THE SPATIAL ECOLOGY, HABITAT SELECTION, AND BEHAVIOR OF BIG EYE PIT VIPERS (*TRIMERESURUS MACROPS*) IN HUMAN DOMINATED AND PROTECTED AREAS IN THE SAKAERAT BIOSPHERE RESERVE

Curt Hrad Barnes

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science in Environmental Biology

Suranaree University of Technology

Academic Year 2016

การศึกษานิเวศวิทยาเชิงพื้นที่การเลือกแหล่งที่อยู่อาศัย และพฤติกรรมของงูเขียวหางไหม้ตาโตในเขตที่อยู่อาศัยและเขตคุ้มครอง ณ พื้นที่สงวนชีวมณฑลสะแกราช

นายเคิร์ท ฮแรด บาร์นส

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต

สาขาวิชาชีววิทยาสิ่งแวดล้อม

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ปีการศึกษา 2559

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Suranaree University of Technology has approved this thesis submitted in partial fulfillment of the requirements for a Master's Degree.

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นายเคิร์ท ฮแรด บาร์นส : การศึกษานิเวศวิทยาเชิงพื้นที่การเลือกแหล่งอยู่อาศัย และพฤติกรรมของงูเขียวหางไหม้ตาโตในเขตที่อยู่อาศัยและเขตคุ้มครอง ณ พื้นที่สงวนชีวมณฑลสะแกราช (THE SPATIAL ECOLOGY, HABITAT SELECTION, AND BEHAVIOR OF BIG- EYE PIT VIPERS (*TRIMERESURUS MACROPS*) IN HUMAN DOMINATED AND PROTECTED AREAS IN THE SAKAERAT BIOSPHERE RESERVE). อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน โทมัส สไตร์น. 141 หน้า.

งูเขียวหางไหม้/การรบกวน/การอาศัย/การใช้พื้นที่/แหล่งอาศัย/พฤติกรรม

ถึงแม้ว่าจะมีการถูกคุกคามมากมายในภูมิภาคเอเชียตะวันออกเฉียงใต้ แต่การศึกษาเกี่ยวกับธรรมชาติวิทยา ในการค้นคว้าข้อมูลต่อสัตวชาติในแหล่งอาศัยของมนุษย์กลับมีน้อยมาก ชุมชนในถิ่นทุรกันดารและพื้นที่เกษตรกรรมถือเป็นพื้นที่ที่มีความสำคัญต่อความหลากหลายทางชีวภาพเป็นอย่างมาก กระนั้นยังมีค่าความเสี่ยงต่อการถูกกัดจากอยู่มีพิษสูงด้วยเช่นกัน งานวิจัยชิ้นนี้รวบรวมข้อมูลธรรมชาติวิทยาของงูเขียวหางไหม้ในพื้นที่อาศัยของมนุษย์ตั้งแต่ เดือนพฤศจิกายน 2557 จนถึง เดือน มกราคม 2560 ณ พื้นที่สงวนชีวมณฑลสะแกราช ในภาคตะวันออกเฉียงเหนือของประเทศไทย ข้อมูลพื้นฐานในการดำรงชีวิตและการตอบสนองต่อการปรับเปลี่ยนพื้นที่ในถิ่นทุรกันดารถูกประเมินด้วยการสำรวจแบบพบเห็นตัวเพื่อค้นหาการอาศัยและการพบเจอ การติดตามด้วยคลื่นวิทยุของความหลากหลายทั้งเพศและชนิดของงูเขียวหางไหม้ ด้านการใช้แหล่งอาศัยถูกสังเกตด้วยการติดตามด้วยคลื่นวิทยุและการสำรวจ โดยการเทียบแหล่งอาศัยที่มีอยู่เดิมและการเลือกแหล่งอาศัย การประเมินพฤติกรรมทั่วไปถูกจัดเก็บผ่านการติดตามด้วยคลื่นวิทยุและการสำรวจ มีการติดตั้งกล้องเก็บข้อมูลใกล้กับงูเขียวหางไหม้ที่ถูกติดตามในพื้นที่ที่แตกต่างกันทั้งพื้นที่คุ้มครองและพื้นที่อาศัยของมนุษย์ภายในพื้นที่สงวนชีวมณฑลสะแกราช มีการจัดทำการสำรวจทั้งหมด 174 ครั้ง รวมเป็นระยะเวลา 480.5 ชั่วโมง ตั้งแต่เดือนกันยายน 2558 จนถึง เดือนพฤศจิกายน 2559 โดยพบเจองูเขียวหางไหม้ทั้งสิ้น 31 ตัว และมี 0.34 ± 0.15 ต่อพื้นที่อาศัยทั้งหมด และพื้นที่ที่มีความน่าจะเป็นอยู่ที่ 0.22 ± 0.04 งูเขียวหางไหม้ที่ถูกติดตามมีค่าเฉลี่ยอยู่ที่ 96.10 ± 9.54 วัน และ 97.79 ± 1.59 จุด การศึกษานิเวศวิทยาเชิงพื้นที่และการเคลื่อนที่ของงูเขียวหางไหม้ตาโต *(Trimeresurus macrops)* เพศเมียในพื้นที่อาศัยของมนุษย์และพื้นที่คุ้มครองไม่มีความแตกต่างที่มีนัยยะสำคัญแต่อย่างใด อย่างไรก็ตามการใช้แหล่งอาศัยของงูเขียวหางไหม้ตาโต (*T. macrops)* เพศเมีย กลับมีความแตกต่างในแหล่งอาศัยขนาดกลาง และแหล่งอาศัยขนาดย่อยทั้งในพื้นที่อาศัยของมนุษย์และพื้นที่คุ้มครอง และมีการใช้พื้นที่ป่าที่ถูกบุกรุกที่หลากหลายเป็นแหล่งอาศัยขนาดใหญ่ ณ

