การศึกษานิเวศวิทยาของงูเขียวหางไหม้ในสถานีวิจัยสิ่งแวดล้อมสะแกราช จังหวัดนครราชสีมา

นายคอลิน โทมัส สไตรน์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
สาขาวิชาชีววิทยาสิ่งแวดล้อม
มหาวิทยาลัยเทคโนโลยีสุรนารี
ปีการศึกษา 2557

THE ECOLOGICAL STUDY OF GREEN PIT VIPERS IN SAKAERAT ENVIRONMENTAL RESEARCH STATION, NAKHON RATCHASIMA

Colin Thomas Strine

A Thesis Submitted in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy in Environmental Biology

Suranaree University of Technology

Academic Year 2014

THE ECOLOGICAL STUDY OF GREEN PIT VIPERS IN SAKAERAT ENVIRONMENTAL RESEARCH STATION, NAKHON RATCHASIMA

Suranaree University of Technology has approved this thesis submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy)

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คอลิน โทมัส สไตรน์ : การศึกษานิเวศวิทยาของงูเขียวหางไหม้ ในสถานีวิจัยสิ่งแวดล้อมสะแกราช จังหวัดนครราชสีมา (ECOLOGICAL STUDY OF GREEN PIT VIPERS IN SAKAERAT ENVIRONMENTAL RESEARCH STATION, NAKHON RATCHASIMA). อาจารย์ที่ปรึกษา : ผู้ช่วยศาสตราจารย์ ดร.พงศ์เทพ สุวรรณวารี, 245 หน้า.

งูเขียวหางไหม้เป็นงูที่อาศัยและหากินอยู่ตามต้นไม้ มีลำตัวเรียวยาวกว่างูพวกเดียวกันที่อยู่ตามพื้นดิน ช่วยให้เคลื่อนที่ไปตามต้นไม้และพุ่มไม้เหนือพื้นดินได้อย่างคล่องแคล่ว งานวิจัยนี้มีวัตถุประสงค์เพื่อศึกษาความหลากหลาย ความชุกชุม ลักษณะภายนอก ถิ่นที่อยู่อาศัย และพฤติกรรมบางอย่างของงูเขียวหางไหม้ ในสถานีวิจัยสิ่งแวดล้อมสะแกราช ตั้งแต่เดือนพฤษภาคม พ.ศ. 2555 ถึงเดือนกุมภาพันธ์ พ.ศ. 2558

จากการศึกษาพบงูเขียวหางไหม้จำนวน 3 ชนิด คืองูเขียวหางไหม้ตาโต งูเขียวหางไหม้ท้องเหลือง และงูเขียวไผ่หางเขียว งูทั้งหมด 35 ตัว (งูเขียวหางไหม้ตาโตเพศเมีย 27 ตัว เพศผู้ 4 ตัว งูเขียวหางไหม้ท้องเหลืองเพศเมีย 1 ตัว และงูเขียวไผ่หางเขียวเพศเมีย 2 ตัว เพศผู้ 1 ตัว) ที่อาศัยอยู่บริเวณป่าเบญจพรรณและป่าดิบแล้ง ได้รับการฝังเครื่องส่งสัญญาณวิทยุติดตามเป็นระยะเวลา 11 - 208 วัน จากการหาขนาดถิ่นที่อยู่อาศัยโดยวิธี Minimum Convex Polygon พบว่า งูเขียวหางไหม้ตาโตมีขนาดถิ่นที่อยู่อาศัยเฉลี่ย 0.0201 เฮกแตร์ โดยมีพื้นที่หากินทั่วไป 0.038 เฮกแตร์ (50% Fixed kernel) และพื้นที่อาศัยหลัก 0.0199 เฮกแตร์ (95% Fixed kernel)

ลักษณะภายนอกของงูเขียวหางไหม้ตาโต 139 ตัว งูเขียวหางไหม้ท้องเหลือง 3 ตัว และงูเขียวไผ่หางเขียว 3 ตัว ที่จับได้จากการสำรวจและการพบโดยบังเอิญ ในระหว่างเดือนพฤษภาคม พ.ศ. 2555 และเดือนตุลาคม พ.ศ. 2557 ได้ถูกนำมาเปรียบเทียบกัน นอกจากนี้ การเปรียบเทียบลักษณะภายนอก 7 ลักษณะ รวมทั้ง Residual index และ Scaled Mass Index (SMI) ของงูเขียวหางไหม้ตาโตเพศผู้และเพศเมีย พบว่ามีความแตกต่างกันอย่างมีนัยสำคัญ ขนาดหัวของงูเขียวหางไหม้ตาโตเพศผู้มีความสัมพันธ์อย่างผกผันกับขนาดของลำตัว (SMI) แสดงให้เห็นถึงการแข่งขันระหว่างเพศในงูเขียวชนิดนี้ และลักษณะที่แตกต่างกันทางเพศในงูเขียวหางไหม้ตาโตอาจมีวิวัฒนาการมาจากการใช้ทรัพยากรและอาหารที่แตกต่างกัน

การวิจัยครั้งนี้ใช้วิธีการอันหลากหลาย เพื่อประเมินความชุกชุมของงูเขียวหางไหม้ทั้ง 3 ชนิด จากการจับงูทั้งหมด 285 ครั้ง พบว่าเป็นงูเขียวหางไหม้ที่แตกต่างกัน 203 ตัว แบ่งเป็นงูเขียวหางไหม้ตาโต 190 ตัว งูเขียวหางไหม้ท้องเหลือง 9 ตัว และงูเขียวไผ่หางเขียว 4 ตัว ซึ่งความชุกชุมของงูเขียวหางไหม้ตาโตและงูเขียวหางไหม้ท้องเหลืองไม่เกี่ยวข้องกับสภาพพื้นที่ที่อาศัยอยู่ ขณะที่งูเขียวไผ่ท้องเขียวมักพบลึกเข้าไปในป่าดิบแล้งเท่านั้น

การศึกษาสถานที่ซุ่มจับเหยื่อของงูเขียวหางไหม้ตาโตพบว่า งูชนิดนี้เลือกแหล่งที่มีเศษใบไม้ปกคลุมบนพื้นดินจำนวนมาก มีกิ่งไม้ขนาดใหญ่ และมีแหล่งกำบังตัวหลากหลายในการซุ่มรอเหยื่อ งานวิจัยนี้มีการสังเกตพบพฤติกรรมใหม่ๆ ของงูเขียว ซึ่งช่วยเพิ่มองค์ความรู้ด้านประวัติศาสตร์ธรรมชาติของงูเขียวหางไหม้ตาโตและงูเขียวไผ่ท้องเขียว

งานวิจัยชิ้นนี้แสดงให้เห็นว่าการประเมินความชุกชุมของงูที่มักซ่อนตัวอยู่ตามต้นไม้ ต้องใช้ความความละเอียดอ่อนและความระมัดระวังอย่างมาก และแสดงให้เห็นว่ายังมีความรู้ที่สำคัญอีกมากที่ยังไม่มีการศึกษาในงูกลุ่มนี้

สาขาวิชาชีววิทยา
ปีการศึกษา 2557

ลายมือชื่อนักศึกษา
ลายมือชื่ออาจารย์ที่ปรึกษา P. Suwan
ลายมือชื่ออาจารย์ที่ปรึกษาร่วม

COLIN THOMAS STRINE: THE ECOLOGICAL STUDY OF GREEN PIT VIPERS IN SAKAERAT ENVIRONMENTAL RESEARCH STATION, NAKHON RATCHASIMA. THESIS ADVISOR: ASST.PROF.PONGTHEP SUWANWAREE, Ph.D. 245 PP.

HABITAT SELECTION/ SEXUAL SIZE DIMORPHISM/ SIZE DIMORPHISM/ SPATIAL ECOLOGY/ TRIMERESURUS

Green Pit Vipers (GPV) are arboreal, crotalid snakes with more slender elongate bodies than most terrestrial pit vipers which facilitates movement through trees and bushes above the ground. The aims of this research were to investigate diversity, abundance, morphology, home range, behavior of GPVs in Sakaerat Environmental Research Station (SERS) from May 2012 to February 2015.

Three species of GPVs *Trimeresurus macrops*, *T. albolabris* and *T. vogeli* were captured in SERS. Total of 35 snakes (27 females and 4 males of *T. macrops,* 1 female of *T. albolabris* and 2 females and 1 male of *T. vogeli*), inhabiting mixed deciduous and dry evergreen forest, were implanted with internal radio transmitters and tracked from 11 to 208 days. Individual Minimum Convex Polygon home ranges for *T. macrops* averaged 0.0201 ha, with activity areas of 0.038 ha (95% Fixed kernel) and core areas 0.0199 ha of (50% Fixed kernel).

Adult morphological characters of 139 *T. macrops*, 3 *T. vogeli* and 3 *T. albolabris* obtained by active searches and opportunistic captures from May 2012 to October 2014 were compared. Additionally, 7 external characters including residual index and scaled mass index (SMI) between male and female *T. macrops* were significantly different. Male head size in *T. macrops* was negatively correlated with SMI, which may reveal intersexual competition in *T. macrops*. Sexually dimorphic characters in *T. macrops* may have evolved through intraspecific resource partitioning.

We assessed relative abundance of the three GPV species at SERS using a variety of sampling methods. A total of 285 GPV captures were recorded during the study period, with 203 individuals (190 *T. macrops*, 9 *T. albolabris* and 4 *T. vogeli*). *Trimeresurus macrops* and *T. albolabris* did not show site specific tendencies in relative abundance; however, *T. vogeli* was found exclusively in deep evergreen forest.

We used randomly selected microhabitat quadrats to test ambush site selection of *T. macrops*. This snake selected sites with deeper leaf litter, larger stems, and greater numbers of shelter sites surrounding the site than random points in the forest. Four novel behavioral observations were recorded for GPV during the study period, which have expanded the knowledge base of the natural history of *T. macrops* and *T. vogeli*.

Our research has demonstrated the need for careful consideration when attempting to assess relative abundance among secretive arboreal snakes, and highlights the knowledge gap in this little studied snake group.

School of Biology

Academic Year 2014

Student's Signature____________________

Advisor's Signature____________________

Co-advisor's Signature____________________

ACKNOWLEDGEMENTS

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The SERS staff members have been unquestionably patient with me throughout this research program, and have given assistance in various ways, so much that without them, undoubtedly this project would have failed. I thank the technology division in particular for their tolerance of venomous snakes in close proximity to students, and the kitchen staff for always being on the lookout for Green Pit Vipers (in addition to feeding my entire team).

I express my sincere gratitude to Asst. Prof. Dr. Pongthep Suwanwaree, for his help, guidance and the opportunity to pursue the projects that deeply interested me. My thesis co-advisor Dr. Jacques Hill III reminded me with clarity and conciseness what the underlying goal of ecology truly is. I also thank Dr. Matt Goode for training me in surgical procedures, anesthetic use and for donating transmitters to my initial program.

Director Taksin Artchawakom, has not only given permission for this program, but has also acted as a mentor in the field and has shown me how to lead effectively. I thank him for use of facilities, support, and guidance. Dr. Nareerat

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My field team, (The Sakaerat Conservation and Snake Education Team) are deserving of more gratitude than can be expressed through text. In particular Jacob Bukoski's enthusiasm for research inspired me to expand my work. Matt Crane's love of education pushed me to strive to always learn. Ines Silva's aptitude for data guided me to methodological revisions. Bartosz Nadolski's love of snakes helped raise my morale when times were difficult, and Curt Barnes reminded me that there is still so much to learn and build toward with this program..

It is with much gratitude that I thank my family. My mother (Sharon Strine), and father's (Russell Strine) support and guidance throughout my early years. I am in debt all of my extended family for their love and understanding throughout this program, but my Grandfather Gail T. Guyton will always hold a particular place in my mind. It is to him that I owe my love of the natural world and curiosity to question it's workings always.

Final thanks go to my wife (Supunnee Potijun Strine), who has endured the sleepless nights, long working hours, and challenging times, with good graces and a positive outlook. She has celebrated the successes of my work, and supported me in failure, and it is to her and my son (Thanabordee Potijun), that I dedicate this work.

Colin Thomas Strine

CONTENTS

CHAPTER

CONTENTS (Continued)

CONTENTS (Continued)

Page

CONTENTS (Continued)

Page

CONTENTS (Continued)

CONTENTS (Continued)

Page

LIST OF TABLES

LIST OF TABLES (Continued)

Table **Page**

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

Figure **Page**

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure **Page**

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure **Page**

LIST OF FIGURES (Continued)

Figure **Page**

LIST OF ABBREVIATIONS

a.s.l. = above sea level

AIC = Akaike's Information Criterion

AN = Human disturbance

BCI = Body condition index

BF = Bamboo forest

BPM = Beeps per minute

DDF = Dry dipterocarp forest

DEF = Dry evergreen forest

DF = Deep forest

DV = Dead vegetation

FK = Fixed kernel

FK50 = Fixed kernel 50% utilization area

FK95 = Fixed kernel 95% utilization area

FS = Field station

GIS = Geographic Information System

GLM = Generalized linear model

GLMM = Generalized linear mixed models

GPS = Global Positioning Systems

LIST OF ABBREVIATIONS (Continued)

GPV = Green Pit Viper

GV = Green vegetation

HL = Head length

HW = Head width

IUCN = International Uninon for Conservation of Nature

LC = Least Concern

LL = Leaf litter

MAB = Man and Biosphere

MCP = Minimum convex polygon

MDD = Mean daily displacement

MDF = Mixed deciduous forest

NA = Not Assessed

PF = Plantation forest

RK = Rock

SBR = Sakaerat Biosphere Reserve

SCSET = Sakaerat Conservation and Snake Education Team

SE = Standard Error

SERS = Sakaerat Environmental Research Station

SMI = Scaled mass index

SSD = Sexual size dimorphism

SVL = Snout- to- ventral length

LIST OF ABBREVIATIONS (Continued)

TBL = Total body length

TISTR = Thailand Institute of Scientific and Technological Research

TL = Total length

TRAL = *Trimeresurus albolabris*

TRMA = *Trimeresururs macrops*

TRVO = *Trimeresurus vogeli*

TVL = Tail to ventral length

UC = Uncovered

UDOI = Utilization distribution overlap index

WA = Water associated

WDV = Woody dead vegetation

WV = Woody vegetation

CHAPTER I

INTRODUCTION

1.1 Background and problem

The ultimate goal of ecology is to determine the influence of the environment on the distributions and abundances of organisms (Begon *et al*., 1996). The ecology of large, charismatic vertebrate taxa is relatively well studied (Perry *et al*., 2007). Snakes, Suborder *Serpentes,* are often overlooked as ecological study taxa in regards to ecology because their secretive natural history strategies require intensive effort to obtain acceptable sample sizes (Shine, 1994; Pawar, 2007). This is particularly true for the Asian Green Pit Vipers (*Trimeresurus* spp.) which are members of the sub-family Crotalinae, nested within Viperidae family. The Green Pit Viper (GPV) is one of the most widespread snake taxa in Southeast Asia, with species found from Southern China to Indonesia (Chanhome *et al*., 2011). As venomous snakes, GPV are thought to make up a significant proportion of snakebites in Southeast Asia (Warrell *et al.*, 1999) each year. High abundance and camouflage defense behaviors make this group particularly susceptible to human-snake interactions.

The venom structure among GPV species can be markedly different even among closely related GPV species, and populations (Chanhome *et al*., 2002; Soogarun *et al*., 2006). Frequent misunderstanding of the life history and the morphological characters has led to frequent misidentifications of these species (Malhotra and Thorpe, 1997) even by medical professionals treating envenomated patients (Viravan *et al*., 1992). In order to reduce the chance of bites it is necessary to understand how GPV live, which sites they prefer and in what abundances are they present. Therefore, this thesis provides an opportunity to assess the spatial ecology of relatively unstudied group of tropical snakes, with the side benefit of generating knowledge that may be valuable in bite prevention.

Green Pit Vipers (GPV) are small nocturnal, arboreal sit and wait ambush predators occurring throughout Southeast Asia. Although they are relatively common, even so far as to be found in major city centers such as Bangkok (Mahasandana and Jintakune, 1990), a considerable knowledge gaps exist on the basic ecology of GPV, especially in Thailand. There are presently more than 20 recognized species of GPV in Thailand, and taxonomic revisions based on both morphological and genetic variation are constantly being proposed (Malhotra *et al*., 2011). Yet, virtually all knowledge on habitat use and seasonal activity of GPV is anecdotal or from captive husbandry (Chanhome *et al*., 2011). As understudied, yet arguably the most widespread and commonly encountered snake Taxa in Thailand, GPV serve as ideal candidates for study

Thus, this is an opportunity to investigate spatial ecology, habitat use, and relative abundance of the three *Trimeresurus* sp. found within Sakaerat Environmental Research Station (SERS) which is part of the Sakaerat Biosphere Reserve. Due to sample size limitations, much of the inferences hereafter will be limited to The Big Eyed Pit Viper (*Trimeresurus macrops*), however information on the White Lipped Pit Viper (*Trimeresurus albolabris*) and The Vogel’s Pit Viper (*Trimeresurus vogeli*) will also be included.

Big Eyed Pit Vipers (*Trimeresurus macrops*) are native to Southeast Asia, predominantly occupying the understory of forests (1-3 m); they are active nocturnally in Dry Evergreen Forests (DEF) and Mixed Deciduous Forests (MDF) in SERS and in many other areas throughout their range (Das, 2010). Typically up to 710 mm in females, the body is slender and the temporal scales are strongly keeled which distinguishes the species from the White Lipped Pit Viper (*Trimeresurus albolabris*) and the Vogel's (*Trimeresurus vogeli*) pit viper. Dorsally, the species has a pale green coloration with the chin and gular region bluish (Cox *et al*., 2012). The Big Eyed Pit Viper was once considered broad reaching throughout Southeast Asia; recently, it was split using multivariate molecular analyses into three separate species (Malhotra *et al*., 2011). For the purposes of the thesis *T. macrops* present in the study area of SERS will be the only species to be considered as the Big Eyed Pit Viper following Malhotra *et al*. (2011).

The distribution and abundance of *T. macrops* species remains poorly studied and has been determined from fragmented museum collections. A detailed database may yield insight into morphological and genetic variation across The Big Eyed Pit Viper's range. Little ecological information exists on for *T. macrops* and most of the literature dealing with *T. macrops* is aimed towards the toxic effects of venoms and post-bite treatment which are thought to be the least severe of the GPV complex (Hutton *et al*., 1990).

The White Lipped Pit Viper (*Trimeresurus albolabris*) is an arboreal, nocturnal species thought to forage actively on the ground periodically but the robust body structure indicates the species is mostly an ambush (sit and wait) predator (Cox *et al*., 2012). The White Lipped Pit Viper is recorded in both urban landscapes and forested areas up to 1600 m a.s.l. and likely breeds between September-November, with litters born between February-May according to Cox *et al*. (2012). This species is the most common GPV found at Suranaree University of Technology located roughly 60 km N of the study area, and has been confirmed present at SERS, albeit in very low population densities. With a total length of approximately 1,040 mm, *T. albolabris* is a medium sized robust bodied pit viper. Generally, the coloration is lime-green or bright green dorsally with a smooth or very weak keel to the scales. The ventral surface varies between light green and yellow. The temporal scales are generally smooth with an ovate triangular shaped head. The tail is usually reddish brown in color. Usually the eye color is sexually dimorphic; however in T. albolabris both males and females have yellow irises (Das, 2010).

The Vogel's Pit Viper (*Trimeresurus vogeli*) is physically similar to *T. albolabris* (Malhotra *et al*., 2004) but is a darker green. It is thought to inhabit upland evergreen forests, and is sometimes found in vegetated grasslands at high elevations (Malhotra *et al*., 2004). Primarily it preys upon skinks, and frogs at ground level within a few meters of water (Malhotra *et al*., 2004). Little is known of the reproductive behaviors and the foraging ecology for the The Vogel's Pit Viper. The project confirmed the presence of *T. vogeli* at SERS, and performed the first radio-telemetry on the species. Although listed as Least Concern (LC) by the IUCN (2012), the main threats to this species likely include illegal logging and poaching in primary forests it is thought to prefer (Cox *et al*., 2012). The species is likely common in areas where it occurs, but confirming presence of snake species in an area can be effort intensive (Dorcas and Willson, 2009). The Vogel's Pit Viper is remarkably rare in SERS and only one adult male and three adult females were captured deep in the evergreen forest.

It is imperative that we understand the ecology of GPV, because they are arguably the most commonly encountered vertebrate predators at SERS, and likely play a critical role in the food web. If GPV are present in high abundances, they would make good model organisms for studies of ambush predation strategies. Detection probabilities among snakes are often too low to provide any level of confident inference (Steen, 2010).

As the group of snakes which hospitalize the highest proportion of people in Thailand each year (Viravan *et al*., 1992) studies of the GPV are also important from a medical standpoint. Thus, my project is an opportunity to investigate lowland communities of GPV in various aspects of their ecology. Furthermore, information obtained through this study may be used for both conservation, and snake bite prevention.

1.2 Objectives

The objectives of this study are:

1) To examine the home range, seasonal movement patterns and microhabitat site selection for *T. macrops* at Sakaerat Environmental Research Station, and to perform preliminary study on the spatial ecology of *T. albolabris* and *T. vogeli*.
2) To study morphometric sexual dimorphism in *T. macrops,* and preliminarily examine differences in morphometrics between Green Pit Viper (GPV) species at Sakaerat Environmental Research Station.

3) To investigate relative abundance, population structure, survivorship and capture effectiveness for different methods among *GPV* (primarily *T. macrops*) in Sakaerat Environmental Research Station.

4). Record novel behavioural observations for SERS cryptic GPV species, and confirm the timing of the breeding season for *T. macrops* in SERS.

1.3 Scope and limitations of study

The study focuses on a resident community of GPV species in Sakaerat Environmental Research Station, Nakhon Ratchasima, a small (80 km^2) well-protected lowland forest area. The study area consists of 4 main 100 m x 100 m intensive sites, as well as the South central deep evergreen forest. Because males often were too small to accommodate the 1.2 g transmitters, only 5 snakes out of 32 tracked GPV were male, thus the spatial ecology questions were primarily limited to the abundant female *T. macrops*. All snakes were followed until 1 week before transmitter expiration, or mortality of the individual due to predation or other causes. Green Pit Vipers were tracked for varying intervals throughout the year including all seasons except for the Thai summer (March-May) due to transmitter battery life (12-16 weeks). By tracking the snakes, home range, habitat use patterns, and ambush sites selection were investigated. In addition, quantified active surveys, as well as drift fenced plots with attached funnel trapping sessions were conducted from May 2012 to February 2015, and May 2012 to August 2013, respectively. Relative abundance was roughly estimated during the rainy seasons (periods of high GPV visibility and activity) of 2012, 2013 and 2014 within dry evergreen fragments and mixed deciduous forest fragments, using mark and recapture methods to evaluate capture methods for GPV.

1.4 Benefits of study

The ultimate goal of my study was to increase knowledge of the natural history, provide fundamental population information, and offer advice to local communities in addition to management authorities on a lowland GPV forest community in the region, in order to manage, and protect the often misunderstood *Trimeresurus* spp. in forested areas and national parks throughout Thailand. Furthermore, the information compiled by the study may be used to compare forest GPV communities and populations to communities in disturbed areas as part of a broader-wide scale research program, particularly for *T. macrops*, and other *Trimeresurus* species for which natural history information is virtually absent. The data presented here may also be used toward building a better local understanding of *T. macrops* in order to prevent bites to humans as opposed to focusing solely on treatment post-bite.

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CHAPTER II

LITERATURE REVIEW

2.1 Vipers (family Viperidae)

The vipers (family Viperidae), including true vipers (Viperinae), pit vipers (Crotalinae), night adders (Causinae) and Fea's viper (Azemiopinae) are considered one of the most dangerous snake families, and are responsible for a large proportion of bites in rural areas throughout the world (Simpson and Norris, 2009). The viperids are all venomous to varying degrees of potency, with a hinged fang venom apparatus, which has allowed for the evolutionary development of disproportionately long fangs in comparison to other venomous taxa (Zug *et al*., 2001). The fangs are folded against the roof of the mouth when the mouth is closed, and as the snake strikes, the fangs rotate forward to an angle of approximately 90 degrees with the roof of the mouth (Cox *et al*., 2012). The angle of the solenoglyphous (hinged) fangs upon strike allows for deep penetration into muscle tissue where the typically haemotoxic and cytotoxic venom cocktails are most effective for subduing prey items (Lillywhite, 2014).

Vipers are found worldwide except for on Papau-Australia, Antarctica, oceanic islands, and some areas north of the Arctic Circle (McDiarmid *et al*., 1999) (Figure 2.1). There are 36 genera and 256 accepted viper species worldwide, with at least 50 species residing in Southeast Asia alone (Alirol *et al*., 2010). Of the 256 species 7 species are critically endangered, 18 species are endangered, 19 species are vulnerable, 12 species are near threatened, and 17 species are listed as data deficient (IUCN, 2013). Although only 192 species have been assessed by the IUCN most species are listed as either least concern or data deficient.

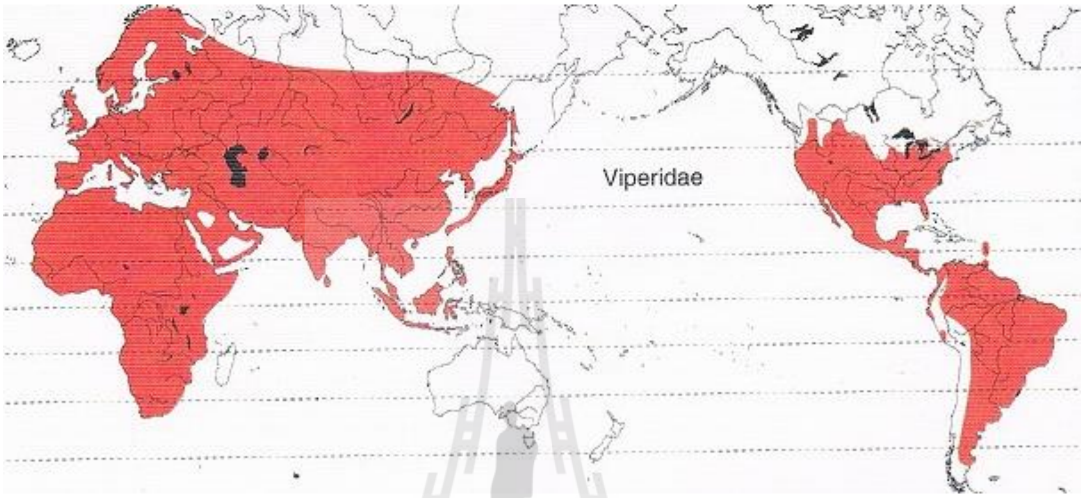

Figure 2.1 Worldwide distribution map of family Viperidae, showing the cosmopolitan distribution of the family, in addition to the absence of vipers in Oceana (Zug *et al.*, 2001).

Vipers are a significant cause of injury to humans, however their viper venom has the potential to be used in medicine (Finn, 2001) making them of interest for conservation and so losing populations of vipers also reduces access to potentially unique venom compounds. Some vipers are incredibly tolerant to the risks of exploitation and habitat degradation (Jetic *et al.*, 2013) but others are threatened by habitat fragmentation in the form of roads and human settlements (Filippi and Luiselli, 2004). Despite the prevalence of vipers, only limited information is available on the basic biology, for the majority of the taxon especially in Southeast Asia where new species are constantly being discovered (Malholtra *et al.*, 2011; Vogel *et al.*, 2014).

2.2. Pit Vipers (subfamily Crotalinae)

Pit vipers (Crotalines) are widely distributed throughout Asia and the Americas (including North, Central and South America), and are thought to have evolved out of Asia (O'Shea, 2011). Crotalids are the only vipers found in the new world, and only a single species (*Gloydius halys*) extends into Eastern Europe (Nilson and Gutberlet, 2004; Figure 2.2). The size range includes the smallest (300 mm) to some of the largest vipers (3.75 m) in the world.

Crotalid vipers all have a well-developed loreal pit which acts as an infrared receptor; in addition they tend to have a choanal process on the palantine (Zug *et al*., 2001). Pit vipers also have a specialized muscle between the venom gland and the ectopterygoid, when contracted the venom is forced out of the venom gland, perhaps giving them greater control over venom delivery than other vipers (Campbell and Lamar, 2004).

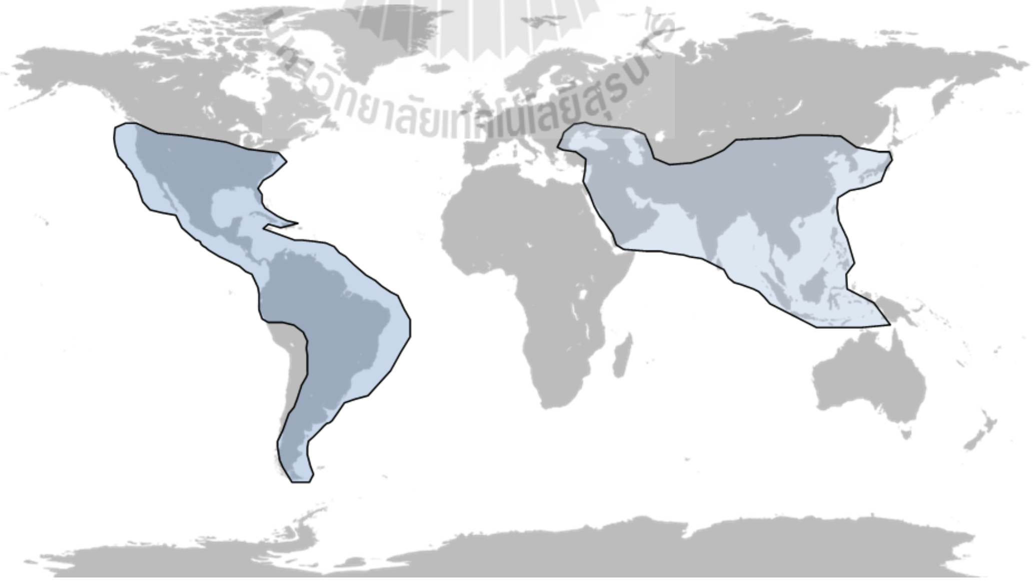

Figure 2.2 World range map of subfamily Crotalinae displaying the absence of pit vipers in Europe and Australia (Zug *et al*., 2001).

Table 2.1 Worldwide pit viper genera and number of species per genus (IUCN Redlist 2014; McDiarmid *et al.*, 1999).

Genus	Common name	Species	Vulnerable	Endangered	Continental Geographic range
Agkistrodon	Moccasins	3	0	0	North, Central and South America.
Atropoides	Jumping Pit Vipers	3	0	1	Mexico and Central America
Bothriechis	Palm-Pit Vipers	7	2	1	Southern Mexico to South America.
Bothriopsis	Forest-Pit Vipers	7	0	1	Central and South America
Bothrops	Lanceheads	32	2	3	Central and South America to Argentina
Calloselasma	Malayan Pit Viper	1	0	0	Southeast Asia from Thailand to Indonesia.
Cerrophidion	Montane Pit Vipers	3	0	0	Central America
Crotalus	Rattlesnakes	29	0	2	The Americas, from southern Canada to northern Argentina.
Deinagkistrodon	Hundred-pace Pit Viper	1	NA	NA	Southeast Asia.
Gloydius	Asian moccasins	9	1	0	North Asia, South Asia, Central Asia
Hypnale	Hump-nosed Pit Vipers	3	0	0	Sri Lanka and India.
Lachesis	Bushmasters	3	NA	NA	Central and South America.
Ophryacus	Mexican horned Pit Vipers	2	1	0	Mexico.
Ovophis	Mountain Pit Vipers	3	0	0	South, Southeast and East Asia
Porthidium	Hognose Pit Vipers	7	0	0	Central America
Sistrurus	Ground rattlesnakes	3	0	0	North and Central America
Trimeresurus	Asian lanceheads	46	0	3	Southeast Asia from India to southern China and Japan
Tropidolaemus	Temple vipers	2	0	0	Southern India and Southeast Asia.

There are currently more than 18 genera with 151-228 accepted species depending upon the classification system (ITIS, 2004; Nilson and Gutberlet, 2004; Uetz and Hollermann, 2014). Pit vipers are cryptic in nature and population trends are difficult to assess (Steen *et al*., 2010). In spite of the knowledge gap, the IUCN (2014) has classified 5 pit vipers as near threatened, 9 species as vulnerable, 9 as endangered and 2 as critically endangered (IUCN, 2014; Table 2.1). Table 2.1 illustrates the genera of the crotaline snakes.

Pit vipers are primarily nocturnal ambush hunters with few exceptions (Beaupre, 2002) and employ a variety of niches worldwide, including semi-aquatic, terrestrial, desert dwelling, and arboreal taxa (Beaupre and Duvall, 1998). In most cases, pit vipers are relatively long lived (>15 years in captivity). They obtain prey through ambush low energy sit and wait foraging tactics, which allow them to remain in the same location for relatively long periods, perhaps reducing predation risk because of camouflaged coloring which breaks up the snake’s outline making them more difficult to pick out from above (Stevens and Merilaita, 2009).

By remaining in one place, little energy is invested in foraging, using the Jacobson’s organ in combination with the heat sensing pit likely increases foraging success (Zamudio and Greene, 1997). Because pit vipers typically forage passively through ambush methods, much of their energy is allocated to growth and storage, thus pit vipers often have heavier robust bodies and larger heads than other snakes (Cundall, 2002). The sessile nature of pit vipers (Scharf *et al*., 2006), makes them ideal candidates for habitat selection studies. They often remain in a selected site for multiple days; even weeks in some cases (Shine and Bonnet, 2000).

Crotalines usually undergo ontogenetic shifts in diet, primarily from ectotherms to endotherms as they mature and are able to take larger more nutritious prey (Greene, 1997; Holycross and Mackessy, 2002; Martins *et al*., 2002). In some cases accidental altruism has been recorded based on foraging pit vipers killing prey items too large to consume simply because they were in ambush position when large animals passed by, as is often the case on the island of Shedao where the Shedao pit viper (*Gloydius shedaoensis*) has been studied for more than 20 years because it is an isolated island dwelling snake with unique ecological characteristics (Shine *et al*., 2003). With the exception the Shedao pit viper of China and the Golden lancehead (*Bothrops insularis*) there is limited information on long term pit viper foraging ecology outside of North America (Guimaraes *et al*., 2014).

Typically, strong sexual size dimorphism (SSD) exists in pit viper species (Andersson, 1994; Shine 1993), in cases where there is male to male combat there is typically male biased SSD (Cox *et al*., 2007). Mating systems among pit vipers are variable, ranging from (rarely recorded) multiple paternity for example in the Halys Pit Viper (*Gloydius halys*), especially in locations with high population densities (Simonov and Wink 2011) to intensely competitive male to male combat systems as is seen in the Malayan Pit Viper (*Calloselasma rhodostoma*) found in Thailand (York 1984; Strine *et al*., 2015). In addition, numerous species are thought to store sperm, especially species that mate during the proximal months of the activity season (Olsson and Madsen, 1998).

2.3 Asian Green Pit Vipers

2.3.1 Description and distribution

Green Pit Vipers (GPV) are all arboreal or semi-arboreal crotalid snakes with more slender elongate bodies than most terrestrial pit vipers to facilitate movement through trees and bushes above the ground (Malhotra *et al*., 2011). Most Asian GPV (also known as Asian lanceheads, or Asian moccassins) are currently classed as *Trimeresurus* (Lacépède, 1804), although members of *Tropidolaemus* (Wagler, 1830), and *Gloydius* (Hoge and Romano-Hoge, 1981) are also considered GPV. They are usually identifiable by the slender neck and body, compiled with a triangular head and a distinctly green coloration. Some snakes in this group display interstitial banding (the *albolabris* group), while others are primarily solid in skin color. *Trimeresurus* (Lacepede) is the largest genera of Asian snakes consisting of more than 40 species in the Asian subtropics and tropics (Tu *et al*., 2000; Vogel *et al*., 2014).

Phylogenetic analyses have split the genus *Trimeresurus* into several genera (*Cryptelytrops*, *Popeia*, *Pareas*, and *Viridovipera*) based on phylogenetic and morphological characters (Malhotra and Thorpe, 2004; Malhotra *et al*., 2011), however not all taxonomists accept the revisions (David *et al*., 2001, 2011). Here we follow David *et al*. (2011), treating *Trimeresurus sensu lato* as a valid generic term, and we treat *Cryptelytrops*, *Popeia*, *Pareas* and *Viridovipera*, as sub-genera following Cox *et al*. (2012).

Table 2.2 Conservation status and extraterritorial distributions of *Trimeresurus* spp. in Thailand (Cox *et al*., 2012).

Species	Sub Genus	Common Name	Status	Distribution
T. albolabris	*Cryptelytrops*	White lipped Pit Viper	LC	Thailand (cosmopolitan) Bangladesh, Cambodia, China, India, Indonesia. Laos, Vietnam, Myanmar
T. kanburiensis	*Cryptelytrops*	Kanchanaburi Pit Viper	EN	Thailand (Kanchanaburi)
T. macrops	*Cryptelytrops*	Big Eyed Pit Viper	LC	Thailand (Nakhon Ratchasima, Ayutthaya, Bangkok, Chiang Mai, Chiang Rai, Kanchanaburi, Sing Buri *et al*.) Cambodia, Laos, and Vietnam
T. purpureomaculatus	*Trimeresurus*	Shore Pit Viper	NA	Thailand, Indonesia, Western Malaysia, Myanmar, Singapore
T. venustus	*Trimeresurus*	Beautiful Pit Viper	NA	Southern Thailand, Prachuap Khiri Khan, below Isthmus of Kra
T. hageni	*Parias*	Hagen's Pit Viper	LC	Thailand (Narathiwat, Songkhla, Surat Thani, Trang), Indonesia, Western Malaysia, and Singapore
T. sumatranus	*Parias*	Sumatran Pit Viper	LC	Thailand (Narathiwat, Pattani, Yala), Malaysia, Indonesia, Singapore

Table 2.2 (Continued).

Species	Sub Genus	Common Name	Status	Distribution
T. phuketensis	*Popeia'*	Phuket Pit Viper	NA	Thailand (Phuket)
T. popeiorum	*Popeia*	Pope's Bamboo Pit Viper	LC	Thailand (Chiang Mai, Chiang Rai, Phetchaburi, Lampang, Uthai Thani) India, Laos, Western Malaysia, Vietnam
T. gumpretchi	*Viridovipera*	Gumprecht's Green Pit Viper	NA	Thailand (Chayaphum, Chiang Mai, Chantaburi, Loei, Phetchabun, Phitsanulok, Udon Thani), China, Laos, Vietnam
T. vogeli	*Viridovipera*	Vogel's Green Pit Viper	NA	Thailand (Chantaburi Nakhon Ratchasima, Prachin Buri, Trat), Cambodia, Laos Vietnam
T. fucatus	*Popeia*	Siamese Peninsular Pit Viper	LC	Thailand (Chumphon, Krabi, Nakhon Si Thammarat, Phang-nga, Surat Thani, Trang) Western Malaysia, Myanmar
T. wiroti	*Craspedocephalus*	Thai Palm Viper	LC	Thailand (Krabi, Nakhon Si Thammarat, Narathiwat, Surat Thani, Trang)

Worldwide 46 species of *Trimeresurus* exist, 13 of which are found in Thailand, including one Asian mocassin the Wagler's pit viper (*Tropidolaemus wagleri*), which occupies a similar niche as *Trimeresurus* in Thailand thus we treat it as a GPV. (Cox *et al*., 2012; Vogel *et al*., 2014;IUCN, 2014 Table 2.2). A single species *T. kanburiensis* is endangered in Thailand, restricted to upland deciduous and evergreen forests in Kanchanaburi Thailand (Chan-Ard *et al*, 2012).

2.3.2 Natural history

As nocturnally active ambush hunters, they use their solenoglyphous fangs to envenom and kill prey which, typically consists of: birds, small mammals, lizards, and amphibians (Cox *et al*., 2012; Das, 2010). Asian GPV are often euryphagous taking anything from arthropod prey to vertebrates (Koba, 1961; Mori and Moriguchi 1988; Mori *et al*., 1989; Creer *et al*., 2002). A study in Taiwan examined 229 male and 65 female Taiwanese bamboo pit vipers (*Trimeresurus stejnegeri*), and found that only 13% of the snakes contained prey items and of these more than 10 amphibian species were found in the stomach along with mammalian and reptilian evidence (Creer *et al*., 2002). In comparison with Tsai, 2008, who studied the Taiwanese mountain viper (*Trimeresurus gracilis*) with 16% of snakes containing prey items, the *T. stejnegeri* had fewer identifiable prey items in the digestive tract. In some cases, secondary evidence of arthropods in the stomach of prey items (Lee and Lue 1996; Creer *et al*., 2002). Rapid venting of prey items may be the reason for the absence of food matter found in *T. stejnegeri* digestive systems, rapid venting of fecal matter would be adaptive for arboreal species needing to move through trees. In addition the arboreal three dimensional matrix may reduce the chance of encountering prey because there is more available space for prey items to travel through, although the matrix provides protection from predators (Creer *et al*., 2002). Thus, because of their arboreal lifestyle Asian GPV often are found without prey items inside the stomach. Lilywhite *et al.* (2002) suggests that male snakes are more often discovered with prey items in the digestive tract perhaps because of their energy allocations towards feeding as opposed to growth (Asian GPV have a female biased SSD).

Most *Trimeresurus* species are viviparous, producing between 3–30 neonates during birthing (Das, 2010, Chanhome *et al*., 2011). Although multiple paternity has not been recorded in the genus, it is probably present because most *Trimeresurus* mate at the end of the of the activity period before the cool season of their range (Tsai and Tu, 2001), which is typically an indicator of multiple paternity, as is long term sperm storage. At least some species exhibit long term sperm storage, for example the Stejneger’s pit viper (*T. stejnegeri*) of Taiwan showed direct evidence of long term sperm storage in over 90% of the reproductive individuals captured by examining hormone levels (N=132) and reproductive organ morphology (Tsai and Tu, 2001). In addition, it is likely that some (if not all) *Trimeresurus* sp. undergo a biennial reproductive cycle, because the ratio of reproductive to non-reproductive (Tsai and Tu, 2001) snakes was 1:1, typically indicative of biennial reproductive systems found in north American crotalids, but it is thought that the mechanisms for sperm storage and biennial reproduction are different in the subtropics and tropics (Tsai and Tu, 2001; Lin and Tu, 2008).

2.3.3 Human health consideration

Thousands of people are bitten by GPV in Southeast Asia every year, in fact within even industrial nations such as Hong Kong and Singapore, GPV can account for up to 50% of all human envenomation (Warrell, 2010). The excellent camouflage GPV's employ allows them to avoid detection even in urban areas, increasing the risk for people who are unaware of the snake's presence (Chotenimitkhun and Rojnuckarin, 2008) and especially in rural areas where agricultural workers and children are at greatest risk when low level hanging fruits are picked from trees. Although the group as a whole is considered dangerous, envenomations are rarely lethal, particularly for *T. macrops* which is thought to have weaker venom than other GPV (Hutton *et al*., 1990). Typically GPV bites are not lethal, although they can be extremely painful, requiring expensive hospital visits and long term recovery especially in the case of *Trimeresurus albolabris*, which can cause excess bleeding and the inability to clot (Soogarun *et al*., 2006). Non-lethal envenomations contribute significantly to the medical costs of the state of Thailand, often multiple serum vials are needed to treat a bite victim (Pak Thong Chai Hospital, 2014). Hospital records from Nakhon Ratchasima, Pak Thong Chai Hospital, and Wang Nam Khiao Hospital, which are adjacent to the study site to the North and South respectively, indicated that GPV accounted for 44 of the 141 serious hospitalizations from snakebites from 2011 to 2014. Thus, even near the study area GPV account for more than 30% of the total snakebites, even though GPV compose less than 5% of the total species in the region.

Treatment for GPV envenomations is usually through the use of polyvalent antivenin from Thailand, it is even used in adjacent nations as far as Hong Kong, as was the case with a 6 year old child who developed severe coagulopathy after being bitten by a *T. albolabris*, native antivenin of *Akistrodon halys* was administered with no effect, but when *T. albolabris* antivenin from Thailand was administered the symptoms were significantly reduced (Yang *et al*., 2007). Bite prevention is always preferable to treatment via serum because serum can have detrimental health effects especially if the patient is allergic to the serum (Morais and Massaldi, 2009), antivenin prices are lower in Thailand than other Asian nations in part due to the ready supply of serum produced by the Queen Saovapha Memorial Institute and Snake Farm (Chanhome, 2008).

Thailand is fortunate, in that it is home to the Bangkok Snake Farm, which is associated with the Thai Red Cross, and has continually expanded the capacity to produce effective antivenin for the entire Southeast Asian region (Chanhome *et al*., 2002). Although polyvalent (effective on bites from multiple species) serum is typically used with GPV bites, the toxic effects among different species vary significantly in potency (Hutton *et al*., 1990), with *T. albolabris* showing the most severe toxic effects in the group. These taxa are not restricted exclusively to agricultural areas, and as human population continues to spread GPV's will continue to come into conflict with humans and most likely the number of envenomations yearly will increase, in fact both *T. albolabris* and *T. macrops* were still found in major cities in recent years (Mahasandana and Jintakune, 1990; Cox *et al*., 2012).

2.4 GPV found in SERS

2.4.1 White Lipped Pit Viper (*Trimeresurus (Cryptelytrops) albolabris* GRAY, 1842)

The White Lipped Pit Viper has a maximum total body length of 1,040 mm in females (averaging 600–940 mm) this species is a medium sized robust bodied pit viper (Gray, 1842). Adults range from 105 g – 260 g (Cox *et al*., 2012). The coloration is lime-green or bright green dorsally with a smooth or very weak keel to the scales, while the ventral surface varies between light green and yellow. The temporal scales are generally smooth with an ovate triangular shape to the head (Cox *et al*., 2012). The tail is usually a reddish brown color and makes up approximately 14–21% of the total length (TL). Unusual for green pit vipers, the sex is indeterminate by eye color as males and females both possess yellowish brown eyes with vertically elliptic pupils (Das, 2010; Cox *et al*., 2012). Males and females are dimorphic in that females are larger and males have a white stripe running down the first dorsal scale to the venter (Figure 2.3). The lateral white stripe is often (but not always) absent in females. The extensive diagnostic characters used for clarifying *T. albolabris* in our study following Cox *et al.* (2012) are listed in Table 2.3.

Figure 2.3 Adult male *T. albolabris* (Left) and Female *T albolabris* (Right). Photo Credit: Edward Lau, Cowan Belanger.

T. albolabris is found in much of Thailand (Figure 2.4), and extraterritorially as far south as Indonesia, and as far-east as Bangladesh (Cox *et al*., 2012). *Trimeresurus albolabris* is recorded in both urban areas and forested areas up to 1600 m a.s.l. in Thailand and extraterritorially up to 2000 m a.s.l. (Orlov *et al*., 2002) This species is the most common GPV found at Suranaree University of Technology roughly 60 km N of the study area (Strine *et al*., 2011), and has been confirmed present at SERS by our methods (Figure 2.3), albeit in very low population densities. *T. albolabris* is thought to breed between September–November in Thailand, with litters born between February and May (Cox *et al*., 2012), but; outside of Thailand the species is recorded to mate from March–May and bear young from July–August (Orlov *et al*., 2002). This species typically gives birth to between 3–30 neonates weighing between 3.6 and 5.2 g at birth.

Figure 2.4 Distribution of *T. albolabris* within Thailand (Cox *et al*., 2012).

Although they prefer forested areas and edge habitat, *T. albolabris* are found in urban, suburban and agricultural areas, typically spending daytime hours in shelter of low bushes, trees, and bamboo (Das, 2010; Cox *et al*., 2012) As an arboreal, nocturnal species it is thought to forage on ground periodically but the robust body structure indicates the species is mostly an ambush (sit and wait) predator (Cox *et al*., 2012). Orlov *et al*. (2002) observed *T. albolabris* feeding mostly on frogs from the Rhacophorid and Microhylid families, but they also took mammals such as soricids (shrews). Occasionally during heavy rains *T. albolabris* was observed by Orlov *et al.* (2002) foraging on ground, on one particular occasion a female *T. albolabris* (590 mm SVL) consumed seven adult common tree frogs (*Polypedates leucomystax*).

