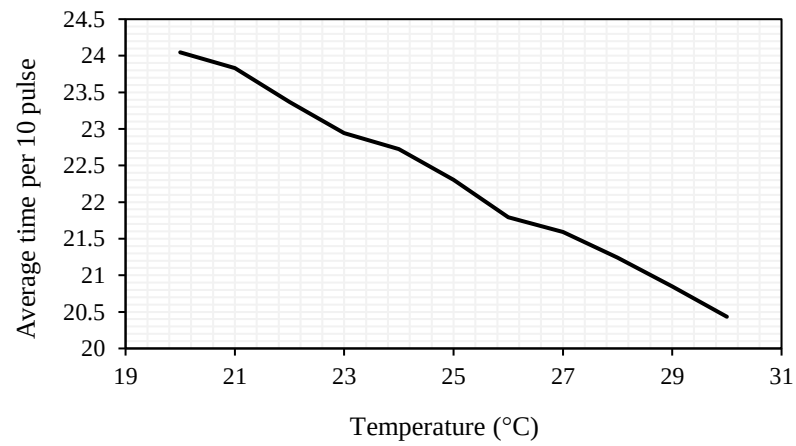
Transmitter 150.890MHz



Transmitter 150.910MHz



Transmitter 150.970MHz



Transmitter 150.990MHz