บริเวณพื้นที่ศึกษาในแหล่งชุมชน โดยงูเขียวหางไหม้ทั้งสองชนิดปรากฏตัวอยู่ทั้งแหล่งอาศัยขนาดกลางและย่อยในพื้นที่ศึกษาทั้งหมด งูเขียวหางไหม้ที่ถูกติดตามมีอัตราการเคลื่อนไหวที่สูงกว่าในพื้นที่คุ้มครองมากกว่าพื้นที่อาศัยของมนุษย์ โดยมีการบันทึกทั้งหมด 14,293 ครั้งเป็นระยะเวลาต่อหนึ่งนาทีแสดงให้เป็นว่าพวกมันใช้เวลาในการซุ่มโจมตีอย่างชัดเจนมากกว่าการลอบซุ่มโจมตี โดยงานวิจัยชิ้นนี้ เสนอว่างูเขียวหางไหม้ โดยเฉพาะงูเขียวหางไหม้ตาโต (*T. macrops*) อาจไม่มีผลกระทบที่เจาะจงต่อการบุกรุกของมนุษย์แต่อย่างไร แต่ควรมีการศึกษาต่อไปในภายภาคหน้าเพื่อที่จะสร้างความเข้าใจต่อการคงอยู่ของงูชนิดนี้ การศึกษานิเวศวิทยาเชิงพื้นที่และการเคลื่อนที่การเลือกแหล่งอาศัย และพฤติกรรมของงูเขียวหางไหม้ทั้งในพื้นที่คุ้มครองและพื้นที่อาศัยของมนุษย์สืบไป

สาขาวิชาชีววิทยา

ปีการศึกษา 2559

ลายเซ็นนักศึกษา Curt H. Barnes

ลายเซ็นอาจารย์ที่ปรึกษา ______

ลายเซ็นอาจารย์ที่ปรึกษาร่วม P. Suwan

CURT H. BARNES : THE SPATIAL ECOLOGY, HABITAT SELECTION, AND BEHAVIOR OF BIG- EYE PIT VIPERS (*TRIMERESURUS MACROPS*) IN HUMAN DOMINATED AND PROTECTED AREAS IN THE SAKAERAT BIOSPHERE RESERVE. THESIS ADVISOR : COLIN THOMAS STRINE, Ph.D. 141 PP.