As low energy ambush predators, they likely only forage on ground when anuran prey items are unusually abundant, such as during heavy rainstorms.

2.4.2 Big Eyed Pit Viper (*Trimeresurus (Cryptelytrops) macrops* KRAMER, 1977)

Trimeresurus macrops is a diminutive species of green pit viper typically between 520–660 mm as adults with a maximum TL of 720 mm in rare cases (Das, 2010; Cox *et al*., 2012). The body is slender and cylindrical; with the head very distinct from the neck and narrow (Kramer, 1977). Adults rarely exceed 100g and range between 36 and 108 g making them the smallest GPV found in SERS (Cox *et al*., 2012).

The tail accounts for between 11–16% of the TL and is prehensile with a brown coloration. The head is triangular with strongly keeled temporal scales distinguishing it from the White Lipped Pit Viper and the Vogel's pit viper; however the first labial is either partially fused or entirely fused with the nasal (Das *et al*., 2012). Dorsally, this species has a pale green coloration with the chin and the gular region bluish. The eyes are large and variable in coloration with sex. Strong sexual dimorphism exists in this species, with females being significantly larger than males **(**See Ch. IV**).** Males also have bright golden eyes, while females typically have orange-colored eyes (Das, 2010). The males also have a white post ocular stripe to adulthood, in females this stripe fades as they mature (Figure 2.4). The diagnostic characters we used to distinguish *T. macrops* from other GPV in Sakaerat are found in Table 2.3 following Cox *et al*. (2012).

Figure 2.5 Big eyed pit vipers (*Trimeresurus macrops*) in SERS. Adult male (A) Female (B) Photo credit: Andrew Brown.

The big eyed pit viper (*T. macrops*) was once considered broad reaching; recently, it was split using multivariate molecular analyses into three separate species which all have similar coloration and diagnostic features, fortunately the nova taxa *Trimeresurus (Cryptelytrops) cardamonensis* is only present in the Cardamom mountains of southwestern Cambodia, and southeastern Thailand, and the new species *Trimeresurus (Cryptelytrops) rubeus* is only found in southern Vietnam and eastern Cambodia (Malhotra *et al*., 2011). Thus little taxonomic confusion exists for the *T. macrops* found in northeast Thailand, however Malhotra *et al*. (2011) suggest that cryptic species may exist in isolated Thai populations. For the purposes of this thesis we will only consider *T. macrops* ss as the Big Eyed Pit Viper following Malhotra *et al*. (2011). Currently it is thought to reside in North, Northeast and Western Thailand in isolated populations (Figure 2.6; Cox *et al*., 2012). It is also recorded from Laos, Cambodia and Vietnam (Orlov *et al*., 2002).

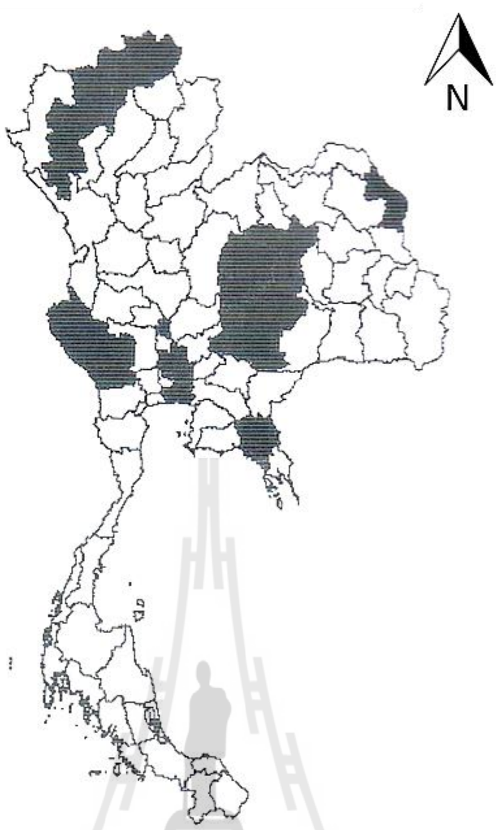

Figure 2.6 Distribution of *T. macrops* within Thailand (Cox *et al.*, 2012).

Cox *et al.* (2012) consider *T. macrops* to be a lowland species living in areas below 500 m, but Orlov *et al.* (2002) recorded specimens of *T. macrops* at heights of 1,670 m a.s.l. in Thailand. In contrast to Cox *et al.* (2012), they are thought to prefer evergreen forest patches and edges near water according to Das (2010). The basic ecology of this species is still poorly understood, and conflicting reports exist. For example, they are considered either semi-arboreal (Figure 2.7), or arboreal, which may be attributed to what season observers sampled in, or perhaps the specific *T. macrops* population (Hill, 2003; Das, 2010; Cox *et al*., 2012). Little is known of their diet preference; however they are thought to take anurans, reptiles, small mammals, and potentially birds (Cox *et al*., 2012). In contrast, Gumprecht (1998) argued that they primarily consume lizards and frogs which is logical considering the small body size, and the more limited narrow elongate gape when compared to other GPV present in SERS (Orlov *et al*., 2002).

Figure 2.7 Female *T. macrops* (ID No. TRMA062) perched on woody vegetation 30 cm off ground in typical bamboo habitat at SERS.

2.4.3 Vogel’s Pit Viper (*Trimeresurus* (*Viridovipera*) *vogeli,* DAVID, VIDAL and PAUWELS, 2001)

Vogel’s pit vipers are primarily dimorphic both in coloration and size between males and females (David *et al*., 2001). Male *T. vogeli* rarely reach above 950 mm, TL, while females often attain sizes of greater than 1300 mm making them one of the largest GPV in Thailand, and the largest found in SERS (Cox *et al*., 2012). Male *T. vogeli* are a dark green, on the dorsum with white vertebral flecks running along the dorsum spaced equidistant from one another (Das, 2010; Cox *et al*., 2012). They often have a red edged ventrolateral stripe, which is bordered above by a white stripe, the dorsum typically has dark or deep purple crossbands (Figure 2.8).

Figure 2.8 Male *T. vogeli* in tongs captured at SERS in August of 2013. Photo Credit: Daniel Worthen.

Females on the other hand, are typically bright green and lack the white vertebral flecks, the ventrolateral stripes are usually visible but are subdued (Cox *et al*., 2012; Figure 2.9). In a single case, a female *T. vogeli* was found with a red ventrolateral stripe beneath the white ventrolateral stripe from SERS (Malhotra *et al*., 2004). According to Vogel *et al.* (2001) males have golden yellow to yellowish green eyes. Malhotra *et al*. (2004) examined *T. vogeli* characters and found that males from northeastern Thai populations have orange to red eyes with elliptical pupils, which darken from yellow as they age. In both sexes the venter is light green, and the tail is reddish brown (Cox *et al*., 2012). The tail is usually between 18–20% of the body length in *T. vogeli*. The diagnostic characters used to identify *T. vogeli* are presented in Table 2.3.

Figure 2.9 *Trimeresurus vogeli* captured in Sakaerat in October 2014, one of three individuals found between 2011 – 2014. Photo credit: Elliot Lewis Hails.

The distribution in Thailand is limited to only five provinces from central and northeastern Thailand (Table 2.3; Figure 2.10). Vogel's pit vipers are found on the Khorat Plateau from SERS, and Khao Yai national park in the western Dongraek Mountains and in a patch of isolated southeastern mountains known as the Khao Si Dao Wildlife Sanctuary (Malhotra *et al*., 2004). Little is known of the extraterritorial distribution of *T. vogeli* but specimens have been collected in Cambodia, Laos and Vietnam (Cox *et al*., 2012). Malhotra (2004) claims that the snake is found in the

Cardamon Mountains in Cambodia and the Bolovens Plateau in Laos as well as the Kontum Plateau in central Vietnam.

Of the 32 specimens examined by Malhotra *et al*. (2004) 16 individuals were found in dry evergreen forests, 11 were found in wet evergreen forests, and the remainder were found in various vegetation types. Most individuals were found less than 3 m from ground, but this may be a bias in detection probability as searching higher levels of the canopy is often less efficient. According to Cox *et al*. (2012), they predominantly occupy dense evergreen forests from 200–1200 m a.s.l., however Malhotra and colleagues (2004) found the majority of specimens from 200 m a.s.l. and only rarely at high elevations.

Primarily it is thought to prey upon skinks, and frogs at ground level within a few meters of water (Cox *et al*., 2012). However, Malhotra *et al*. (2004) found frogs were the dominant prey type found in the digestive tract, followed by mammalian prey. The study also found a single skink inside the gut of an adult female, and arthropod remains inside a juvenile specimen. Virtually nothing is known of the potential ontogenetic shift in *T. vogeli*, leaving a distinct knowledge gap in the understanding of their foraging ecology, further diet study is warranted.

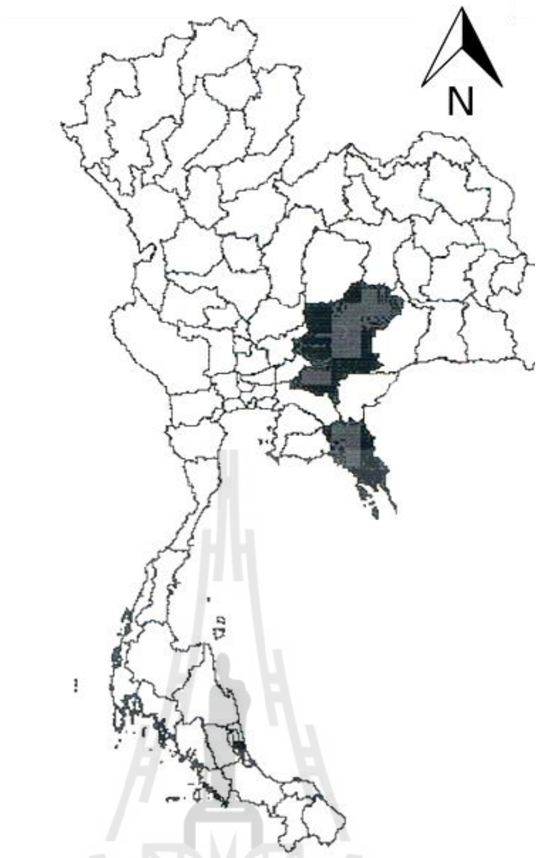

Figure 2.10 The currently accepted distribution of *Trimeresurus vogeli* within Thailand (Cox *et al*., 2012).

The reproductive cycle and timing within this species (unlike *T. macrops* and *T. albolabris*) has not been recorded from heavily disturbed ecotypes, and likely requires un-fragmented forest area to thrive (Malhotra *et al*., 2004; Das, 2010; Cox *et al*., 2012). Therefore major threats to this species likely include illegal logging and poaching in primary forests where it is thought prefer although they are still considered a species of least concern. (Stuart and Nguyen, 2012; IUCN Redlist, 2014). The population status and trends remain unknown and this species is only rarely encountered in SERS.

2.4.4 Gumprecht's Green Pit Viper (*Trimeresurus gumprechti* DAVID, VOGEL, PAUWELS, and VIDAL, 2002)

Trimeresurus gumprechti are large GPV attaining maximum total lengths in females of approximately 1200 mm and around 850 mm in males (David *et al.*, 2002; Cox *et al.*, 2012). Like all GPV the head is distinct from the neck and is triangular (Cox *et al.*, 2012). As in the Vogel's pit viper the first supralabial is completely separated from the nasal (Table 2.3 diagnostic characters). However distinguishing it from the Vogel's the supraoculars are separated by 10–12 smooth scales. Males are typically bright green on the dorsum but there is a postocular stripe white with a thicker red stripe above (Figure 2.11). Males also have a ventrolateral stripe that is red below and white above, sometimes with white vertebral flecks (Cox *et al.*, 2012).

Figure 2.11 *T. gumpretchi*, with the diagnostic bright green coloration and deep red above the white postocular stripe. Photo credit: Gernot Vogel (World Wildlife Foundation, http://www.scientificamerican.com).

Females are a much darker green on the dorsum, and have no dark crossbars, they often have a thin ventrolateral stripe and the vertebral flecks are almost always absent (Figure 2.11; Figure 2.12). Females usually have yellow eyes, while males have brightly colored red eyes with elliptical pupils (David *et al*., 2002; Das, 2010). In both sexes the interstitial skin is black, and the venter is yellow-yellowish green (Figure 2.12). They both have rust-brown tails but are sexually dimorphic in the tail proportion of body, in males the tail accounts for 15–21% of the TL, and in females the tail only makes up for 14–16% of the TL (Cox *et al*., 2012). For diagnostic characters and distinguishing marks of this species see Table 2.3.

Figure 2.12 *Trimeresurus gumpretchi* (female) perched arboreally in an alert position from Loei province. Photo Credit: Wolfgang Wuster (http://www.herpnation.com).

According to David *et al.* (2002) this species is only known from Northeastern Thailand in the provinces of Loei, Phitsanulok, Phetchabun, and Chayaphum, but because of taxonomic uncertainty (specimens thought to be *T. stejnegeri*, which is one of the previous names for *T. gumpretchi* prior to phylogenetic splitting, were collected from SERS, but were confirmed to actually be *T. vogeli*) it is possibly present within SERS (Figure 2.13). It was found in Dong Phaya Yenin Range (Gumprecht, 1997; David *et al*., 2002). Although unconfirmed, it is likely present in southern and western Laos and in the Annamite mountains (Das, 2010). According to Cox *et al*. (2012), this species is also present in China (Hainan and Yunnan provinces) as well as Myanmar and southern Vietnam. Although most of the past records for *T. stejnegeri* in Thailand were those of *T. (Viridovipera) gumpretchi*, some may have been confused with *T. vogeli* as well, thus it remains unconfirmed whether or not *T. gumpretchi* is present in SERS.

Figure 2.13 The range map of *T. gumpretchi* in Thailand (Cox *et al*., 2012).

Gumprecht's Pit Viper (*Trimeresurus gumprechti*) inhabits hilly and mountainous evergreen forests or dry seasonal forests from 800–1200 m a.s.l. (David *et al*., 2002). However Cox *et al*. (2012), describe the snake to be often found in thick brush, and bamboo thickets from 350–1350 m a.s.l, and usually found near streams. Although they are reported to prey upon small mammals and skinks, no in field observation of foraging strategy or diet preferences have occurred, what little is known of their diet is recorded from captive individuals and examined specimens (Gumprecht, 1997; David *et al*., 2002). They were found perching 1.5 m above ground resting in branches at times, but have also been recorded on ground (David *et al*., 2002; Das, 2010; Cox *et al*., 2010).

The species is listed as Least Concern (Stuart *et al*., 2012), and currently has stable populations, likely the major threats to the perpetuity of this species are the constant slash and burn agriculture, and fragmentation from timber logging occurring in Northeast Thailand, because like *T. vogeli*, this species is thought to prefer undisturbed forested areas well away from humans (Cox *et al*., 2012; Stuart *et al*., 2013). Although *T. gumprechti* are potentially present in SERS they have never been recorded in the reserve and were not found by our methods.

Table 2.3 Diagnostic characters of the four potential species of *Trimeresurus* in SERS (Cox *et al*., 2012).

Trait	***Trimeresurus albolabris***	***Trimeresurus macrops***	***Trimeresurus vogeli***	***Trimeresurus gumprechti***
Dorsum	green/ yellowish green	Pale green/bluish green, keeled on 1st –3rd ventral scale rows.	Bright pale green (m) dark green (f) white posterior flecks. Strongly keeled.	Bright green with numerous white dots across the vertebral (m) females are darker and lack crossbars.
Head	Triangular, with internasals larger than head scales	Triangular to ovate, with bluish green labials with a small scale sometimes between them.	Triangular with smooth scales, internasals are separated with 8 small scales	Triangular with smooth dorsal scales, and slight keels. Internasals are in contact or separated by a small scale.
Supralabial	9–13 Supralabrial 1 partially or entirely fused to nasal. 3rd is largest.	9–12 separate from orbit by small row of scales, 1st entirely or partially fused with nasal	10–13 1st supralabial separated from the nasal. 3rd is the largest supralabial	9–11 with the first entirely separated from the nasal third is the largest supralabial
Below eye	yellow white or pale green	bluish green to bluish white	light green	Pale green
Infralabral	10–15, 4 pairs of chin shields	10–12, 2 pairs of chin shields	14–16, 2 chin shield pairs both distinct	10 to 14
Post ocular	Absent	white (m,j) absent (f)	thin white (m) absent (f)	Bicolored red/white(m)/White (f)

Table 2.3 (Continued).

Trait	***Trimeresurus albolabris***	***Trimeresurus macrops***	***Trimeresurus vogeli***	***Trimeresurus gumprechti***
Eye color	Brownish, yellow	orange (m) golden yellow (f)	red (m) yellow (f)	red (m) yellow (f)
Temporals	Smooth	Strongly keeled	weakly keeled or smooth	Smooth, or weakly keeled
lateral stripe	White (m) absent (f)	pale blue (mostly)	white (red edged) (m)/ white	bicolor white red (m)/white or blue (f)
Interstitial skin	Unbanded (usually)	Banded with black	Black	bright blue
Midbody scale rows	19–21	19–21	21–23	21 rows
Ventrals	149–176	143–178	163–173	162–168
Subcauals	44–78 paired	41–76 paired	48–72 paired	51–71 paired
Tail	reddish brown short prehensile	reddish brown short prehensile	Long prehensile	long prehensile rusty or brown
Hemipenis	Extends to 20th–25th subcaudals and is forked 5th–6th.	Extends to the 25th subcaudal forked spinose then spongy.	short and spinose, 14.5 mm with six large spines and six shorter spines	10–20 short spines largest at the base.

2.5 Relevant research in Asian Green Pit Vipers

Despite detailed taxonomic information for many Asian GPV species, most species lack information regarding the basic biology, reproductive, foraging and spatial ecology. An exception, which has been well studied for the past 20 years is the insular Chinese pit viper (*Gloydius shedaoensis*). As an island dwelling arboreal GPV, it has offered a unique opportunity to study the ecological mechanisms in a semi-closed ecosystem (Shine *et al*., 2003). Sixteen island dwelling insular pit vipers (*Gloydius shedaoensis*) were tracked for a year by Shine and colleagues (2003) on the island of Shedao in northeastern China. The snakes were primarily sedentary with daily displacements of less than 2 m per day. Shine *et al*. (2003) posited that the ectothermic nature and the ambush strategy employed by *G*. *shedaoensis*, allow them to capitalize on a limited food resource (migratory birds) available only twice each year.

The overall Minimum Convex Polygon (MCP) home ranges were smaller than 3 ha with no obvious difference in home range size between males and females (Shine *et al*., 2014). There was no correlation between the snake home range size and the number of times it was located. Snakes thermoregulated but maintained a fairly consistent optimal temperatures year round between 15–25^{o}C.

The Chinese green tree viper (*Trimeresurus s. stejnegeri*) is an abundant nocturnal green pit viper inhabiting Taiwan and other Asian nations and it has been one of the model organisms for understanding diet composition (Lee, 1996) and reproductive cycles in other *Trimeresurus* species (Tsai *et al*., 2001). Fascinatingly *T. stejnegeri* is also one of the only Asian GPV to be studied in terms of shelter site selection through the design of artificial enclosures used over multiple seasons (Lin *et* *al*., 2007). In order to test the hypotheses that distance to prey, vegetation density, and thermal quality are important factors in retreat site selection, Lin *et al.* (2007) experimentally placed *T. stejnegeri* in large shaded artificial enclosures with experimentally controlled vegetation density and distances to prey items. Only during the warm season was thermal quality important for retreat site selection, when *T. stejnegeri* choose lower retreat sites, as opposed to higher sites (Lin *et al*., 2007). The temperature was cooler at lower retreat sites, and thus it appeared that temperature was the most important factor influencing retreat site selection by the Chinese pit vipers. Although the study takes place in outside of nature, it provides valuable insight into the importance of thermal ecology in shelter site selection for Asian GPV.

In Thailand a single study represents the literature for the ecology of *Trimeresurus* sp. At Sakaerat Environmental Research Station (SERS) in Nakhon Ratchasima, Thailand from May–August 2007 Hill (2014) tracked 4 adult male and 3 adult male *T. ma*crops using radiotelemetry. He tested the hypothesis that *T. macrops* (considered *C. macrops*) does not actively thermoregulate in the dry evergreen forest (DEF) of SERS. By constructing temperature models and comparing with radiotracked snakes, Hill (2014) was able to determine that *T. macrops* are thermo conformers in the DEF. Although daily locations were taken, he was unable to calculate home ranges for the tracked snakes because of high error values from the Garmin Global Positioning Systems (GPS) that were used in DEF forest fragments (Hill, 2014). Thus, the home range sizes for *T. macrops* remain unknown. Further information, regarding the seasonality of *T. macrops*, activity period, foraging ecology and larger sample sizes are necessary to identify the role of thermo conforming in the evergreen habitat.

2.6 Study site

2.6.1 Location and history

The Sakaerat Environmental Research Station (SERS) operated under the auspices of the Thailand Institute of Scientific and Technological Research (TISTR) in association with the UNESCO Man and Biosphere (MAB) reserve network program and is situated on the southernmost portion of the Khorat Plateau, around 14° 30’N and 101° 55’ E. The station is approximately 300 km northwest of Bangkok, and close to 60 km east-southeast of Nakhon Ratchasima (Figure 2.14 Map of SERS and Thailand). The protected area of the research station covers 7809 ha, with six sub-districts of Nakhon Ratchasima Province included inside the boundaries of the research station. The subdistricts of Lam Nam Kaew, Phu Luang, Ta Khob, Wang Mi, Wang Ngam Khiao, and Udom Sap are all part of the research station. The altitude within the station ranges from 250–790 a.s.l. with three main peak hills of 790–682 m a.s.l, approximately 35% of the protected area ranges between 300–400 m a.s.l (TISTR, 2012a).

Sakaerat serves as a small well-protected area surrounded by a matrix of heavily used agricultural land with intermittent human settlements particularly along the border of highway 304, which borders SERS to the South. The surrounding settlements and agricultural areas have encroached upon the natural forested landscape especially in the northeastern boundary, in part due to illegal expansion of farmland into natural protected areas and illegal logging (Maninan *et al.*, 1976). Much of the encroachment initially was in response to 15 villages, which were present inside SERS before 1983.After that all inhabitants were resettled off site in Wang

Nam Khiao subdistrict in order to reduce the chance of illegal logging and encroachment (Khernark, 1991).

The forest regeneration project, initiated by the Royal Forestry Department of Thailand intended to rehabilitate the degraded forests and recover forest over abandoned settlement land was established in 1982. Subsequently the total forest cover within SERS has increased from 63.15% in 1986 (Ongsomwang, 1986) to 72.62% in 2002 (Trisurat, 2009). The trend of regeneration is expected to increase with >90% forest cover in the station boundaries by 2020 (Döbert, 2010) but unfortunately the regrowth forests are primarily composed of *Eukalyptus* sp. and *Acacia* sp. plantations, which have not successfully regenerated (reptile and ambhibian) faunal diversity with the forest cover (Strine *et al.*, *Unpublished Data*).

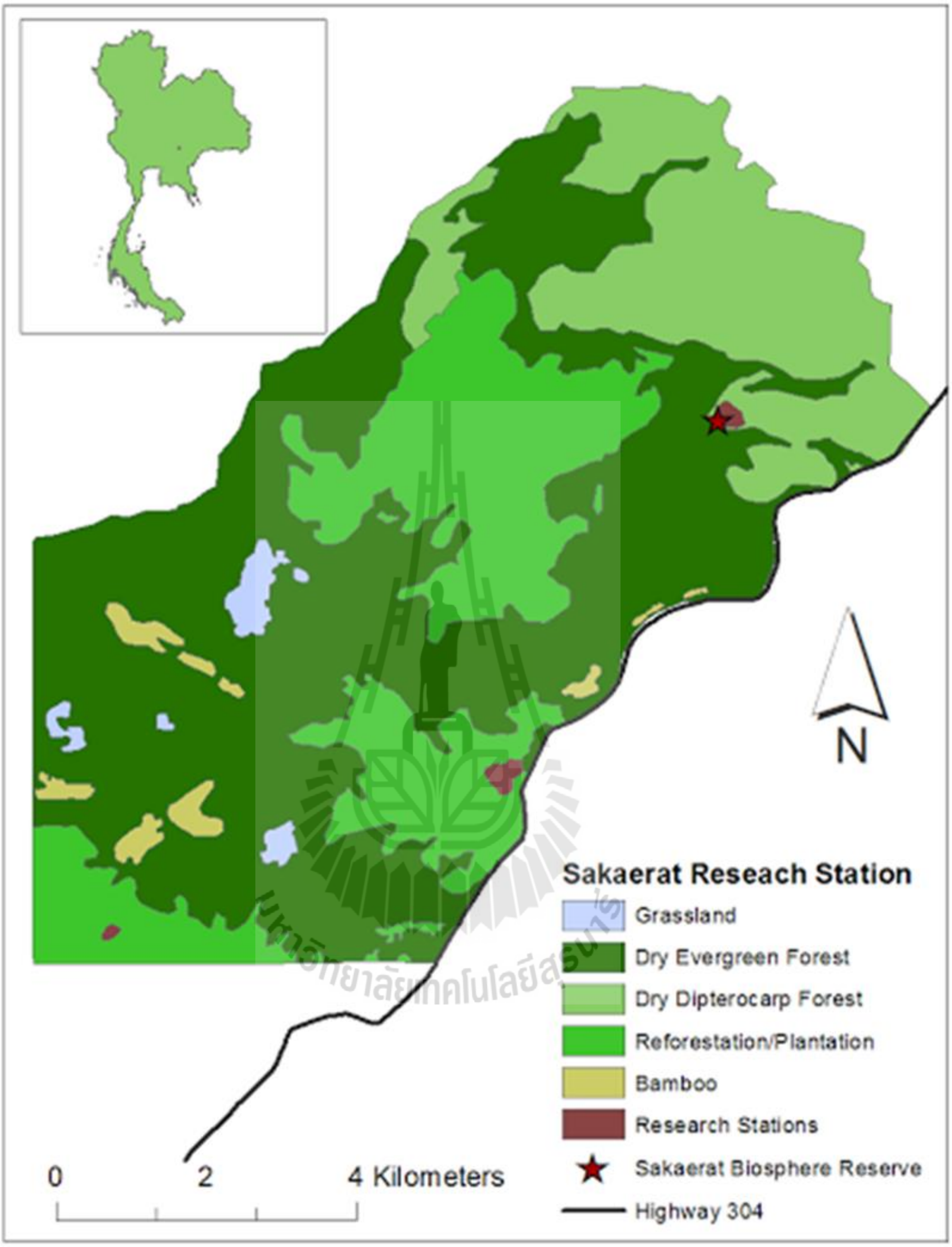

Figure 2.14 Sakaerat Environmental Research Station predominant forest types.

2.6.2 Vegetation associations

There are two main natural forest types found in SERS. The dry deciduous (dipterocarp) forest (1451 ha, 18.6%) dominated by fire resistant common dipterocarpaceous trees such as *Shorea siamensis*, *Shorea obtusa*, and *Dipterocarpus intricatus* at the canopy level (TISTR 2014b; Figure 2.15), and *Bamboo vietnamensis* at the understory level which grows up to 3 m each year, and then burns between February and March (Figure 2.15).

The dry evergreen forest (4682 ha, 60.0%) is dominated by evergreen tree species such as *Hopea ferrea*, *Hopea odorata* and *Hydnocarpus ilicifolia*, forming a multistory dense canopy typically greater than 85% coverage at the ground story level (Figure 2.16). The closed canopy system is complimented with heavy liana (woody vine) coverage, and with the presence of diagnostic Ebenaceae transitional trees that become lianas as they mature (Kanzaki *et al*., 1995; TISTR 2014b). There are also two large (1446 ha, 18.5%) mature (> 20 year) forest plantations composed of mixed *Acacia* sp. and *Eukalyptus* sp. which have almost no understory, but a very dense leaf litter layer. The grounds also contain several patches of bamboo forest (112 ha, 1.4%), and grassland (93 ha 1.2%), the offices and operational buildings at SERS make up the rest of the area (25 ha, 0.3%).

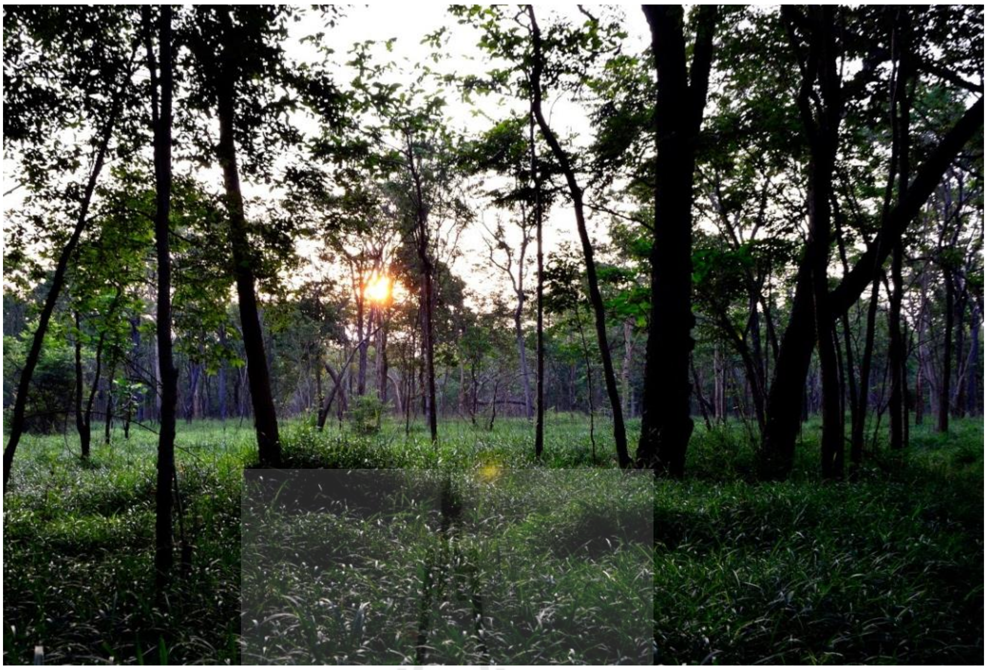

Figure 2.15 Dry Dipterocarp Forest (DDF) in Sakaerat Environmental Research Station (SERS), Nakhon Ratchasima. Photo Credit: Elliott Hails.

Figure 2.16 Dry Evergreen Forest (DEF) at Sakaerat Environmental Research Station (SERS).

2.6.3 Wildlife

For a small protected area SERS supports high faunal diversity, likely because there are a variety of habitat types in a small area, and there is strong protection of the pristine habitats found in SERS, in fact more than 80 mammalian wildlife species are found in SERS (TISTR, 2014c). The natural forest and plantations of SERS are home to approximately 230 birds (TISTR, 2014c), including the national bird of Thailand the Siamese fireback (*Lophura diardi*), and to more than 80 species of mammals including the Southern serow (*Naemorhedus sumatraensis*), which is both a protected and threatened species (Duckworth *et al*., 2008).

Also present are apex level predators such as the crested serpent eagle (*Spilornis cheela*) which is a major predator of ground dwelling and arboreal snakes in the reserve (TISTR, 2014d) as well as other snake predators such as the hog badger (*Arctonyx collaris*) and the Javan mongoose (*Herpestes javanicus*) and opportunistic predators such as the common wild pig (*Sus scrofa*) which is relatively common in SERS (TISTR, 2014c). There are 86 accepted species of reptiles, including 62 snake species, in Sakaerat. The most notorious predator of other snakes being the king cobra (*Ophiophagus hannah*) which is the longest venomous snake on Earth. (TISTR, 2014c). There are 26 recorded amphibian species present in SERS, but likely more species are found in remote areas, such as the Khorat large mouthed frog (*Limnonectes megastomias*), which was discovered in 2008 and named new to science (McLeod, 2008).

2.6.4 Climate

Sakaerat is a seasonal tropical climate, which never frosts. With cool dry winters attaining minimum temperatures of approximately 8–10°C, and hot humid summers with maximum temperatures above 45°C, there is a distinct seasonality in the reserve. The SERS staff collects and records daily maximum and minimum temperature, as well as relative humidity and rainfall from five established meteorological stations, and deposits the data on an online database for use by researchers as references. Here we report the information from weather stations 1 and 3 because the two stations are in close proximity to our study sites within SERS. The average monthly temperature, relative humidity, and rainfall at SERS for 2012, 2013, and 2012 are displayed as references in Figures 2.17, 2.18, and 2.19 (TISTR, 2014a).

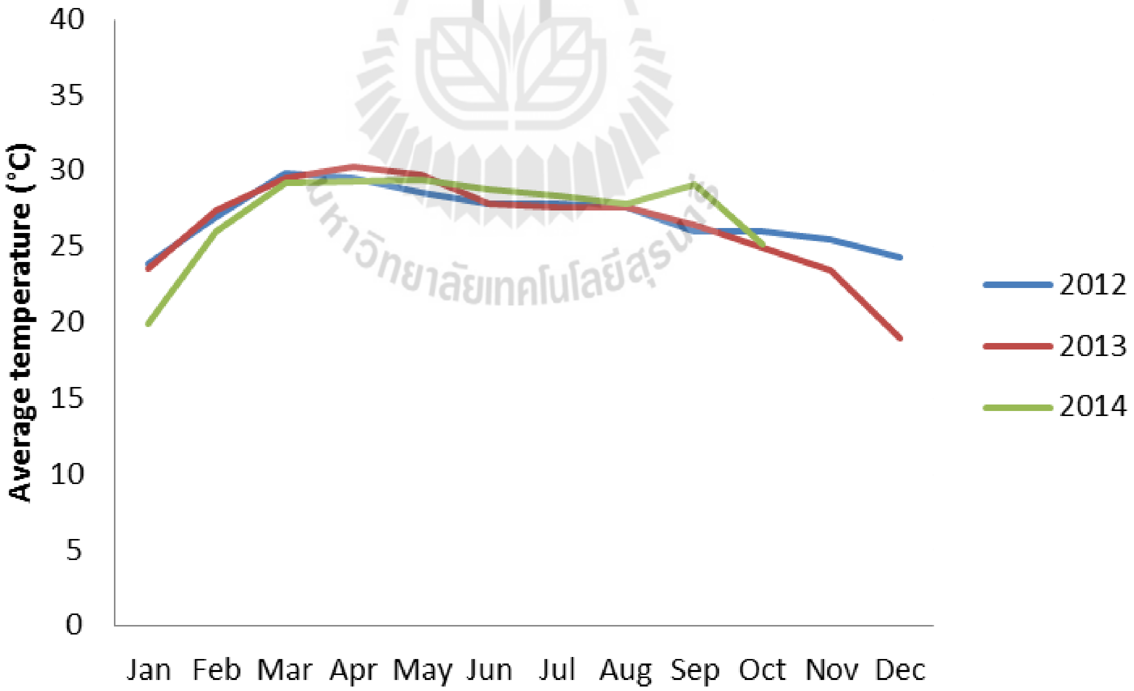

Figure 2.17 Average monthly temperature at Sakaerat Environmental Research Station (SERS) from 2012–2014.

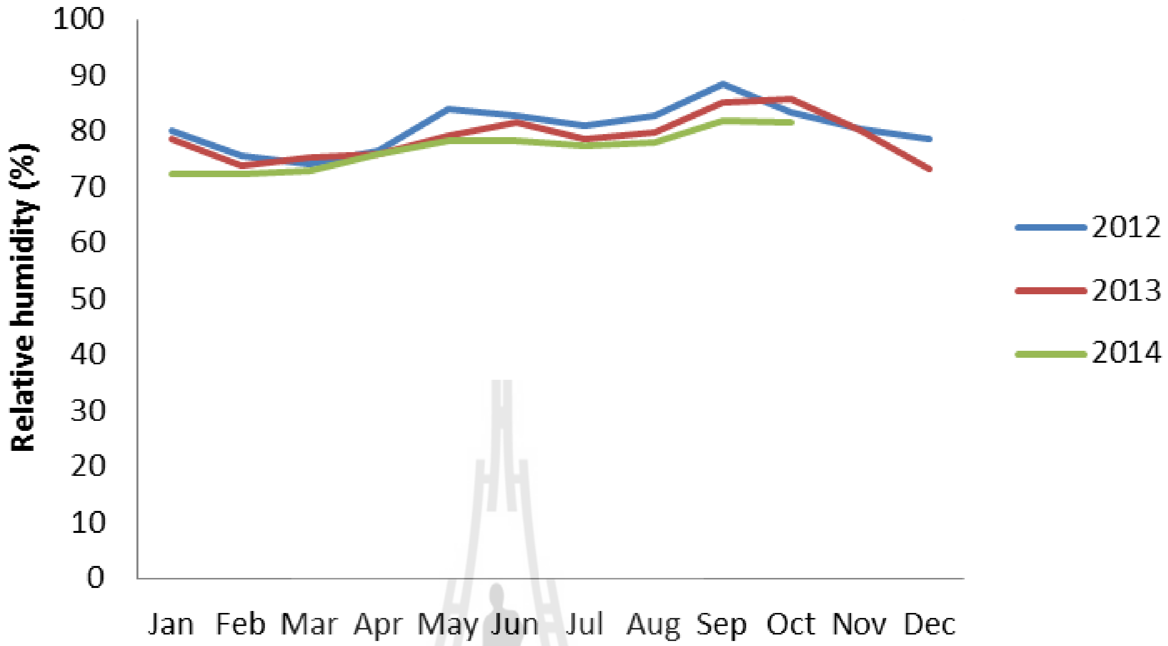

Figure 2.18 Average monthly relative humidity at Sakaerat Environmental Research Station (SERS) from 2012–2014.

During the three year period (2011–2014) the average annual rainfall was approximately 1,150 mm, but this discounts November and December of 2014. The dry season occurs from November to April (Figure 2.9), and there are two peak wet seasons a first rainfall peak from May–June, and then a second From August to November. In 2014 the general trend of rainfall was lower than in 2012 or 2013. The average annual temperature was 26.7°C (range 20.0–30.5), and the average annual humidity is 81.6% (range 71–89%). Humidity also appeared to be slightly lower for 2014 than the previous two years of the study.

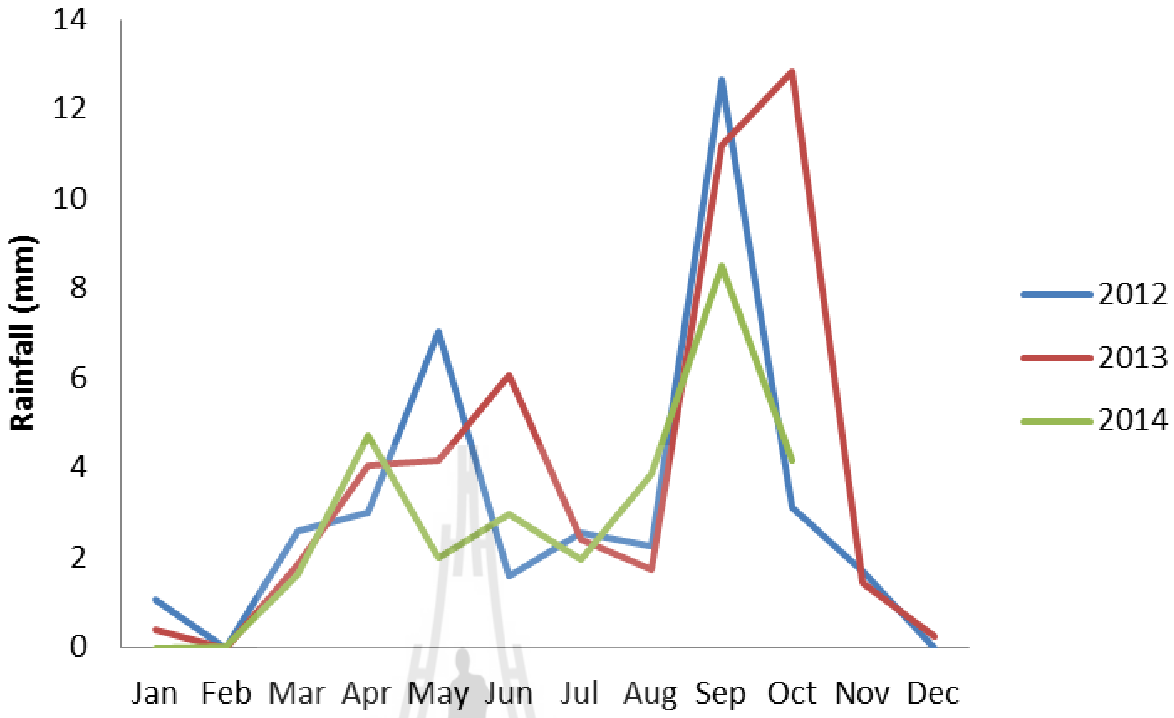

Figure 2.19 Average monthly rainfall at Sakaerat Environmental Research Station (SERS) from 2012–2014.

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CHAPTER III

GREEN PIT VIPER HOME RANGE AND HABITAT USE

3.1 Abstract

The Big-Eyed Green Pit Viper (*Trimeresurus macrops*) is one of three Green Pit Vipers (GPV) found sympatric in Sakaerat Environnmental Research station, and is by far the most commonly encountered species. Little is known about the spatial ecology of this species, and even less is known about the less frequently encountered White-lipped Green Pit Viper (*Trimeresurus albolabris*), and The Vogel's Pit Viper (*Trimeresurus vogeli*). Considering all three species have the potential to inject health hazardous venom, and that habitat fragmentation and isolation may bring these species into conflict with humans, it is important to study the impact of human presence and expansion on these snake species. During 2012–2014, 27 adult female *T. macrops,* 4 adult male *T. macrops*, 1 adult female *T. albolabris,* 1, adult male *T. vogeli*, and 2 adult female *T. vogeli* inhabiting Sakaerat Environmental Research Station were implanted with internal radio transmitters and tracked from 11-208 days, with 22-187 fixes on snakes included. Individual MCP home ranges for *T. macrops* averaged 0.0201 ha, with Fixed kernel 95% activity areas 0.0199 ha, and core areas (50%) ranging from 0.038 ha. Comparisons between *T. macrops* and other species were all non-significant likely due to insufficient sample sizes in *T. albolabris* and *T. vogeli*. There was little overlap between conspecific tracked females in deep forest

sites, especially for the most used areas of their home ranges, and even less overlap for congeners tracked in the same site. Significant differences in home ranges, movement patterns, or behavior between individuals living in forested areas and near the research station were not detected. The study suggests that *T. macrops* are not significantly affected by human disturbance, likely due to their cryptic behavior and limited movement patterns. This study also suggests preliminarily that *T. vogeli* may be a deep evergreen forest specialist, which would put it at risk to habitat fragmentation. Future studies should focus on prey abundance, habitat selection and survival rates in heavily disturbed areas.

3.2 Introduction

Understanding the mechanisms driving animal movement patterns such as trophic status, body size, seasonality, predation risk, resource availability and habitat structure animal movement patterns even among relatively sessile species to develop a unified home range behavioral theory is crucial for understanding ecological processes in animal taxa (Harestad and Bunnel, 1979; Osborn, 2004; Edelman and Koprowski, 2006; Börger *et al*., 2008). Home ranges are the area which is typically utilized during the course of everyday activities by an individual or group of animals during a specific time frame (Burt, 1943; Jennrich and Turner, 1969; Ford and Krumme, 1979). Home ranges typically have a smaller area which is used more extensively and typically has more resources or key important resources available (Kaufman, 1962; Seaman and Powell, 1989; Mitchell and Powell, 2012).

Large home ranges are costly because the time and energy allocated for travel are greater, in addition to the fact that the chances of interacting with predators and competitors (Powell, 2000; Yoder *et al*., 2004; Lendrum *et al*., 2014). Thus, theoretically animals should minimize the adequate home range size, and that home range size will be positively correlated with the resources needed for particular groups, and with body size (Harestad and Bunnell, 1979; Badyaev *et al*., 1996). Home range size should be inversely related to resource availability, habitat quality and the individual fitness (Whitaker *et al*., 2007; Breininger *et al*., 2011).

Habitats refer to a set of physical environmental parameters that are used by a species for survival, life activities and reproduction (Hall *et al*., 1997). A habitat can influence the distribution of the available food resources and shelter sites, as barrier against predators, and in the case of arboreal animals the three dimensional matrix of vegetation (M’Closkey *et al*., 1990; Lima, 1993).

Habitat quality, resources, and adequate shelter site availability influence survivorship and fitness in snakes (Larsen and Gregory, 2006; Shoemaker *et al*., 2009). The most endangered snake the Antiguan racer (*Alsophis antiguae*), has been successfully repatriated along a number of islands, because the conservation strategies incorporated study of habitat quality and the improvement of their habitat condition including removing the invasive mongoose (Daltry *et al*., 2001; Daltry, 2008). Successful conservation measures should incorporate habitat structure and selection preferences, for the management of threatened populations or potentially invasive pest snakes (Wiles *et al*., 2003; Shoemaker *et al*., 2009).

Habitat structure may influence foraging behavior in snakes, many of which are stationary for multiple days in the same location through an ambush strategy which requires low energy input, but requires careful selection based on prey movement and physical parameters of the site (Reinert *et al*., 1984; Theodoratus *et al*., 1997; Sun *et al*., 2000).

In the case of snakes and other ectothermic organisms, the habitat structure also influence thermal variability, which is important for thermoregulation, and thus site selection particularly in temperate environments (Secor and Nagy, 1984; Blouin-Demers and Weatherhead, 2002a; Blouin-Demers and Weatherhead, 2002b). Thermal factors can influence foraging site selection by ectothermic predators, especially species that must remain immobile (ambushing) for long periods of time (Shine *et al*., 2002). As mid-level predators, snakes must select sites that are both sufficiently sheltered, and likely to encounter prey, thus there may be concessions for maximizing safety or likeliness of capturing prey depending on the energetic requirements of the snake (Duval and Chiszar, 1990; Hayes and Duvall, 1991; Perry, 1999; Tsairi and Bouskila, 2004).

Foraging strategy, and site selection have direct influences in fitness, body condition, and fecundity in many snake species (Van Orsdol, 1984; Radcliffe *et al*., 1996; Shine and Fitzgerald, 1996). Consequently, understanding the microhabitat variables selected as foraging and retreat sites will undoubtedly benefit overall habitat-snake relationships, particularly for understudied venomous arboreal snakes.

Arboreality (use of above ground sites) offers an advantage in prey detection, and in some cases better vantage point for striking and therefore envenomating prey items as well as a three dimensional matrix through which to escape predators (Shine, 1983; Shine *et al*., 1996; Shine and Sun, 2002). For example, snakes preying upon birds would be able to detect warm bodied animals more easily against the colder arboreal background and might have a higher chance of successfully subduing avian prey (Chiszar, 1986; Grace *et al*., 1999). Arboreal sites are thought to be more complex than ground sites. With increasing habitat complexity the chance of encountering prey in the habitat matrix reduces (James and Heck, 1994). Although arboreality may increase exposure to predators, cryptic coloring likely combats detection by avian predators, as most arboreal snakes typically have a mottled or green coloration which serves as camouflage (Curio, 1976; Li, 1995).

Tradeoffs in arboreal sites exist for ectothermic animals, because often the arboreal sites are cooler than ground sites, which may reduce potential strike speed, and capture success depending on the thermal environment (Lillywhite *et al*., 1998; Sun *et al*., 2001). The ideal arboreal site for ambush or resting may vary with conspecific size, sex, age class or between closely related species with similar structure, based on body size or perhaps antipredator responses (Shine *et al*., 2002b; Shine *et al*., 2002c, Eskew *et al*., 2008). Niche partitioning among species or conspecifics may result from differences in site selection in habitats or physical dimorphism of characters (Shine *et al*., 2002) or at the microhabitat level (Edgehouse *et al*., 2014).

Green Pit Vipers (GPV), members of the genus *Trimeresurus sensu lato* are mostly listed as species of least concern, despite limited understanding of the basic ecology and population trends of most species (Cox *et al*., 2012; Vogel *et al*., 2014; IUCN, 2014), with the exception of a single endangered species in Kanchanaburi Thailand (Chan-Ard, 2012), the Kanchanaburi pit viper (*Trimeresurus kanburiensis*). Population trends for most species remain unknown, but several species are thought to require pristine forest habitats with limited fragmentation such as the Vogel's pit viper (*Trimeresurus vogeli*) and Gumprecht's pit viper (*Trimeresurus gumpretchi*) found in

Thailand (David *et al*., 2002; Malhotra *et al*., 2004). While some species require large tracts of undisturbed habitat, other GPV appear to be relatively resiliant to human disturbance, the white lipped pit viper (*Trimeresurus albolabris*), and the big eyed pit viper (*Trimeresurus macrops*) for example, can be found in degraded ecosystems as well as forest habitats (Mahasandana and Jintakune, 1990; Cox *et al*., 2012; Hill, 2014).

The four species are thought to be sympatric across Thailand , especially in Nakhon Ratchasima where the distributional ranges converge (See Chapter 2; Cox *et al*., 2012). The natural history, and basic ecology of Thai GPV in Nakhon Ratchasima province is poorly understood, with most information coming from field collected specimens, captive populations, and short term single season studies (Malhotra *et al*., 2004; Chanhome *et al*., 2011; Cox *et al*., 2012). This study will expand our understanding of GPV natural hisory in terms of habitat selection, space use and vertical stratification, and will attempt to elucidate the ecological relationship between GPV in a site where at least 3 species are known to be sympatric, occupying the same forest type.

This study used minimum convex polygons (MCP), and Kernel 95%, 50% core area isopleths to examine home ranges of *T. macrops*, *T. albolabris* and *T. vogeli* using successive daily locations of radio-transmitter implanted snakes from the three species. More advanced spatial analyses were not used, due to the limited number of relocations per individual. Initially the hypothesis, that home range size between *T.albolabris* and *T. macrops* would differ, with *T. albolabris* displaying greater movement was of primary interest. However, the hypotheses were revised to focus specifically on *T. macrops*, in a site specific capacity based on insufficient sample sizes the other species. Thus, the hypothesis that *T. macrops* females have similar home range sizes between different sites in SERS was subsequently tested.

The hypothesis, that body size does not influence home range size in *T. macrops*, and that there is distinct seasonality in *T. macrops* home ranges was tested. Due to limited sample size in *T. albolabris* and *T. vogeli* the hypotheses different GPV species will will have non random habitat site selection, and that different species of GPV would have different habitat selection parameters were unable to be tested. Thus habitat selection was forced to focus solely on *T. macrops*.

3.3 Methods

3.3.1 Study area

This study was conducted at Sakaerat Environmental Research Station (SERS, Figure 3.1), which operates under the auspices of the Man and Biosphere (MAB) Program, classed as a UNESCO Biosphere Reserve since 1967. The Biosphere Reserve covers 821 km^2, with the core protected area of SERS boundaries delineated at 78.09 km^2, located in north-eastern Thailand at the border of the Khorat plateau (14°30’N and 101°55’E). The elevation at SERS ranges from 280-762 m asl.

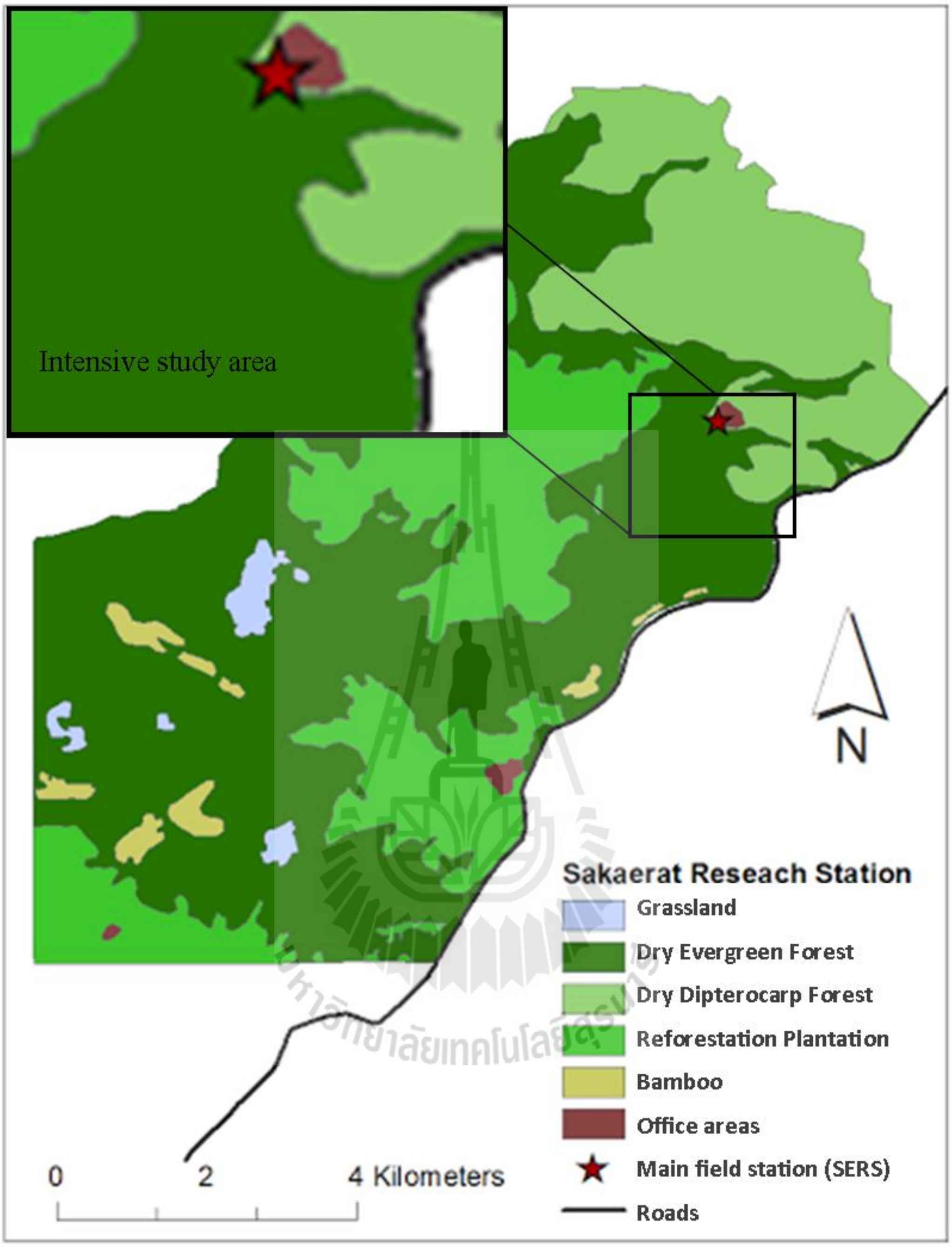


Figure 3.1 Forest types of the intensive study area at Sakaerat Environmental Research Station (SERS) which is expanded at the top left corner.

The core area has two main forest types: dry evergreen forest (4682 ha, 60.0%) dominated by members of the *Hopea* genus and *Hydnocarpus* sp., and dry dipterocarp forest (1451 ha, 18.6%) dominated by fire resistant common dipterocarpaceous trees such as *Shorea siamensis*, *Shorea obtusa*, and *Dipterocarpus intricatus* at the canopy level, and *Bamboo vietnamensis* at the ground story level. There are also two large patches of mature plantation forest (>20 y), with mixed *Acacia* and *Eukalyptus* (1446 ha, 18.5%). In addition SERS hosts several patches of bamboo forest (112 ha, 1.4%), and grassland (93 ha 1.2%), the offices and operational buildings at SERS make up the rest of the area (25 ha, 0.3%) (TISTR, 2014a).

The intensive study area within Sakaerat includes the operational area (here after referred to as Field Station (FS), and the dry evergreen forest from the tower 2 trail to the lower dam pond off of the main road of SERS. The intensive study area is approximately 300 ha, with elevations ranging from 310-540 m. The average annual precipitation was 1,150 mm excluding November and December of 2014, with a peak wet season from May-June, then a short intermittent dry season, followed by a second rainy season from August-November. The average annual temperature was 26.7°C (range 20.0-30.5), and the average annual relative humidity is 81.6% (range 71-89%), there was a general trend of lower rainfall and humidity in 2014 when compared to prior years (TISTR. 2014b).

3.3.2 Snake capture for radio telemetry

Green Pit Vipers (GPV) were collected via opportunistic captures and active searches in well-known sites at Sakaerat Biosphere Reserve. Because GPV are mainly arboreal (meaning they move through the trees), standardized drift fences and funnel traps are not adequate for finding and capturing GPV (See Chapter V). Thus after-dark surveys with head-lamps to illuminate snakes were performed in various habitat types. During preliminary snake collection, all captured individuals were permanently marked with a heat branding field captures. Active opportunistic searches of optimal habitat types observers with quantified effort in unit man hours calculated as number of observers x number of hours searched to the nearest hour for each survey to standardize detection rate and probability. Weather was recorded during surveys in order to compare similar weather surveys with one another for relative abundance analyses. Optimal survey weather was post rain, and light evening rain, all surveys for GPV were conducted after sundown before 02:00 am.

Observers noted the locations and behavioural characteristics of each captured animal during the detection and capture. If a snake was found unmarked, then it was removed to the lab for diagnostics and standard marking under anaesthesia. Snakes that had not been captured for more than one month were also brought back for biometrics, growth and diet analyses. If a radio transmitter of an appropriate size was available and criteria for surgery were met (good body condition, mass >30g, available transmitters) then after a brief period of observation, snakes were prepared for surgery.

3.3.3 Radio transmitter implantation

Green Pit Vipers were housed in affordable plastic tubs following (Llewelyn *et al*., 2009, 2011) in the open air Sakaerat Laboratory until the completion of quarantine and implantation of transmitters. After a brief observation period, each snake selected for radiotelemetry was prepared for surgery. Adult *Trimeresuru*s > 30g in good body condition were implanted with a small radio transmitter inserted into the body cavity. After applying isoflurane as an inhaled anaesthetic, we implanted BD-2 1.8g or 1.2g Holohil transmitters based on body size following the 5% body mass rule to reduce impact on snake behaviours. Implantation techniques were performed following (Reinert and Cundall, 1982; Hardy and Greene, 2000) where the transmitter is inserted to the coelomic cavity and the antennae is run laterally between the subcutaneous tissue and the peritoneum (Figure 3.2).

Figure 3.2 The author performing a transmitter insertion surgery on *T. macrops.*

Aseptic procedures were followed, including boiling all equipment prior to use, followed by an ethanol (95%) bath for at least 15 minutes before surgery. Equipment was stored in a sterile ethanol container until surgery and was only handled by the surgeon, who wore plastic gloves and avoided touching any non-aseptic surfaces for the duration of surgery. The incision was made roughly one third of the body length from the tail tip toward the anterior, along the lateral line on the first row of dorsal scales. The coelomic body cavity was pierced using a blunt incision with curved hemostats, which prevented further damage to the snake. Once the body cavity was opened, the transmitter was inserted while the coelom was held open. In GPV no coelomic stitch is necessary because the transmitter is so large and the muscle tissue is nearly impossible to attach a suture. Sutures were stitched using hemostats and tied off with square knots (Figure. 3.3). During surgery there were no mortalities of the 32 implanted snakes, thus less than the critical 5% of mortality limit was acceptable for research ethics.

Figure 3.3 *Trimeresurus macrops* post-surgery with sutures visible.

Surgeries were performed by Colin T Strine after training by Dr. Matthew J. Goode. After a short observation period (< 24 hours), snakes were returned to the original capture locations. Upon removal from study, if snakes were recaptured, transmitters were removed using the same surgical protocols. Surgical techniques were carried out following the Animal Care and Use Committee Guidelines (ACUCG) of Suranaree University of Technology. No GPV died during surgery or as a result of Anaesthesia overdoses. However 1 GPV was visibly predated by a King Cobra (*Ophiophagus hannah*), a second was predated by red weaver ants, and three individuals of 32 died prematurely during tracking. Although mortality rates are unknown for untracked snakes, there appears to be low survivorship between years (See Chapter V).

3.3.4 Radio tracking snakes

Green Pit Vipers from four field sites were selected at SERS (Figure 3.4) for radiotelemetry; the tower trail (deep forest), the main station (disturbance associated), the lower dam pond (water associated) and the upper dam pond (water associated). Snakes were tracked with the same protocols at all field sites. A combination of homing in on the snakes, and pinpointing visually using the antenna was used to obtain fixes of animals in the field. Fixes were defined as actual certain locations of an individual where a GPS point could be taken, fixes were not necessarily visual confirmation, because often snakes were found under cover or in the canopy, in the case where snakes were not visible, notes were described.

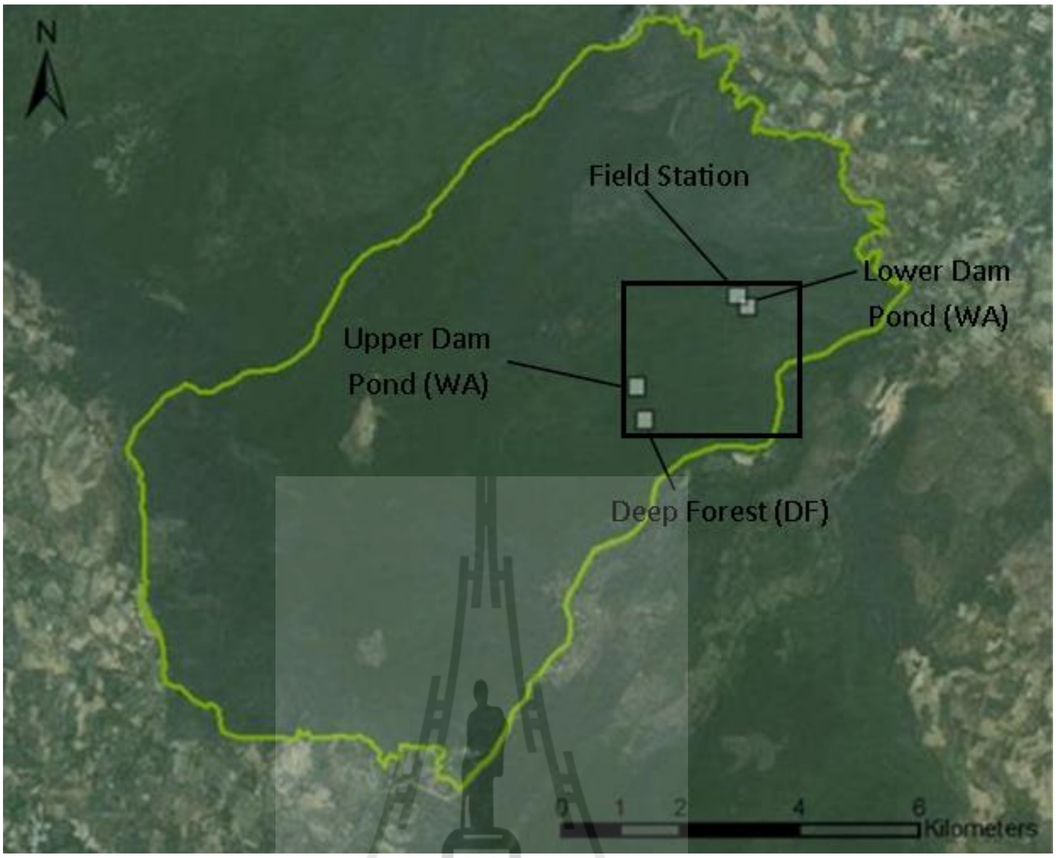


Figure 3.4 Satellite overlay intensive 100 m x 100 m selected study sites for tracking GPV at SERS.

Upon pinpoint we used the Iform application available for Android and IOS systems, we recorded date of location, time, personnel who locate the snake and the habitat type. We compiled detailed location description at the initial pinpoint including cover type and perch type to the lowest taxonomic level. A Global Positioning System (GPS) point was taken with the highest possible accuracy and the accuracy of each pinpoint was recorded in order to minimize error. If snakes had moved from the previous location the GPS was used to estimate the straight line distance the snake had moved from the previous location. If the snake moved less than 100 m observers paced the distance to verify GPS estimates at approximately

1 m per pace. Possible barriers or features snakes may have crossed to arrive at new locations were also recorded.

Habitat types were classified by the canopy cover and dominant vegetation group in the general vicinity. Habitat categories were listed as the following: Dry Evergreen Forest (DEF), Mixed Deciduous Forest (MDF), and Bamboo Forest (BF). Upon location, a general description was given of the microhabitat so that observers could identify movement from microhabitat readily on future visits to the animal, distinguishing characteristics such as termite mounds or human influence were noted in the location descriptions.

If the snake was spotted during tracking, whether it was perched (off the ground with the body draping over a branch or other hard surface) or not was recorded. The height of perch was estimated to the general layers of underground (< 0 m), On ground (0 m), ground story (0.1-1 m), understory (1-3 m), midstory (3-10 m), overstory (>10 m). When snakes were perched, the perch type was recorded with the following available categories: ground, rock, woody vegetation, non woody vegetation, manmade, and other (Figure 3.5). Estimated body support (%) of full body was estimated for each individual.

Figure 3.5 *Trimeresurus vogeli* in ambush position, on groundstory woody vegetation.

During data collection both ambient temperature and humidity were recorded (at chest level approximately 120 cm from ground in the same thermal quality of the snake, if known). We also recorded ground temperature and relative humidity at ground level 1cm from the ground. Number of beeps per minute (BPM) were recorded using a stop watch for temperature sensitive transmitters. BPM rise with higher temperatures allowing us to estimate temperature inside the snakes, which can then be compared to the ambient and substrate level temperatures. Photographs were taken in order to verify snake locations at a further date and back up data (Figure 3.6).

Figure 3.6 Photographing a tracked GPV at the upper dam pond, water associated site.

Seasonally collected movement data was logged into Arc-Map (ESRI, California, USA) Minimum Convex Polygons (MCP) were used to estimate home ranges. To avoid loss of snakes and expensive transmitters, snakes were re-captured approximately one week before the expected nominal battery life is to end. We removed transmitters through aseptic surgical techniques. If the snake was in excellent body condition, and new transmitters were available, we inserted a new transmitter. After the procedure, we returned snakes to the exact capture location.

3.3.5 Statistical analyses

Body condition was estimated using the scaled mass index (SMI; Peig and Green, 2009), as it can be readily compared across populations (Labocha *et al*., 2014). The assumptions of homogeneity of variances and normality for each variable were tested using the Shapiro-Wilk’s test, and the Levine test for homogeneity. The non-parametric Kruskal-Wallis was used to compare body condition and study areas, and to compare MDD, average distance and maximum distance moved. As the number of fixes, relocations and days tracked did not differ between forest and field station individuals (Mann–Whitney *U* test, $p > 0.05$), these three samples could be readily compared on all other analyses.

Home-range size for each individual using 100% Minimum Convex Polygons (MCP) and fixed-kernel density methods (FK; Worton, 1989), enabling comparisons with previous studies. For the kernel estimates, we used the least-squares cross-validation method to select the smoothing parameter h, obtaining fixed 95% (activity range) and 50% (core area) utilization distributions for each individual (Tiebout and Cary, 1987). Although the accuracy of both MCP and kernel methods have been questioned (Row and Blouin-Demers, 2006), both have been included for comparative purposes with previous studies. All estimated home-range sizes were calculated in hectares (ha). Overall differences in home-range size (MCP, 95% and 50% FK) were compared using an ANCOVA. This analysis allowed us to include the number of fixes each individual was tracked as a covariate, as it was positively correlated with bigger FK areas (Pearson’s r: $p < 0.05$).

Spatial overlap was initially quantified as the MCP area shared between individuals. However, as this home range overlap includes unused areas (and as such is a poor indicator of interaction), we also assessed spatial overlap using the UD overlap index (UDOI; Fieberg and Kochanny, 2005) of both 50% and 95% fixed-kernels. This index equals 0 for two non-overlapping home ranges and 1 for complete overlap.

Generalized linear mixed models (GLMM) with binomial error distributions were used to evaluate potential behavior patterns, selecting snake ID as the random variable (to account for non-independence of locations for each individual) and dominant behavior as the binomial response variable. We considered habitat (highly disturbed versus low impact areas), forest layer and time (night versus daytime) as predictor variables. We also used GLMMs to reveal differences in microhabitat selection between habitats, using temperature and humidity at substrate as well as ambient levels for another set of predictors. Top models were selected by AIC corrected for small samples sizes (AICc), using R package AICcmodavg (Mazerolle, 2010). To validate each model, we used marginal R^2 (mR^2) and conditional R^2 (cR^2; Nakagawa and Schielzeth, 2013). These R^2values can be interpreted respectively as the variance explained by only fixed effects and the variance explained by both the fixed and random effects.

We analyzed movement data using Geographic Information System (GIS) software (ArcGIS 10.1; ESRI, 2011) and R statistical software version 3.0.2 (R Development Team, 2013). Unless otherwise stated, all descriptive statistics are reported as means ± standard error and the significance threshold was set at $\alpha < 0.050$.

3.4 Results

3.4.1 Green Pit Viper captures from 2012-2014

Between May 2012 and November 2014, 293 GPV captures occurred including recaptures (Table 3.1). Non-recaptured individuals made up 219 of the 293 GPV captures (See Appendix 1). There were 91 unique male captures and 122 female individual GPV captured. The station site (site 1) had the highest captures 97, with 72 individuals, (25.7%). The Lower Dam Pond (site 2) 28 total GPV captures with 14 unique individuals. The Upper Dam Pond (site 3) had 21 captures with 15 individuals captured and the deep forest had 28 GPV captures with 9 individuals. Capture locations for the three species in SERS are displayed in figure 3.7. All other captures came from various sites in SERS (9 captures with 8 individuals). Capture proportions of the three different species sex ratios and effort for snakes found in SERS are presented in Chapter V.

During the study period from May 2012- February 2015, 203 individual *T. macrops* 270 times (73 recaptures) were captured. All juvenile and neonate *T. macrops* were removed as candidates for radio telemetry because they violate the 5% body mass rule juvenile and neonate snakes (*n* = 43).

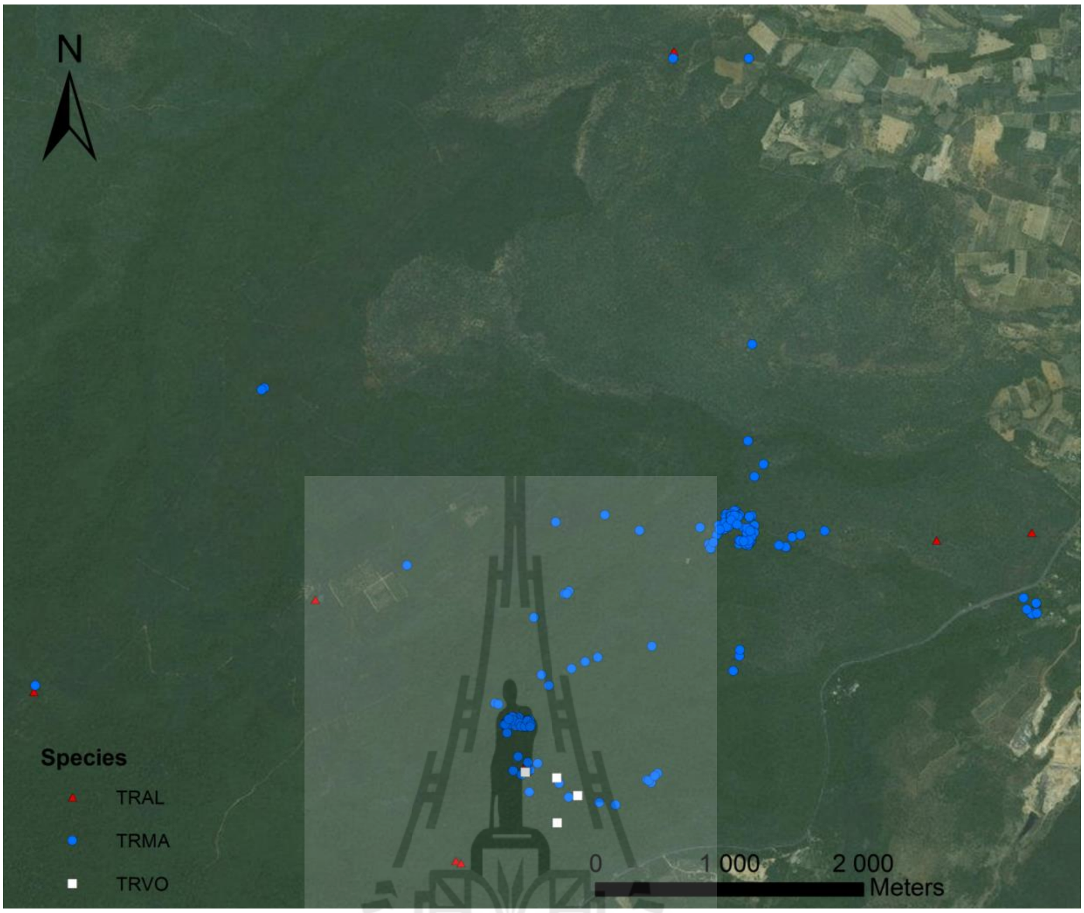


Figure 3.7 Capture locations for GPV captured in SERS from May 2012- February 2015.

Table 3.1 Number of GPV captures from different study sites, sex ratios and age classes from each site.

			Sex			Age class			
Sites	**No. of captures**	**No. of individuals**	**F**	**M**	**U**	**A**	**J**	**N**	**YoY**
Deep forest	59	47	28	17	2	34	5	8	0
Field station	87	58	36	19	3	50	5	3	0
Lower dam pond	72	45	28	15	2	34	2	9	0
Upper dam pond	42	30	9	21	0	25	5	0	0
Other	25	23	11	11	1	16	2	4	1
Grand Total	**285**	**203**	**112**	**83**	**8**	**159**	**19**	**24**	**1**

Age classes: Adult (A), Juvenile (J), Neonate (N), YoY (Young of the Year).

Sex:Female (F), Male (M), Unknown (U).

3.4.2 Tracked Green Pit Vipers

From September of 2012 to February of 2015 a total of 32 (Table 3.2, Table 3.3) individual GPV were tracked for a mean 69 ± 7.6 days (range = 11-208 days). There were 27 female GPV tracked on average for 72 ± 7.7 days (range = 11-208). Only 5 male GPV were tracked for a mean of 53± 7.08 days (range =16-108 days) throughout the duration of the study because they were often too small to meet the 5% rule for transmitter implantation and they were rarely of adequate girth in order to implant a transmitter without disturbing the snake’s behaviour. Of the 32 tracked GPV only a single individual was *T. albolabris* (female, 193 days), therefore differences in spatial ecology between *T. albolabris* and *T. macrops* were unable to be assessed, due to an insufficient sample size.

Three *T. vogeli*, were tracked during the study period, a single male (106 days) and two females which were tracked on average for 203± 4.5 days (199- 208 days). The 28 *Trimeresurus macrops* were tracked on average for 66 ± 6.5 days (range = 11-147) days in three main sampling sessions between September 2012 and February 2015. A total of 24 Female *T. macrops* were tracked on average for 70 ± 7.5 days (range = 11-147 days).

The sample sizes for *T. vogeli* and *T. albolabris* were limited, but substantial information was garnered using individuals as focal animals for study. Individuals with less than 5 relocations before transmitter failure, inability or relocate, or death of the individual were excluded from (female *n* = 5, male *n* = 3) the spatial ecology study on the grounds that they would bias the dataset. The Upper Dam Pond (*n* = 2) female *T. macrops* were not combined with the lower dam pond based on the high levels of students (*n* = 17,000 per annum, pers.comm) which disturb the area making it difficult to combine with the Lower Dam Pond, which had minimal human disturbance.

Table 3.2 Morphometrics, body condition at tracking initiation, and duration of tracking for female T. macrops (*n*=22) T. albolabris (*n*=1), Oct 2012- Feb 2015 at SERS.

Snake ID	SVL (mm)	TVL (mm)	Mass (g)	HL (mm)	HW (mm)	First track	Condition	Final track	Track Days
T. macrops									
TRMA006	630	111	81.8	20.2	31.27	06.11.13	Excellent	02.01.14	57
TRMA014	470	82	56.9	20	32	25.10.12	Good	19.12.12	55
TRMA023	443	56	45.5	NA	NA	26.10.12	Good	13.12.12	47
TRMA024	660	100	68.8	10	30	28.10.12	Good	19.12.12	52
TRMA025	316	138	64.2	22	24	04.11.12	Good	17.03.13	133
TRMA029	460	76	38.1	18.19	26.5	05.01.13	Excellent	13.06.13	43
TRMA048	569	101	30	22	27.2	05.01.13	Good	02.07.13	62
TRMA050	494	44	44.6	19	27	05.01.13	Good	24.05.13	23
* TRMA052	586	106	55.1	20	32	23.05.13	Good	24.06.13	33
TRMA062	618	119	70.2	24	32	23.05.13	Good	14.07.13	52
TRMA069	630	115	67.6	27	34	22.11.13	Good	20.01.14	59
TRMA080	566	74	50.9	22	24	09.09.13	Good	05.12.13	87
TRMA088	668	110	33.49	20	22	22.09.13	Good	24.01.14	124
TRMA090	540	96	46.2	16	23.5	09.09.13	Excellent	03.02.14	147
* TRMA094	505	84	41.7	18.23	26.27	11.11.13	Good	18.01.14	68
TRMA095	497	99	56.85	19.03	27.59	05.11.13	Good	20.01.14	76
* TRMA096	508	84	44.2	15.31	23.23	09.12.13	Good	26.01.14	48
* TRMA099	544	83	40.1	23.28	27.4	16.11.13	Good	27.11.13	11
* TRMA102	621	119	98.05	21.51	30.86	04.12.13	Good	30.01.14	57
TRMA174	534	100	42.1	26.75	16.99	07.10.14	Good	27.01.15	144
TRMA178	456	115	46.2	21.38	13.76	11.11.14	Good	13.02.15	95
TRMA186	550	96	45.8	25.89	17.39	08.11.14	Good	13.02.15	98
Mean	539.79	93.83	55.49	20.56	26.14				70.54
SE	17.32	4.49	4.57	0.8	1.1		N = 24		7.51
T. vogeli									
TRVO002	642	119	104.2	37.53	25.9	20.07.14	Good	13.02.15	208
TRVO003	729	138	109.7	39.21	26.23	29.07.14	Good	13.02.15	199
Mean	685.5	128.5	106.95	38.37	26.065				203.5
SE	43.5	9.5	2.75	0.84	0.165		N = 2		4.5
T. albolabris									
TRAL006	765	140	122.9	28	36	25.08.13	Excellent	06.03.14	193

* Indicates that the snake had fewer than 5 relocations (and thus individuals not included in the analyses).

Table 3.3 Morphometrics, body condition at tracking initiation, and duration of tracking among male *T. macrops* (*n*=4) and T. vogeli (*n*=1)from Oct 2012- Feb 2015 at SERS.

Snake ID	**Sex**	**SVL (mm)**	**TVL (mm)**	**Mass (g)**	**HL (mm)**	**HW (mm)**	**First Track**	**Condition**	**Final Track**	**Total Days**
T. macrops										
TRMA026*	M	603	237	33.2	22	19	11.09.13	Good	27.09.13	37
TRMA110*	M	534	43	49.5	15.92	25.77	11.11.13	Good	05.02.14	86
TRMA065	M	613	136	40.4	22	14	06.06.13	Good	23.08.13	123
TRMA093*	M	487	122	33.2	14.68	23.01	04.11.13	Good	11.12.13	16
	Mean	545.4	129.2	38.32	18.52	20.556			**Mean**	53.6
	SE	60.2	69.9	6.9	3.39	4.438			**SE**	94.58
T. vogeli										
TRVO001	M	490	108	35.3	18	21	10.10.13	Good	24.01.13	106

3.4.3 General observations

Data from 21 adult female *T. macrops*, with a mean total body length 63.9 of ± 2.2 cm (range: 45.4–77.8 cm), and 55.49 ± 4.57 g body mass (range: 30–113 g; Table 3.4) are presented in this section, along with data from 1 male *T. macrops* (> 5 relocations), which was 60.9 cm total body length and had a body weight of 40.4 g. The spatial data from 2 female *T. vogeli* with a mean total body length of 81.85 ± 5.7 (range: 76.1-87.6 cm) and mean body mass of 106.9 ± 2.75 (range: 104.2-109.7 g, Table 3.4), and one male *T. vogeli* with a total body length of 49.8 cm and a mass of 35.3 g are presented here as well. In addition the data from a single female *T. albolabris* 90.5 cm total body length, and 122.9 g are presented in this chapter.

Female *T. macrops* were separated into three study groups, station snakes (mild disturbance) *n* = 7, water associated snakes *n* = 9 and deep forest snakes *n* = 5. All tracked *T. vogeli* (*n* = 2 female, 1 male), and *T. albolabris* (*n* = 1) were within the deep forest areas, none were caught at the station sites or the water associated sites.

The female *T. macrops* Field Station (FS) group (Figure 3.4a, $n = 7$) were tracked on average 96.43 ± 9.49 (range: 69-133 days), while the Deep Forest (DF) group (Figure 3.4b, $n = 5$) were tracked on average 92.6 ± 14.94 (range: 59-144 days, $n = 9$), females from the Water Associated (WA) group were (Figure 3.4c) tracked on average 54.1 ± 7.56 (range: 23-97 days). There are differences in the mean number of days tracked for the three *T. macrops* groups (ANOVA = $F_{2,18} = 6.245$, $p = 0.012$), the data was normal ($W = 0.98$, $p = 0.87$) and the dispersion was equal ($F = 0.25$, $df = 2$, $p = 0.78$).

The mean number of fixes between sites, were not different (*Kruskal-Wallis* = 1.850, $df = 2$, $p = 0.397$), the data were not homoscedastic ($F = 4.8096$, $df = 2$, $p = 0.0212$) and not normal ($W = 0.84$, $p = 0.003$). Although all other GPV groups had either an N of 1 or 2, the non-female *T. macrops* groups were only used as a comparison with the three field site groups (Table 3.4d).

The mean body condition (SMI) of the tracked female *T. macrops* upon release did not differ between sites (Table 3.4, $W = 0.4673$, $df = 2$, $p = 0.7916$). Total body length between female *T. macrops* from different sites was not different (Table 3.4, $W = 1.6074$, $df = 2$, $p = 0.4477$), the data were normal ($W = 0.944$, $p = 0.3704$), and there was equality of variances according to the Levine test ($F = 0.5788$, $df = 2$, $p = 0.5734$), but non-parametrics were once again chosen. The mean SVL was not different between FS, DF, and WA female *T. macrops* (Table 3.4, $W = 1.1979$, $df = 2$, $p = 0.5494$), the data were normal ($W = 0.9165$, $p = 0.1288$), and dispersion ($F = 0.2692$, $df = 2$, $p = 0.7678$) was equal the sample size limitation restricted tests to non-parametrics.

The mean mass between snakes from each of the test sites was not different (Table 3.4, $W = 0.0486$, $df = 2$, $p = 0.976$), the data were homoscedastic ($W = 0.3793$, $p = 0.6912$), and normal ($W = 0.9137$, $p = 0.1153$). Because morphometric data among all groups were not significantly different, further comparisons of sites in terms of spatial patterns were possible.

Table 3.4 Tracking information on the Female *T. macrops* radiotracked in SERS from 2012-2014 at the different tracking sites, field station (FS) $n = 7$, deep forest (DF) $n = 5$, and water associated (WA).

ID	Group	Days	Fixes	Start date	Ending date	TBL	Mass (g)	SMI	MCP	FK50	FK95
6	FS	69	30	06/11/2013	15/01/2014	741	59.3	28.1	0.279	0.044	0.199
25	FS	133	61	26/10/2012	15/01/2013	658	64.2	36.4	0.075	0.022	0.121
80	FS	87	39	09/09/2013	06/12/2013	622	55.6	38.9	0.275	0.05	0.265
88	FS	122	50	22/09/2013	24/01/2014	696	45.6	26.7	0.158	0.042	0.177
90	FS	110	47	13/10/2013	03/02/2014	622	56.9	35.8	0.219	0.047	0.226
95	FS	75	31	05/11/2013	20/01/2014	596	39.2	55.5	0.349	0.029	0.197
102*	FS	79	33	11/11/2013	30/01/2014	738	98.1	48.7	0.049	N/A	N/A
	Mean	96.4	41.6			668	59.8	38.6	0.201	0.039	0.198
	SE	9.5	4.4			22	7.1	3.9	0.042	0.005	0.020
69	DF	59	23	22/11/2013	20/01/2014	745	67.6	31.9	0.015	0.028	0.092
94*	DF	67	29	11/11/2013	18/01/2014	589	41.7	39.9	0.012	N/A	N/A
174	DF	144	187	07/10/2014	27/01/2015	634	42.1	36.6	0.448	0.056	0.312
178	DF	95	152	11/11/2014	13/02/2015	571	46.2	55.8	0.225	0.053	0.284
186	DF	98	138	08/11/2014	13/02/2015	646	45.8	33.3	0.214	0.06	0.265
	Mean	92.6	105.8			637	48.7	39.5	0.183	0.049	0.238
	SE	14.9	33.6			30	4.8	4.3	0.081	0.007	0.050

Table 3.4 (Continued).

ID	Group	Days	Fixes	Start date	Ending date	TBL	Mass (g)	SMI	MCP	FK50	FK95
14	WA	97	92	28/05/2013	05/09/2013	635	81.8	28.3	0.246	0.052	0.255
23	WA	47	22	26/10/2012	13/12/2012	499	45.5	66.2	0.413	0.054	0.298
24	WA	55	93	01/05/2013	26/06/2013	673	41.8	26.8	0.094	0.035	0.168
29	WA	41	85	01/05/2013	25/06/2013	649	47.5	39.2	0.228	0.024	0.158
48	WA	72	88	01/05/2013	13/07/2013	685	62.8	30.9	0.169	0.029	0.148
50	WA	23	47	01/05/2013	24/05/2013	538	62.5	44.7	0.068	0.023	0.112
52*	WA	31	55	23/05/2013	24/06/2013	692	55.1	32.7	0	N/A	N/A
62	WA	52	61	23/05/2013	14/07./2013	733	70.2	35.2	0.121	0.034	0.185
96*	WA	69	23	17/11/2013	26/01/2014	592	44.2	41.5	0.119	N/A	N/A
	Mean	54.1	62.9	41404.33333	41459.875	633	56.8	38.4	0.162	0.036	0.189
	SE	7.6	9.5	32.46408272	40.00332017	25	4.5	4.0	0.040	0.005	0.025

Table 3.5 Tracking information on the *Trimeresurus* spp. in SERS from 2012-2014 at the deep forest site.

ID	Group	Days	Fixes	Start date	Ending date	TBL	Mass (g)	SMI	MCP	FK50	FK95
65	TRMA-M	185	111	06.06.13	11.12.13	749	40.4	20.8	0.676	0.026	0.229
1	TRVO-M	106	56	10.10.13	24.01.13	598	35.3	NA	0.404	0.076	0.358
6	TRAL-F	193	55	25.08.13	06.03.14	943	122.9	NA	0.234	0.064	0.255
2	TRVO-F	208	302	20.07.14	13.02.15	835	104.2	NA	1.574	0.128	0.859
3	TRVO-F	199	285	29.07.14	13.02.15	854.1	109.7	NA	5.107	0.124	0.709
N = 5	**Mean**	203.5	293.5			844.5	106.95		3.34	0.126	0.784
	SE	4.5				9.55	2.75		1.766	0.002	0.075

3.4.4 Female *T. macrops* number of relocations

Overall, there were an average of 14.6 ± 2.5 (range = 1 – 80 movements) relocations (> 5m moves) per individual GPV. Female *T. macrops* had a mean of 14.6 ± 2.5 (range = 1 – 35 moves). Female *T. macrops* differed in number of moves between sites (Table 3.4). The mean number of days tracked differed significantly between the three sites (ANOVA = $F_{2,18} = 6.245$, $p = 0.012$) with Water Associated snakes tracked the shortest periods of time (Figure 3.8). When applying the site as a covariate the number of fixes (ANCOVA: $F_{1,10} = 3.746$, $p = 0.075$) was not influenced by the number of days, however site was a strong predictor for the number of fixes (ANCOVA: $F_{1,10} = 12.539$, $p < 0.001$).

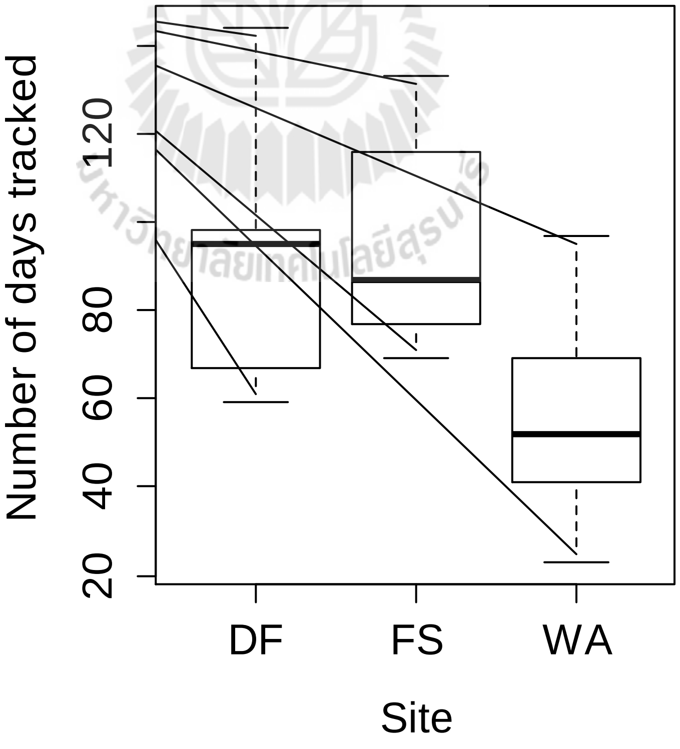


Figure 3.8 Comparison of the number of days that female *T. macrops* were tracked between the three field sites selected at SERS.

The number of days tracked was correlated with the number of moves (Figure 3.9A), yet was a non-significant correlation (Pearson's product correlation, t = 1.00, df = 19, p = 0.331). The number of fixes was more strongly correlated with the number of moves per individual (Figure 3.9B) (Pearson's product-moment correlation, t = 5.64, df = 19, p < 0.001) and therefore home range sizes, thus the number of fixes was selected as a covariate for further statistical analyses on movement patterns.

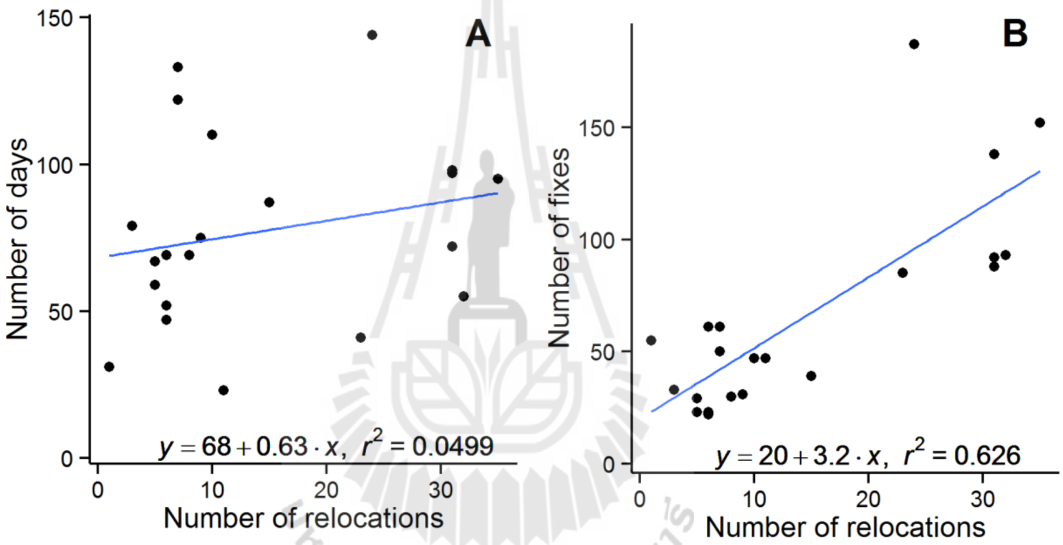


Figure 3.9 Correlation between number of days a female *T. macrops* was tracked at SERS and number of relocations (A), and the correlation between the number of fixes (B) and the number of relocations throughout the tracking period.

3.4.5 Female *T. macrops* movement patterns

Movement patterns differed somewhat between sites (Table 3.6). The total number of days stationary between FS, WA, and DF snakes was different (ANOVA: $F_{2,18}$ = 7.94, p < 0.01). The maximum number of days stationary differed between sites (ANOVA: $F_{2,18}$ = 4.74, p < 0.03). The average mean number of days stationary between sites was different ($W = 6.95$, $df = 2$, $p < 0.04$). Deep forest snakes were stationary on average for 8.7 ± 1.1 days, FS snakes were stationary on average for 12.0 ± 1.5 days, and WA snakes were stationary on average 7.9 ± 2.8 days, with a recorded maximum of 50 days with no relocations greater than 5 m. Female *T. macrops* had relocated on 27.9% of all observation attempts (Table 3.6), with DF snakes moving on average 16.9 ± 4.02 times, FS snakes moving on average 9 ± 1.51 occurrences, and WA snakes relocating on average 10.6 ± 2.67 times ($W = 0.919$, $p = 0.144$), even when number of fixes was used as a covariate (ANCOVA: $F = 28.163$, $df = 2$, $p = .864$), number of relocations did not differ between sites.

Table 3.6 Number of relocations, and total time spent stationary presented for tracked *Trimeresurus* spp. at SERS.

					Days spent stationary (<5 m move)		
ID	Site	Sex	Relocations	Days	Total	Mean ± SE	Max
TRMA069	DF	F	5	58	54.0	10.8 ± 10.0	24.0
TRMA094	DF	F	5	67	63	10.5 ± 7.5	48.0
TRMA174	DF	F	23	110	100.0	9.1 ± 10.8	38.0
TRMA178	DF	F	16	92	78.0	8.7 ± 6.6	19.0
TRMA186	DF	F	21	94	77.0	4.5 ± 4.2	17.0
					mean of Total	mean ± SE	Max
					74.4	8.7 ± 1.1	48.0
TRMA006	FS	F	5	67	61.0	12.2 ± 9.4	28.0
TRMA025	FS	F	12	130	104.0	9.5 ± 15.6	50.0
TRMA080	FS	F	13	87	77.0	5.9 ±8.5	28.0
TRMA088	FS	F	8	122	115.0	14.4 ± 10.7	36.0
TRMA090	FS	F	9	110	100.0	11.1 ± 13.3	39.0
TRMA095	FS	F	7	75	70.0	11.7 ± 10.5	26.0
TRMA102	FS	F	3	79	76	19.0 ± 9.2	44.0
					mean of Total	mean ± SE	Max
					86.1	12.0 ± 1.5	50.0

Site: Deep Forest (DF), Field Station (FS), Water Associated (WA), Total is the total number of days spent stationary.

Table 3.6 (Continued).

					Days spent stationary (<5 m move)		
ID	**Site**	**Sex**	**Relocations**	**Days**	**Total**	**Mean ± SE**	**Max**
TRMA014	WA	F	16	94	89.0	6.4	23.0
TRMA023	WA	F	11	46	44.0	7.3	30.0
TRMA024	WA	F	20	50	44.0	3.4	13.0
TRMA029	WA	F	12	41	37.0	4.6	20.0
TRMA048	WA	F	10	72	64.0	7.1	28.0
TRMA050	WA	F	6	23	18.0	3.0	7.0
TRMA052	WA	F	1	31	30	30.0 ± 0	30
TRMA062	WA	F	5	19	17.0	3.4	10.0
TRMA096	WA	F	5	69	63.0	6.0 ± 2.3	23
					mean of Total	mean ± SE	Max
					45.1	7.9 ± 2.8	30.0
TRMA065	WA	M	12	77	70.0	6.4 ± 6.1	19.0
TRVO001	DF	M	14	104	92.0	7.1 ± 5.0	16.0
TRVO002	DF	F	59	202	149.0	5.1 ± 7.2	30.0
TRVO003	DF	F	32	194	157.0	7.1 ± 8.8	28.0
					mean of Total	mean ± SE	Max
					153.0	6.1 ± 0.8	30.0
TRAL006	DF	F	14	184	172.0	15.5 ± 12.3	46.0

In general, most moves were short distance and within 13.3 meters of the individual's last known location, with 43.4% of all moves within 5 meters. The maximum recorded single-night move was 102.2 meters, which was by a WA individual.

When accounting for the number of fixes as a covariate, movement patterns of different *T. macrops* females did not differ significantly between sites, total distance moved (ANCOVA: $F_{2,17}$ = 0.275, p = 0.763), mean distance (ANCOVA: $F_{2,17}$ = 1.937, p = 0.175), or maximum distance moved (ANCOVA: $F_{2,17}$ = 0.133, p = 0.876) (Table 3.6). Mean daily displacement (MDD) is also not significantly different between sites (ANCOVA: $F_{2,17}$ = 2.630, p = 0.101), although the mean for WA individuals is higher than either DF or FS (Figure 3.10).

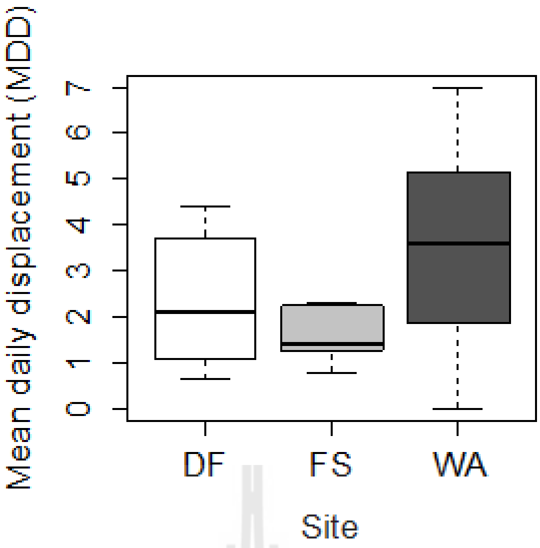


Figure 3.10 Comparison of the mean daily displacement for female *T. macrops* in FS, DF, and WA sites.

Table 3.7 Relocation and movement patterns for tracked *Trimeresurus* spp. at SERS.

					Distance moved (m)		
ID	**Site**	**Sex**	**Relocations**	**Days**	**Total**	**Ave ± SE**	**Maximum**
TRMA069	DF	F	5	58	63.5	12.7 ± 3.8	24.2
TRMA094	DF	F	5	67	42.1	10.5 ± 4.8	23.4
TRMA174	DF	F	23	110	302.1	25.2 ± 4.9	60.0
TRMA178	DF	F	16	92	419.6	28.0 ± 6.2	89.7
TRMA186	DF	F	21	94	363.6	20.2 ± 3.0	46.1
					mean total	mean ± SE	Max
					238.2	22.0 ± 7.7	89.7
TRMA006	FS	F	5	67	154.8	19.4 ± 0.8	84.0
TRMA025	FS	F	12	130	104.6	10.5 ± 2.4	28.6
TRMA080	FS	F	13	87	195.1	15.0 ± 3.0	36.1
TRMA088	FS	F	8	122	139.3	19.9 ± 5.3	41.6
TRMA090	FS	F	9	110	150.3	15.0 ± 4.5	46.9
TRMA095	FS	F	7	75	174.0	21.8 ± 7.9	63.9
TRMA102	FS	F	3	79	174.0	21.8 ± 7.9	63.9
					mean total	average ± SE	max
					146.9	17.4 ± 7.00	84.0

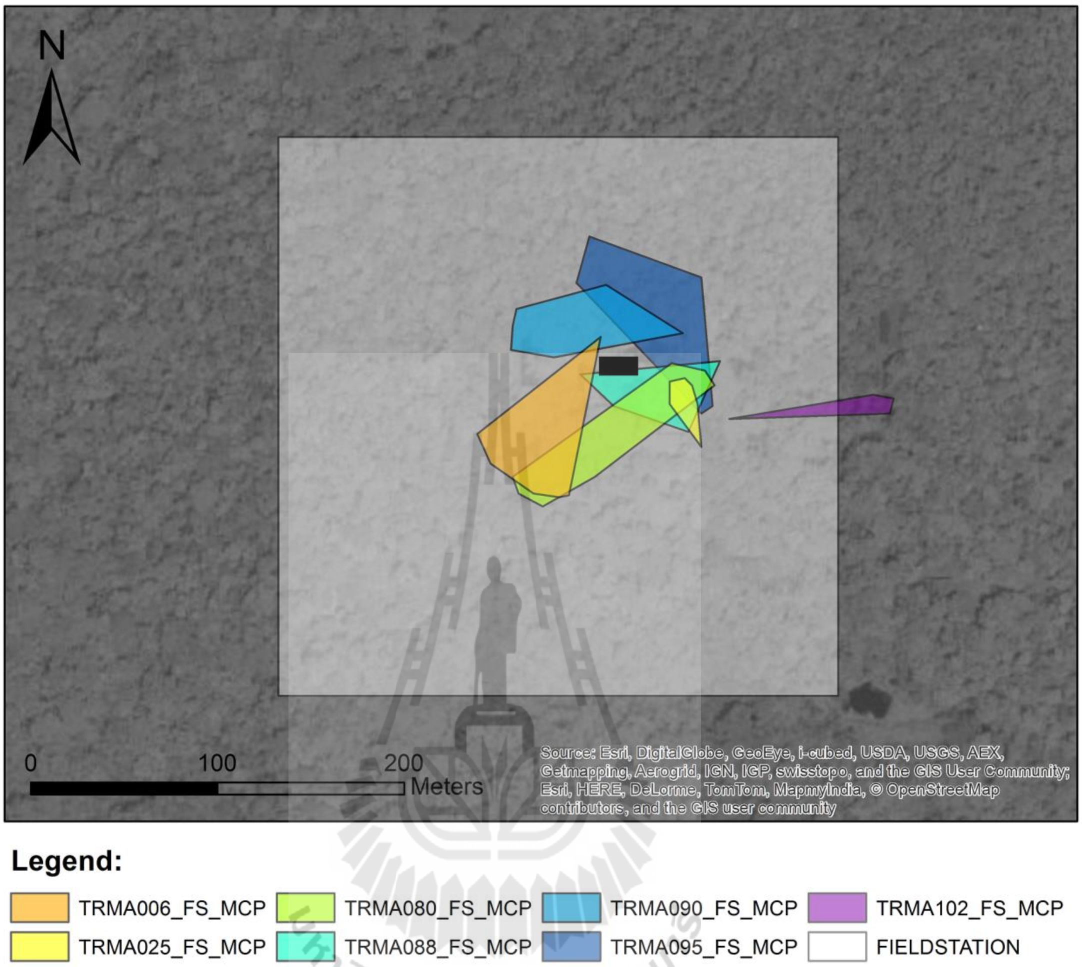
Table 3.7 (Continued).

					Distance moved (m)		
ID	**Site**	**Sex**	**Relocations**	**Days**	**Total**	**Ave ± SE**	**Site**
TRMA014	WA	F	16	94	347.4	13.9 ± 5.5	102.2
TRMA023	WA	F	11	46	214.5	21.5 ± 7.4	61.2
TRMA024	WA	F	20	50	282.4	8.6 ± 2.0	39.4
TRMA029	WA	F	12	41	286.1	15.1 ± 4.8	62.1
TRMA048	WA	F	10	72	194.4	8.1 ± 4.7	63.7
TRMA050	WA	F	6	23	143.6	14.4 ± 9.9	77.6
TRMA052	WA	F	1	31	0	0 ± 0	0
TRMA062	WA	F	5	19	73.9	14.8 ± 4.6	29.8
TRMA096	WA	F	5	23	127.1	21.2 ± 4.2	35
TRMA065	WA	M	12	77	381.3	22.4 ± 9.9	141.4
					mean total	average ± SE	max
					185.5	12.6 ± 5.8	102.2
TRVO002	DF	F	59	202	1350.5	18.8 ± 2.4	86.8
TRVO003	DF	F	32	194	992.6	26.1 ± 6.4	130.6
TRVO001	DF	M	14	104	339.2	26.1 ± 5.7	67.7
					mean total	average ± SE	max
					1171.6	22.4 ± 6.7	130.6
TRAL006	DF	F	14	184	304.5	21.7 ± 6.9	77.8

3.4.6 Site specific home range size

Home range polygons are displayed with snake tracking locations on figure 3.11, clear overlap is present, and snakes were shown to sometimes leave the intensive study sites. In the case of the DF site the majority of non-macrops individuals were tracked outside of the intensive study site. Disturbance is visible on the map at both the WA site (limited) and FS site (moderate human disturbance). The map also displays the excluded Upper Dam Pond site.

On average MCP home ranges were small 0.237 ± 0.037 (range: 0-0.676 ha) for all tracked *T. macrops* including the one male (*n* = 22 snakes). Upon first examination *T. vogeli* (*n* = 3) MCP 2.36 ± 1.41 (range: 0.404-5.107 ha) home ranges appear larger than *T. macrops*. However the only *T. albolabris* had a superficially similar MCP home range size (MCP = 0.234 ha) to the tracked *T. macrops*.

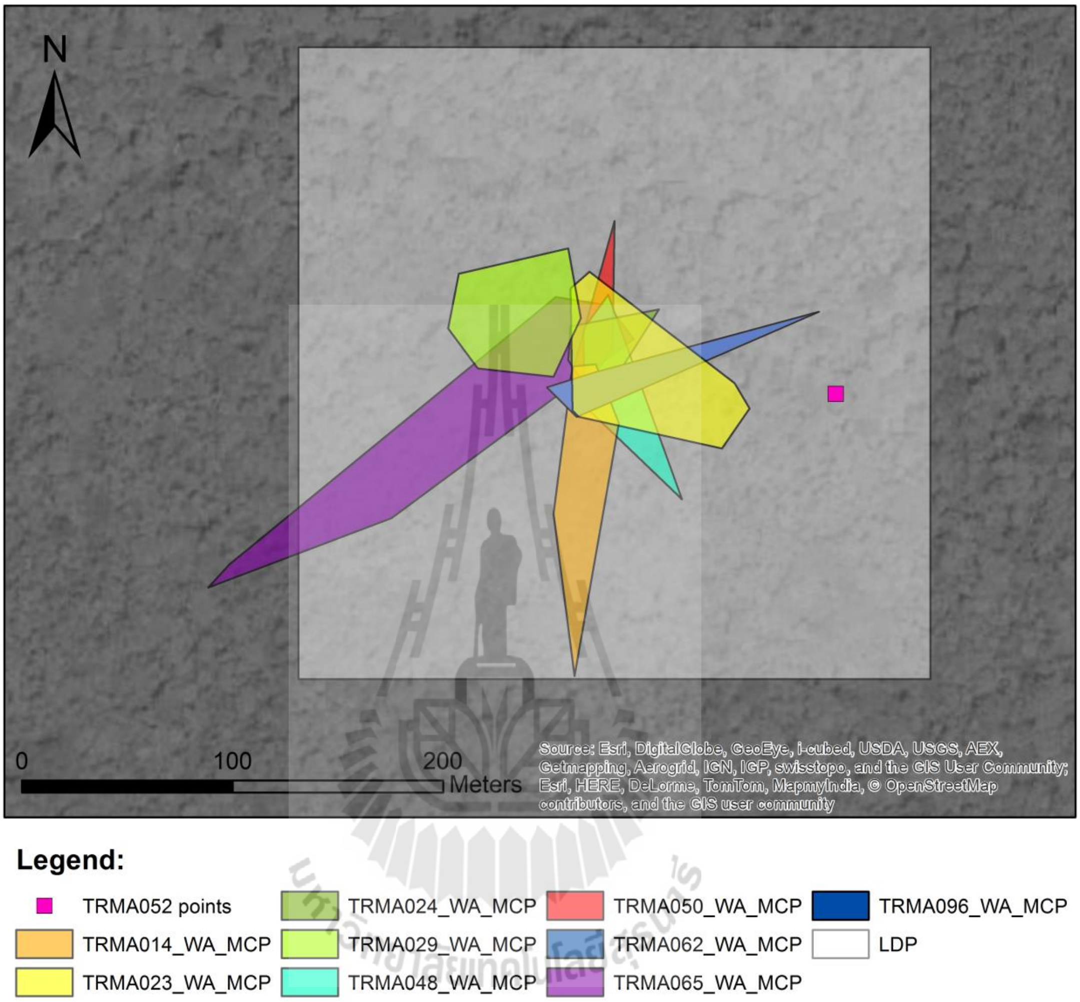


Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; Esri, HERE, DeLorme, TomTom, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 3.11 Field station MCP polygons of *T. macrops* tracked in the intensive site. Displaying the site in reference to SERS, and the overlap of the polygons.

The mean home range size for adult the 21 female adult *T. macrops* using the MCP method was 0.171 ± 0.028 (range: 0-0.448 ha). The mean MCP home range size between sites did not differ ($W = 0.559$, $df = 2$, $p = 0.756$) between any of the three selected sites. The mean home range sizes for FS ($n = 7$) *T. macrops* (Figure 3.11) was 0.195 ± 0.045 (range: 0.049-0.349 ha), DF ($n = 5$) (Figure 3.13), 0.183 ± 0.080

(range: 0.012-0.448 ha), and WA ($n = 9$) group (Figure 3.12) (range: 0-0.358 ha) showed no clear patterns.

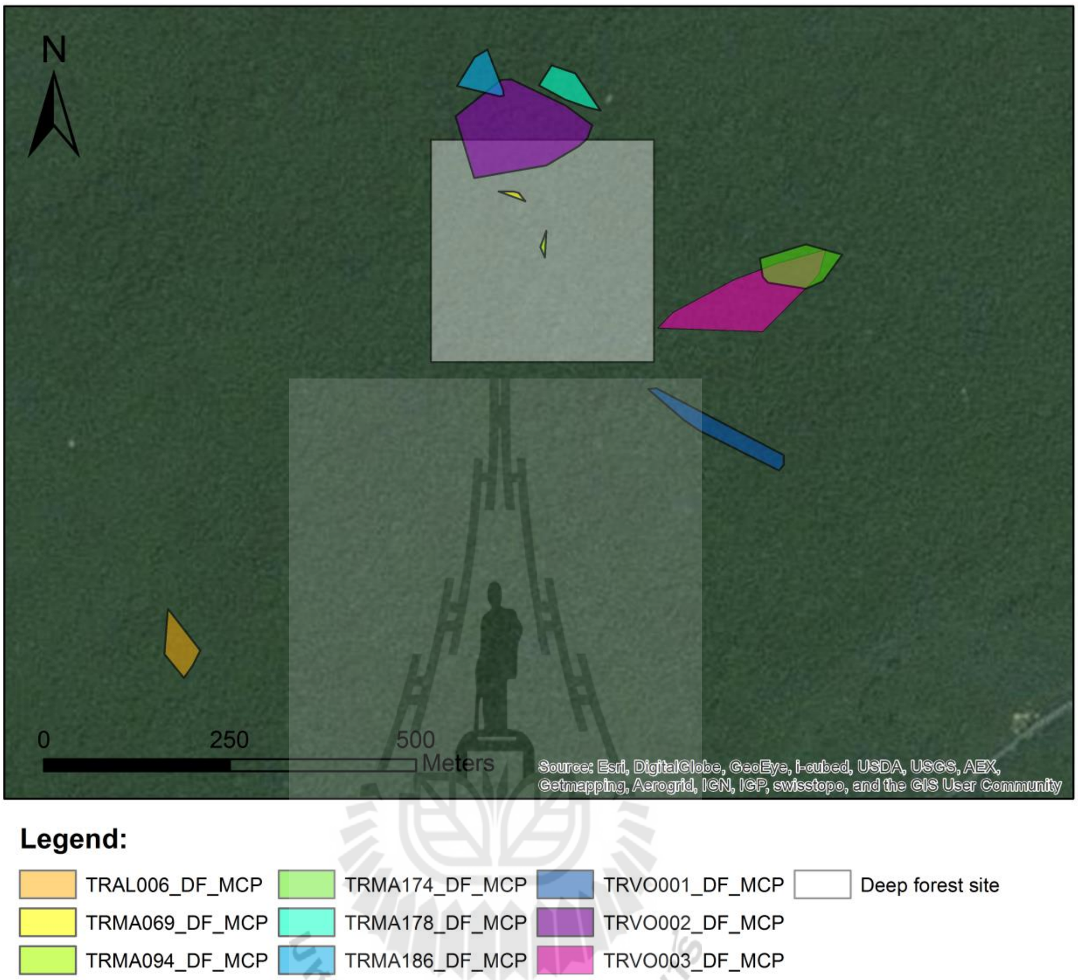


Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; Esri, HERE, DeLorme, TomTom, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 3.12 Water associated site of MCP polygons of *T. macrops* tracked in the intensive site. Displaying the site in reference to SERS, and the overlap of the polygons.

Home ranges did not differ between sites and forest habitats for any of the estimate methods (FK50: $F_{1,10} = 0.122$; $p = 0.734$; FK95: $F_{1,10} = 1.557$, $p = 0.241$). Nonetheless, the mean size of core and activity areas were slightly larger for deep forest (FK50: 0.049 ± 0.007 ha; FK95: 0.238 ± 0.049 ha; Figure 3.13) than either field station (FK50: 0.039 ± 0.004 ha; FK95: 0.197 ± 0.019 ha), or water associated

(FK50: 0.035 ± 0.0047 ha; FK95: 0.189 ± 0.024 ha; Figure 3.12) snakes.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 3.13 Deep forest site of MCP polygons of *Trimeresurus* spp. tracked in the intensive site, displaying the site in reference to SERS, and the overlap of the polygons.

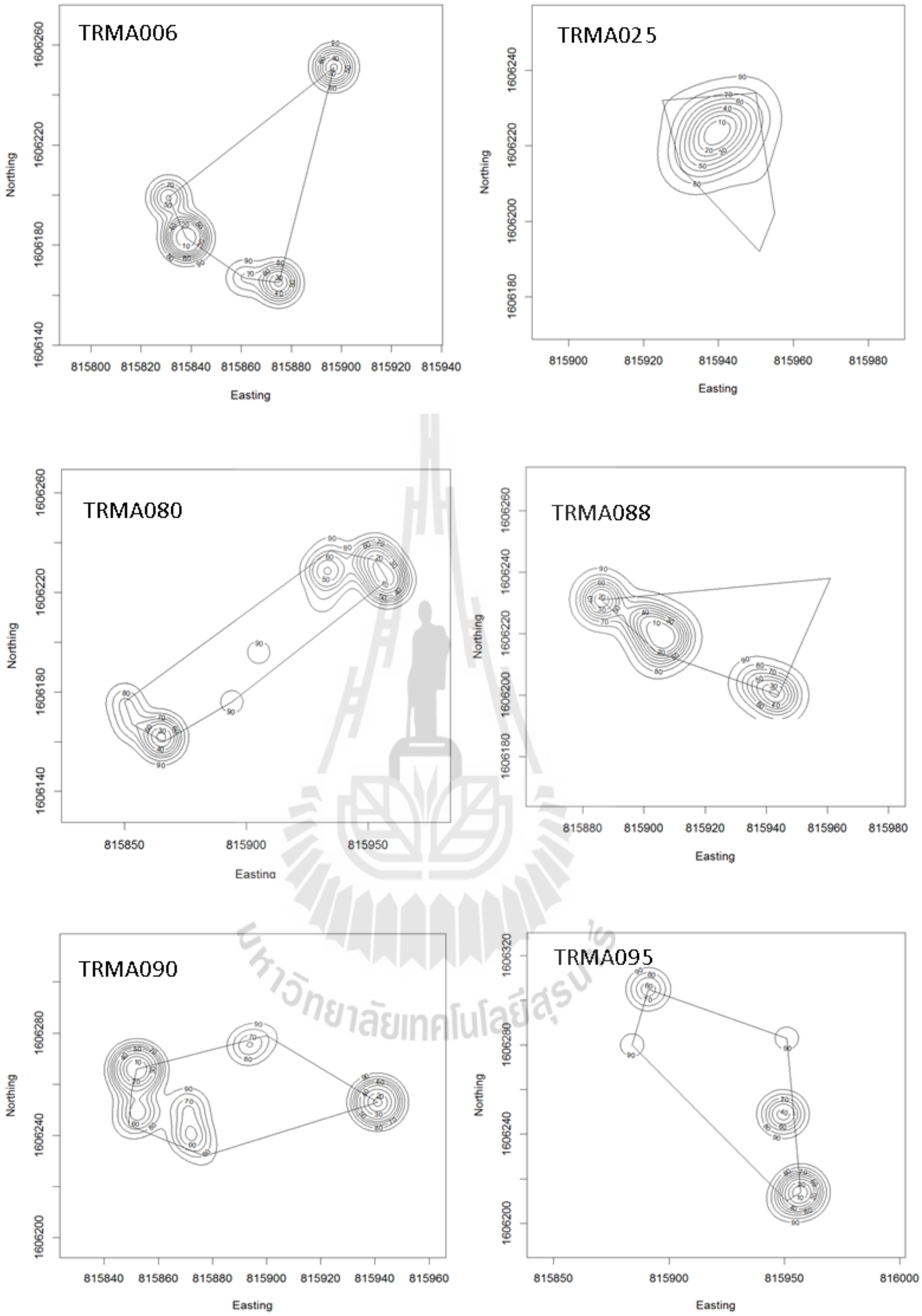


Figure 3.14 Minimum Convex Polygon, home ranges for station snakes, and fixed kernel 95% and 50% activity centers for *T. macrops* centered at the field station (FS) site.

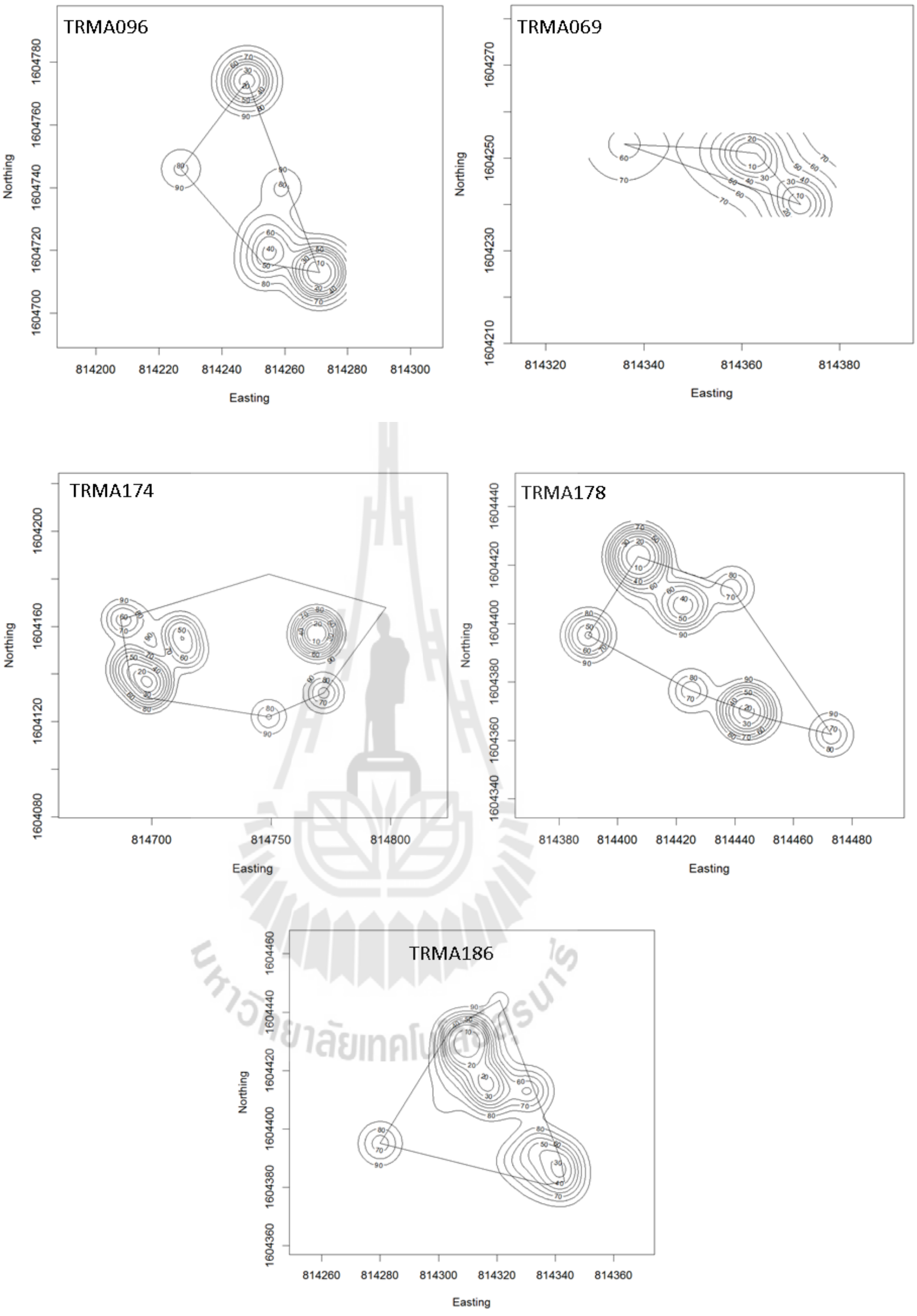


Figure 3.15 Minimum Convex Polygon, home ranges for deep forest (DF) snakes, and fixed kernel 95% and 50% activity areas for *T. macrops* tracked in the deep evergreen forest of SERS.

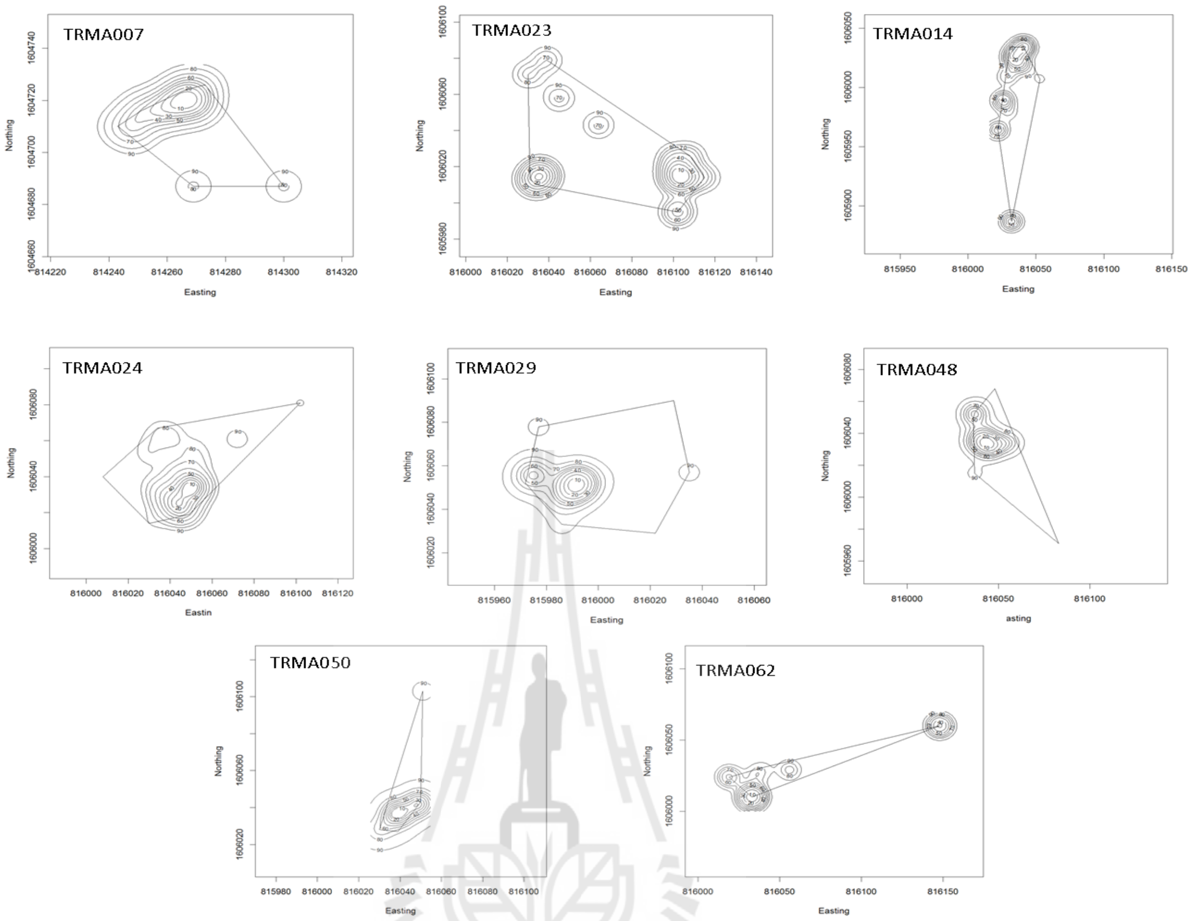


Figure 3.16 Minimum Convex Polygon, home ranges for Water Associated (WA) snakes, and fixed kernel 95% and 50% activity areas for *T. macrops* tracked near standing ponds (upper and lower dam pond) at SERS.

3.4.7 Home range overlap

The overall mean percentage of MCP overlap was 41.4 ± 22.8% (station: 42.1 ± 15.6%; t: 40.6 ± 28.2%), although differences between habitats were not statistically significant (*p* > 0.050 for all comparisons). For activity areas, however, there was little overlap among conspecifics, as UDOI averaged only 0.039 for station snakes and 0.045 for forest individuals (*i.e.* Figure 3.14). Core area overlap was even lower, with station overlap averaging 0.001, while forest was 0.005.

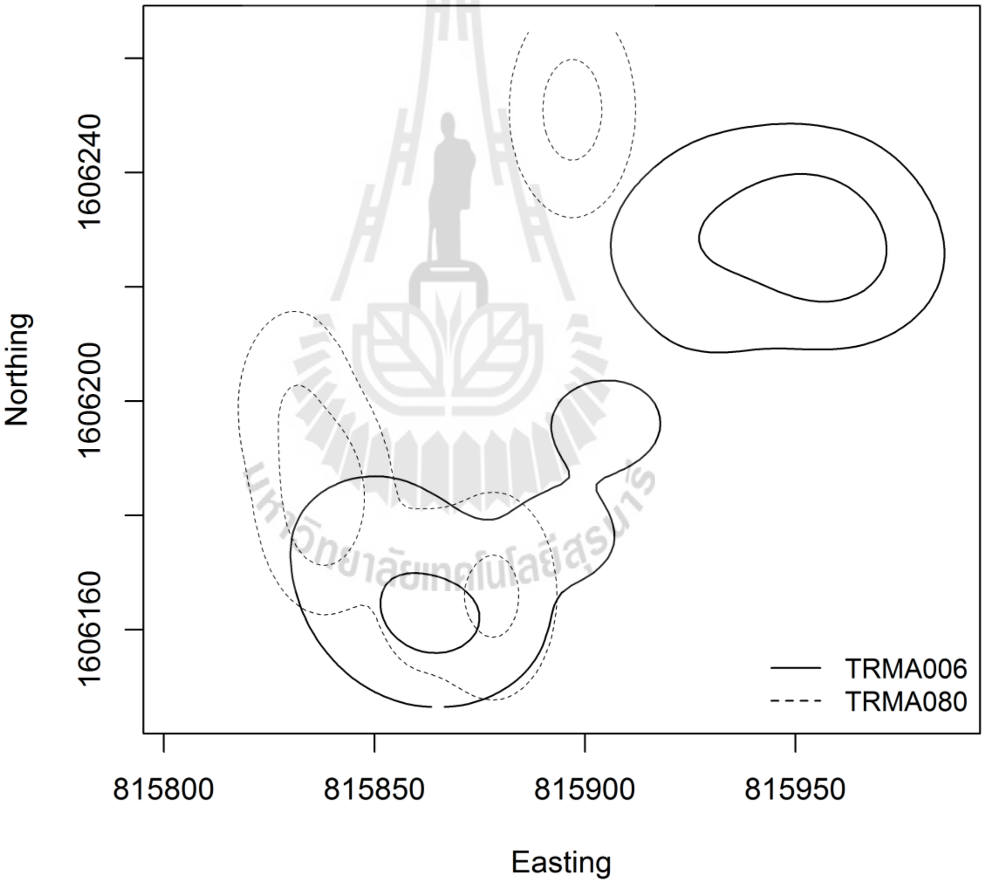


Figure 3.17 Example Utilization Distribution Overlap Index (ODOI) for the home ranges of two female *T. macrops*, individuals TRMA080 and TRMA006, from the field station (FS) site.

3.4.8 Spatial ecology of *T. vogeli* and deep forest *T. macrops*

The number of fixes ($W = 0.899$, $p = 0.428$), and number of days tracked ($W = 0.829$, $p = 0.1669$) were not different between the two randomly selected *T. macrops*, and two tracked *T. vogeli*. The total number of days stationary ($W = 0$, $p = 0.2$), maximum number of days stationary ($W = 2$, $p = 0.8$), and average mean number of days stationary were not different between the 2 randomly selected deep forest female *T. macrops* and sympatric deep forest *T. vogeli* ($W = 4$, $p = 0.8$) (Table 3.5). Home range size MCP (ANCOVA: $F = 0.02$, $df = 1$, $p = 0.909$), home range FK95 (ANCOVA: $F = 0.151$, $df = 13.676$, $p = 0.764$) and activity center FK50 (ANCOVA: $F = 1.34$, $df = 1$, $p = 0.453$). However there is a clear pattern of larger home ranges when displayed in graphical form (Figure 3.12), the non-significance of home range size difference is likely a result of very small sample sizes.

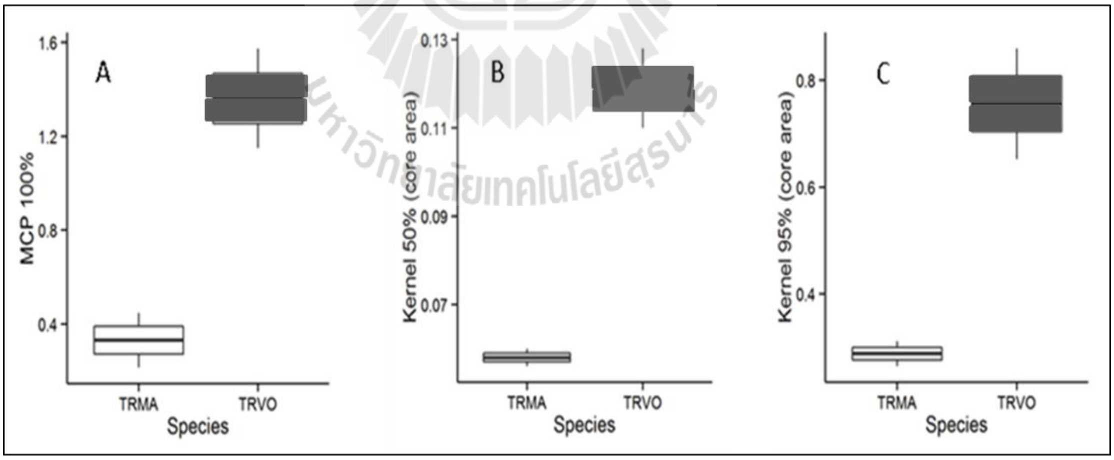


Figure 3.18 Comparison of home range size for tracked female *T. macrops* and *T. vogeli* in the deep forest sites using, MCP (100%) (A) FK (50%) (B) and FK (95%) (C).

Home range sizes for all tracked *Trimeresurus* spp. excluding female *T. macrops* used for site comparisons are displayed in figure 3.12. The male *T. macrops* had the largest MCP home range but not the largest fixed kernel home ranges of all the *T. macrops* (95%=0.229, 50% 0.026). The male *T. vogeli* appeared to have a smaller fixed kernel home range (95% 0.358, 50% 0.076) than the mean fixed kernel home ranges of the two female *T. vogeli* (95% 0.784 ± 0.002, 50% 0.126 ± 0.075, however but with *n* = 1, no true statistical comparison could be performed. MCP home ranges for individuals.

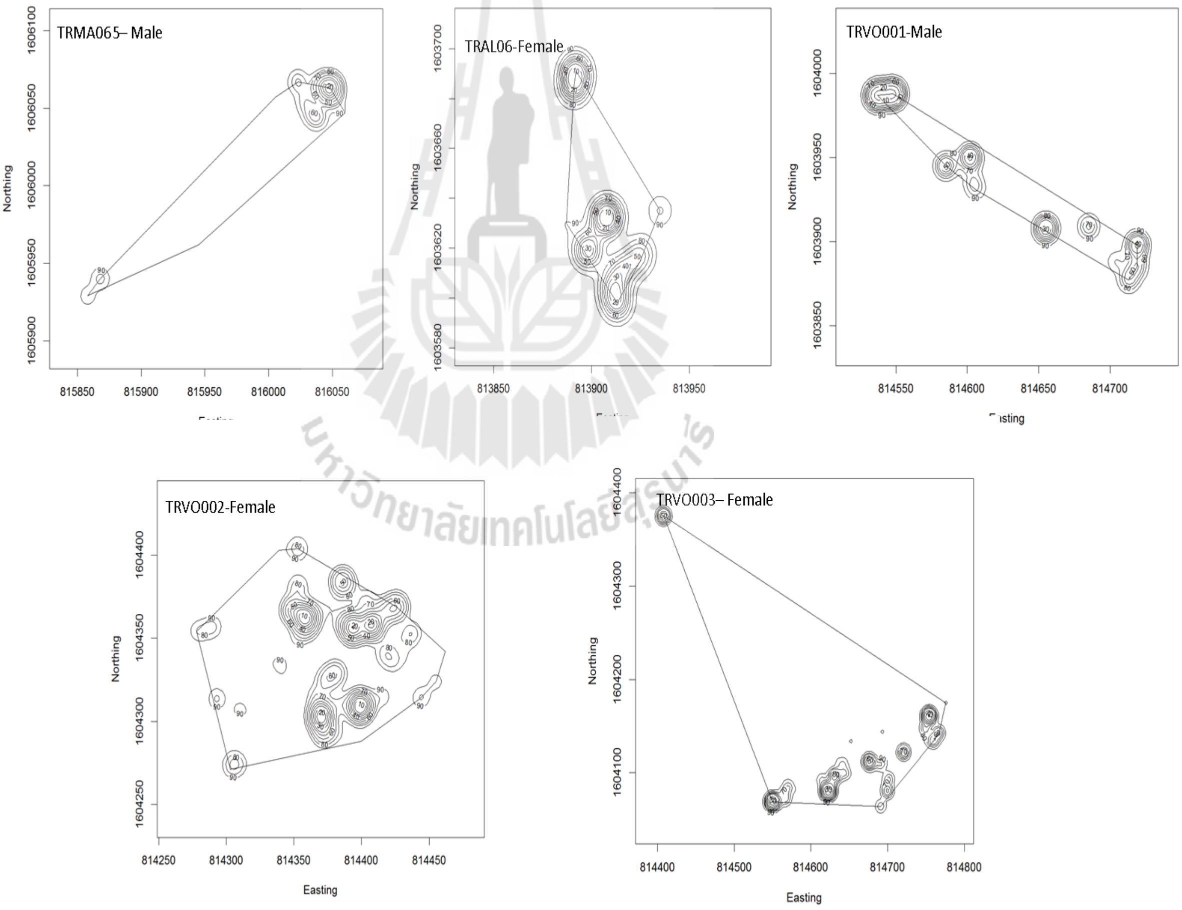


Figure 3.19 Display of the home ranges for *T. vogeli*, *T. albolabris* and *T. macrops* snakes found in various sites throughout SERS and tracked between 2012 and 2014.

Home range overlap was minimal for the deep forest *T. macrops* individuals did not overlap with one another (Table 3.7), however *T. macrops* 174 shared 83% of its MCP home range *with T. vogeli* 003. Additionally *T. macrops* 186 shared 10% of its MCP home range with *T. vogeli*. Interestingly very little of the FK 95% range = 0-0.035 and FK 50% range = 0-0.006 overlapped with other snakes of either species.

Table 3.8 Home range overlap patterns for deep forest *T. macrops* with the sympatric *T. vogeli*.

SNAKE	**Overlap with**	**MCP HOME RANGE**		**FK 50%**		**FK 95%**	
	Snake ID #	**HRO (ha)**	**PHR**	**PHR**	**UDOI**	**PHR**	**UDOI**
TRMA174	TRMA178	0	0	0	0	0	0
vs	TRMA186	0	0	0	0	0	0
	TRVO002	0	0	0	0	0	0
	TRVO003	0.373	83.3	0.017	0.006	0.048	0.035
TRMA178	TRMA186	0	0	0	0	0	0
vs	TRVO002	0	0	0	0	0.014	0.001
	TRVO003	0	0	0	0	0.014	0.001
TRMA186	TRVO002	0.023	10.8	0	0	0.003	0.001
vs	TRVO003	0	0	0	0	0	0
TRVO002	TRVO003	0.142	9.0	0	0	0.059	0.008

HRO is home range overlap, PHR is percent of home range, UDOI utilization distribution overlap index. FK is fixed kernel.

3.4.9 Behavior and microhabitat selection

Individuals were visually detected on 1218 of 2043 (59.6%) overall observation attempts. Female *T. macrops* were visible 785 of 1364 (57.5%). When separated into sites, the FS snakes were visible 182 of 289 (63.0%) observations, the DF snakes were visible 329 of 529 (62.2%) observations, and the WA snakes were visible 274 of 546 observations (50.2%). The male *T. macrops* was only visible 17 out 111 (15.8%) observation attempts.

The female *T. albolabris* was visible 38 of 55 observation attempts (69.0%). The two female *T. vogeli* were visible 367 of 587 observation attempts (62.5%), while the single male *T. vogeli* was visible only 10 of 56 attempts (17.8%).

Female *T. macrops* from the FS spent the highest proportion of time sheltering (21.5%), while only 17.6% on average of FS were in ambush during data collection. Female DF *T. macrops* were found in resting position (31.6%), and sheltering (18.0%) on the majority of all visual observations; however 20.6% of observations revealed ambushing *T. macrops*. Interestingly WA snakes (40.0% of all observations) were observed ambushing most often and were only spotted resting (15.8%) and sheltering (14.8%) occasionally. In all groups, less than (~1.6%) 2% of observations were on moving snakes. The proportion of visible observations in each behavior is displayed in Figure 3.18, making the trend of the greater proportion of ambush position datapoints for WA snakes more evident, as well as showing that the combination of resting and sheltering observations make up the greatest proportion of observed behaviors for FS snakes. Slight variations in behavior can be seen between sites, but sample size limitations made statistical inferences on behavioral differences inappropriate.

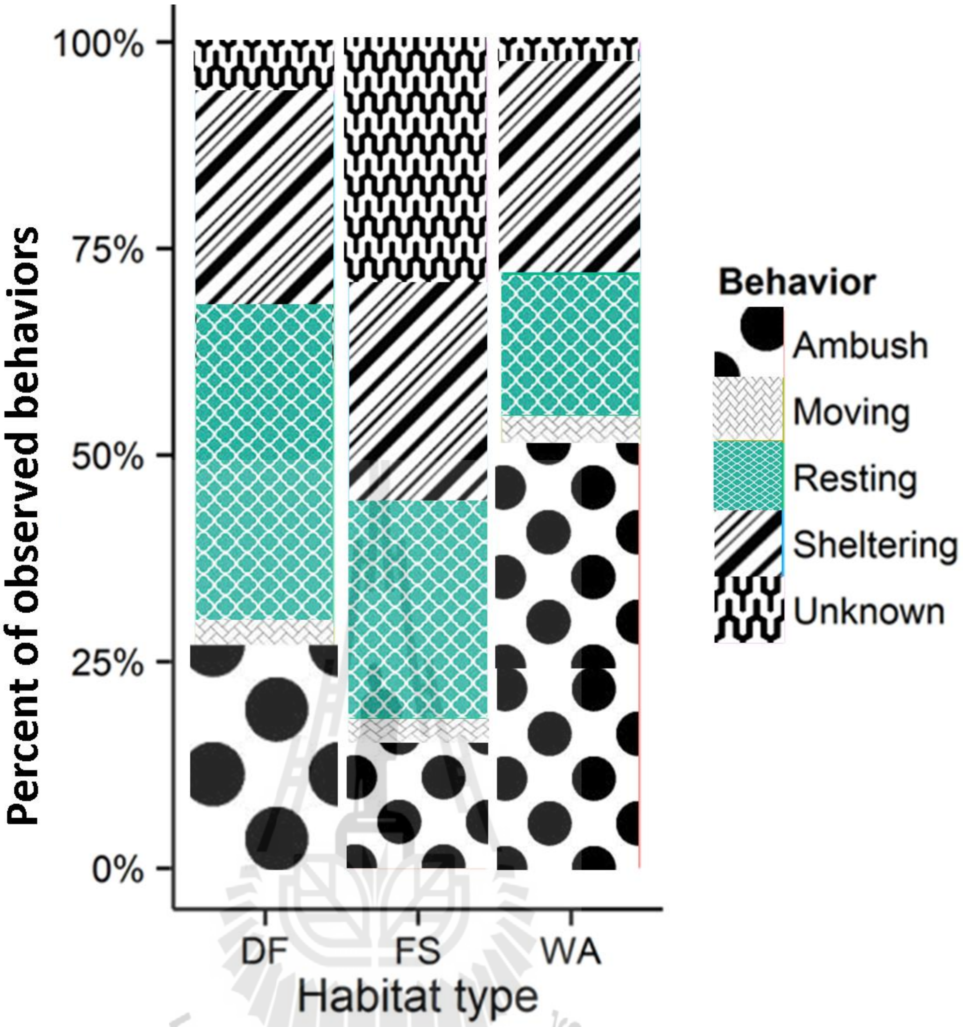


Figure 3.20 Comparison of the proportion of observed behaviors spent in categorized behavior types between deep forest (DF), field station (FS), and water associated (WA).

When perched, female *T. macrops* selected for woody vegetation (*i.e.* branches, twigs, trunks and lianas) approximately 51.3% of the time, only 9.9% of observations were snakes found perching on non-woody (green) vegetation. The dominant perch type was unable to be identified in more than 20% (24.4%) of all visual observations.

When snakes were underground, and observed from above, they were almost ubiquitously sheltering, except in one case, where a female T. macrops was in ambush position beneath the entrance to a burrow. The snakes appeared to spend the highest proportion of on ground datapoints sheltering (Figure 3.21). In the groundstory, snakes tended to spend a large proportion of observed datapoints ambushing for prey, followed by resting as the second highest. When snakes were in the understory, they were typically found either resting, or ambushing for prey. In contrast, when snakes were found in the mid-story, they were very rarely spotted in ambush position, and were most often seen in resting position. Snakes were never spotted moving through the midstory or underground. Visuals did not occur in the overstory.

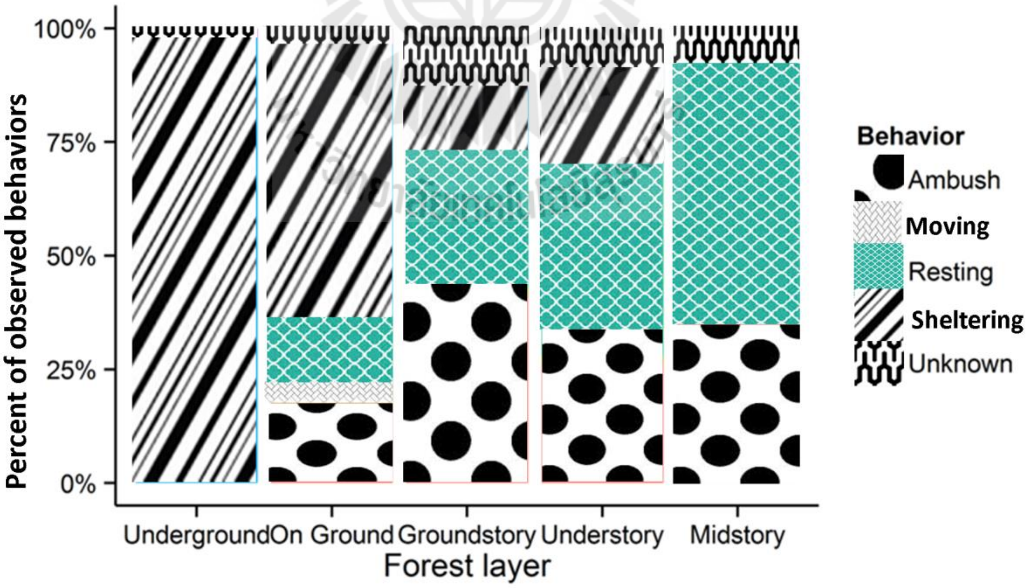


Figure 3.21 Comparison of the proportion observed behaviors spent in categorized behavior types between each forest layer.

Human disturbance did not have any significant influence on behavior, as habitat was not a significant predictor in any models. Movement occurred predominantly during night times although there were too few movement data points to run any models for movement, as we had only one recorded move during the day, from a forest snake. Due to few movement observations, no environmental variables were selected as predictors by AICc.

T. macrops were less often resting in the WA (β = -1.8512 ± 0.3696, z = -5.008, $p < 0.001$; $mR^2 = 0.710$, $cR^2 = 0.741$) and FS (β = -0.880 ± 0.375, z = -2.346, $p < 0.001$; $mR^2 = 0.710$, $cR^2 = 0.741$) associated sites than DF. During datapoints at night female *T. macrops* were less likely to be resting (β = -1.787 ± 0.140, z = -12.786, $p = 0.019$; $mR^2 = 0.710$, $cR^2 = 0.741$), and snakes were somewhat more likely to be observed resting in the understory (β = 2.787 ± 1.075, z = 2.594, $p = 0.009$; $mR^2 = 0.710$, $cR^2 = 0.741$) (Table 3.9). Both increased ambient humidity (β = 0.037 ± 0.005, z = 7.538, $p < 0.001$; $mR^2 = 0.057$, $cR^2 = 0.364$) and ground temperature (β = 0.080 ± 0.022, z = 3.593, $p < 0.001$; $mR^2 = 0.057$, $cR^2 = 0.364$) led to an increase in resting behavior (Figure 3.22).

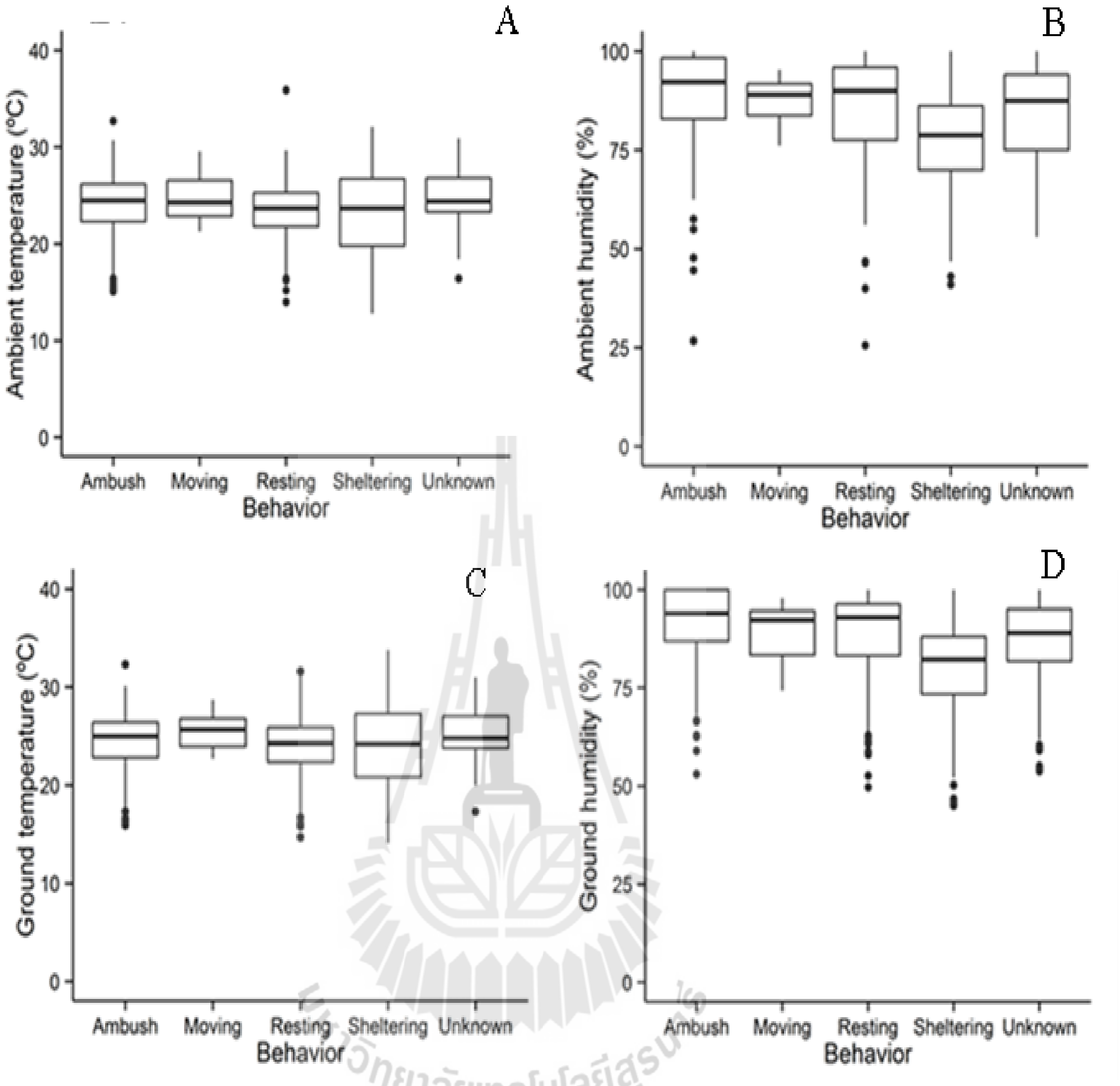


Figure 3.22 The influence of ambient temperature (A), ambient humidity (B), ground temperature (C), and ground humidity (D) on likelihood of finding a female tracked *T. macrops* in a given behavior.

Table 3.9 Model results for temporal, weather, and spatial patterns influencing *T. macrops* resting behaviors.

Variable	Coefficient	SE	*z*-value	*p*-value
(Intercept)	-1.911	± 1.091	-1.752	0.080
Site, Forest Station	-0.88	± 0.375	-2.346	0.019*
Site, Water Associated	-1.851	± 0.37	-5.008	< 0.001*
Cycle, night time	-1.787	± 0.14	-12.786	< 0.001*
Layer, Groundstory	2.374	± 1.075	2.209	0.027*
Layer, Midstory	1.789	± 1.079	1.657	0.097
Layer, On Ground	1.161	± 1.11	1.045	0.296
Layer, Underground	-13.507	± 64.006	-0.211	0.833
Layer, Understory	2.787	± 1.075	2.594	0.009*
(Intercept)	-6.417	± 0.77	-8.33	< 0.001*
Ambient humidity	0.037	± 0.005	7.538	< 0.001*
Temperature on ground	0.08	± 0.022	3.593	< 0.001*

* is significance value of *p* <.05

Table 3.10 Model results for temporal spatial and weather patterns influencing *T. macrops* ambush behaviors.

Variable	Coefficient	SE	*z*-value	*p*-value
(Intercept)	-2.985	± 0.746	-4.001	< 0.001*
Season, Dry	-1.216	± 0.398	-3.054	0.002*
Season, Rainy	-0.538	± 0.208	-2.592	0.010*
Cycle, Night time	2.379	± 0.153	15.521	< 0.001*
Layer, Groundstory	1.042	± 0.725	1.438	0.150
Layer, Midstory	-0.470	± 0.728	-0.646	0.518
Layer, On Ground	-0.691	± 0.768	-0.900	0.368
Layer, Underground	-2.392	± 1.257	-1.902	0.057
Layer, Understory	-0.100	± 0.723	-0.138	0.890
(Intercept)	-5.770	± 0.568	-10.154	< 0.001*
Relative humidity on ground	0.048	± 0.006	7.954	< 0.001*

* is significance value of *p* <.05

Snakes were observed in ambush position more often during nighttime (β = 2.379 ± 0.153, z = 15.521, p < 0.001; $mR^2 = 0.340$, $cR^2 = 0.474$) and less often during the dry season (β = -1.216 ± 0.398, z = -3.054, p = 0.002; $mR^2 = 0.340$, $cR^2 = 0.474$), than either daytime or cold season (Table 3.10). Higher ground humidity (β = 0.048 ± 0.006, z = 7.954, p < 0.001; $mR^2 = 0.340$, $cR^2 = 0.474$) led to an increase in ambush activity (Figure 3.19).

Table 3.11 Model results for temporal spatial and weather patterns influencing *T. macrops* sheltering behaviors.

Factors influencing *T. macrops* sheltering behavior	Coefficient	SE	*z*-value	*p*-value
(Intercept)	-16.497	± 618.279	-0.027	0.979
Site, Field Station	0.422	± 0.605	0.697	0.486
Site, Water Associated	2.815	± 0.685	4.108	< 0.001*
Layer, Groundstory	14.187	± 618.278	0.023	0.982
Layer, Midstory	13.625	± 618.278	0.022	0.982
Layer, On Ground	16.500	± 618.278	0.027	0.979
Layer, Underground	19.544	± 618.279	0.032	0.975
Layer, Understory	14.245	± 618.278	0.023	0.982
Cycle, Night time	-0.545	± 0.187	-2.920	0.004*
Season, Dry	-3.726	± 1.179	-3.159	0.002*
Season, Rainy	-3.507	± 0.539	-6.508	< 0.001*
(Intercept)	7.775	± 0.983	7.907	< 0.001*
Ambient humidity	-0.028	± 0.015	-1.835	0.066
Ambient temperature	-0.146	± 0.025	-5.739	< 0.001*
Relative humidity on ground	-0.049	± 0.017	-2.875	0.004*

* is significance value of p <.05

Sheltering behavior was more often observed at the WA sites (β = 2.815 ± 0.685, z = 4.108, p < 0.001; $mR^2 = 0.576$, $cR^2 = 0.680$), and less frequently during nighttime than daytime (β = -0.545 ± 0.187, z = -2.920, p < 0.001; $mR^2 = 0.576$, cR^2 =

0.680) and during the dry (β = -3.726 ± 1.179, z = -3.159, p = 0.002; mR^2 = 0.576, cR^2 = 0.680) and rainy seasons (β = -3.507 ± 0.539, z = -6.508 p < 0.001; mR^2 = 0.576, cR^2 = 0.680). Sheltering behavior was significantly more prevalent when the ambient temperature was lower (β = -0.146 ± 0.025, z = -5.739, p < 0.001; mR^2 = 0.576, cR^2 = 0.680) and the ground was less humid (β = -0.049 ± 0.017, z = -2.875, p = 0.004; mR^2 = 0.576, cR^2 = 0.680; Table 3.11; Figure 3.15).

3.5 Discussion

These results indicate that these species does not appear to be significantly affected by low level human disturbance, nor habitat association, as individuals from both study areas had similar body condition and behaviors. Home-range sizes were, although not significantly slightly smaller for forest snakes and for water associated *T. macrops*. When 2 *T. macrops* were selected at random and comparing the mean MCP home range size to *T. vogeli*, the *T. macrops* MCP home ranges were not significantly smaller, but the pattern showed a very clear pattern that may be elucidated with a larger sample size. A slightly higher proportion of sheltering behaviors and lower proportion of daily displacements in field station individuals compared to forest snakes, as well as longer stationary periods and less moving days was observed, although none were significant. These results might be partially explained by the higher proportion of fixes during the cold season for the low impact study area. However, as this species' defense mechanism is cryptic behavior, it is likely that they would move less when there are more potential disturbances in the area. More successful predations, or higher prey abundance, may also have led to higher inactivity periods and reduced ambush observations in highly disturbed areas, as home-range size may be correlated to prey abundance (Hoss *et al.*, 2010).

The results confirmed *T. macrops* as a highly nocturnal ambush predator. Movement pattern was largely sedentary with very short moves between relocations, similar to other ambush-hunting vipers (*Bothrops asper*; Wasko and Sasa, 2009). Individuals tended to choose higher perch sites for their daytime resting sites, likely to avoid predation, and then moved short distances into more exposed areas during the night for their nocturnal ambush sites. Mostly, *T. macrops* females chose thin branches in the ground story (68 out of 184 ambush observations) and although we observed one instance of diurnal ambush behavior, it was likely an atypical observation.

Higher humidity led to higher ambush opportunities, as prey items are likely to be more active and abundant during higher humidity. Movement, aside from small scale shifts from shelter to ambush sites, was rare and mostly limited to nighttime and cooler temperatures. Although the ambient temperature reached a maximum of 39.4°C, we only observed movement below 31.2°C, and even that instance was with a snake basking in full sun within 3 meters of a human settlement. And while the lowest value recorded was 12.8°C, we did not observe any movement below 23.2°C.

Unlike another ambush cryptic pit viper (*i.e. B. asper*; Wasko and Sasa, 2009), *T. macrops* did not avoid heavily disturbed areas with reduced canopy and ground cover. Field station individuals used these disturbed areas, even when their more typical perch sites (*i.e.* branches, vegetation complexes, fallen logs) were unavailable, selecting man-made structures instead. During the cold season (with lower temperatures and lower humidity), snakes were under cover for long periods of time; selecting hollow logs, crevices under rocks and even man-made structures as shelters.

Body size did not influence home range sizes in *T. macrops*, even though it has been shown to have an effect on home ranges of other snake species (Whitaker and Shine, 2003; Roth, 2005). Individuals within the field station had on average larger home ranges, which may suggest an effect of human disturbance on space use, but no specific pattern. These results are likely due to individual variation and the small sample size available for analysis. However, proximity to human settlements likely has the same effect as edges: facilitating thermoregulation since they provide access to open sunny areas which increased body temperature, and shaded areas that decreased body temperatures (Carfagno and Weatherhead, 2006).

Home-range sizes for *T. macrops* were also significantly smaller when compared with other pit vipers of similar size: *Crotalus viridis* had an MCP home range of 8.0 ha (Macartney, 1985), *C. horridus* had 27.4 ha (Reinert and Zappalorti, 1988), *B. asper* had 5.95 ha (Wasko and Sasa, 2009), and even the smallest viper, *Bitis schneideri*, had a home range of 0.10 ha for adult females (Maritz and Alexander, 2012).

However, MCP does not take into account the number of occurrences (*i.e.* highly versus rarely used areas) or allow areas outside of the polygon to be included in the activity area. It also significantly overestimates the area used by an individual (Reed and Douglas, 2002), causing bias for small sample sizes (Nilsen *et al.*, 2008). *T. macrops* in the study remained in the same areas for long periods of time with little to no movement, so both MCP and kernel estimates included large areas of unused space. Kernel methods usually produce larger estimates than polygons, as their probabilistic contours may extend beyond the polygon boundaries. As such, and taking into consideration their foraging strategy, small home ranges and low frequency of movement, we believe both methods are not a biologically meaningful estimate of spatial use for *T. macrops*. Recent research as also suggested that this method is not an accurate measure for home range sizes in reptiles due to their sedentary nature (Row and Blouin-Demers, 2006).

Home-range overlap was not significant, core area overlap especially was very limited. We observed 42 instances of proximity between tracked snakes (within less than 5 meters of each other), although the individuals did not interact directly.

3.6 Conclusion

Although when accounting for number of fixes movement patterns and home range sizes do not differ between *T. macrops* from different sites, behavioral patterns are slightly different between the sites, as water associated sites are areas where prey congregate, it is a logical conclusion, that *T. macrops* spend more time foraging in sites that will have high anuran prey abundances, because they are thought to be anurophagus (Cox *et al*., 2012).

As any reliable conclusions on spatial ecology require large sample sizes (Kernohan *et al.*, 2001), thus these results can only provide preliminary data on this group of species. In addition, these data are primarily based on the active seasons between May-July and Oct-Dec, thus they do not represent the full seasonal cycle of GPV. Further study is warranted into comparing sympatric deep forest *T. macrops* with *T. vogeli*, because although sample sizes were extremely small, different movement patterns were visible, which may become more evident with a larger sample size, and thus be incorporated into a large body of theory into the theory of niche partitioning, or prematurely as vertical stratification.

However the continuing use of moderately human-disturbed areas indicates a tolerance for human presence for *T. macrops* females. However, the area selected as moderately disturbed is still a protected environment where non-destructive research and education takes place, and we should not extrapolate these conclusions to all other disturbed environments. Further studies on habitat utilization and selection for both male and female *T. macrops* are necessary, and how this selection relates to prey availability between highly disturbed areas and low impact forested areas also requires more investigation.

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CHAPTER IV

GREEN PIT VIPER MORPHOMETRICS

4.1 Abstract

Body size for vipers is normally biased toward large males and smaller females. Sexual dimorphism in adult and sub-adult Green Pit Vipers was evaluated, primarily in (*Trimeresurus macrops*) which is a small, arboreal Green Pit Viper commonly found in Southeast Asia, but severely understudied. Morphological characters of 139 adult *T. macrops* (3 female *T. vogeli* and 3 female *T. albolabris*) obtained by active and opportunistic searches were compared. External characters (N=7) including residual index (R_i) and scaled mass index (SMI) between male and female *T. macrops* were evaluated. Body length measurements and mass were different between males and female *T. macrops*. Females had greater snout-vent length, body mass and head length and width, while males had greater tail lengths. A postocular stripe was always present on males, but never on female *T. macrops*. Male head size in *T. macrops* was negatively correlated with body condition (SMI), which may reveal intersexual competition in *T. macrops*. Sexually dimorphic characters in *T. macrops* may have evolved through intraspecific resource partitioning, which may be an indicator of further partitioning among the GPV species present in Sakaerat based on the differences found in *T. albolabris* and *T. macrops*.

4.2 Introduction

Snakes are unique among reptiles in that they typically swallow their prey items whole, in fact snakes take prey items very large relative to their own size using the adaptation of a highly mobile quadrate bone that articulates as opposed to being directly fused to the skull (Cundall and Greene, 2000; Vincent *et al.*, 2006). Thus body size and structure influence snake diet and overall niche breadth, for example maximum gape can predict the maximum prey size in certain snake species (King, 2002). Snakes frequently show ontogenetic, sexual, geographic, and congeneric dimorphism among body measurements (Forsman, 1991; Shine, 1991; King, 1997; King *et al.*, 1999).

In some cases the larger heads lead to improved fitness, which is perhaps explained by the ability to swallow larger prey and thus allocate more resources toward growth, storage and reproduction (Forsman *et al.*, 1993), as is the case in European adders (*Vipera berus*). As body size increases, prey size typically increases proportionately, however the pattern varies among species (Shine, 1991a; Arnold, 1993). Often times young snakes have larger heads relative to body size, to consume prey that would likely not otherwise be possible, because young snakes are already constrained by a small body size, with larger heads, a greater variety of prey items are available, especially when prey can be subdued through the use of venom (Gans, 1974; Greene, 1977; King, 2002).

In snake species, female-biased sexual size dimorphism (SSD) is recurrent in many lineages (e.g. Natricinae, Xenodontinae, Boidae, Scolecophidia), but only the Viperidae family is characterized by nearly universal-biased SSD (Cox *et al.*, 2007). Male-biased SSD is especially prevalent in viperid species which display male-male combat behaviour, as it is one of the selective pressures leading to larger body length and mass in males (Shine, 1978). However, male-biased SSD is not ubiquitous and some species follow the common pattern of females being the larger sex, despite also displaying ritualized male-male combat behaviour (i.e. *Calloselasma rhodostoma*; York, 1984; Strine *et al*., 2015).

While male-biased SSD may offer individual fitness advantages based on the ability to out-compete other males and gain access to females (Shine, 1978), female-biased SSD may also result in reproductive advantages, such as greater fecundity (King, 2000) and larger clutch sizes for larger females (Seigel and Ford, 1987; Shine, 1993; Manjarrez et al., 2014). In addition, larger females are often able to produce larger offspring, which are in better body condition at birth and therefore have a higher chance of surviving to a reproductive age (Bronikowski, 2000; Kissner and Weatherhead, 2005; Manjarrez *et al*., 2014). For males, it also seems to be beneficial to mature earlier at the cost of a smaller size (Bronikowski, 2000; Sparkman *et al*., 2007).

Head size and head shape can also be dimorphic among male and female snakes, which may relate to resource or even diet partitioning (Houston and Shine, 1993; Pearson *et al*., 2002; Manjarrez *et al*., 2014). The role of SSD in resource partitioning has attracted great attention, with reproductive success in fecundity and parturition (Andersson, 1994; Manjarrez *et al*., 2014), as well as dietary intake (Cox, *et al*., 2008), being considered the strongest drivers of SSD. As snakes swallow prey whole, and are therefore gape limited, the head size limits the prey size the snake is able to ingest (King, 2002; Shetty and Shine, 2002: Vincent *et al*., 2004). Females should theoretically be able to capture and ingest larger prey than conspecific males with smaller heads, as well as eat less frequently since vipers are low energy specialists (Shine, 1991, 1993; Pearson *et al*., 2002; Shine and Sun, 2003).

The morphological differences may allow females and males to occupy separate ecological niches, influencing their food requirements and reducing intersexual resource competition (Shine, 1991, 1993; Houston and Shine, 1993, Pearson *et al*., 2002; Manjarrez *et al*., 2014). This could be particularly significant in the tropics, where niche breadth among taxa is typically narrower than in temperate communities (Krasnov *et al*., 2008). This narrower niche breadth leads to an increased extinction risk (Slatyer *et al*., 2013), and is therefore critical to assess the influence of SSD on trophic ecology and specifically on body condition (Madsen, 2011; Manjarrez *et al*., 2014).

Green Pit Vipers (*Trimeresurus* spp.), a primarily tropical and sub-tropical pit viper group (sub-family Crotalinae), exhibit sexual dimorphism as well as considerable geographic variation in morphological characters, leading to frequent misidentifications. Vogel *et al*., (2014) claim that there are currently 46 accepted species within the genus, and describe new cryptic species in Sumatra.

Sexual dimorphism has been described in some species of Asiatic *Trimeresurus* species (Shine, 1994). Captive female *T. albolabris* were significantly heavier than males, but no differences in head shape were found (Herrel *et al*., 2011). Female *T. vogeli* captured in Laos and Cambodia had significantly shorter tails, larger heads, and reached overall larger body lengths than conspecific males (Malhotra *et al*., 2004). Initial studies on *T. stejnegeri stejnegeri* in Northern Taiwan documented it as a sexually dimorphic species (Tsai and Tu, 1998), though recent studies did not find any significant size differences between sexes (Tu and Lin, 2000; Creer *et al*., 2002). For *T. macrops*, one of the most common and widespread green pit vipers in central and northern Thailand, Cambodia and Laos (IUCN, 2014), very little detailed morphometric information is available.

In Sakaerat Environmental Research Station there are three confirmed species of GPV, The Big Eyed Pit Viper (*Trimeresurus macrops*), the White Lipped Pit Viper (*Trimeresurus albolabris*), and the Vogel's Pit Viper (*Trimeresurus vogeli*). *Trimeresurus macrops* is a small species of green pit viper, typically between 520-660 mm as adults, with a maximum total length of 720 mm in some rare cases (Das, 2010; Cox *et al*., 2012). The body is slender and cylindrical; with a narrow head very distinct from the neck (Kramer, 1977). Adults rarely exceed 100 g and range between 36–108 g (Cox *et al*., 2012). The tail accounts for 11-16% of the total length and is prehensile with a brown coloration.

The head is triangular with strongly keeled temporal scales distinguishing it from the White Lipped Pit Viper and the Vogel's Pit Viper; however the first labial is either partially fused or entirely fused with the nasal (Das, 2010). Dorsally, this species has a pale green coloration with the chin and the gular region bluish, and blue and black interstitial bands. The eyes are large and males typically display a white postocular stripe, which is absent in females (Kramer, 1977). Green Pit Vipers are considered an arboreal and nocturnal, setting up ambush sites at dusk and moving to shelter sites near dawn (Chanhome *et al*., 2011).

Most of the literature on Green Pit Vipers is limited to the toxic effects of venoms and post-bite treatment. Soogarun *et al*. (2006) stated that *T. albolabris and T. macrops*, the two pit vipers most likely to be found in disturbed areas, had biting rates increase by 76% since 1977. *Trimeresurus albolabris* and *T. macrops* (1.7:1

envenomations) are the only Green Pit Vipers present in Bangkok, and 90% of bites from these species were classified as mild envenomations, with only bites from *T. albolabris* classified as severe (Mahasandana and Jintakune, 1990). Hospital records in Wang Nam Khiao and Pak Thong Chai districts indicate that Green Pit Vipers were responsible for 44 of the 141 (31.2%) serious hospitalizations from snakebite between 2011 and 2014 in the region. Because this group is responsible for a large proportion of bites, it is also important to assess how their biometrics may influence their basic ecology.

The goals of this study were to: 1) assess sexual dimorphism mature *T. macrops* using various morphometric characters, including body mass, body and tail length, as well as head measurements, and the presence or absence of a postocular stripe. 2) Examine the morphological variation between female individuals of the three sympatric species found in SERS. Because morphological variation is often an indicator of diet or niche partitioning (Temeles *et al.*, 2010), it is important to understand the morphometric variations in potential model organisms such as GPV, which are arguably the most commonly encountered snake species in Northeastern Thailand.

4.3 Methods

4.3.1 Study site

This study was conducted in Dry Evergreen Forest (DEF) and Mixed Deciduous Forest patches at Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Thailand (14.44–14.55°N, 101.88–101.95°E). SBR has a core area of approximately 80 km^2 and a further 360 km^2 comprising buffer and transitional zones. The protected area ranges in elevation from 280 to 762 m and is comprised of a patchy matrix of contiguous vegetation associations. Greater than 60% of the protected area is classed as DEF (for map see Chapter 2 and 3), which is characterized by closed canopy multi-story forest dominated by robust evergreen tree species such as *Hopea adorata* and *H. ferrea*). Dry Dipterocarp Forest makes up approximately 18% of the total core area and is an open canopy ecotype with a dense understory of *Bamboo* grasses and fire resistant dipterocarpaceae trees, such as *Shorea siamensis* and *S. obtusa*.

4.3.2 Capture information

Various sampling methods (See Chapter 5 for details) resulted in *T. macrops* 220 times, including recaptures, between May 2012 and August of 2014. All recaptures from analyses (*n* = 80) were excluded, using only the most recent capture for morphometric analysis as opposed to the initial capture, resulting in 160 individual *T. macrops*. All juvenile and neonate captures were excluded from dimorphism analyses (*n* = 29) and an additional an 11 individuals were removed due to erroneously measured base characteristics. Snakes were captured snakes via opportunistic captures and active time-area constrained surveys, where we searched four 100 x 100 m selected sites in the evergreen and mixed deciduous forest patches of SERS. Additional individuals were captured either opportunistically, or through a drift fence trapping program, which ran only from May 2012 to August 2013.

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4.3.3 Laboratory techniques

Prior to measuring biometrics, snakes were anesthetized in transparent plastic tubes with vaporized Isoflurane anesthesia. Anesthetic measurements are preferred to traditional methods such as the squeeze box, as the measurement process is less stressful and both precision and accuracy are greater when measuring anesthetized snakes (Setser, 2007).

After complete body tone loss, all individuals of all species were measured on a semicircular custom made measuring pipe from the tip of the snout to the posterior tip of the anal scale, commonly defined as snout-venter length (SVL in mm), and from the anterior tip of the first sub-caudal scale to the tip of the tail (tail length; TL in mm). Total body length (TBL in mm) was obtained by adding SVL and TL. For TBL, SVL, TL, mass and body condition, we used all 120 individuals. However, for head length (HL in mm) and head width (HW in mm), The analysis only include 74 individuals, because before October 2013 individuals heads were measured with a different method manually using string, only later obtaining hand held digital calipers, which has lower accuracy. Therefore, all head measurements before October 2013 were not comparable.

Body mass was measured (g) using a digital scale. Sex was determined by inserting a probe into the cloaca and gently easing it into one of the cavities at the base of the tail and recording the distance the probe travelled in number of sub-caudal scales. In females, it was possible to pass the probe back only as far as the musk glands, which lie beneath the first one or two sub-caudal scales, while in males the probe could extend to at least the ninth sub-caudal scale. Each captured individual was given a unique mark (Figure 4.1) with a Bovie ™ cauterizing unit for future identification following Winne *et al*. (2006). Pictures of every individual's body, head, ventrals, sub-caudal scales, tail, brand and any other identifying characteristics such as scars were taken to aid in future identification (Figure 4.2).

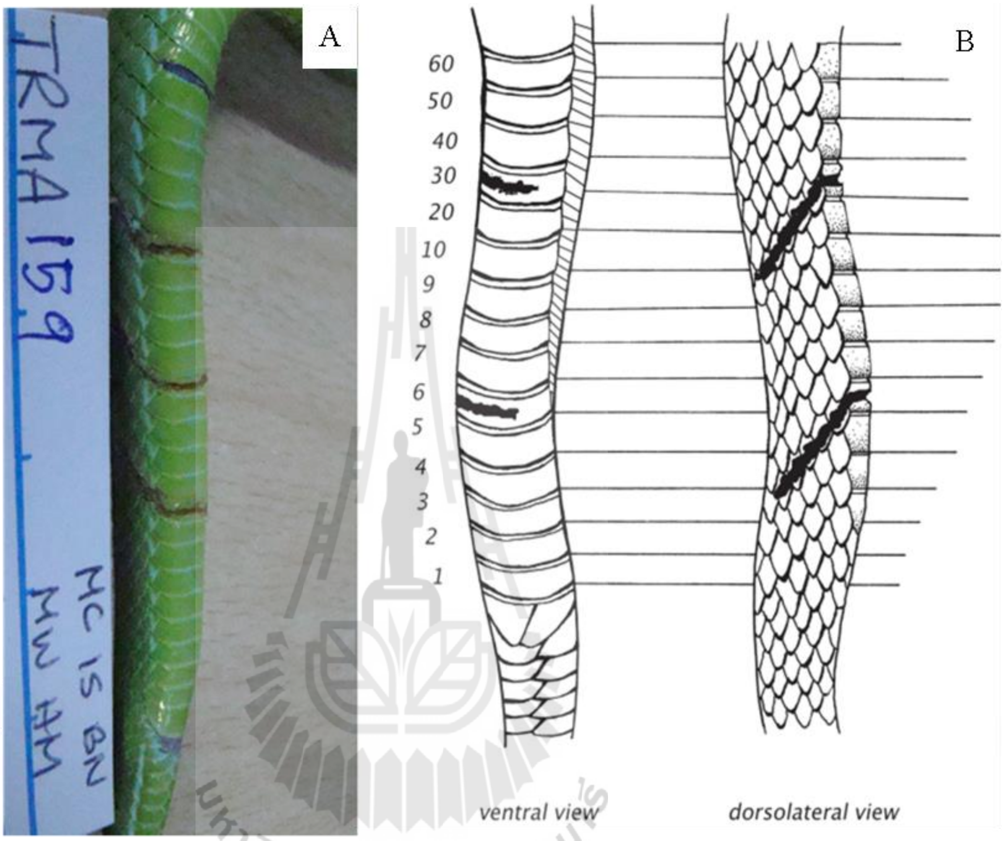

Figure 4.1 Unique marking scheme for snakes, showing the branding system on individual TRMA 159 (A) and the artistic rendition (B) of the numerical system (Winne *et al*., 2006).

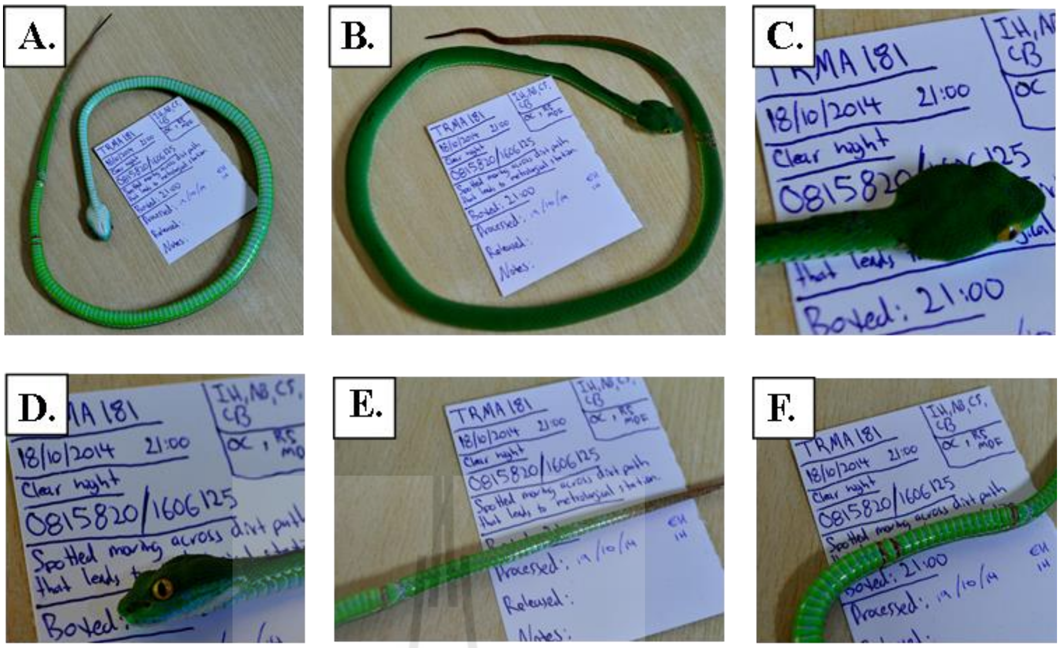

Figure 4.2 Photographic records post processing of individual *T. macrops* number 181.

4.3.4 Data analysis for sexual dimorphism in *T. macrops*

For *T. macrops*, individuals of both sexes greater than 450 mm TBL were considered to be sexually mature, based on the smallest gravid female captured during the study period in SERS. Neonates and juveniles were excluded from the analyses (*n* = 39) as they might confound the SSD patterns present in adults, while pseudoreplication was eliminated by excluding recaptures.

Body condition was calculated using residuals from a linear regression of log-transformed mass and SVL (Body Condition Index (BCI); Bonnet and Naulleau, 1994), and scaled mass index (SMI; Peig and Green, 2009). Scaled Mass Index adjusts the mass of all individuals as if they had the same body size and, unlike most residual indices, can be readily compared across populations (Labocha *et al*., 2014).

To test for dimorphism between male and female *T. macrops* the mean values for each variable were compared by applying linear or generalized linear models (G/LM), using sex as a predictor and mean SVL, TL, TBL, mass, body condition indexes, and head measurements (HL, HW) as dependent variables. Each variable for normality, homoscedasticity and independence and fitted the appropriate family (Gaussian for SVL, HL, HW, BCI; log-normal for TBL, TL, mass, SMI). All models using residuals and standardized residuals versus fitted and predicted values by Cook's distances. Akaike's Information Criterion (AIC, Akaike, 1974) was used to compare each model with and without the categorical variable "sex".

To separate variability in SVL within male and female *T. macrops* from intersexual differences, we conducted an ANCOVA using HL or HW as main factors and SVL as a covariate to control for the differences in body length (Fabien *et al*., 2004). Pearson correlations were used to explore the relationships between TL and TBL in both sexes, as well as between both head measurements and SMI, which were confirmed using tests for association between paired samples.

All statistical calculations using R statistical software version 3.0.2 (R-Development Core Team, 2013) and significance level was set at p <0.05. All descriptive statistics reported as means ± standard deviation.

4.3.5 Analysis of daily growth rates for adult and juvenile *T. macrops*

Daily growth rates (DGR) for 21 individual *T. macrops* recapture events from 01/05/2013 to 27/10/2014 were assessed. Multiple recaptures of the same individuals were excluded from analysis along with individuals recaptured in less than 30 days and greater than 250 days apart (range 18-247). Daily and weekly growth rates for SVL, TL, and TBL were not normally distributed and therefore the Mann-Whitney test was used to compare mean growth rates between adult males and adult females (*n* = 8 and *n* = 7 respectively) and between juveniles (*n* = 14) and adults (*n* = 15).

4.3.6 Data analysis for morphometric variation between *Trimeresurus* spp.

In order to compare the species, a random sample of *T. macrops* from the total population of 197 captured individuals was selected using the random number generator function in program R (R-Development Core Team, 2013) to match the extremely limited sample size of 3 *T. vogeli* for body measurements, and 2 *T. albolabris* because the prior individuals were caught before October 2013 and head measurement technique differed between years.

To test for morphometric variation between female *T. macrops, T. vogeli,* and *T. albolabris* the mean values for each variable were compared using the non-parametric Kruskall-Wallis Chi squared test using species as the predictor and mean SVL, TL, TBL, mass, and head measurements (HL, HW) as the test variable. Each variable for normality, homoscedasticity and independence and fitted the appropriate family (Non-parametric).

The body condition indices of SMI and Residual index were not compared between species because the sample sizes were too small to generate reliable base population means for *T. vogeli* and *T. albolabris,* in comparison to *T. macrops*.

4.4 Results

4.4.1 *Trimeresurus macrops* sexual dimorphism

Trimeresurus macrops were captured 270 times (73 recaptures) for a total of 97 snakes (including unmarked individuals). After removing measurements from the first captures of recaptured snakes, juvenile and neonate snakes (n = 43), and 15 erroneously measured snakes, the sample size for our analyses was 139 individuals. In general males were more slender and elongate than females (Figure 4.3; Figure 4.4), and all adult and sub-adult males (n = 61) displayed a postocular stripe (Figure, 4.4), which was absent on all sub-adult and adult females (n = 78). For HL and HW we removed all individuals measured without digital calipers (n = 36) prior to October 2013 with an additional 9 snakes removed due to erroneous measurement for a total of 42 males and 51 females (n = 93).

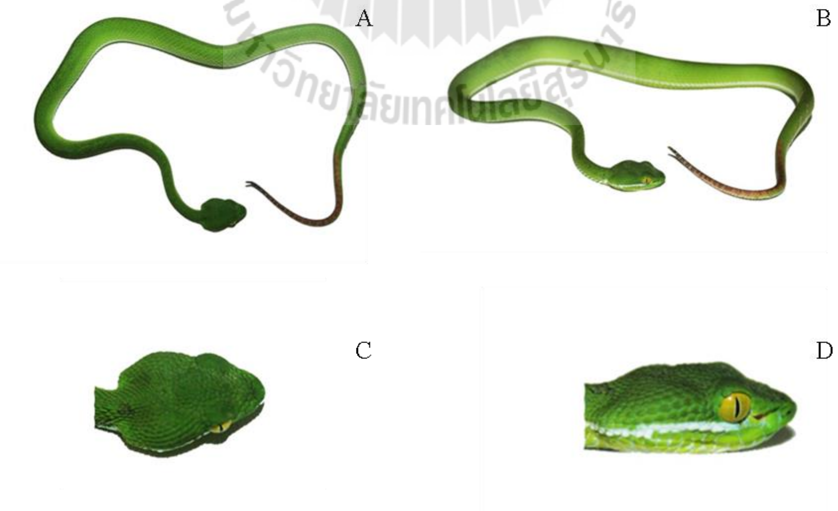

Figure 4.3 Male *T. macrops* body structure from above (A) and side (B) and head structure from above (C) and from the side (D) displaying the clear postocular stripe. Photo credit: Andrew Brown.

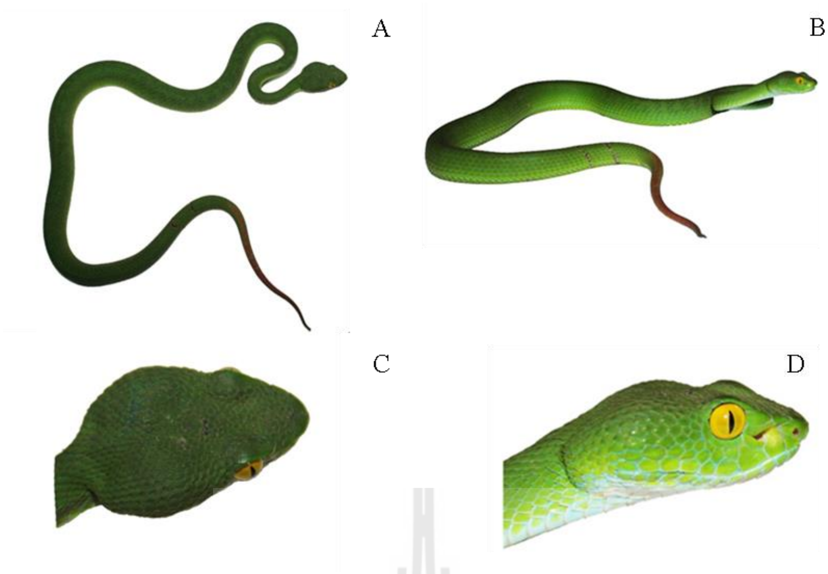

Figure 4.4 Female *T. macrops* body structure from above (A) and side (B) and head structure from above (C) and from the side (D). Displaying branding technique. Photo credit: Andrew Brown.

Model parsimony results for all external characters as well as R_i and SMI using AICc are presented in Table 4.1 . Total body length was significantly greater in females than males (GLM: β = –27.08 ± 11.63; t = –2.328, p = 0.021; Figure 4.5A; Table 4.1), Mean SVL was significantly higher in females than males (β = –47.76 ± 10.23; t = –4.667, $p < 0.001$; Figure 4.5B, Table 4.1), and males attained longer TL (17.6%) than females (β = 0.194 ± 0.037; t = 5.265, $p < 0.001$; Figure 4.5C, Table 4.1).

Body mass was also significantly greater in females (32.1%) than males (β = –0.389 ± 0.065; t = –5.939, p = 0.001, Figure 4.5D, Table 4.1), even after removing gravid females (n = 21; β = –0.301 ± 0.062; t = –4.865, $p < 0.001$). Significant differences between sexes for R_i (β = –0.126 ± 0.035; t = –3.558, p < 0.001; Table 4.1) but not for SMI (β = –0.126 ± 0.035; t = –3.558, $p < 0.001$; Table

4.1), and even after removing gravid females both results showed the same pattern (R_i: β = –0.080 ± 0.034; t = –2.365, p = 0.020; SMI: β = 0.020 ± 0.042; t = 0.439, p = 0.661). Body mass was also significantly greater in females (32.1%) than males (β = –0.389 ± 0.065; t = –5.939, p = 0.001, Figure 2D, Table 4.2), even after removing gravid females (n = 21; β = –0.301 ± 0.062; t = –4.865, p < 0.001).

Significant differences were detected between sexes for R_i (β = –0.126 ± 0.035; t = –3.558, p < 0.001; Table 4.2) but not for SMI (β = –0.126 ± 0.035; t = –3.558, p < 0.001; Table 4.1), and even after removing gravid females both results showed the same pattern (R_i: β = –0.080 ± 0.034; t = –2.365, p = 0.020; SMI: β = 0.020 ± 0.042; t = 0.439, p = 0.661).

Table 4.1 Model selection results for predicting body length, head measurements and body conditions indexes. Models are ranked by AICc differences (ΔAICc). K: number of parameters, ω: AICc weight, LL: log-likelihood.

Variables	Rank	Model	K	AICc	ΔAICc	w	LL
Total body length (mm)	1	TBL ~ Sex	3	1571.9	0.0	0.8	–782.9
	2	TBL ~ 1	2	1575.2	3.3	0.2	–785.6
Snout–vent length (mm)	1	SVL ~ Sex	3	1536.3	0.0	1.0	–765.1
	2	SVL ~ 1	2	1554.7	18.4	0.0	–775.3
Tail length (mm)	1	TL ~ Sex	3	1270.3	0.0	1.0	–632.1
	2	TL ~ 1	2	1293.8	23.5	0.0	–644.9
Body weight (g)	1	Mass ~ Sex	3	1124.5	0.0	1.0	–559.1
	2	Mass ~ 1	2	1158.1	33.7	0.0	–577.0
Head length (mm)	1	HL ~ Sex	3	418.2	0.0	1.0	–206.0
	2	HL ~ 1	2	472.7	54.6	0.0	–234.3
Head width (mm)	1	HW ~ Sex	3	367.6	0.0	1.0	–180.7
	2	HW ~ 1	2	415.5	47.8	0.0	–205.7
Residual index (R_i)	2	R_i ~ Sex	3	–40.0	0.0	1.0	23.1
	1	R_i ~ 1	2	–29.8	10.2	0.0	16.9
Scaled mass index (SMI)	1	SMI ~ 1	2	993.9	0.0	0.6	–494.9
	2	SMI ~ Sex	3	995.0	1.0	0.4	–494.4

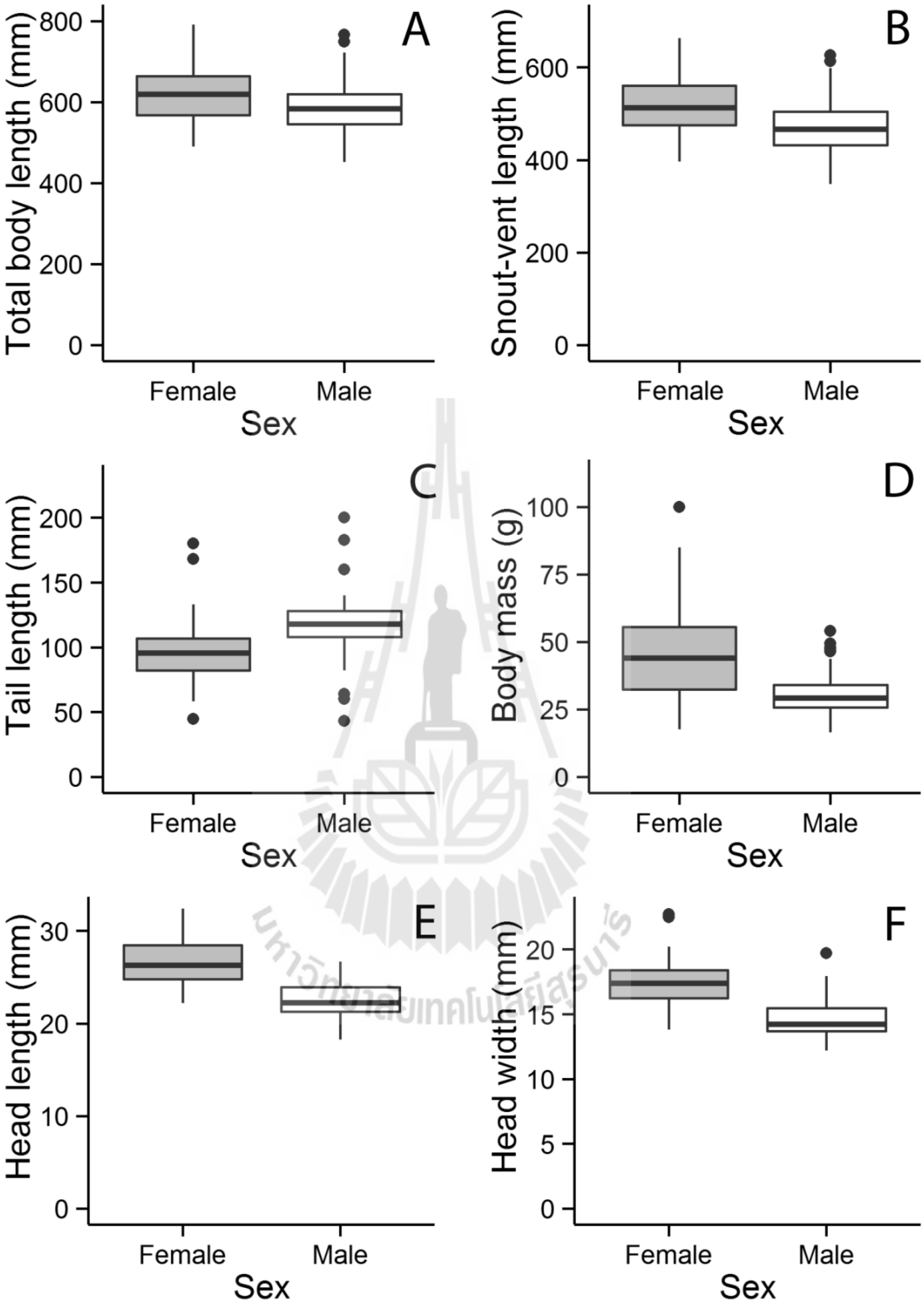

Figure 4.5 Dimorphic characters total body length (A), snout to vent length (B), tail length (C), body mass (D), head length E, and head width (F) of adult *T. macrops* captured at SERS between March 2012 and February 2015.

Both HL (β = –4.080 ± 0.467, t = –8.740, $p < 0.001$; Figure 45E, Table 4.2) and HW (β = –2.862 ± 0.356, t = –8.046, $p < 0.001$; Figure 4.5F, Table 4.2) were significantly higher (15.1%, 16.1%) in females (n = 51) than males (n = 42).

Sexual differences were also significant when HL and HW measurements were adjusted for SVL; for any given SVL, females had larger HL (ANCOVA: $F_{1,90}$ = 32.4; $p < 0.001$; Figure 4.6A) and HW ($F_{1,90}$ = 22.3, $p < 0.001$; Figure 4.6B) than males. Pearson's coefficient showed significant negative correlations between TBL and SMI for both females (test for association of paired samples: r_{76} = –0.250, t = –2.253, p = 0.027) and males (r_{59} = –0.637, t = –6.345, $p < 0.001$). We also found positive correlations between HL/HW and SVL in both females (HL: r_{49} = 0.725, t = 7.362, $p < 0.001$, Figure 4.6A; HW: r_{49} = 0.658, t = 6.117, $p < 0.001$, Figure 3B) and males (HL: r_{40} = –0.913, t = 14.199, $p < 0.001$, Figure 4.6A; HW: r_{40} = 0.655, t = 5.487, $p < 0.001$, Figure 4.6B). We found a significant positive correlation between SMI and HW in females only (r_{49} = 0.284, t = 2.073, p = 0.043; Figure 4.6B) not between SMI and HL (r_{49} = 0.206, t = 1.476, p = 0.147; Figure 4.6A).

Table 4.2 Measurements for female and male adult *T. macrops*, as well as both body condition indexes (R_i and SMI) and the parameters, coefficients and estimates (β) for all final models used to predict these variables.

Set	**Sex**	***n***	**Mean ± SD**	**Min**	**Max**	**Coefficients**	**Estimate**	**SE**	***t***	***P***
TBL (mm)	F	78	616.4 ± 70.0	490	791	(Intercept)	616.4	7.7	79.979	< 0.01
	M	61	589.3 ± 65.0	452	766	SexM	-27.1	11.6	-2.328	**0.021**
SVL (mm)	F	78	519.9 ± 59.1	396	663	(Intercept)	519.9	6.8	76.684	< 0.01
	M	61	472.1 ± 59.8	348	626	SexM	-47.8	10.2	-4.667	**< 0.01**
TL (mm)	F	78	96.5 ± 21.7	44.6	180	(Intercept)	4.6	0	169.27	< 0.01
	M	61	117.2 ± 24.2	43	200	SEXM	0.2	0	5.265	**< 0.01**
Mass (g)	F	78	45.8 ± 16.6	17.5	100	(Intercept)	3.8	0	113.65	< 0.01
	M	61	31.1 ± 8.0	16.5	54.1	SexM	-0.4	0.1	-5.939	**< 0.01**
HL (mm)	F	51	26.5 ± 2.5	22.2	32.4	(Intercept)	26.5	0.3	84.59	< 0.01
	M	42	22.5 ± 1.9	18.2	26.7	SexM	-4.1	0.5	-8.74	**< 0.01**
HW (mm)	F	51	17.4 ± 1.9	13.8	22.7	(Intercept)	17.4	0.2	72.991	< 0.01
	M	42	14.6 ± 1.5	12.2	19.7	SexM	-2.9	0.4	-8.046	**< 0.01**
Residual index (R_i)	F	78	-0.07 ± 0.19	-0.53	0.63	(Intercept)	0.1	0	2.357	0.02
	M	61	0.06 ± 0.22	-0.63	0.39	SexM	-0.1	0	-3.558	**0.01**
Scaled mass index (SMI)	F	78	37.4 ± 8.5	17.1	68.3	(Intercept)	3.6	0	140.26	< 0.01
	M	61	36.0 ± 8.5	15.8	69.3	SexM	0	0	-1.018	0.31

SD: standard deviation, Min: minimal value measured, Max: maximal value measured, n: sample size. SE: standard error.

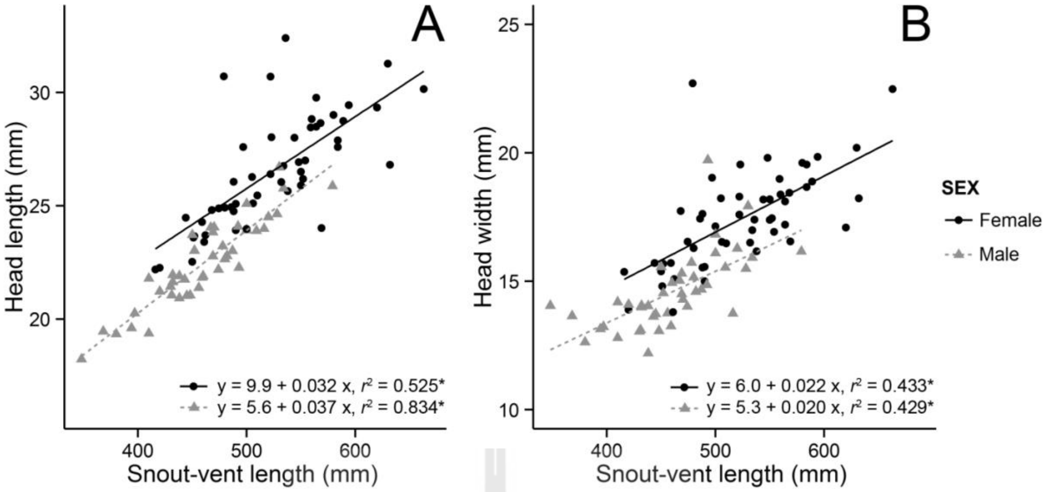

Figure 4.6 The relationship between SVL and HL (A) of male (*n* = 42) and female (*n* = 51), and between SVL and HW (B) of male (*n* = 42) and female (*n* = 51) *T. macrops*. Linear regression fits and associated r^2 values are displayed in each sub-figure

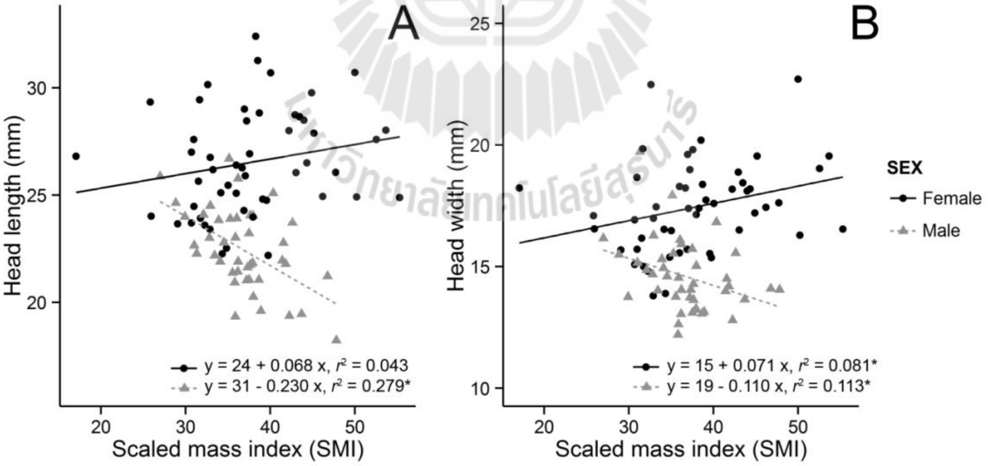

Figure 4.7 The relationship between SMI and HL (A) of male (*n* = 42) and female (*n* = 51), and between SMI and HW (B) of male (*n* = 42) and female (*n* = 51) *T. macrops*.

Males with either longer HL or HW had poorer body conditions than males with smaller heads (HL: $r_{40} = -0.528$, $t = -3.936$, $p < 0.001$, Figure 4.4A; HW: $r_{40} = -0.336$, $t = -2.257$, $p = 0.030$, Figure 4.3B).

A significant positive correlation between this R_i and both HL ($r_{49} = 0.324$, $t = 2.398$, $P = 0.020$) and HW in females ($r_{49} = 0.407$, $t = 3.123$, $p = 0.003$) was detected, but no significant correlations in males (HL: $r_{40} = -0.208$, $t = -1.345$, $p = 0.186$; HW: $r_{40} = -0.067$, $t = -0.427$, $p = 0.671$) were detected. Table 4.3 displays the slope, intercept, r^2, and sample sizes for all correlations between TL/SVL, HL/SVL, HW/SVL, HL/SMI, HW/SMI for males and females.

Table 4.3 Slope (*m*), intercept (*b*), coefficient of determination (r^2) and sample size (*n*) for the standardized major axes of the relationship for all correlations between female (F) and male (M) adult *T. macrops*.

	TBL vs SMI		**HL vs SVL**		**HW vs SVL**		**HL vs SMI**		**HW vs SMI**	
	F	M	F	M	F	M	F	M	F	M
n	78	61	51	42	51	42	51	42	51	42
m	-0.03	-0.08	0.03	0.04	0.02	0.02	0.07	-0.23	0.07	-0.11
b	56	85	9.9	5.6	6	5.3	24	31	15	19
r^2	0.063	0.406	0.525	0.834	0.433	0.429	0.043	0.279	0.081	0.113

4.4.2 Growth rates of juvenile and adult *T. macrops*, and comparison of growth rate among sexes

The mean DGR for adult male SVL, TL, and TBL were 0.138 mm/day, 0.094 mm/day, and 0.898 mm/day (= 0.120, 0.055, and 0.155 respectively). Adult females exhibited higher DGR means for SVL (0.426 mm/day $\sigma = 0.427$), TL (0.095 mm/day, σ = 0.063), and TBL (0.521 mm/day, σ = 0.481) than adult males; however, the results from the Mann-Whitney test revealed no significant difference in growth rates for SVL, TL, and TBL between adult males and females ($p = 0.3357$, $p = 0.5358$, and $p = 0.3357$).

Juveniles exhibited larger mean DGR values for SVL (μ = 1.034, σ=1.347), TL (μ = 0.122, σ = 0.147), and TBL (μ = 1.156, σ = 1.411) than adults (μ = 0.273,σ = 0.328; μ = 0.081 , σ=0.058; μ=0.058 , σ=0.354 SVL, TL, and TBL respectively). Despite differences in means, no significant difference in DGR was detected between juveniles and adult *T. macrops* for SVL ($p = 0.4389$), TL ($p = 1$), and TBL ($p = 0.4859$). The high variance in DGR within all groups suggests that the sample size may be too small to detect variation.

4.4.3 Morphometric characters between female *T. vogeli, T. macrops, and T. albolabris*

The mean morphometric character (Table 4.4, Table 4.5) for *T. albolabris* SVL (635.7 ± 195.2 mm), TVL(105 ± 39.5 mm) TBL (740.7 ± 228.9 mm), Mass(105.2 ± 83.1 g) HL (34.5 ± 12.0 mm) HW (24.0 ± 8.5 mm); *T. macrops* SVL (519.0 ± 52.0 mm), TVL (94.3 ± 23.0 mm), TBL (613.3 ± 74.6), Mass (39.5 ± 1.0 mm), HL (17.3 ± 1.4 mm), HW (26.4 ± 0.21 mm) and *T. vogeli* SVL (697.2 ± 48.0 mm), TVL (130.2 ± 9.9 mm), TBL (827.4 ± 57.8mm), Mass (38.3 ± 7.4 g), HL (25.7 ± 1.0) and HW (26.4 ± 0.21) were not significantly different.

Although the mean measured morphometric characters (Table 4.3), between the three species appeared different (Figure 4.8.) based on initial results none of the body size metrics between species ($n = 3$) SVL (Kruskal-Wallis = 2.7556, *df* = 2, *p* = 0.252), TVL (Kruskal-Wallis = 2.7556, *df* = 2, *p* = 0.252), TBL (Kruskal-Wallis = 2.7556, *df* = 2, *p* = 0.252), Mass (Kruskal-Wallis = 3.4667, *df* = 2, *p* = 0.1767), evaluated showed any statistical differences, nor did head size (n = 2) biometrics HL (Kruskal-Wallis = 2.0, *df* = 2, *p* = 0.3679), HW (Kruskal-Wallis = 2.0, *df* = 2, *p* = 0.3679).

Table 4.4 Mean body morphometrics for randomly selected female *T. macrops* and for the total population of captured *T. albolabris* and *T. vogeli*.

Body measurements	**Mean ± SE**	**Range**
Trimeresurus albolabris		
Snout-vent length (mm)	635.7 ± 195.2	419 – 798
Tail length (mm)	105 ± 39.5	76 – 150
Total body length (mm)	740.7 ± 228.9	495 – 948
Mass (g)	105.2 ± 83.1	30.5 – 194.7
Trimeresurus vogeli		
Snout-vent length (SVL) mm	697.2 ± 48.0	642 – 729
Tail length (TL) mm	130.2 ± 9.9	119 – 138
Total body length (mm)	827.4 ± 57.8	761 – 867
Mass (g)	97.9 ± 18.5	76.5 – 109.7
Trimeresurus macrops		
Snout-vent length (mm)	519.0 ± 52.0	459 – 552
Tail length (mm)	94.3 ± 23.0	69 – 114
Total body length (mm)	613.3 ± 74.6	528 – 666
Mass (g)	38.3 ± 7.4	29.8 – 42.7

Table 4.5 Reported mean head measurements for randomly selected *T. macrops* and the total population of captured female *T. vogeli*, and *T. albolabris*.

Head measurements	**Mean ± SE**	**Range**
Trimeresurus albolabris (*n* = 2)		
Head length (mm)	34.5 ± 12.0	26.0 – 43.0
Head width (mm)	24.0 ± 8.5	18.0 – 30.1
Trimeresurus vogeli (*n* = 2)		
Head length (mm)	39.5 ± 1.0	39.2 – 39.9
Head width (mm)	26.4 ± 0.21	16.3 – 18.3
Trimeresurus macrops (*n* = 2)		
Head length (mm)	25.7 ± 1.0	24.9 – 26.4
Head width (mm)	17.3 ± 1.4	26.2 – 26.5

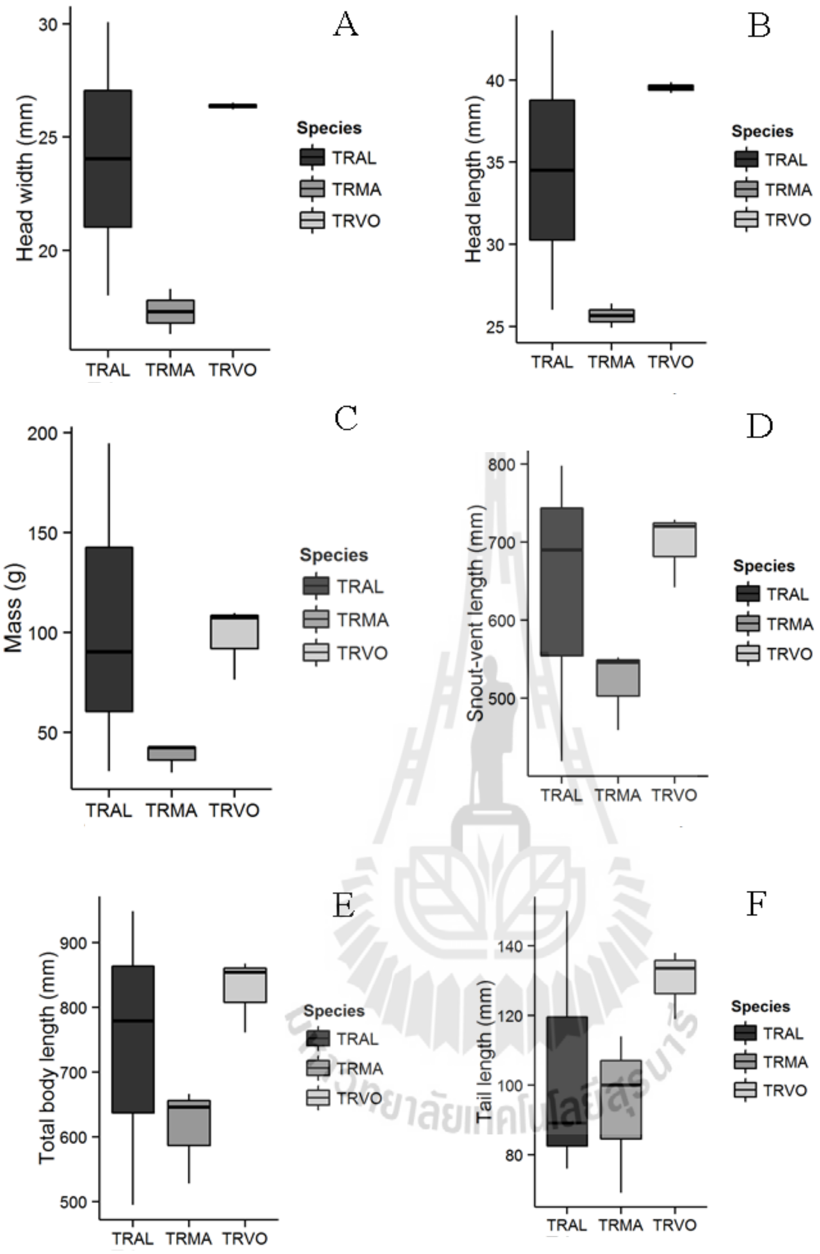

Figure 4.8 Comparisons of morphometrics: head length (A) head width (B), body mass (C), snout to vent length (D), total body length (E), and tail length (F), between *Trimeresurus macrops* (TRMA), *T. vogeli* (TRVO) and *T. albolabris* (TRAL) showing clear trends of *T. macrops* being in general smaller than congeners. The differences were non-significant.

4.5 Discussion

4.5.1 *Trimeresurus macrops* sexual dimorphism

Clear evidence of female-biased sexual dimorphism in *T. macrops* was displayed. Overall larger body size of females is consistent with other Green Pit Vipers with clear SSD, such as *T. vogeli* (Malhotra *et al.,* 2004), where females had larger heads, shorter tails but overall larger body length and mass than conspecific males. In addition males retain a white postocular stripe into adulthood, while in females the stripe fades within the first year as they reach reproductive maturity (as observed by our recaptures of neonates later in the season of 2013 in three individuals).

Female-biased SSD likely leads to increased fitness in larger females, since they can produce more and larger offspring with better body condition at birth. However, at least in *Vipera aspis*, the actual benefit appears to be a reduction in the costs of reproduction, and the ability to take larger prey (Bonnet *et al*., 2000). Offspring from larger females also have higher survival rates, due to a greater range of available prey items and better defensive capabilities (Rivas and Burghardt, 2001; Kissner and Weatherhead, 2005).

Smaller size in males is likely favored by natural selection because allocating resources to reproductive activities, and earlier maturity, rather than growth leads to higher fitness. Smaller size of males increases mobility to track females and reduces their vulnerability to predation (Rivas and Burghardt, 2001). In contrast, for nearly every species of colubrid, females mature later than males regardless of size, perhaps because they invest energy in fat reserves in preparation for reproduction

(Parker and Plummer, 1987). Large body size in males is usually only expected in the case of mating systems that favor physical strength (*i.e.* male-male combat behavior; Andersson, 1994), though not all species follow this pattern (York, 1984; Strine *et al*., 2015).

The larger TL in male *T. macrops* was expected due to the presence of the hemipenis contained within the tail base. Tail length is likely an indicator of sexual fitness: longer hemipenes lead to higher mating success rates (Shine *et al*., 1999). Regression slopes between head measurements were different for both sexes (Figure 3 and 4), indicating larger heads in females may not be simply an outcome of larger body sizes, but might instead be due to selective pressure towards resource partitioning, as is the case for divergent diet composition in male and female Australian Carpet Pythons (*Morelia spilota imbricata*; Pearson *et al*., 2002). If females are able to consume bigger prey items than males, both sexes can occupy different ecological niches and intersexual competition for food should be reduced (Pearson *et al*., 2002).

Body condition index R_i was significantly lower in males; however, SMI showed no difference between male and female body conditions, which we interpret to be more accurate following Peig and Greene (2009), as well as Labocha *et al*. (2014). Although we would expect females to have poorer body condition than males as they bear the majority of the reproductive costs (Baron *et al*., 2012), such as depletion of fat reserves while gravid, and thermoregulatory costs, which may increase predation risk, we saw no evidence of this trend. With the bearing of live young, female *T. macrops* are particularly susceptible to the increased reproductive costs, and, as arboreal snakes, the rapid gain in mass may hinder movement to optimal perch or foraging sites. In fact, *T. macrops* may display dimorphism in order to offset the costs of reproduction.

Although snakes have remarkably flexible jaws, they ingest prey whole and thus head size is still thought to limit optimal prey size; in fact, the maximum prey size is directly correlated with the head size (King, 2002). Female body condition as measured by R_i was positively correlated with both HL and HW. However, female SMI was correlated with HW only. Body condition is likely related to the snake's reproductive state, and might be more variable throughout the year in females than males (Naulleau and Bonnet, 1995; Aubret *et al*., 2002). While the female R_i showed a significantly positive correlation with head size, we again interpret SMI as a more accurate representation of body condition.

Both HW and HL correlation with SMI (Figure 4.) revealed that males with larger heads, had poorer body condition. Males with large heads overlap with female head sizes, which may potentially increase interspecific competition for prey of the optimal size (Shine, 1991; Shine, 1993; Houston and Shine, 1993; Pearson, *et al*., 2002; Manjarrez *et al*., 2014).

The potential of intraspecific niche partitioning to explain the findings warrants further research on the diet of both male and female *T. macrops* and may reveal further information on ecological mechanisms maintaining sexual size dimorphism in arboreal pit vipers. We have observed female *T. macrops* preying upon anurans, and small mammals, but because of their small size and cryptic behaviors, we have never recorded a male predation event. However, dimorphism in head size does not necessarily imply differences in consumed prey sizes (Manjarrez *et al*., 2014). Therefore, further work should determine whether or not males are taking different prey than females in nature, and if foraging success varies among the different sexes, by conducting studies on prey selection and consumption for *T. macrops* and other Green Pit Vipers.

Direct identification of prey items (particularly of anurophagus snakes) from examining the digestive tract is very difficult (Creer *et al*., 2002) and, in some cases, up to 46% of prey items are unidentifiable. In addition, the snake has to be killed, which reduces the opportunity to observe individual variations in diet. We suggest that the use of infrared cameras on ambush sites, similar to those used to monitor bird nest predations (Pierce and Pobprasert, 2007), may yield insight into the diet of ambush predators such as *T. macrops*.

4.5.2 Body structure between Green Pit Viper species

The mean measured morphometric characters (Table 4.3), between the three species appeared different (Figure 4.8.), with Vogel's pit vipers (*T. vogeli*) displaying the largest body and head sizes superficially, however no statistical analyses revealed any variation when species is used as a predictor (n = 3). The clarity of the patterns is confounded by the extremely small sample sizes for *T. vogeli*, and *T. albolabris*. Further sampling effort may elucidate morphological patterns in the two non-*macrops* species in Sakaerat. Although it would require substantial effort to obtain acceptable sample sizes for *T. vogeli*, and *T. albolabris* the potential rewards are vast. By understanding the morphometrics, spatial ecology, and trophic ecology of SERS Green Pit Vipers, a major contribution to niche partitioning theory could be made.

Morphological variation influences both diet and energetics (Shine, 1991a; Arnold, 1993), with larger maximum body sizes *T. vogeli* and *T. albolabris* may be able to avoid competition for food with the primarily anurophagus and diminutive but highly abundant (arguably the most abundant) snakes in SERS. Considering the limitations of the study design, and the amount of effort required to attain acceptable sample sizes for *T. albolabris* and *T. vogeli* make morphometric study of the species of unfeasible. However, numerous questions remain concerning the relative abundance of the two species in SERS. In addition, innovative methods for finding and tracking the two rarely encountered species may yield insight into the population dynamics of highly cryptic low abundance species in the region.

4.6 Conclusion

This study provided quantitative data regarding the sexual dimorphism of a small and commonly encountered GPV *Trimeresurus macrops*, in the mixed deciduous and dry evergreen forests, and provided evidence for a correlation between body condition and head size in males, which had higher overlap with conspecific females. In addition, this study preliminarily examined the morphological differences between the three GPV species found in SERS, however found no differences. Limited sample size inhibited statistical inference when comparing the three species which must be considered. In *T. macrops* female biased dimorphism was present in nearly all variables measured, and may be a result of the reproductive strategy employed by the species. These results may be used as a baseline population means across Thai populations for comparison of *T. macrops* morphometrics and body condition. In addition, the non-significant trends between the three species warrants further study at different study sites. Further effort should also be extended to obtain bigger sample sizes of neonates and juveniles so an intersexual comparison of growth rates and maturation time can be attained.

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CHAPTER V

GREEN PIT VIPER RELATIVE ABUNDANCE, HABITAT SELECTION, AND BEHAVIOR

5.1 Abstract

Green Pit Vipers were captured in Sakaerat Environmental Research Station (SERS) from May 2012 to February 2015. A variety of sampling methods were utilized in order to maximize the number of captures throughout the study period; active searches, passive trapping (drift fence arrays), opportunistic captures, notations and actively tracking snakes to shelter sites were used in order to assess relative abundance of the three main GPV species in SERS. A total of 285 GPV capture events were recorded during the study period, with 203 individuals. Of these individuals 190 were *T. macrops*, 9 individuals were *T. albolabris*, and 4 individuals were *T. vogeli*. *T. macrops* and *T. albolabris* did not show site specific tendancies in relative abundance, however *T. vogeli* was found exclusively in deep evergreen forest. Randomly selected microhabitat quadrats were established to test ambush site selection of the most commonly encountered GPV species in SERS (*T. macrops*). Ambushing *T. macrops* selected sites with deeper leaf litter, larger stems, and greater numbers of shelter sites surrounding the site. Four novel behavioral observations were recorded for GPV during the study period, which have expanded the knowledge base of the natural history of *T. macrops* and *T. vogeli*.

5.2 Introduction

Studying the abundance of animals often yields critical information for defining the protective status of a species and therefore management strategies for the conservation of said species (Parker and Plummer, 1987; Pollock, 2007). Many techniques exist for assessing population abundance and density in herpetofauna including plot or quadrant sampling (Jaeger and Inger, 1994), distance sampling (Smolensky and Fitzgerald, 2010; Thomas *et al*., 2012), various photographic mark and recapture methods (Karanth and Nichols, 2002; Karanth *et al*., 2004), time area constrained surveys (Sun *et al*., 2001), active searches (Peterson *et al*., 2002), as well as drift fences (Burgdorf *et al*., 2005; Todd *et al*., 2007) associated with funnel traps or pitfall traps (Enge, 2001). However, many of these techniques incorporate assumptions that are difficult, or in some cases impossible to meet for extremely cryptic arboreal snake species such as Green Pit Vipers (GPV). For example, distance sampling assumes that along the line of sampling detection rates will be 100%, in the case of arboreal snakes, it is highly unlikely that this assumption actually applies, whereas photographic mark and recapture techniques are of limited use with green pit vipers at present because individuals do not have variable color patterns (Karanth and Nichols, 2002).

Of the 228 viper species worldwide only 10% are classified as threatened or near threatened, most species are either listed as data deficient or of least concern (IUCN, 2014). Poor detection probabilities and low recapture rates likely confound these estimates in snakes (Steen *et al.*, 2010). However Reading *et al*. (2010) postulate that a large proportion of the snake species worldwide are in steep population declines due to habitat degradation and human disturbance.

Green Pit Vipers (GPV) are small arboreal snakes making up 46 species of the Genus *Trimeresurus sensu lato* in Southeast Asia (IUCN, 2014). Of the 46 species only one is critically endangered, while all others are considered least concern or data deficient. Although GPV may be one of the most commonly encountered venomous snake groups in Southeast Asia, relatively little is known about their basic biology. Secretive life history strategies as well as cryptic coloring and avoidance behavior, as well as arboreal behavior make traditional drift fence arrays and visual encounter surveys of limited practical use. Thus there are no reliable estimates of abundance are lacking for most species in Thailand. For example, the only critically endangered *Trimeresurus* species, the Kanburi Pit Viper (*Trimeresurus kanburiensis*), is thought to be endangered because of its very small range and endemism, yet nothing is known of its actual abundance (IUCN, 2014).

In Sakaerat Environmental Research Station, four GPV species were thought to be present, *T. albolabris*, *T. gumpretchi*, *T. macrops* and *T. vogeli.* They are abundant in evergreen forest fragments (< 1200 m elevation) in Thailand (Cox *et al*., 2012). Although no conservation concern exists for these species, they are thought to be responsible for at least 38% of all snake bites resulting in hospitalization in the region for the last five years (Pak Thong Chai Hospital, 2014). Because the animals bite so many people each year it is essential to understand develop an understanding of their abundance in the station.

This study focused on the population of three of the four recorded species in Sakaerat Environmental Research Station (SERS), Nakhon Ratchasima. Opportunistic captures, active searches, drift fence arrays, and captures during telemetry activities were used to initiate a mark and recapture program, in addition to generating relative abundance indices for four selected Dry Evergreen Forest (DEF) sites in Sakaerat. The objectives of this study were (1) to estimate the abundance and density of each of the GPV species in SERS;(2) compare the effectiveness of the different sampling techniques; (3) compare the relative abundance of the three species found in SERS, and (4) assess the habitat type preferences between a mildly disturbed site at the research station, two water associated sites, and a deep forest site at the research station.

5.3 Methods

5.3.1 Study area

The study was conducted at Sakaerat Environmental Research Station (SERS; Figure 5.1) which is UNESCO biosphere reserve established in 1967. The reserve covers 78.09 km^2, and is located in northeastern Thailand just south of the Khorat Plateau (14° 30’ N, 101° 55’ E). Sakaerat’s elevation is from 280–762 m, with two natural forest types: dry evergreen forest (46.82 km^2) and dry dipterocarp forest (14.51 km^2) as well as two large patches of mature (>20 y) plantation forests (14.51 km^2), which are made up of acacia and eucalyptus trees. The rest of the reserve is made up of bamboo forest (1.12 km^2), grassland (0.93 km^2), and the office and operational buildings (0.25 km^2) (TISTR, 2012a). The average annual temperature was 26.1° C (ranging from 19.3–32.8°C) during the study period. The average relative humidity was 82.2% (ranging from 74 to 87%), the average annual precipitation was 1,071 mm with a distinct dry season from November to April (average monthly rainfall of 210 mm) with a pronounced bimodal wet season (average monthly rainfall of 860 mm) from May to October (TISTR, 2012b).

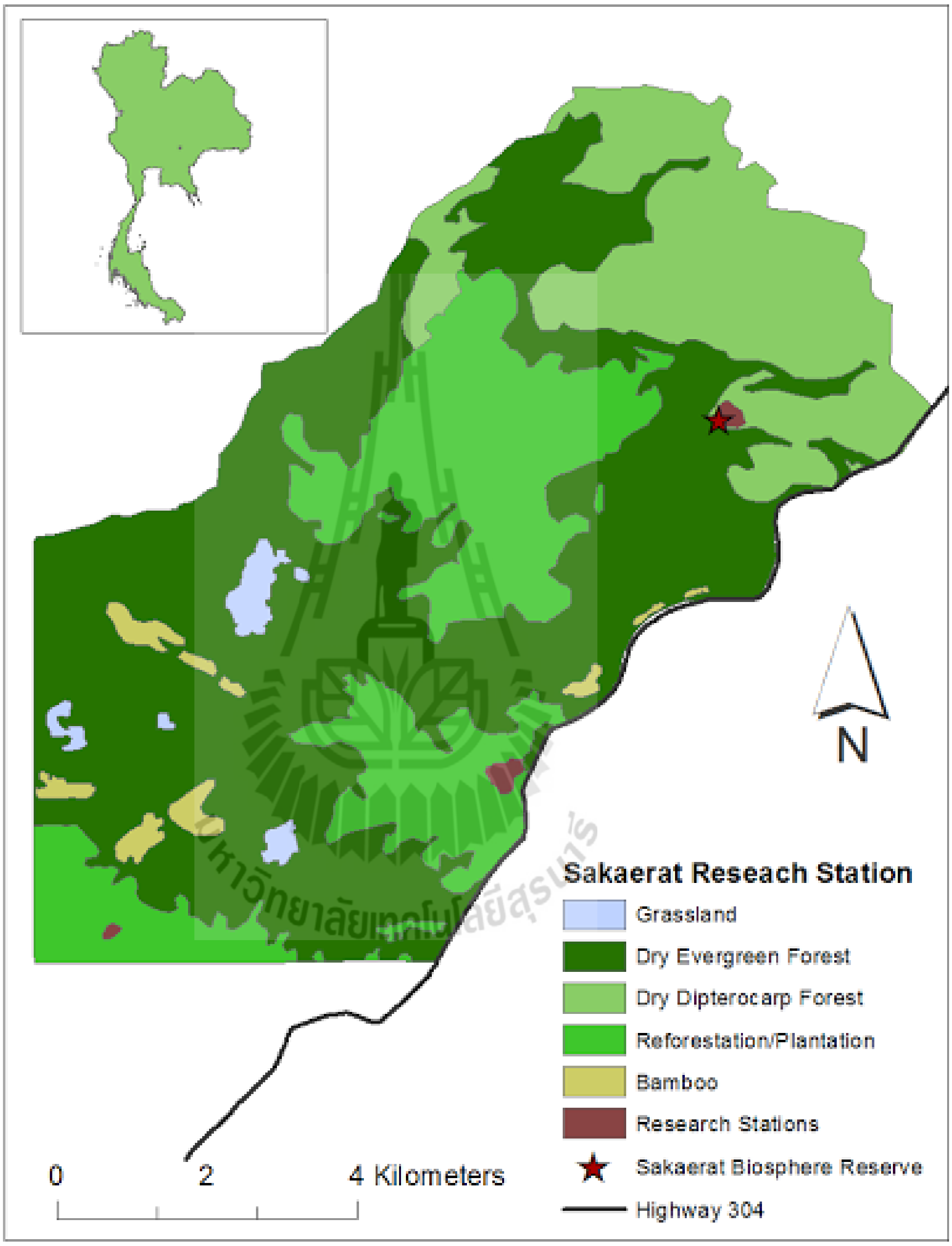

Figure 5.1 Sakaerat Environmental Research Station illustrating the study area, and forest types where sampling for Green Pit Vipers occurred.

5.3.2 Study species

Green Pit Vipers (GPV) in Sakaerat are small (< 300 g) solitary arboreal snakes which rely on ambush foraging strategies (Cox *et al*., 2012). There are three species confirmed by this study present in SERS; the white lipped pit viper (*Trimeresurus albolabris*), the big eyed pit viper (*Trimeresurus macrops*), and the Vogel's pit viper (*Trimeresurus vogeli*). The three species are sympatric in Northeast Thailand (Chanhome *et al*., 2011; Cox *et al*., 2012). While superficially similar there has been an effort to split each into the separate genera of *Cryptelytrops*, and *Viridovipera* by Malhotra and colleagues (2011). Much of the evidence supporting the split in genera comes from molecular as opposed to morphology, structure, or the ecological role (Malhotra *et al*., 2011). For the purposes of this study, *Trimeresurus* is considered as a valid genus until there is a consensus among taxonomists.

5.3.3 Snake capture and collection methods

Active searches: The Dry Evergreen (DEF) Forest in the central region of SERS was selected as the focal point for surveys. Well marked trails in addition to paved roads to sample remote areas of the DEF. Satellite imaging projects a clear difference between the canopies covered DEF (seen to the south west) and the open canopy DDF (northeast). Active sampling in DDF was minimized because preliminary studies showed minimal presence of GPV within the ecotype at SERS. Active searches were conducted by 1–5 observers with quantified effort in unit man hours calculated as number of observers x number of hours searched to the nearest hour for each survey to standardize detection rate and probability. Sampling was conducted between May and August 2012, 2013, and 2014, there were 18 total surveys (82 man hours) in the 2012 season, 96 (453 man hours) in the 2013 season, and 44 (119 man hours) in the 2014 season. Weather was recorded during surveys in order to compare similar weather surveys with one another for relative abundance analyses. Optimal survey weather was post rain, and light evening rain, all surveys for GPV were conducted after sundown before 02:00 am. It is important to note, that although AS were quantified, equal effort between seasons and between sites was not performed. Thus, interpretations of relative abundance and capture efficacy should be strongly cautioned for quantified AS.

Upon capture, the location was marked (UTM), the date, time, habitat type, site, initial occurring behaviour and, (*i.e.* moving, ambushing, resting position) the perch location type and height were recorded. Upon successful bagging the snake were subsequently removed to the laboratory for morphometric measurements (see Chapter 4 for details), and marking and then returned usually within 24 hours of capture to the original capture location.

Passive trapping plots: Although passive trapping has biases against trapping arboreal and semi-arboreal snakes, 12 50 m x 50 m plots, consisting of 2 Y shaped 20 m x 20 m x 20 m drift fence arrays with funnel traps attached to the center and the edges of the fence arrays for a total of 30 traps per plot (n=360). Plot locations were randomly selected on a grid overlain on the SERS map, extensive ground trothing led to the re-randomization of the plot selections 6 separate instances, because ground truth sites proved to be different habitat types than targeted map sites.

Four plots per main habitat type DEF, DDF and Plantation Forests (PF) were established. The traps were opened for seven nights per month from May 2012 to August 2013. Traps were not opened in March 2013, and July 2013 based on time constraints and the partial burn of the dry dipterocarp forest during February of 2013 for a total of 14 months of sampling. Total trap nights were calculated as 7 (nights) x 14 (months) x 360 (traps) for a total of 35,280 trap nights. All captured snakes were recorded and marked, following standard SCSET protocols, morphometrics and photographs were taken under anaesthesia, and snakes were released between 24 and 48 hours of capture within the plot < 10 m from the capture trap.

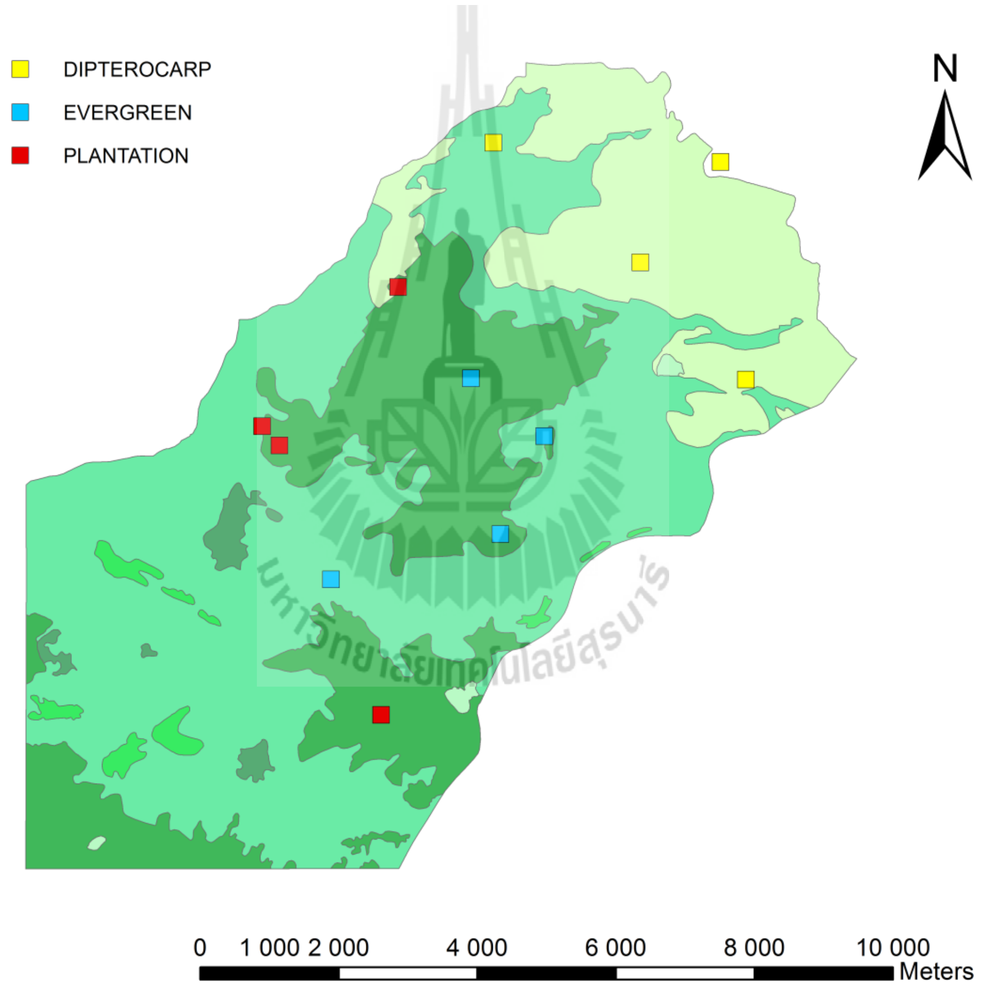

Figure 5.2 Randomly selected plot locations for sampling snake diversity among three main habitat types in SERS between May 2012 and October 2013.

Opportunistic Captures: Although standardized approaches are ideal for population studies, in order to improve sample sizes *Trimeresurus* sp. were collected on an opportunistic basis, while it is impossible to quantify the amount of effort spent attempting to capture snakes in this manner. The total study period serves as a general measure of effort; inferences from this method are strongly cautioned due to the biased nature of opportunism. Effort for this method is quantified by number of nights throughout the study period which was roughly defined from May 01 2012 to October 31 2014 (n = 913 days). During the study period when personnel were available to capture snakes opportunistically, observers were on site, either performing duties in SERS or available to capture snakes during free un-quantified time.

When a snake was captured opportunistically, the location was marked (UTM), the date, time, habitat type, site, initial occurring behaviour and, (*i.e.* moving, ambushing, resting position) the perch location type and height were recorded. Upon successful bagging the snake were subsequently removed to the laboratory for morphometric measurements (see Chapter IV for details), and marking and then returned usually within 24 hours of capture to the original capture location.

Notifications: When personnel were approached by research station staff or villagers and given the details of a snake’s location, the capture type was considered a notification. Observers responded calmly, and captured snakes using proper equipment and techniques during notification captures. Once captured the same protocol used for opportunistic captures was followed in order to collect site specific and capture location data. Radio tracking snakes to capture was defined as Active Tracking, and was performed when transmitters were near expiration.

5.3.4 Ambush Site Selection of *T. macrops*

Captured individual *T. macrops* from May 2012 to January 2014 were selected at the capture site for habitat data collection, if captured from an ambush position. Use versus availability was tested using available sites 5 and 10 m from the selected site. Random sites were selected using a random number generator which determined which direction away from the site observers travelled. A novel designed vertical multiple-layered quadrat (Figure 5.3) which was able to raise the level to 3 different layers (50 cm, 100 cm, and 150 cm) on each of these layers the stem density and number of leaves were counted. For all sites the same observer performed estimates and counts to reduce potential observer biases.

Figure 5.3 Vertical layered 1 m x 1 m quadrat structure of selected sites at 0 cm ground level (A), at 100 cm (B) and at 150 cm (C).

Upon establishment of the quadrat, the *Trimeresurus* ID, capture date and Site ID were recorded. If the site was not selected by the *T. macrops* of interest and was generated using the random number generator then it was considered a random site. If known, the perch height of the snake was also recorded. A single observer looking down over the ground story estimated ground level cover. The categories were: rock (RK), green vegetation (GV), woody vegetation (WV), human disturbance (AN), dead vegetation (DV), woody dead vegetation (WDV), leaf litter (LL), and uncovered (UC). These were estimated as a categorical variable: none (0%), very light (1–15%), light (16–25%), medium (26–65%), heavy (65–80%), very heavy (81–99%), and completely (100%). While the observer was estimating ground cover, a second observer measured litter depth at 5 points within the quadrat, these five points were then averaged to give an overall profile of the litter depth in the quadrat.

Vertical touch poles were used to count the total number of vegetation points touching the pole in the same 5 points where litter depth was taken in each quadrat, to create an overall profile of the vertical vegetation structure, which we expected might be important for GPV site selection. Once completed, slope was measured using a clinometer available on IOS by the same observer who counted the vertical vegetation density.

A third observer used a spherical hand held densitometer to estimate total canopy cover, subsequently the observer stepped back to estimate the different forest story layers using the defined categorical variables listed above. Ground story (<1m), understory (1–3 m), mid-story (3–10 m) and above story (>10 m) were all estimated by the same observer. Dominant vegetation was recorded when possible and further notes were clearly stated.

A 2 minute quantified search of the area within 2 m of the central point of the quadrat (same location as the snake), shelter sites were classed into category based on the entrance type: rock, tree, manmade, log, other were all categories present. We also classed shelter sites by size: small (0.5–5 cm) entrances, medium (5–10 cm), and large (> 10 cm). These were all recorded as a single observer performed the 2 minute quantified search, so equal effort was expended by the observer in every habitat type.

5.3.5 Novel behavior observations

Through a combined effort of both actively radio tracking the three species of GPV throughout SERS, and observing novel interactions, several unique behaviors were recorded during the study period. Upon encountering a snake performing a unique behavior, observers began recording via photographs or video. The time and date when the behavior was initially observed was recorded, as was the location, and snake ID number if known. The behavior was observed until completion and if the individual was not a tracked snake and had not been captured within 1 month prior to the observation it was brought in for processing. In the cases of mating observations extensive effort was applied to avoid disturbing snakes during copulation. During predation events observers attempted to identify species of the prey item but not to spook the snake off of the prey item. Where possible full video recordings were taken of the behaviors, three main behavioral interactions are reported from this thesis: 1) Arboreal mating of *T. macrops* 2) *T. macrops* mating in a high activity and disturbance station area, 3) Bird mobbing of a resting *T. vogeli*, 4) Predation of a common tree frog (*Hylarana nigrivittia*) during the day.

5.4. Results

5.4.1 Green Pit Viper captures

A total of 285 GPV captures occurred during the study period from May 2012– February 13, 2013. There were 203 individual GPV captured throughout the study period (Table 5.1). *Trimeresurus macrops* accounted for the vast majority of total captures (Table 5.2 *n* = 267, 190 individuals) A total of 12 captures of *T. albolabris* occurred, with 9 unique individuals caught (Table 5.2). There were only 6 captures with 4 individual *Trimeresurus vogeli* caught throughout the study period. A total of 10 recorded capture events, and 8 individuals were excluded from data presentation based on the inability to identify the individuals, because of either observer error or marking error.

Green Pit Viper Captures were variable between sites (*n* = 5), with a mean of 57 (range = 25–87 captures), with an average of 40 (range = 23–47 individuals) brought in per site (Table 5.1). In general Field station had the highest number of captures with 87 GPV captures and 58 unique individuals, whereas the Other sites had the lowest (*n* = 25) captures and lowest number of individuals (*n* = 23).

Table 5.1 Green Pit Viper captures from all sites and methods at SERS during the study period from May 2012 to February 2015.

Sites	No. of captures	No.of individuals	Sex			Age class			
			F	M	U	A	J	N	YoY
Deep forest	59	47	28	17	2	34	5	8	0
Field station	87	58	36	19	3	50	5	3	0
Lower dam pond	72	45	28	15	2	34	2	9	0
Upper dam pond	42	30	9	21	0	25	5	0	0
Other	25	23	11	11	1	16	2	4	1
Total	**285**	**203**	**112**	**83**	**8**	**159**	**19**	**24**	**1**

*Female (F), Male (M), Unknown sex (U), Adult (A), Juvenile (J), Neonate (N), Young of the year (YoY)

The sex ratio of GPV was overall biased toward females (57.4%) (Table 5.1). Female biased sex ratio was highest in field station site (65% female), but the only male biased site was the UDP site (70% males). There were 8 individuals where the sex could not be determined for various reasons. The captured GPV were primarily adults (*n* = 159, 78% of captures), however there were more neonate snakes (*n* = 24), than juveniles (*n* = 19) captured.

The deep forest (DF) site produced 41 individual *T. macrops* with 7 recaptures (Table 5.2) The field station (FS) had 58 individual *T. macrops* with 29 recaptures (Table 5.2). While the lower dam pond (LDP) and upper dam pond (UDP) had 45 individuals (recaptures = 27), and 30 individuals (recaptures = 12) respectively, among other sites there were 18 captures, with 16 unique individuals. The LDP had the highest proportion of recaptures (60%), while the field station had the second highest recaptures (50%), the UPD had lower recaptures (40%), the other sites had more than 88% unique individuals indicating very low recaptures. *T. macrops* were cosmopolitan throughout SERS (Figure 5.4).

Overall for *T. macrops* individuals captured where the sec could be identified (*n* = 182), there was a female biased sex ratio (F = 57.6 %), *T. macrops* sex ratios appeared to differ between sites (FS = 65.4%F, WA = 65.1% F, DF = 61.5%F, OT = 53.3 %, UDP = 30% F), while sex ratio was at least slightly biased towards females in almost every site, the UDP site had a male biased sex ratio (70% males).

The age classes for *T. macrops* were heavily biased overall towards adults (147/190 individuals) however the highest ratio of adults to juveniles was found at the FS where 86% of all individuals were adults in contrast to the lowest ratio of adults to juveniles at the OT sites where only 50% of individuals were adults. The proportion of neonates was highest proportion of neonates (20% of unique *T. macrops*) was found in the LDP (Table 5.3). The mean % of snakes found with a bolus (food item in the gut) was 22.1%, the highest proportion (*n* = 22) 30.6% were highest at water associated sites LDP, and the UDP (*n* = 13) 31%.

Table 5.2 Number of *T. macrops* captures and sites including unique individuals and sex ratios at each site, as well as the life history profile of each sampled site.

Sites	**No. of captures**	**No. of individuals**	**Sex**			**Age class**			
			F	**M**	**U**	**A**	**J**	**N**	**YoY**
TRMA_*Trimeresurus macrops*									
Deep forest	48	41	24	15	2	28	5	8	0
Field station	87	58	36	19	3	50	5	3	0
Lower dam pond	72	45	28	15	2	34	2	9	0
Upper dam pond	42	30	9	21	0	25	5	0	0
Other	18	16	8	7	1	10	2	3	1
Total	267	190	105	77	8	147	19	23	1
TRAL_*Trimeresurus albolabris*									
Deep forest	5	2	1	1	0	2	0	0	0
Other	7	7	3	4	0	6	0	1	0
Total	12	9	4	5	0	8	0	2	0
TRVO_*Trimeresurus vogeli*									
Deep forest	6	4	3	1	0	4	0	0	0

*Female (F), Male (M), Unknown sex (U), Adult (A), Juvenile (J), Neonate (N), Young of the year (YoY)

Throughout the study period May 2012 to February 2015, only 12 total captures of *T. albolabris* were recorded with 9 individuals. There were 7 snakes from other locations and from deep forested locations, no other sites yielded *T. albolabris* captures (Table 5.2). The female T. albolabris (4), and males (5) were nearly equal sex ratios, however only adult (*n* = 8) and neonate (*n* = 2) snakes were captured. All but two *T. albolabris* were brought in with good body condition, however only one processed individual had a bolus. 3 of the four females were gravid. The majority of *T. albolabris* were captured through Opportunistic Capture methods (*n* = 6).

Trimeresurus vogeli were captured 6 times with four total individuals (females = 3, males = 1). All snakes were adult (Table 5.2), and they were all caught from deep forest sites. In 4 of the 6 capture cases, the individuals were brought in with good body condition, the remainder were brought in with excellent condition. Only one of four individuals was ever captured with a bolus, and equal captures of Active Search (*n* = 2), Active Tracking (*n* = 2), and Opportunistic Captures (*n* = 2) were recorded.

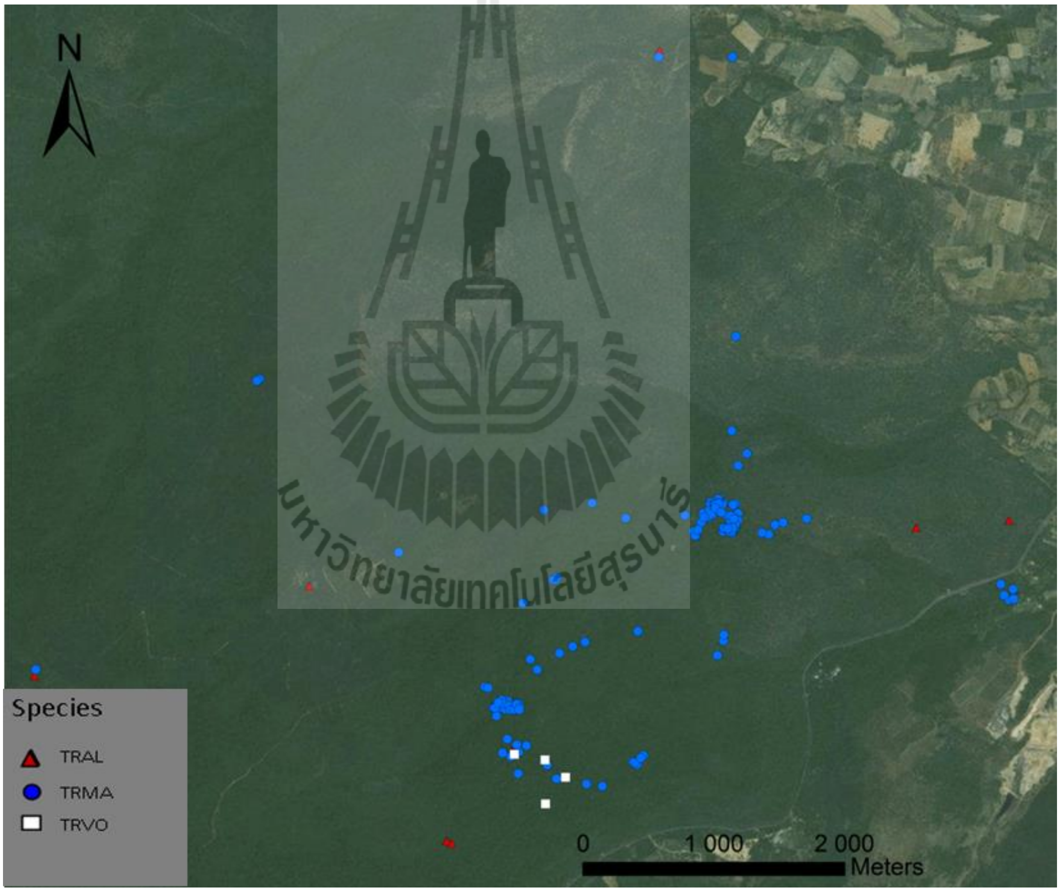

Figure 5.4 Green Pit Viper captures displayed on Sakaerat Environmental Research Station (SERS) map with each species displayed by color.

The total number of monthly captures did not correlate with mean monthly relative humidity, rainfall, or temperature (Figure 5.5). The number of active survey captures did not correlate with any of the three recorded monthly weather parameters (Figure 5.5). Even when accounting for the number of man hours per capture, no weather patterns correlated with the number of snakes captured (Figure 5.5).

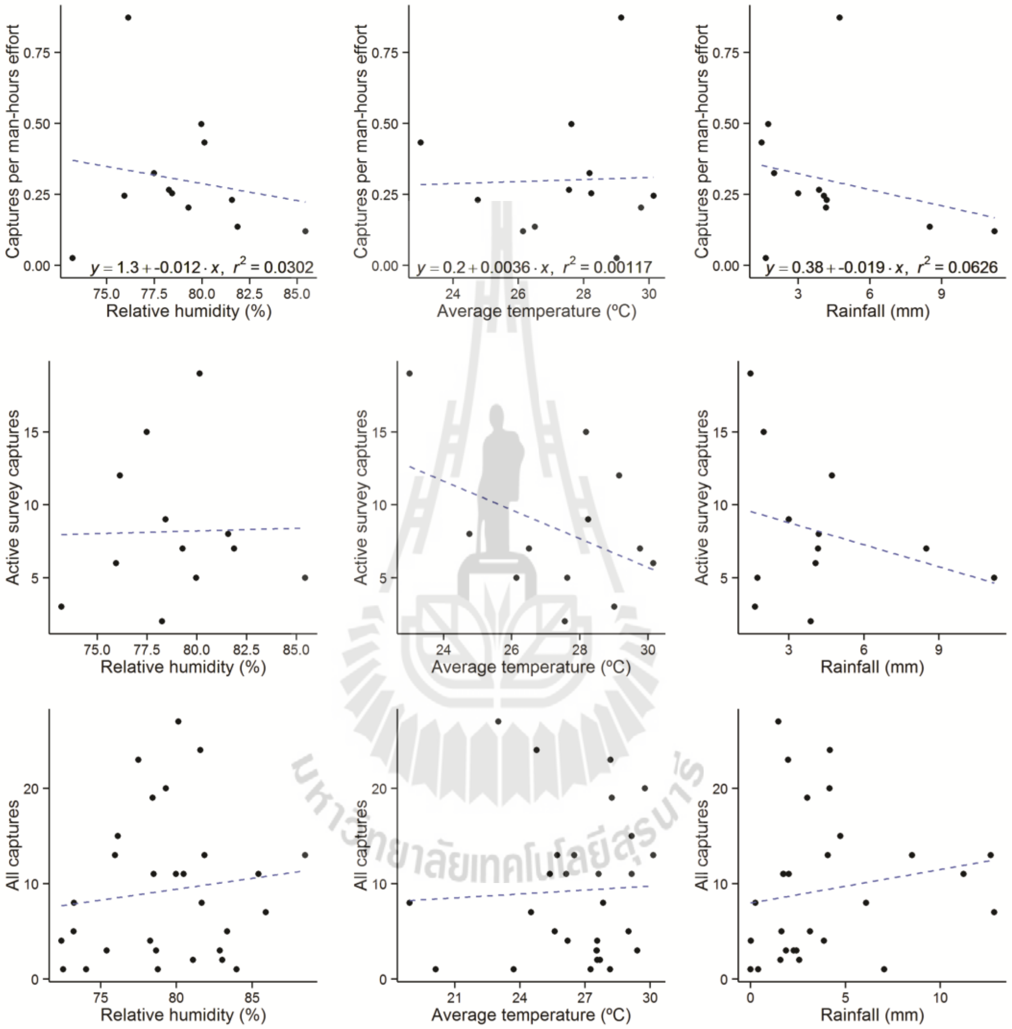

Figure 5.5 The influence of mean monthly environmental parameters recorded from weather station 1 SERS (Ambient temperature and humidity and rainfall) on number of monthly *Trimeresurus* spp. captures.

5.4.2 Recapture information and survivorship

In 2012 a total of 60 adult, 7 juvenile, and 30 neonate *T. macrops* were captured during active searches in the active season with a total of 18 surveys and 83 man hours. Recorded capture rate in 2012 was 0.96 snakes per man hour surveyed. However in 2013 a total of 66 adult, 13 juvenile and 8 neonate *T. macrops* were captured through 96 active surveys and 453 man hours. With a capture rate of 0.176 snakes per survey man hour. In 2014, 20 adult, 6 juvenile, and 2 neonate *T. macrops* were captured during 44 surveys with 119 total man hours (capture rate = 0.243 snakes per man hour). Only two individuals were confirmed survivors of any August–August reproductive season years (Table 5.3; Figure 5.6). Total recaptures throughout SERS are mapped in figure 5.6.

Table 5.3 Total *T. macrops* captures (not individuals) during the three year study period, incorporating survivors, number of surveys, and number of man hours.

	Total	Adult	Juvenile	Neonate	Survived previous year	# of Surveys	Man hours	
							Total	Mean/ survey
May, 2012 to Aug, 2013	80	60	7	30	_	18	83	4.61
Aug, 2013 to Aug, 2014	80	66	13	8	0	96	453	4.71
Aug, 2014 to Dec, 2014	29	20	6	2	2	44	119	2.704
Total	189	146	26	40	2	105	655	4.08

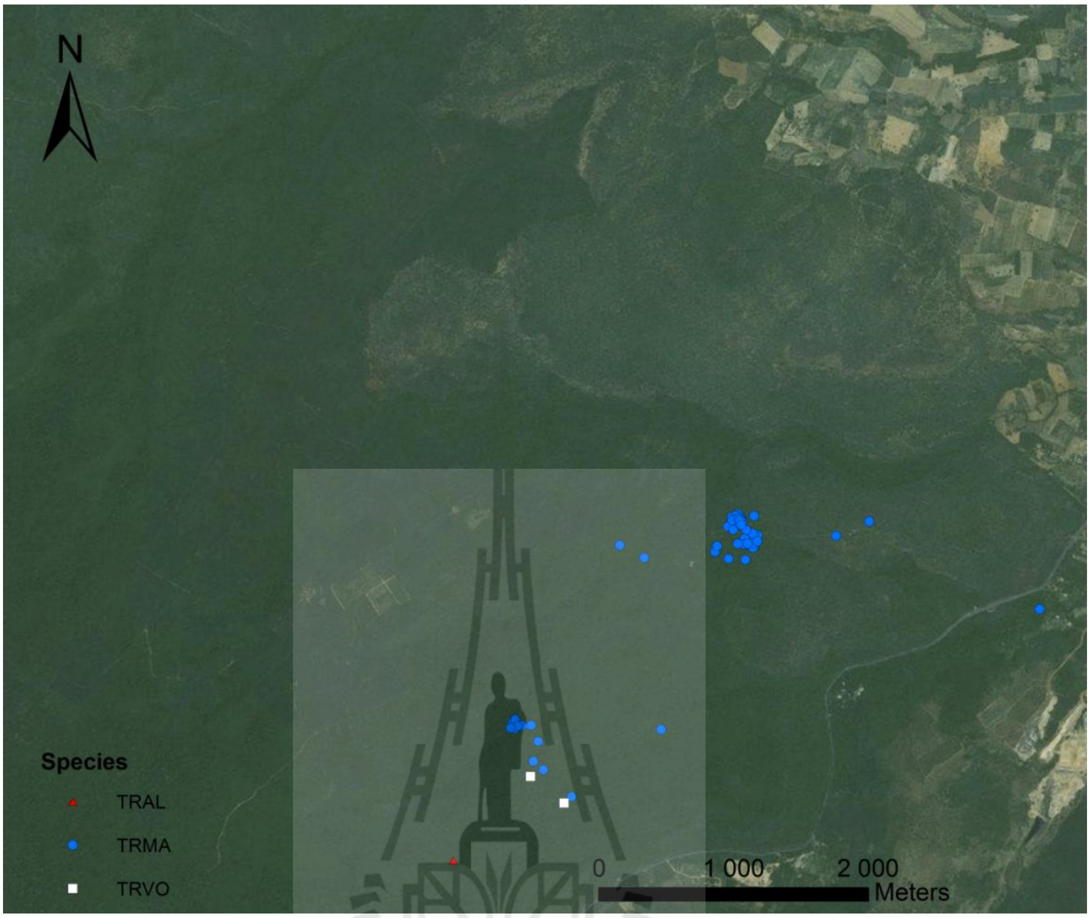

Figure 5.6 Green Pit Viper recapture locations throughout SERS from all sites and in all areas displaying *T. macrops*, *T. albolabris*, and *T. vogeli*.

5.3.4 Ambush site selection

Stem sizes in selected (*n* = 40) habitats were larger than in randomly chosen habitat sites (*n* = 80) at the 5 and 10 m quadrats using the non-parametric Wilcox Test (*W* = 1178.5, *p* = 0.03047). There was no difference in number of leaves along all planes between selected and random sites (*W* = 224871.5, *p* = 0.34). Leaf density among planes was not significantly different between selected and random microhabitat sites. In contrast, instead that the number and size of stems (including green and woody) overall at all layers was higher in sites selected than sites that were not.

Percent of selected sites with different levels of cover were different. Very light (32%), and light (30%) cover were more often selected in the ground story in selected ambush sites than in random sites (Table 5.4). However medium cover (12.5%), and very heavy (20%) cover were less proportionate in selected ground-story sites than random sites. In the understory no cover was selected less than the (43%) of available random sites, in contrast medium cover was selected 17.5% more than the time when only 9.9% of the available sites had medium cover. In the mid-story 43% of the random sites had no cover but were selected only 22% of the time, where-as medium cover was available in only 25% of random sites, but selected in 40% of all ambush sites (Table 5.4).

Table 5.4 Percent of selected ambush sites recorded from captured *T. macrops* until December 2013, in varying degrees of categorical cover in random and selected sites.

	Category of Vegetation Cover							
	None	**VL**	**L**	**M**	**H**	**VH**	**C**	**Total**
Ground-story (0-1 meters)								
Random	6.2	28.4	22.2	22.2	3.7	17.3	0.0	100.0
Selected	0.0	32.5	30.0	12.5	5.0	20.0	0.0	100.0
Understory (1-3 meters)								
Random	43.2	13.6	29.6	9.9	3.7	0.0	0.0	100.0
Selected	27.5	17.5	35.0	17.5	2.5	0.0	0.0	100.0
Midstory (3-10 meters)								
Random	43.2	11.1	13.6	25.9	6.2	0.0	0.0	100.0
Selected	22.5	5.0	25.0	40.0	2.5	0.0	5.0	100.0
Abovestory (>10 meters)								
Random	32.1	6.2	16.0	24.7	21.0	0.0	0.0	100.0
Selected	27.5	5.0	12.5	30.0	25.0	0.0	0.0	100.0

Percent rock cover at ground level was not different between selected and random sites (W = 1398.5, p = 0.2793) nor was % of area covered by human disturbance (W = 1630.5, p = 0.7212). However woody vegetation ground cover was significantly greater in selected habitats than in random microhabitat sites (W = 1195.5, p = 0.02358) in addition, woody dead vegetation was more prevalent in the selected habitat types (W = 1161.5, p = 0.01471). We expected leaf litter cover percent and percent of uncovered ground to be strongly significant in site selection proved to be non-significant (W=1537, p = 0.8067) and (W=1621, p = 0.8116).

In contrast to forest layer selection, overall canopy cover did not differ at all between random and selected sites supporting our inference that canopy cover (W= 1665, p = 0.6343), is not a significant factor in habitat selection.

Slope of selected sites was not significantly different to random sites (*W* = 1239.5, *p* = 0.05564), however there was a general trend of greater slope at selected sites (Figure 5.7). We may have an insufficient sample size to determine whether or not the slope is a significant factor in habitat selection. Litter depth however, was significantly deeper (*W* = 1227.5, *p* = 0.04693).

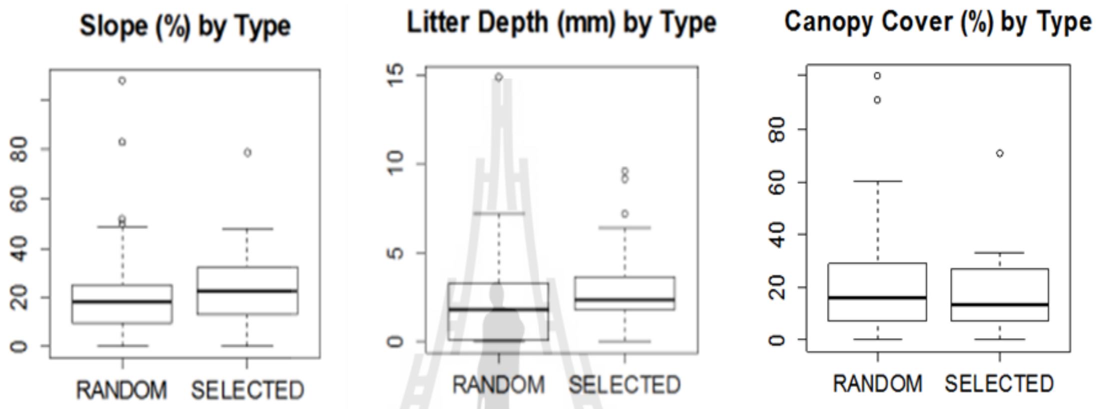

Figure 5.7 Comparison of the measured habitat characteristics between selected ambush sites chosen by *T. macrops*, and random (available) site slope, litter depth, and canopy cover between selected ambush sites and random sites.

Litter depth may be an important factor in site selection because it functions as a refuge for prey items. Heavier litter layer cover also may offer greater chance of escape for GPV when near ground. Most disturbed GPV will flee upward (away from the ground) before choosing to flee along the ground, therefore it is more likely that prey availability is the key component in the importance of litter depth in site selection.

Shelter site number were initially analysed by categories because it was thought that GPV are small therefore small shelter sites (0.5–1 cm) would have a greater influence on site selection strategy than other size categories, because small prey items would be more likely to utilize these sites. However, upon analyses there was no pattern in any category of shelter site. Instead we summed the total number of shelter sites and found a very significant relationship with the total number of shelter sites being higher between (W = 12211.5, p = 0.00892).

Table 5.5 Measured ambush site variables for *T. macrops* for random and selected sites, incorporating the Wilcox test result and significance results.

Measured variable	**Site type**		***W***	***P***
	Selected **Mean ± SE**	**Random** **Mean ± SE**		
canopy cover (%)	22.125 ± 2.18	22.103 ± 2.15	1665	0.63
ground cover types (%)				
Rock (%)	13.726 ± 1.99	13.495± 1.96	1398.5	0.27
woody vegetation	12.478 ± 1.48	12.722 ± 1.48	1195.5	0.02*
anthropogenic disturbance	12.905 ± 2.69	12.689 ± 2.65	1630.5	0.72
woody dead vegetation	15.598 ± 1.59	15.789 ± 1.58	1161.5	0.01*
leaf litter	53.264 ± 3.06	53.512 ± 3.03	1537	0.80
uncovered	16.786 ± 2.27	16.747 ± 2.23	1621	0.81
litter depth (cm)	2.519 ± 0.21	2.512 ± 0.21	1227.5	0.04*
No. shelters within 2 m	2.42 ± 0.19	2.494 ± 0.18	12211.5	<.01*
Slope (%)	21.247 ± 1.54	21.336 ± 1.52	1239.5	0.05
Stem diameter (cm)	0.864 ± 0.141	0.86 ± 0.14	1178.5	0.03*
Leaf density (no./m^2)	4.519± 0.616	4.46 ±0.602	224871.5	0.34

5.4.4 Behavioral observations

Diurnal mating observation: Disturbance is thought to influence reproductive success in a number of taxa. However, reported here is the observation of mating in a heavily disturbed station area in Sakaerat Environmental Research Station. The observation occurred at the main research station within 6 m of the main mechanical shop which is a structure of approximately 10 m x 10 m, concrete with space for 3 parked cars at any given time which consists of primarily equipment and electrical tools. The observation occurred in a small raised nursery bed, the nursery contained 16 small plastic pots with early growing saplings, directly adjacent to mixed clay and concrete bricks approximately 20 cm high. The observation occurred at 14:20 as a notification from Sakaerat staff members. Observers arrived, and placed a time lapse camera over the two snakes which were splayed out in loose loping coils, the female (larger individual) was initially resting the head on the margin of the plastic pot (Figure 5.8). The male initially was resting the head on the midbody coils of the female, the cloaca were directly opposite of one another. Observers moved back after placing the camera to avoid disturbing the snakes. While observing from a distance (approximately 1 hr) the snakes appeared to be immobile making no moves. However, when the snakes sped up via time lapse appeared to be twitching and convulsing. Mating ceased at 21:20 when observers removed the pot to the laboratory to capture the two snakes. It is possible that the observers spooked snakes into ceasing the behavior.

During the mating observation of *T. macrops* 93 and *T. macrops* 06, two major inferences were made. As nocturnally active snakes an observation of mating during the day time is both surprising and novel. In addition, the mating behaviour was in an area of high level disturbance and human traffic, yet both individuals remained in place near humans for more than 7 hours. This observation may be interpreted as *T. macrops* having the capacity to adapt to human disturbance.

Figure 5.8 Mating behavior of *T. macrops* female number 6, and male *T. macrops* number 93, captured at the main station, after copulating for 7 hours.

Arboreal mating observation: Although it may be expected that arboreal species, such as the *Trimererus macrops*, mate off the ground; there are few records of such behaviours, this observation represents the first report of arboreal mating behavior in wild *T. macrops.*

The observation occurred within the transitional zone of the Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Thailand (14.504°S, 101.952°W, datum: WGS84, elev. = 250.85 m). The two *T. macrops* were approached at about 22:50 on 28 Oct 2014.Upon approaching within capture range it became obvious that the two snakes were mating. As soon as observers realized the snakes were mating, the observers moved back to limit disturbance to the individuals.

The snakes were already arboreal approximately 40 cm high in brush/branch complex on a stream bank beside a stream which was approximately 150 cm deep within a disturbed forest. The tree in which the mating occurred was hanging over water with dense leaf litter circling the tree like a floating platform in a fairly open area. During observation, the female began climbing up slightly at 23:00, but then moved back down slightly at 23:04. The female initiated climbing up again at 23:10, pulling the male up the tree with her. The male moved up behind her at 23:12. The female started to move up again at 23:14, this time pulling the male up with her. The male then hooked his tail around the female's body just above the cloaca, and was pulled vertically until the female came to a stopping point (Figure 5.9).The male moved backwards towards the female at 23:15. After the male moved towards the female, the male's head was approximately 80 cm above the water and the female's head was approximately 130 cm above the water.

The snakes then became stationary until 00:02. At that time the female began to move up again pulling the male with her, the same as before, and then became stationary again at 00:03. At 00:20 the snake began to move their tails intensely, and the male started to back up towards the female. Shortly after that the snakes began to move away from each other. The male moved down about 5 cm. The female moved up again at 00:35, pulling the male once again. The male backed up towards the female and un-wrapped his tail from around the female's body. The snakes stopped moving at 00:36, now hanging approximately 150 cm above the water. The female and male started moving away from each other at 01:00, and untangled, disconnecting at 01:01. The male immediately fled away from the female.

The two snakes were captured after completion of mating at 01:04 h. The female was 540 mm snout to vent length (SVL), 98 mm tail length (TL), and weighed 61.6 g. The male involved in the mating behavior was 520 mm SVL, 133 mm TL, and weighed 33.8. The female was in excellent body condition. Her whole body was swollen, which could have been a sign that she was receptive for mating and she had 2 small boluses. The male was in very good body condition, but had no detectable boluses. After the snakes were processed, they were both released at the same location as captured.

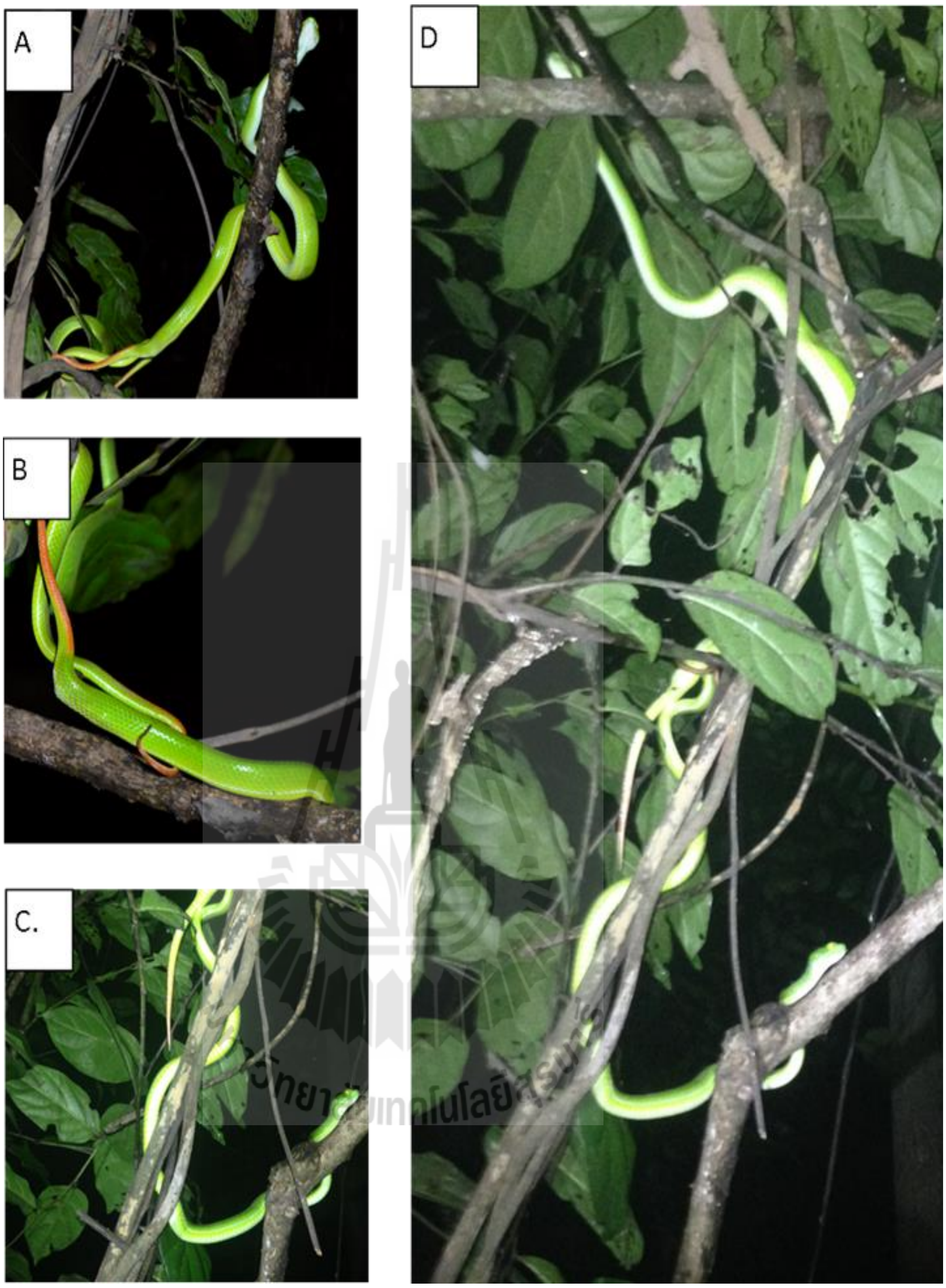

Figure 5.9 Arboreal mating observations of *T. macrops* in a mixed deciduous forest, displaying the female pulling (A) the male vertically during copulation (B), resulting in both snakes perching on separate limbs (C,D).

As an arboreal nocturnal species *T. macrops* likely spend most of their time in trees (Cox *et al*., 2012; Chanhome *et al*., 2011). Although the species is arboreal, this observation represents the first reported sighting of an arboreal mating event for this species. This observation concurs with findings from Chanhome *et al*. (2011) on the timing of reproduction for captive *T. macrops*.

Bird mobbing of T. vogeli: Pit viper species from the *Trimeresurus* genus have been reported to prey on birds, namely *T. macrops, T. albolabris* and *T. purpureomaculatus* (Chanhome *et al*., 2011), but for the recently described *T. vogeli* information is still scarce regarding diet composition and depredation behavior.

While radio tracking an adult female *T. vogeli* as part of a larger snake ecology project at the Sakaerat Biosphere Reserve in Nakhon Ratchasima Province, Thailand, a mixed flock of birds was observed in dry evergreen forest exhibiting mobbing behavior near the previous known location of the snake at 13:13 on January 05, 2015. Observers remained beyond five meters of where the snake was believed to be and the location the birds appeared to be focusing mobbing efforts on thus, limiting disturbance during the event.

At least 2 species, Asian brown flycatchers (*Musicapa dauurica*) and Turdidae spp, at least 10 individual birds were present. Individuals of the flock appeared to act independently, mobbing underneath and to the sides of the snake but not from above, never making physical contact with the viper.

Asian brown flycatchers (*Musicapa dauurica*) flew in and hovered briefly within five centimeters on two occasions and perched within twenty centimeters multiple times as well. The snake was stationary during the event and in a loosely coiled resting position with the head horizontal to the rest of the body, perching in a branch complex in the midstory layer (3 to 5 meters). The snake did not appear to be visibly disturbed, nor did it retreat even as observers approached to verify the snake presence.

Prey animals mob predators by repeatedly emitting loud and easily detectable calls, and displaying movements that gather more conspecifics around the threat. This behaviour, although risky to the mobbers, aims to distract or deter the predator from attacking. On occasion mobbing on snakes has been observed, among others, towards Viperidae predators both for a life-like model of *Cerastes gasperetti* and *Bothrops lateralis*, with the latter being a heterospecific behaviour. However it still has not been formally described for green pit vipers of the genus *Trimeresurus*.

Diurnal Predation: On 29 July 2014 an adult female *T. macrops* was observed predating upon a dark sided frog (*Hylarana nigrivittata*) at 07:57. Observers arrived on scene based on a notification from Sakaerat staff. The prey item was already envenomated and likely had already died, however the snake had ingested to the anterior hindlegs of the frog (Figure 5.11A). Initially the snake was stationary facing black plastic mesh lining while perched atop an electrical wire which was situated approximately 1 m above ground. The wire was resting on the concrete ledge of a large covered water basin which was approximately 6 x 2 m. The snake was initially perched with the head vertical leaning against the mesh, after 40 seconds of contracting the muscles in the neck the snake had positioned itself flat against the concrete ledge, and had ingested to the hinged joint on the hind limbs of the frog (Figure 5.11B).

Through a combination of jaw walking and repositioning of the body the snake completely ingested the frog after a brief pause from minute 2:40–2:45 (Figure 5.11C). The frog was completely engulfed by 03:02.

Thus the entire predation event was very short. After slowly moving the prey item down the stomach through repeated muscle contraction and body repositioning the snake began to retreat at 04:12 (Figure 5.11C) and began tongue flicking rapidly at 04:15 after moving approximately 6 cm, the snake paused and perched on the margin between concrete and plastic wire, no further movements were observed and video recorded until 07:02. Observers did not attempt capture on the snake, and therefore morphometrics of neither the individual, nor the snake identification number could be verified. 4) The diurnal predation event of a dark sided frog (*Hylarana nigrivittia*) confounds the typical assertion that *T. macrops* is primarily active nocturnally (Cox *et al*., 2014). This observation suggests that *T. macrops* may be an activity period generalist, and likely takes prey items whenever they become available much like the low energy (*Gloydius shedaoensis*) on the island of Shedao, that rarely move and will prey upon even previously killed birds if the item falls nearby a snake (Shine *et al*., 2003).

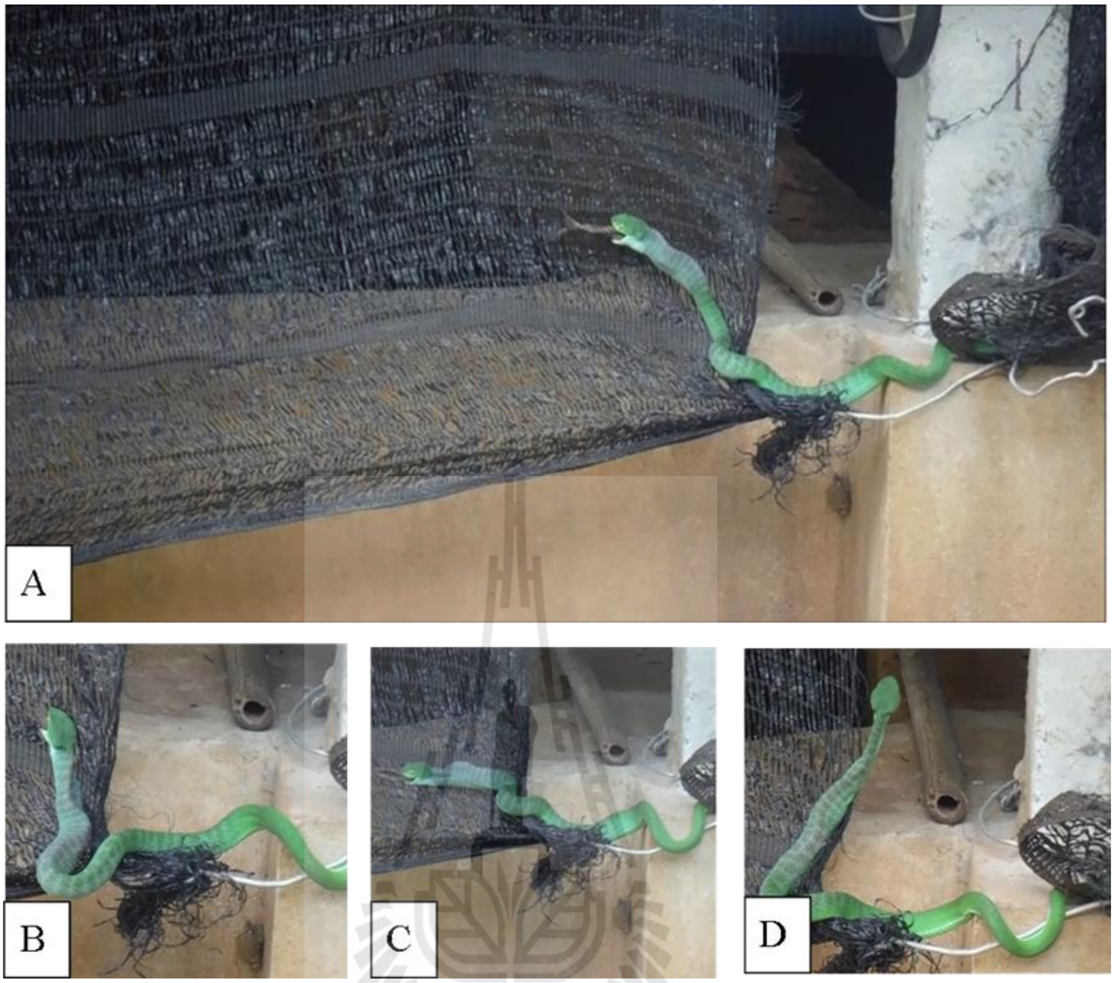

Figure 5.10 Female *T. macrops* predating a (*Hylarana nigrovittata*) diurnally, in a disturbed area. The hindlegs are initially visible (A), but the snake uses the support from a vertical silt fence (B) to swallow the prey item whole, the snake alternates between horizontal (C) and vertical movements (D) in order to complete ingestion.

5.5 Discussion

5.5.1 Snake captures

Green Pit Vipers were relatively abundant throughout SERS during the study period with a total of 285 GPV captures throughout the sampling period. Active search and opportunistic captures were the most effective methods of capturing large numbers of GPV (*n* =237 captures). Although these methods suffer in the ability to make statistical inference based on standardized effort, and violate a number of assumptions for mark and recapture programs (Steen *et al*., 2010), they have the added benefit of building sample sizes with limited effort.

T. macrops was the most abundant species (*n* = 190 individuals), found in all sites and all ecotypes. Female biased sex ratios were observed in all but one site (UDP site was 70% biased towards males) which is similar in sex ratios to studies conducted on congeners *T. stegnegeri* in Taiwan (Lin *et al*., 2007; Lin *et al*., 2008). In addition, *T. macrops* near sources of water were more often found with a food bolus, as *T. macrops* are thought to be primarily anurophagus (Cox *et al*., 2012). Interestingly, snakes captured at the water associated sites were less often found gravid than deep forest areas, or field station areas. It is possible that *T. macrops* gives birth and feeds in areas where water is prevalent, but then during the reproductive cycle it moves away to areas with lower predator abundances similar to the neotropical vipers *Bothrops asper*, which were given supplementary food (Wasko and Sosa, 2012).

While *T. macrops* appear to be found (58 individuals in field stations) throughout both disturbed and undisturbed areas (41 individuals in deep forest sites) in the MDF and DEF of Sakaerat, *T. vogeli* seems to be restricted to deep evergreen (*n* = 3) fragments with little human activity in Sakaerat. Although there are clear trends in relative abundance favoring *T. macrops* over *T. vogeli* and *T. albolabris* in Sakaerat, premature inference should be strongly cautioned. Because survey locations, seasons and durations were not standardized sites cannot be readily compared. Furthermore, *T. vogeli* appear to use multiple forest strata which may confound detection probability in comparison to *T. macrops*. Further study should include standardized Time Area Constrained Surveys in areas suspected to house both species such as deep evergreen streambeds, and cliff-sides, which limit disturbance.

5.5.2 Ambush site selection

It is possible our results may be limited by the lack of available habitat variation, or perhaps insufficient sampling size, but the data appear to indicate non-random selection of microhabitat with canopy cover as a factor (Table 5.4).

Sites with VL ground story canopy occupied a greater proportion of the sampled sites than random sites (Table 5.5), while lightly covered understory sites made up a greater proportion of the total sample than in random sites. Medium cover occupied a higher proportion of the selected sites in mid story than in random sites while the same pattern was true for the above story.

5.6 Conclusion

The most common GPV found in SERS is likely *T. macrops*. The ambush strategy employed by *T. macrops,* allows it to be cosmopolitan throughout SERS because it can tolerate mild anthropogenic disturbance and is commonly found at the field station. However, because survey effort was not standardized between field station sites, and deep forest sites, the relative abundance of *T. macrops* in different areas cannot be assessed. Big eyed pit vipers (*T. macrops*) appear to select ambush sites non-randomly with chosen sites showing deeper litter, more available shelter sites, larger stem sizes, and variable 100–150 cm level cover. Although there has been some attempt to eludicate the drivers in ambush site selection further work should focus on prey abundance as a factor for ambush site selection as well as evidence of predators.

The novel behavioural observations from this chapter have expanded the knowledge base on the range of behaviours and the activity period of *T. macrops* (*i.e* they are sometimes active diurnally). In addition further information has been gleaned on *T. vogeli* defensive behaviours, which simply are to remain stationary even when under duress from a mob of aggressive birds.

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CHAPTER VI

CONCLUSION AND RECOMMENDATION

6.1 Conclusions

This study focused on a resident community of Green Pit Vipers centered in the dry evergreen forests and mixed deciduous forest fragments of Sakaerat Environmental Research Station, Nakhon Ratchasima. It highlights the generally limited information on ecology and biology of green pit vipers in Northeastern Thailand. These results in particular, illustrate how small the home ranges of *T. macrops* female GPV are, and can be used as a baseline reference for studies along different levels of disturbance where the species is thought to occur.

6.1.1 Home range size of Green Pit Vipers in SERS

Kernel estimates (95% 0.0199 ha, 50% 0.038 ha), and MCP home ranges were small (0.0201 ha) for *T. macrops* females throughout the tracking periods. Home range sizes were not different between different sites, including pristine sites and sites with mild disturbance, even when the number of fixes, and the number of days tracked was accounted for. Although there were no significant differences between home range sizes of *T. macrops* in deep forest and sympatric *T. vogeli*, a clear Vogel's biased home range size pattern emerged. The pattern would likely clarify given more appropriate sample sizes for *T. vogeli*. As the technology for smaller transmitters with longer battery lives emerge, serious consideration should be put into studies over multiple seasons, to examine seasonal home range shifts, and potential patterns of temporary emigration.

6.1.2 Spatial ecology of deep forest *T. vogeli* and *T.macrops*

Movement patterns between *T. vogeli* and *T. macrops* did not differ for the total number of days stationary, the maximum number of days stationary or the mean number of days stationary, however *T. vogeli* showed a trend of larger home ranges, although non-significant. This observation may be accounted for based on the larger body sizes of *T. vogeli* (also non-significant). While a significant portion of certain *T. macrops* home range was overlapped by *T. vogeli*, a very small portion of *T. vogeli* MCP home ranges overlapped any *T. macrops* individuals and in the FK 50% less than .006% overlapped with any individual. Thus, with greater sample size there may be greater inference into spatial partitioning and perhaps even vertical stratification.

6.1.3 Environmental influence on *T. macrops* microhabitat selection and behavior

Female *T. macrops* were visible approximately 39% of the tracking fixes, and were used to identify microhabitat selection parameters. Percent of time visible was different between sites. Female *T. macrops* selected woody vegetation perches 62.1% of the time, and were only observed perching on 8% of the time on green vegetation. When *T. macrops* were on ground they showed a strong tendancy to be in ambush foraging positions. Likely foraging primarily occurs on the groundstory (< 1 m in height). Sheltering accounted for the highest proportion of female

T. macrops datapoints in the midstory (3-10 m). Human disturbance was not a significant predictor of where *T. macrops* may be found. The site where snakers were tracked influenced the predominant behaviors observed, for example *T. macrops* in water associated sites were more often found in ambush position than snakes from other sites. Nocturnally *T. macrops* were more likely to be active, and were most likely to be in ambush position nocturnally with higher ground humidity. While snakes were more likely to be sheltering when ground temperatures were cooler and less humid, they were also more frequently sheltering diurnally. These results indicate clear patterns of the solar cycle and environmental parameters influence on *T. macrops* behaviors and activity patterns.

6.1.4 Sexual size dimorphism in *T. macrops*

Female *T. macrops* were in general larger, and heavier than male conspecifics. While males had greater tail lengths (expected, because the tail houses the hemipenes), female *T. macrops* had greater snout to vent length, and body mass as well as head measurements than males. Even when accounting for TBL as a covariate the head measurements are significantly larger in females than males. Interestingly the males with the largest heads, also had the poorest body condition (Scaled Mass Index). The largest headed males overlapped with the mode head size of female snakes, which is perhaps an indicator of interspecific competition, or even potentially selection for resource partitioning among the sexes. The size bias toward females can be interpreted as benefitting reproductive activities by building up fat reserves and smaller body size in males may increase mobility which could impact successfully encountering mates.

6.1.5 Morphological variation between *Trimeresurus* spp.

Morphometric characters were not significantly different between the three species. However the mean TBL for *T. albolabris* (740.7 ± 228.9 mm), *T. vogeli* (827.4 ± 57.8 mm), and *T. macrops* (697.2 ± 48.0 mm) were clearly not the same. The sample sizes were insufficient in both *T. albolabris* and *T. vogeli* to properly compare with *T. macrops,* which means that further captures of GPV in Sakaerat will clarify the observed pattern and yield exciting results on size variation of SERS pit vipers. The preliminary size variation may be interpreted as potential partitioning of resources, and stratification of habitat sites, because different body structures are suited to different forest strata.

6.1.6 Relative abundance and capture effectiveness

Green Pit Vipers were relatively abundant throughout SERS during the study period with a total of 285 GPV captures throughout the sampling period. Active search and opportunistic captures were the most effective methods of capturing large numbers of GPV (*n* =237 captures), while passive trapping (*n* = 11), and road survey (*n* = 3) were largely unsuccessful at capturing GPV. The most abundant species was *T. macrops* (N = 190 individuals), found in all sites and all ecotypes. Female biased sex ratios were observed in all but one site (UDP site was 70% biased towards males). While *T. macrops* appear to be found (58 individuals in field stations) throughout both disturbed and undisturbed areas (41 individuals in deep forest sites) in the MDF and DEF of Sakaerat, *T. vogeli* seems to be restricted to deep evergreen (*n* = 3).

6.1.7 Ambush site selection for captured *T. macrops*

Big eyed pit vipers (*T. macrops*) appear to select ambush sites non-randomly with chosen sites showing deeper litter, more available shelter sites, larger stem sizes, and variable 100-150 cm level cover. Vertical stratification cover appears to have an influence on ambush site selection, but the methods employed by this study were unable to identify the pattern of the relationship. Although there has been some attempt to eludicate the drivers in ambush site selection further work should focus on prey abundance as a factor for ambush site selection as well as evidence of predators.

6.1.8 Novel observed behaviors

Several novel behaviors and events were observed during radiotelemetry and observed opportunistically in Sakaerat Environmental Research Station. 1) Two individual *T. macrops* were observed mating in a heavily disturbed area within 6 m of a mechanic shop in the base of a flower pot in a small raised nursery bed on October 20, 2013 which coincides with previous records of the *T. macrops* reproductive cycle. The observation indicates that anthropogenic disturbance likely has a limited impact on T. macrops reproductive behaviors. 2) Arboreal mating was observed in a mixed disturbed forest just south of the research station boundaries on October 28, 2014, from 22:50-01:014 h in an area of moderately disturbed streamside habitat. This observation is the first reported observation of arboreal mating in *T. macrops* in Thailand, and fits the timing of mating activities recorded by captive individuals. 3) Bird mobbing was observed during tracking of the *T. vogeli*, and it showed a distinctively non-responsive behavior to the mob of birds.

4) Diurnal predation was observed, a *T. macrops* female envenomated and subdued a dark sided frog (*Hylarana nigrovittata*).

6.2 Recommendation

Although this study provided basic information on the spatial ecology and movement patterns of female *T. macrops*, much remains unknown of their basic biology and ecology.

1) As any reliable conclusions on spatial ecology require large sample sizes (Kernohan *et al.*, 2001), expanding the sample size of males in order to explore the spatial relationship and patterns between sexes is the next logical step in this research program

2) Because these results can only provide preliminary data on this group of species, based on the active seasons between May-July and Oct-Dec, they do not represent the full year of GPV, thus longer term radiotelemetry may elucidate seasonal movement patterns.

3) This study confirms the need to compare sympatric GPV because although sample sizes were extremely small, different movement patterns, sizes, and strata use were visible, a larger sample size could potentially be incorporated into a large body of theory into the theory of niche partitioning, or prematurely as vertical stratification.

4) Methodological techniques should be carefully considered when attempting to assess *T. macrops* densities, and population structure. Because in over 35,280 trap nights in plots from multiple habitat types resulted in only 10 *T. macrops* and 1 *T. albolabris* captures in comparison to 138 captures during active surveys. However, standardization and pulsed sampling would potentially allow acceptable

detection probability calculations to be computed, which are essential for density calculations.

5) In order to reduce snakebite from GPV it is best to avoid dense green and woody vegetation from 10 cm - 300 cm at night time, when snakes are most active. Because most snakebites occur on the hand and foot, villagers should always wear proper shoes and have a light when working outside at night time. Extra care should be taken when picking fruit or working in the agricultural landscapes.

APPENDICES

APPENDIX A

RADIOTRACKED GREEN PIT VIPERS

Table A-1 All female *Trimeresurus* sp. used for radiotelemetry (n = 32) during the study period from May 2012 to January 2015.

	Morphometrics							**Location of first track (UTM)**					
Snake ID	**SVL (mm)**	**TVL (mm)**	**Mass (g)**	**HL (mm)**	**HW (mm)**	**First track**	**Condition**	**X**	**Y**	**Site**	**Final track**	**Track Days**	**Fate**
T. macrops													
TRMA006	630	111	81.8	20.2	31.27	06.11.13	Excellent	815875	1606165	FS	02.01.14	57	TF
TRMA007	640	80	113	NA	NA	26.10.12	Good	814363	1604068	UDP	06.12.12	41	Unknown
TRMA014	470	82	56.9	20	32	25.10.12	Good	816039	1606030	LDP	19.12.12	55	Released
TRMA022*	450	64	50.4	NA	NA	26.10.12	Good	816041	1606030	LDP	15.01.13	81	Unknown
TRMA023	443	56	45.5	NA	NA	26.10.12	Good	816035	1606017	LDP	13.12.12	47	Unknown
TRMA024	660	100	68.8	10	30	28.10.12	Good	816036	1606026	LDP	19.12.12	52	Released
TRMA025	316	138	64.2	22	24	04.11.12	Good	815951	1606192	FS	17.03.13	133	Mortality
TRMA029	460	76	38.1	18.19	26.5	05.01.13	Excellent	816022	1606029	LDP	13.06.13	43	Released
TRMA048	569	101	30	22	27.2	05.01.13	Good	816044	1606046	LDP	02.07.13	62	Released
TRMA050	494	44	44.6	19	27	05.01.13	Good	816039	1606027	LDP	24.05.13	23	Predation
TRMA052*	586	106	55.1	20	32	23.05.13	Good	816051	1606041	LDP	24.06.13	33	Predation
TRMA062	618	119	70.2	24	32	23.05.13	Good	816041	1606031	LDP	14.07.13	52	Unknown
TRMA069	630	115	67.6	27	34	22.11.13	Good	814336	1604253	DF	20.01.14	59	Mortality
TRMA080	566	74	50.9	22	24	09.09.13	Good	815958	1606225	FS	05.12.13	87	Released
TRMA088	668	110	33.49	20	22	22.09.13	Good	815961	1606238	FS	24.01.14	124	Released
TRMA090	540	96	46.2	16	23.5	09.09.13	Excellent	815941	1606253	FS	03.02.14	147	Re;eased
TRMA094*	505	84	41.7	18.23	26.27	11.11.13	Good	814398	1604164	DF	18.01.14	68	Released
TRMA095	497	99	56.85	19.03	27.59	05.11.13	Good	815951	1606210	FS	20.01.14	76	Released
TRMA096	508	84	44.2	15.31	23.23	09.12.13	Good	814257	1604721	UDP	26.01.14	48	Unknown
TRMA099*	544	83	40.1	23.28	27.4	16.11.13	Good	814249	1604169	UDP	27.11.13	11	Mortality

*Removed from kernel analyses because the snake had too low relocations to be represented, (TF) Transmitter failure

Table A-1 (Continued).

	Morphometrics							Location of first track (UTM)					
Snake ID	**SVL (mm)**	**TVL (mm)**	**Mass (g)**	**HL (mm)**	**HW (mm)**	**First track**	**Condition**	**x**	**y**	**Site**	**Final track**	**Track Days**	**Fate**
T. macrops													
TRMA102*	621	119	98.05	21.51	30.86	04.12.13	Good	816043	1606220	FS	30.01.14	57	Released
TRMA174	534	100	42.1	26.75	16.99	07.10.14	Good	814691	1604148	DF	27.01.15	144	Released
TRMA178	456	115	46.2	21.38	13.76	11.11.14	Good	814407	1604423	DF	13.02.15	95	Active
TRMA186	550	96	45.8	25.89	17.39	08.11.14	Good	814310	1604430	DF	13.02.15	98	Active
MEAN	539.79	93.83	55.49	20.56	26.14							70.54	
SE	17.32	4.49	4.57	0.8	1.1		N = 24					7.51	
T. vogeli													
TRVO002	642	119	104.2	37.53	25.9	20.07.14	Good	814370	1604307	DF	13.02.15	208	Active
TRVO003	729	138	109.7	39.21	26.23	29.07.14	Good	814753	1604134	DF	13.02.15	199	Active
MEAN	685.5	128.5	106.95	38.37	26.065							203.5	
SE	43.5	9.5	2.75	0.84	0.165		N = 2					4.5	
T. albolabris													
TRAL006	765	140	122.9	28	36	25.08.13	Excellent	813887	1603630	DF	06.03.14	193	Released

*Removed from kernel analyses because the snake had too low relocations to be represented, (TF) Transmitter failure

Table A-2 All male *Trimeresurus* spp. (*n* = 5) used for radiotelemetry (*n* = 32) during the study period from May 2012 to January 2015.

Snake ID	**Morphometrics**					**First Track**	**Condition**	**Location of first track (UTM)**		**Site**	**Final Track**	**Track Days**	**Fate**
	SVL (mm)	**TVL (mm)**	**Mass (g)**	**HL (mm)**	**HW (mm)**			**x**	**y**				
T. macrops													
TRMA026*	603	237	33.2	22	19	11.09.13	Good	0816054	1606058	LDP	27.09.13	37	Unknown
TRMA110#	534	43	49.5	15.92	25.77	11.11.13	Good	0814641	1605639	UDP	05.02.14	86	Unknown
TRMA065	613	136	40.4	22	14	06.06.13	Good	0816051	1606054	LDP	23.08.13	123	Unknown
TRMA093*	487	122	33.2	14.68	23.01	04.11.13	Good	0815871	1606160	FS	11.12.13	16	Mortality
	545.4	129.2	38.32	18.52	20.556						**Mean**	53.6	
N=4	60.2	69.9	6.9	3.39	4.438						**SE**	94.58	
T. vogeli													
TRVO001	490	108	35.3	18	21	10.10.13	Good	0814713	1603877	DF	24.01.13	106	Unknown

*Removed from kernel analyses because the snake had too low relocations to be represented, (TF) Transmitter failure,

Snake translocated

APPENDIX B

GREEN PIT VIPER CAPTURES

Table B-1 All *Trimeresurus* sp. caught (n = 203) during the study period from May 2012 to January 2015

			UTM coordinates						
Species	**Snake ID**	**Capture date**	**x**	**y**	**Sex**	**Age Class**	**Mass (g)**	**TBL (mm)**	**Ecotype at Capture**
TRMA	001	2012-05-02	814595	1606181	M	Adult	140	700	Evergreen Forest
	002	2012-06-24	814318	1604715	M	Adult	100	450	Evergreen Forest
	003	2012-06-25	814318	1604720	M	Juvenile	-	270	Evergreen Forest
	004	2012-07-26	815878	1606172	F	Adult	40.8	540	Evergreen Forest
	005	2012-07-30	815966	1606016	M	Adult	35	580	Evergreen Forest
	006	2012-08-29	816363	1606070	F	Adult	84	760	Evergreen Forest
	007	2012-08-30	816363	1606068	F	Adult	113	720	Evergreen Forest
	008	2012-09-21	814143	1604825	M	Neonate	12.5	360	Evergreen Forest
	009	2012-09-21	814714	1605084	F	Adult	39.8	590	Evergreen Forest
	010	2012-09-21	814816	1605136	M	Adult	28.8	540	Evergreen Forest
	011	2012-09-22	814167	1604818	F	Adult	33.57	590	Mixed-deciduous
	012	2012-09-22	815740	1606015	F	Adult	50.9	622	Evergreen Forest
	013	2012-09-23	816033	1606787	M	Adult	54.05	624	Evergreen Forest
	014	2012-10-26	815231	1605937	F	Adult	54.9	654	Evergreen Forest
	015	2012-09-23	815922	1606179	F	Adult	59.1	690	Mixed-deciduous
	016	2012-09-24	815922	1605067	M	Adult	31.55	610	Mixed-deciduous
	017	2012-09-25	815278	1604253	F	Juvenile	13.3	311	Ecotone-semiclosed
	018	2012-09-24	815308	1604233	F	Juvenile	14.8	333	Ecotone-semiclosed
	019	2012-09-24	815308	1604232	M	Adult	43.61	569	Ecotone-semiclosed

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates		Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
			x	y					
TRMA	020	2012-09-28	815835	1606122	M	Adult	27.5	570	Dipterocarp
	021	2012-10-25	814490	1605038	F	Neonate	13.4	372	Plantation-forest
	022	2012-10-26	816041	1606030	F	Adult	50.4	514	Mixed-deciduous
	023	2012-10-26	815990	1606044	M	Adult	45.5	499	Evergreen Forest
	024	2012-10-28	816055	1606058	F	Adult	68.8	660	Dipterocarp
	025	2012-11-04	815940	1606204	F	Adult	64.2	454	Human Settlement
	026	2012-11-01	816060	1606226	M	Adult	33.2	640	Human Settlement
	027	2012-11-05	815813	1606154	F	Adult	44.1	650	Evergreen Forest
	028	2012-11-05	816081	1606154	M	Adult	34.6	520	Mixed-deciduous
	029	2012-11-07	815947	1606162	F	Adult	38.1	536	Mixed-deciduous
	030	2012-11-07	815798	1606084	M	Juvenile	22	-	Evergreen Forest
	031	2012-11-17	814345	1604664	F	Adult	21	475	Evergreen Forest
	032	2012-11-17	814297	1604699	F	Adult	48	679	Evergreen Forest
	033	2012-11-17	814303	1604698	M	Adult	48	612	Evergreen Forest
	034	2012-11-24	814693	1605662	F	Adult	100	638	Evergreen Forest
	035	2012-11-26	812416	1607181	F	Adult	25	498	Plantation-forest
	036	2013-01-17	815291	1604248	M	Adult	28.8	546	Evergreen Forest
	037	2013-02-25	813483	1605857	M	Juvenile	14.2	394	Evergreen Forest
	038	2013-03-26	815871	1606240	F	Adult	38.1	508	Dipterocarp
	039	2013-04-02	816050	1606045	M	Adult	18.4	484	Dipterocarp

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	UTM coordinates y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	040	2013-04-02	816050	1606047	F	Adult	22.1	485	Evergreen Forest
	041	2013-04-02	816057	1606037	F	Adult	25.2	505	Evergreen Forest
	042	2013-04-03	814249	1604707	M	Adult	34.4	722	Evergreen Forest
	043	2013-04-05	814252	1604706	F	Juvenile	14.5	441	Evergreen Forest
	044	2013-04-05	814256	1604714	M	Adult	24.5	523	Evergreen Forest
	045	2013-04-08	814253	1604685	F	Adult	17.45	502	Evergreen Forest
	046	2013-04-20	816049	1606049	F	Adult	31.3	614	Dipterocarp
	047	2013-04-20	816481	1606044	F	Adult	26	572	Dipterocarp
	048	2013-04-24	816038	1606053	F	Adult	30	670	Dipterocarp
	049	2013-04-22	816052	1606052	F	Adult	32.3	594	Dipterocarp
	050	2013-04-25	816043	1606213	F	Adult	44.6	538.6	Dipterocarp
	051	2013-04-27	816042	1606032	M	Adult	27.7	598	Mixed-deciduous
	052	2013-05-04	816051	1606041	F	Adult	55.1	692	Dipterocarp
	053	2013-05-06	816315	1605993	F	Adult	30.4	562	Dipterocarp
	054	2013-05-07	814351	1604665	F	Adult	43.8	618	Dipterocarp
	055	2013-05-08	816265	1606007	F	Adult	35.3	635	Dipterocarp
	056	2013-05-08	815985	1606037	M	Adult	39	634	Dipterocarp
	057	2013-05-09	816036	1606015	F	Adult	42.7	666	Dipterocarp
	058	2013-05-09	816036	1606015	F	Adult	30.7	573	Dipterocarp
	060	2013-05-14	816064	1607508	F	Juvenile	15.2	430	Evergreen Forest

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	UTM coordinates y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	062	2013-05-24	816031	1606018	F	Adult	70.2	737	Dipterocarp
	063	2013-05-27	816074	1606105	F	Adult	20.7	505	Dipterocarp
	064	2013-05-29	815941	1606266	F	Adult	42.4	646	Human Settlement
	065	2013-05-29	816049	1606051	M	Adult	40.4	749	Dipterocarp
	066	2013-05-30	816033	1606006	-	Neonate	6.7	288	Mixed-deciduous
	067	2013-06-06	816079	1606100	F	Neonate	3	203	Mixed-deciduous
	068	2013-06-02	815966	1606046	F	Neonate	7.6	296	Dipterocarp
	069	2013-06-04	816037	1606043	F	Adult	67.6	745	Dipterocarp
	070	2013-06-05	816426	1606084	F	Neonate	-	232	Dipterocarp
	071	2013-06-05	816426	1606084	F	Neonate	3.7	374	Dipterocarp
	072	2013-06-14	815961	1606238	M	Neonate	-	325	Dipterocarp
	073	2013-06-26	815474	1609647	M	Neonate	5.3	249	Ecotone-semiclosed
	074	2013-07-08	816038	1606053	M	Adult	37.9	640	Dipterocarp
	075	2013-07-27	812397	1607168	M	Adult	24.6	520	Plantation-forest
	076	2013-08-07	814910	1605169	M	Adult	23.2	516	Evergreen Forest
	077	2013-08-12	815861	1606228	F	Adult	26	552	Dipterocarp
	078	2013-09-05	815893	1606228	M	Adult	24.6	565	Mixed-deciduous
	079	2013-08-30	816051	1606041	F	Neonate	8	326	Dipterocarp
	080	2013-08-31	812397	1607168	F	Adult	50.9	640	Plantation-forest
	081	2013-08-25	816037	1606043	M	Neonate	9.7	364	Dipterocarp

Table B-1 (Continued).

			UTM coordinates						
Species	**Snake ID**	**Capture date**	**x**	**y**	**Sex**	**Age Class**	**Mass (g)**	**TBL (mm)**	**Ecotype at Capture**
TRMA	082	2013-08-30	815893	1606228	F	Neonate	10	378	Dipterocarp
	083	2013-08-30	816038	1606053	F	Neonate	11.7	362	Evergreen Forest
	084	2013-09-11	815758	1605981	F	Neonate	8.8	299	Dipterocarp
	085	2013-09-09	815942	1606223	M	Adult	28.7	679	Evergreen Forest
	086	2013-09-05	815958	1606225	M	Adult	30.2	714	Mixed-deciduous
	087	2013-09-12	815871	1606240	F	Juvenile	13.5	394	Mixed-deciduous
	088	2013-09-19	815868	1606214	F	Adult	33.49	778	Mixed disturbed
	089	2013-10-11	815968	1605178	F	Adult	32.2	649	Mixed-deciduous
	090	2013-10-12	815930	1606264	F	Adult	46.2	636	Mixed-deciduous
	091	2013-09-20	815357	1604301	F	Adult	24.3	578	Evergreen Forest
	092	2013-10-20	815946	1606211	M	Adult	22.9	547	Evergreen Forest
	093	2013-10-20	815876	1606166	M	Adult	33.2	609	Mixed-deciduous
	094	2013-11-03	814398	1604163	F	Adult	41.7	589	Evergreen Forest
	095	2013-11-02	815943	1606205	F	Adult	56.85	596	Mixed-deciduous
	096	2013-11-06	815336	1604283	F	Adult	44.2	592	Evergreen Forest
	097	2014-11-06	814302	1604709	F	Adult	82.1	752	Evergreen Forest
	098	2013-11-06	814281	1604698	M	Adult	33.9	594	Evergreen Forest

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	UTM coordinates y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	100	2013-11-07	815964	1606234	F	Juvenile	-	-	Mixed-deciduous
	101	2013-11-07	816003	1606136	M	Adult	16.7	531	Mixed-deciduous
	102	2013-11-07	816043	1606220	F	Adult	98.05	740	Evergreen Forest
	103	2013-11-07	816055	1606072	F	Adult	49.2	577	Evergreen Forest
	104	2013-11-07	815979	1606038	F	Juvenile	16.5	407	Evergreen Forest
	105	2013-11-07	816018	1606014	M	Adult	16.5	462	Evergreen Forest
	106	2013-11-08	814226	1604686	M	Adult	36.3	587	Evergreen Forest
	107	2013-11-08	814230	1604694	F	Adult	42.9	651	Evergreen Forest
	108	2013-11-08	814207	1604664	M	Adult	47.6	717	Evergreen Forest
	109	2013-11-08	814227	1604684	M	Adult	28.9	542	Mixed-deciduous
	110	2013-11-11	814662	1605645	M	Adult	49.5	577	Evergreen Forest
	111	2013-11-12	815973	1605224	Unknown	Juvenile	14.8	415	Mixed-deciduous
	112	2013-11-19	815862	1606175	F	Adult	-	572	Mixed-deciduous
	113	2013-11-21	815974	1606041	F	Adult	41.1	567	Evergreen Forest
	114	2013-11-29	814221	1604673	M	Adult	32.4	578	Evergreen Forest
	115	2013-12-15	814367	1604648	F	Adult	52.4	560.5	Evergreen Forest

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	 y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	116	2013-12-16	814399	1604700	F	Adult	82.7	663	Evergreen Forest
	117	2014-03-15	816035	1606078	M	Juvenile	15.2	448	Mixed-deciduous
	118	2014-03-22	815968	1606234	M	Adult	20.5	488	Mixed-deciduous
	119	2014-04-01	-	-	M	Adult	20.3	487	Ecotone-semiclosed
	120	2014-04-21	814217	1604664	F	Adult	27.5	570	Evergreen Forest
	121	2014-04-21	816034	1606043	M	Adult	33.6	593	Ecotone-semiclosed
	122	2014-04-21	814250	1604669	M	Adult	46.5	668	Evergreen Forest
	123	2014-04-29	814278	1604322	M	Adult	18.1	452	Evergreen Forest
	124	2014-04-29	814231	1604603	M	Adult	39.2	615	Evergreen Forest
	125	2014-04-29	814298	1604655	M	Adult	28.3	562	Evergreen Forest
	126	2014-04-29	814277	1604698	M	Adult	25.7	548	Evergreen Forest
	127	2014-04-30	815884	1606142	M	Adult	27.2	566	Mixed-deciduous
	128	2014-04-30	815917	1606234	M	Adult	32.2	590	Mixed-deciduous
	129	2014-05-03	814216	1604667	M	Adult	28.7	534	Evergreen Forest
	130	2014-05-03	816050	1606074	F	Adult	35.8	580	Evergreen Forest
	132	2014-07-25	815901	1606202	F	Adult	45.2	656	Mixed-deciduous

Table B-1 (Continued).

			UTM coordinates						
Species	**Snake ID**	**Capture date**	**x**	**y**	**Sex**	**Age Class**	**Mass (g)**	**TBL (mm)**	**Ecotype at Capture**
TRMA	133	2014-05-20	815926	1606209	F	Adult	24.3	519	Evergreen Forest
	134	2014-05-20	816049	1606090	F	Adult	21.1	491	Mixed-deciduous
	135	2014-05-22	815854	1606126	F	Adult	38.3	733	Mixed-deciduous
	136	2014-05-23	814433	1605466	M	Adult	40.6	639	Evergreen Forest
	137	2014-05-30	814326	1604678	M	Adult	24.4	538	Evergreen Forest
	138	2014-06-04	815947	1606197	M	Adult	24	512	Mixed-deciduous
	139	2014-06-04	815904	1606224	Unknown	Neonate	4.7	272	Mixed-deciduous
	140	2014-06-05	816023	1606101	F	Adult	28.6	546	Evergreen Forest
	141	2014-06-05	816036	1606021	F	Adult	25.5	541	Evergreen Forest
	142	2014-06-06	816059	1606069	Unknown	Neonate	3.8	242	Mixed-deciduous
	143	2014-06-06	815902	1606240	F	Adult	85	791	Mixed-deciduous
	144	2014-06-19	814245	1604708	M	Adult	30.8	601	Evergreen Forest
	145	2014-06-22	814384	1604698	F	Adult	24.1	504	Evergreen Forest
	146	2014-06-24	814337	1604651	M	Adult	23.6	519	Evergreen Forest
	147	2014-06-27	815221	1606117	F	Adult	27.1	582	Ecotone-open
	148	2014-06-27	816606	1606114	F	Adult	29.8	528	Mixed-deciduous

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates		Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
			X	y					
TRMA	149	2014-06-27	816047	1606123	F	Adult	39.3	600	Mixed-deciduous
	150	2014-07-05	-	-	M	Adult	23.7	518	Mixed-deciduous
	151	2014-07-09	815903	1606226	M	Adult	31.8	607	Mixed-deciduous
	152	2014-07-10	815873	1606145	Unknown	Adult	51.9	619	Mixed-deciduous
	153	2014-07-10	815315	1605253	Unknown	Neonate	2	214	Evergreen Forest
	154	2014-07-13	815675	1606139	Unknown	Neonate	5	263	Mixed-deciduous
	155	2014-07-13	815752	1605985	F	Adult	32.7	558	Roadside
	156	2014-07-14	815950	1606229	M	Adult	28.5	529	Human Settlement
	157	2014-07-19	814365	1604652	F	Neonate	5	269	Evergreen Forest
	158	2014-07-20	814616	1604244	F	Adult	47.8	691	Evergreen Forest
	159	2014-07-20	815042	1604067	F	Adult	21.3	520	Evergreen-closed
	160	2014-07-21	815907	1606224	F	Juvenile	11.4	334	Mixed-deciduous
	161	2014-07-25	814384	1604694	F	Neonate	6.4	268	Evergreen Forest
	162	2014-07-25	815775	1606029	M	Neonate	4.9	349	Evergreen Forest
	163	2014-08-17	814461	1604376	F	Adult	39.4	638	Evergreen Forest
	164	2014-08-23	814622	1604227	F	Adult	50.4	648	Evergreen Forest

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	UTM coordinates y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	165	2014-08-29	815947	1606228	M	Adult	34.9	662	Mixed-deciduous
	166	2014-09-03	815958	1606219	F	Juvenile	7.5	305	Mixed-deciduous
	167	2014-09-06	818155	1605492	F	Juvenile	9.3	333	Agricultural
	168	2014-09-06	818117	1605527	M	YoY	5.8	301	Agricultural
	169	2014-09-06	818094	1605612	F	Neonate	6.3	161	Agricultural
	170	2014-09-08	814401	1604325	F	Neonate	3.5	241	Evergreen Forest
	171	2014-09-23	814544	1604959	M	Adult	34	642	Evergreen Forest
	172	2014-09-26	81439	1604690	M	Juvenile	10.9	348	Evergreen Forest
	173	2014-09-28	816025	1606134	F	Adult	15.4	434	Mixed-deciduous
	174	2014-10-02	814691	1604124	F	Adult	44.5	638	Evergreen-closed
	175	2014-10-13	815932	1606228	M	Adult	26.2	571	Mixed-deciduous
	176	2014-10-04	816081	1606521	M	Adult	8.3	458	Mixed-deciduous
	177	2014-10-10	816049	1606113	M	Adult	31	596	Mixed-deciduous
	178	2014-10-03	814340	1604291	F	Adult	32.1	620	Evergreen-closed
	179	2014-10-15	814386	1604384	M	Adult	22.7	540	Evergreen Forest
	175	2014-10-13	815932	1606228	M	Adult	26.2	571	Mixed-deciduous

Table B-1 (Continued).

Species	Snake ID	Capture date	UTM coordinates x	UTM coordinates y	Sex	Age Class	Mass (g)	TBL (mm)	Ecotype at Capture
TRMA	176	2014-10-04	816081	1606521	M	Adult	8.3	458	Mixed-deciduous
	177	2014-10-10	816049	1606113	M	Adult	31	596	Mixed-deciduous
	178	2014-10-03	814340	1604291	F	Adult	32.1	620	Evergreen-closed
	179	2014-10-15	814386	1604384	M	Adult	22.7	540	Evergreen Forest
	180	2014-10-17	-	-	M	Adult	26.5	570	Evergreen Forest
	181	2014-10-18	815820	1606125	M	Adult	24	553	Mixed-deciduous
	182	2014-10-18	815907	1606195	F	Adult	26.5	600	Mixed-deciduous
	183	2014-10-20	816038	1606043	F	Juvenile	13.6	408	Mixed-deciduous
	184	2014-10-28	818187	1605574	Unknown	Adult	61.6	638	Plantation-forest
	185	2014-10-29	818194	1605498	M	Adult	33.8	653	Mixed-deciduous
	186	2014-11-05	814315	1604427	F	Adult	45.8	646	Evergreen Forest
	187	2014-11-10	816002	1606038	M	Adult	13.5	564	Evergreen Forest
	188	2014-11-19	814679	1605645	F	Adult	65.6	691	Evergreen Forest
	189	2014-12-01	815952	1606162	F	Adult	50.4	571	Human Settlement
	190	2014-12-01	814411	1604664	F	Juvenile	8.1	326	Evergreen Forest
	191	2014-12-01	814405	1604650	M	Juvenile	8.6	364	Roadside

Table B-1 (Continued).

			UTM coordinates						
Species	**Snake ID**	**Capture date**	**x**	**y**	**Sex**	**Age Class**	**Mass (g)**	**TBL (mm)**	**Ecotype at Capture**
TRMA	192	2014-12-02	-	-	M	Adult	41.1	652	Evergreen Forest
	193	2014-12-02	814921	1604083	F	Adult	50	559	Evergreen Forest
TRVO	001	2013-10-07	812397	1607168	M	Adult	35.3	598	Evergreen Forest
	002	2014-07-12	814368	1604310	F	Adult	104.2	835	Evergreen Forest
	003	2014-07-20	814760	1604134	F	Adult	-	-	Evergreen Forest
	004	2014-09-12	814603	1604267	F	Adult	76.5	761	Evergreen Forest
TRAL	001	2012-08-28	813849	1603646	M	Adult	33	540	Plantation-forest
	002	2012-09-29	818155	1606100	F	Adult	90.4	779	Dipterocarp
	003	2013-03-30	812798	1605598	M	Adult	20.7	470	Plantation-forest
	004	2013-05-31	815479	1609699	F	Adult	30.5	495	Dipterocarp
	005	2013-08-17	810693	1604910	F	Neonate	4.8	246	Plantation-forest
	006	2013-08-17	813887	1603630	F	Adult	122.9	905	Evergreen Forest
	007	2013-09-27	817443	1606044	M	Adult	70.7	460	Evergreen Forest
	008	2013-12-06	-	-	M	Adult	24.9	556	Plantation-forest
	009	2014-10-28	818187	1605574	M	Adult	29	541	Plantation-forest

Table B-2 All *Trimeresurus* sp. recaptures (n = 81) during the study period from May 2012 to January 2015.

Species	Snake ID	Capture date	UTM Coordinates x	UTM Coordinates y	Sex	Age Class	Mass (g)	TBL(mm)	Ecotype at Capture
TRMA	006	2013-10-20	815876	1606166	F	Adult	81.8	741	Mixed-deciduous
	014	2013-05-27	816055	1606034	F	Adult	41.8	635	Evergreen forest
	020	2013-11-21	815996	1606034	M	Adult	31.8	609	Mixed-deciduous
	020	2014-05-03	816043	1606044	M	Adult	33.3	615	Mixed-deciduous
	024	2014-04-30	816049	1606028	F	Adult	67.4	674	Evergreen forest
	024	2014-06-05	816049	1606045	F	Adult	47.5	673	Evergreen forest
	025	2013-05-01	815994	1606053	F	Adult	41.3	458	Human Settlement
	026	2013-07-05	816039	1606037	M	Adult	40.3	663	Evergreen forest
	026	2013-08-16	815950	1606234	M	Adult	34.8	662	Dipterocarp
	027	2013-11-18	815876	1606157	F	Adult	67.4	671	Mixed-deciduous
	028	2013-05-22	815857	1605929	M	Adult	25.2	537	Dipterocarp
	028	2013-09-11	815758	1605981	M	Adult	28.4	578	Evergreen forest
	029	2013-06-13	815978	1606078	F	Adult	51.4		Dipterocarp
	029	2013-11-21	815976	1606037	F	Adult	62.8	649	Evergreen forest
	031	2013-03-04	814268	1604665	F	Adult	18	460	Dipterocarp
	031	2013-11-06	814251	1604687	F	Adult	55	602	Evergreen forest
	039	2013-09-22	816038	1606053	M	Adult	27.5	571	Dipterocarp
	039	2014-03-15	816035	1606043	M	Adult	28.3	574	Mixed-deciduous
	039	2014-04-21	816019	1606043	M	Adult	27.4	588	Mixed-deciduous

* TBL (Total body length),

Table B-2 (Continued).

Species	Snake ID	Capture date	UTM Coordinates x	y	Sex	Age Class	Mass g	TBL(mm)	Ecotype at Capture
	039	2014-07-13	816056	1606054	M	Adult	29.8	606	Evergreen forest
	040	2013-05-01	816049	1606059	F	Adult	28.5	521	Evergreen forest
	040	2013-12-10	816059	1606073	F	Adult	44.2	575	Evergreen forest
	041	2014-10-10	816049	1606113	F	Adult	50.1	630	Mixed-deciduous
	046	2013-05-01	816049	1606049	F	Adult	28.5	610	Dipterocarp
	046	2013-12-01	816048	1606246	F	Adult	64.8	616	Dipterocarp
	047	2014-10-10	816049	1606113	F	Adult	55.7	659	Mixed-deciduous
	048	2014-06-10	816657	1606098	F	Adult	62.5	685	Mixed-deciduous
	051	2014-05-05	-	-	M	Adult	32.2	610	Mixed-deciduous
	069	2013-11-07	815925	1606039	F	Adult	61.8	743	Evergreen forest
	072	2013-09-14	815946	1606223	M	Neonate	10.5	375	Dipterocarp
	074	2013-08-03	816041	1606010	M	Adult	28.2	636	Dipterocarp
	079	2014-04-21	816043	1606041	F	Neonate	9.3	353	Evergreen forest
	080	2013-12-06	815853	1606167	F	Adult	59.3	622	Human Settlement
	086	2013-10-13	815927	1606262	M	Adult	30.4	714	Mixed-deciduous
	088	2014-02-18	815892	1606144	F	Adult	72.8	672	Mixed-deciduous
	088	2014-07-05	-	-	F	Adult	55.6	696	Mixed-deciduous

Table B-2 (Continued).

Species	Snake ID	Capture date	UTM Coordinates		Sex	Age Class	Mass g	TBL(mm)	Ecotype at Capture
			x	y					
	090	2014-02-19	815881	1606239	F	Adult	48.5	605	Mixed-deciduous
	090	2014-06-01	815921	1606247	F	Adult	45.6	622	Mixed-deciduous
	092	2013-11-08	815904	1606206	M	Adult	25.9	548	Mixed-deciduous
	092	2014-07-04	816037	1606118	M	Adult	33.9	603	Mixed-deciduous
	095	2014-12-26	-	-	F	Adult	32.3	598	Human Settlement
	096	2014-02-07	-	-	F	Adult	39.2	594	Evergreen forest
	098	2014-03-11	-	-	M	Adult	31.8	596	Evergreen forest
	098	2014-04-20	814265	1604703	M	Adult	33.4	603	Evergreen forest
	100	2014-06-02	815908	1606247	F	Adult	23.5	531	Mixed-deciduous
	102	2014-02-28	815961	1606202	F	Adult	87.6	738	Mixed-deciduous
	102	2014-05-13	815988	1606143	F	Adult	56.5	740	Mixed-deciduous
	102	2014-06-01	815904	1606224	F	Adult	56.8	738	Mixed-deciduous
	104	2013-12-15	-	-	F	Juvenile	16.8	410	Mixed-deciduous
	104	2014-05-03	815999	1606042	F	Adult	24.6	490	Mixed-deciduous
	106	2013-12-16	814251	1604710	M	Adult	37.1	584	Evergreen forest
	111	2014-07-19	815773	1606023	F	Adult	40.9	622	Evergreen forest

Table B-2 (Continued).

Species	Snake ID	Capture date	UTM Coordinates x	UTM Coordinates y	Sex	Age Class	Mass (g)	TBL(mm)	Ecotype at Capture
	111	2014-10-20	815886	1606213	F	Adult	50.8	644	Mixed-deciduous
	116	2014-06-19	814270	1604725	F	Adult	62.3	666	Evergreen forest
	116	2015-01-10	-	-	F	Adult	71.9	671	Evergreen forest
	119	2014-04-20	814271	1604731	M	-	-	-	Ecotone-semiclosed
	127	2014-09-09	815947	1606225	M	Adult	31.15	600	Mixed disturbed
	127	2014-10-27	-	-	M	Adult	29.3	606	Mixed-deciduous
	128	2014-07-11	815949	1606213	M	Adult	29.7	600	Mixed-deciduous
	132	2014-10-24	815943	1606183	F	Adult	57.3	677	Mixed-deciduous
	133	2014-06-30	815929	1606225	F	Adult	27.6	557	Mixed-deciduous
	133	2014-10-10	815938	1606210	F	Adult	40.7	680	Mixed-deciduous
	137	2014-09-05	814289	1604685	M	Adult	27.9	549	Evergreen forest
	141	2014-07-13	815983	1605921	F	Adult	25.3	544	Bamboo
	142	2014-07-04	816065	1606050	F	Neonate	5.8	294	Mixed-deciduous
	142	2014-08-19	816072	1606059	M	Young of Year	15.1	353	Evergreen forest
	145	2014-10-03	814442	1604570	F	Adult	25.3	533	Evergreen-closed
	146	2014-09-05	814237	1604670	M	Adult	25.3	538	Evergreen forest

Table B-2 (Continued).

Species	Snake ID	Capture date	UTM Coordinates		Sex	Age Class	Mass(g)	TBL(mm)	Ecotype at Capture
			x	y					
	156	2014-10-12	815951	1606181	M	Adult	23.9	553	Mixed disturbed
	161	2014-09-09	815356	1604659	F	Neonate	8.6	315	Evergreen forest
	169	2014-10-11	818172	1605554	F	Juvenile	6.6	302	Agricultural
	172	2014-10-27	814391	1604690	M	Juvenile	9.4	360	Evergreen forest
	174	2014-10-29	814691	1604160	F	Adult	42.1	634	Evergreen forest
	178	2014-11-08	814481	1604360	F	Adult	53.1	696	Evergreen forest
	178	2015-01-15	814407	1604423	F	Adult	47.3	634	Evergreen forest
	186	2015-01-15	814337	1604381	F	Adult	63.3	694	Evergreen forest
TRVO	003	2014-12-06	814634	1604113	F	Adult	107.4	854.1	Evergreen forest
	002	2014-12-07	814385	1604310	F	Adult	109.7	867	Evergreen forest
TRAL	006	2013-11-20	813811	1603685	F	Adult	205.3	943	Evergreen forest
	006	2014-01-27		-	F	Adult	191.1	942	Evergreen forest
	006	2014-03-06	-	-	F	Adult	194.7	948	Evergreen forest

APPENDIX C

GENERALIZED LINEAR MIXED MODEL RESULTS

Table C-1 Candidate set of 16 GLMM of environmental variables fitted to explain the occurrence of resting behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAICc**	**wi**	**Cum.wi**	**LL**
1	Ambient temp + Relative humidity, ground	4	683.84	0	0.26	0.26	-34338
2	Temp, ground+ Relative humidity,ground	4	684.33	0.49	0.21	0.47	-338.1
3	Ambient temp + Temperature, ground + Relative humidity,ground	5	685.47	1.63	0.12	0.59	-337.7
4	Ambient relative humidity + Ambient temp + Relative humidity	5	685.5	1.66	0.12	0.7	-337.7
5	Ambient relative humidity+Ambient temp	4	685.56	1.72	0.11	0.82	-338.8
6	Ambient relative humidity+ Temp, ground +Relative humidity ground	5	686.36	2.52	0.08	0.89	-338.1
7	Ambient relative humidity+Ambient temp+Temp,ground+Relative humidity, ground	6	687.34	3.49	0.05	0.94	-337.6
8	Ambient relative humidity+Ambient temp+Temp,ground	5	687.58	3.74	0.04	0.98	-338.7
9	Ambient relative humidity+ Ambient temp	4	688.97	5.13	0.02	1	-340.5
10	Relative humidity, ground	3	697.27	13.42	0	1	-345.6
11	Ambient relative humidity+ Relative humidity, ground	4	699.12	15.27	0	1	-345.5
12	Ambient relative humidity	3	702.56	18.72	0	1	-348.3
13	Ambient temp	3	703.76	19.91	0	1	-348.9
14	Temp, ground	3	705.21	21.36	0	1	-349.6
15	Ambient temp + Temp, ground	4	705.75	21.9	0	1	-348.8
16	Base model	2	714.47	30.63	0	1	-355.2

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models with 0 ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support Ambient temperature is temperature at 120 cm, Ambient relative humidity is at 120 cm, Ground temperature is temp at 1 cm from ground, and 1 ground relative humidity is taken at 1 cm with a Kestrel 3000.

Table C-2 Candidate set of 16 GLMM of environmental variables fitted to explain the occurrence of ambushing behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAICc**	**wi**	**Cum.wi**	**LL**
1	Relative humidity, ground	3	708.62	0	0.35	0.35	-351.29
2	Temp, ground + Relative humidity,ground	4	710.2	1.59	0.16	0.51	-351.07
3	Ambient temp+ Relative humidity,ground	4	710.47	1.85	0.14	0.65	-351.2
4	Relative humidity, ground + Ambient, relative humidity	4	710.59	1.97	0.13	0.78	-351.26
5	Ambient temp + Temp, ground +Relative humidity,ground	5	711.98	3.37	0.07	0.85	-350.94
6	Ambient, relative humidity + Temp, ground + Relative humidity,ground	5	712.14	3.53	0.06	0.91	-351.02
7	Ambient, relative humidity + Ambient temp + Relative humidity,ground	5	712.37	3.75	0.05	0.96	-351.14
8	Ambient, relative humidity +Ambient temp+Temp ground+ Relative humidity,ground	6	714.02	5.4	0.02	0.98	-350.94
9	Ambient, relative humidity	3	716.6	7.99	0.01	0.99	-355.28
10	Ambient, relative humidity + Ambient temp + Temp ground	5	717.69	9.07	0	0.99	-353.8
11	Ambient, relative humidity + Temp ground	4	718.37	9.75	0	1	-355.15
12	Ambient, relative humidity + Ambient temp	4	718.62	10	0	1	-355.28
13	Base model	2	737.97	29.35	0	1	-366.97
14	Temp ground	3	738.51	29.89	0	1	-366.24
15	Temp, ground	3	739.42	30.81	0	1	-366.69
16	Ambient temp + Temp ground	4	739.53	30.92	0	1	-365.73

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models with 0 ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support Ambient temperature is temperature at 120 cm, Ambient relative humidity is at 120 cm, Ground temperature is temp at 1 cm from ground, and 1 ground relative humidity is taken at 1 cm with a Kestrel 3000.

Table C-3 Candidate set of 16 GLMM of environmental variable fitted to explain the occurrence of sheltered behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAICc**	**wi**	**Cum.wi**	**LL**
1	Ambient temp + Relative humidity,ground	4	613.1	0	0.41	0.41	-302.52
2	Relative humidity,ground + Ambient temp + Ambient, relative humidity	5	614.45	1.34	0.21	0.62	-302.18
3	Ambient temp + Temp, ground + Relative humidity,ground	5	615.12	2.02	0.15	0.77	-302.51
4	Temp, ground + Relative humidity,ground	4	615.71	2.61	0.11	0.88	-303.82
5	Ambient, relative humidity + Ambient temp + Temp, ground + Relative humidity,ground	6	616.46	3.36	0.08	0.96	-302.17
6	Ambient, relative humidity + Ambient, relative humidity + Relative humidity,ground	5	617.73	4.63	0.04	1	-303.82
7	Ambient, relative humidity + Ambient temp + Temp, ground	5	628.35	15.25	0	1	-309.13
8	Ambient, relative humidity + Ambient temp	4	628.95	15.84	0	1	-310.44
9	Relative humidity,ground	3	637.21	24.11	0	1	-315.59
10	Ambient, relative humidity + Relative humidity,ground	4	639.05	25.94	0	1	-315.49
11	Ambient, relative humidity + Temp, ground	4	640.2	27.1	0	1	-316.07
12	Ambient, relative humidity	3	661.7	48.6	0	1	-327.83
13	Ambient temp	3	724.92	111.82	0	1	-359.44
14	Ambient temp + Temp, ground	4	725.73	112.63	0	1	-358.84
15	Temp, ground	3	728.71	115.61	0	1	-361.34
16	Base model	2	734.66	121.56	0	1	-365.32

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models with 0 ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support Ambient temperature is temperature at 120 cm, Ambient relative humidity is at 120 cm, Ground temperature is temp at 1 cm from ground, and 1 ground relative humidity is taken at 1 cm with a Kestrel 3000.

Table C-4 Candidate set of 14 GLMM of temporal and spatial variables fitted to explain the occurrence of sheltered behavior of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAIC**	**w_i**	**Cum.w_i**	**LL**
1	SiteID + Habitat + Cycle + Season	10	883.52	0.00	0.64	0.64	-431.63
2	SiteID + Cycle + Habitat	8	885.56	2.05	0.23	0.87	-434.70
3	Season + Cycle	6	889.26	5.74	0.04	0.91	-438.58
4	Cycle	4	889.67	6.15	0.03	0.94	-440.81
5	Habitat + Cycle	7	889.99	6.47	0.03	0.96	-437.93
6	Season + Cycle + Habitat	9	890.43	6.91	0.02	0.98	-436.11
7	Site + Cycle	6	891.00	7.48	0.02	1.00	-439.45
8	Site + Season + Habitat	8	972.28	88.76	0.00	1.00	-478.06
9	Base model	2	974.12	90.60	0.00	1.00	-485.05
10	Site + Season	6	974.77	91.25	0.00	1.00	-481.34
11	Site	4	974.95	91.43	0.00	1.00	-483.45
12	Season	4	975.02	91.50	0.00	1.00	-483.49
13	Habitiat + Season	7	978.17	94.65	0.00	1.00	-482.02
14	Habitat	4	978.17	94.65	0.00	1.00	-482.02

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models with 0 ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support .Site is the area where snakes were tracked in Field Station, Deep Forest, or Water Associated. Season is the season based on rainfall and temperature (Dry, Rainy, or Cold). The cycle is the time at which the snake was spotted (Day or Night), The habitat was the habitat type.

Table C-5 Candidate set of 14 GLMM of temporal and spatial variables fitted to explain the occurrence of sheltered behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAIC**	**w_i**	**Cum.w_i**	**LL**
1	Site + Cycle	6	876.48	0.00	0.47	0.47	-432.19
2	Site + Cycle + Habitat	8	878.34	1.85	0.19	0.66	-431.09
3	Habitats + Cycle	7	878.51	2.02	0.17	0.83	-432.19
4	Cycle	4	879.88	3.39	0.09	0.91	-435.91
5	Site + Habitat + Cycle + Season	10	881.06	4.57	0.05	0.96	-430.40
6	Season + Cycle + Habitat	9	882.24	5.76	0.03	0.99	-432.02
7	Season + Cycle	6	883.88	7.40	0.01	1.00	-435.89
8	Season	4	1018.64	142.16	0.00	1.00	-505.30
9	Site + Season	6	1022.01	145.52	0.00	1.00	-504.96
10	Site + Season + Habitat	8	1022.23	145.74	0.00	1.00	-503.03
11	Habitat + Season	7	1023.28	146.80	0.00	1.00	-504.58
12	Habitat	4	1023.28	146.80	0.00	1.00	-504.58
13	Base model	2	1027.14	150.65	0.00	1.00	-511.56
14	Season	4	1029.74	153.26	0.00	1.00	-510.85

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models 0 with ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support .Site is the area where snakes were tracked in Field Station, Deep Forest, or Water Associated. Season is the season based on rainfall and temperature (Dry, Rainy, or Cold). The cycle is the time at which the snake was spotted (Day or Night), The habitat was the habitat type.

Table C-6 Candidate set of 14 GLMM of temporal and spatial variables fitted to explain the occurrence of sheltered behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAIC**	**w_i**	**Cum.w_i**	**LL**
1	Site + Habitat + Cycle + Season	10	877.67	0.00	1.00	1.00	-428.71
2	Site + Season + Habitat	8	891.94	14.28	0.00	1.00	-437.89
3	Season + Cycle + Habitat	9	893.94	16.28	0.00	1.00	-437.87
4	Season + Cycle	6	901.74	24.07	0.00	1.00	-444.82
5	Site + Season	6	906.21	28.54	0.00	1.00	-447.06
6	Season + Habtiat	7	908.36	30.70	0.00	1.00	-447.12
7	Habitat	4	908.36	30.70	0.00	1.00	-447.12
8	Site + Cycle + Habitat	8	915.95	38.29	0.00	1.00	-449.89
9	Season	4	917.10	39.44	0.00	1.00	-454.53
10	Habitat+ Cycle	7	919.11	41.45	0.00	1.00	-452.49
11	Cycle	4	927.75	50.09	0.00	1.00	-459.85
12	Site + Cycle	6	930.73	53.06	0.00	1.00	-459.31
13	Base model	2	947.91	70.24	0.00	1.00	-471.95
14	Site	4	951.37	73.70	0.00	1.00	-471.66

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models 0 with ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support .Site is the area where snakes were tracked in Field Station, Deep Forest, or Water Associated. Season is the season based on rainfall and temperature (Dry, Rainy, or Cold). The cycle is the time at which the snake was spotted (Day or Night), The habitat was the habitat type.

Table C-7 Candidate set of 14 GLMM of temporal and spatial variables fitted to explain the occurrence of sheltered behaviour of radio tracked *T. macrops.*

	Variables	**K**	**AICc**	**ΔAIC**	**w_i**	**Cum.w_i**	**LL**
1	Site + Habitat + Cycle + Season	10	877.67	0	1	1	-428.71
2	Site + Season + Habitat	8	891.94	14.28	0	1	-437.89
3	Season + Cycle + Habitat	9	893.94	16.28	0	1	-437.87
4	Season + Cycle	6	901.74	24.07	0	1	-444.82
5	Site + Season	6	906.21	28.54	0	1	-447.06
6	Season + Habitat	7	908.36	30.7	0	1	-447.12
7	Habitat	4	908.36	30.7	0	1	-447.12
8	Site + Cycle + Habitat	8	915.95	38.29	0	1	-449.89
9	Season	4	917.1	39.44	0	1	-454.53

Note: LL is log-likelihood: K is the number of parameters in the model ΔAICc is the difference in the AICc (model score), models with 0 ΔAIC have the most support, values between 0 and 2 have substantial support, values that have greater than 2 have less support .Site is the area where snakes were tracked in Field Station, Deep Forest, or Water Associated. Season is the season based on rainfall and temperature (Dry, Rainy, or Cold). The cycle is the time at which the snake was spotted (Day or Night), The habitat was the habitat type.

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Publications

Strine C.T. Silva I., Crane M., Nadolski B., Artchawakom T., Goode M., and Suwanwaree P. (2014) Mortality of a Wild King Cobra, *Ophiophagus hannah* Cantor 1836 (Serpentes: Elapidae) from Northeast Thailand after ingesting a plastic bag. **Journal of Asian Herpetological Research**. 5(4): 284-286.

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