VIPER/DISTURBANCE/OCCUPANCY/SPACE USE/HABITAT/BEHAVIOR

Despite facing a swathe of threats, Southeast Asia is underrepresented in natural history studies investigating faunal communities in human- modified landscapes. Rural communities and agricultural areas serve as important areas for biodiversity, although they also present the highest risk for venomous snakebite. Between November 2014- January 2017 this project assessed green pit viper natural history in human dominated and protected areas in the Sakaerat Biosphere of Northeast Thailand. Basic life history and response to rural- modified landscapes was assessed through multiple methods. Visual encounter surveys were used to determine occupancy and detection and radiotelemetry of multiple sex and species was conducted for home range and movement analysis. Habitat utilization observed during radiotelemetry and surveys was compared to transects to determine available habitat and habitat selection. Basic behavior was assessed during radio telemetry and surveys. Lastly, reviewing minimally invasive but intensive camera recordings set near tracked vipers was used to assess behavior in human dominated and protected habitats. A total of 174 surveys were conducted during 480.5 surveyor hours between September

2015- November 2016, with 31 vipers observed and 0.34 ± 0.15 sites occupied and detection probability of 0.22 ± 0.04. Green pit vipers were radiotracked for a mean of 96.10 ± 9.54 days and 97.79 ± 13.59 fixes. Spatial ecology and movement was not significantly different for female *Trimeresurus macrops* in human dominated and protected study areas. Tracked female *T. macrops* utilized habitat differently at meso- and microhabitat levels in human dominated and protected areas, and utilized heterogeneous disturbed forest habitat most frequently as macrohabitat in the human-dominated study area. These vipers also displayed meso- and microhabitat selection at both the study area and site levels. Tracked vipers were observed higher proportions of fixes active than sedentary in the protected area than human dominated area, and 14,293 scans at 1 minute intervals suggested that they also spent more time clearly ambushing than ambiguously ambushing. This study suggests that generally green pit vipers, particularly *T. macrops*, may not be significantly affected by disturbance but further work is required to better understand their persistence, spatial ecology and movement, habitat selection, and behavior in protected and rural human- modified landscapes.

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ACKNOWLEDGEMENTS

I would like to sincerely thank my thesis advisor, Dr. Colin Strine, for all of his support throughout the course of this project. I owe much gratitude to Dr. Pongthep Suwanwaree who was my initial thesis advisor upon admittance to Suranaree University of Technology, but nonetheless continued to support me through to the end of my thesis. Additionally, I would like to thank my proposal committee and my defense committee members: Dr. Nooduan Muangsan, Dr. Jacques Hill III, and Dr. Pongrit Krubphachaya for all of their suggestions and constructive criticism. I will remember the discussion during my thesis defense regarding the purpose and value of venomous snake and ecological research for many days to come.

I would like to further extend gratitude to Dr. Taksin Artchawakom, former Director of the Sakaerat Environmental Research Station (SERS), for his unending support and assistance. His passion and vision for ecological research and management at SERS were in a large part what made my project a reality. Dr. Surachit Waengsothorn, current (2016 -) Director of SERS, continued to provide valuable support and assistance in the later days of my project. Lastly, I owe many thanks to entire SERS staff who work tirelessly to make the research station one of the best in the world.

I would also like to thank the Sakaerat Conservation and Snake Education Team (SCSET), particularly leaders and graduate students Bartosz Nadolski, Inês Silva, Matthew Crane, Matthew Ward, and Tyler Knierim. Without their encouragement, guidance, and support I would not be where I am. Additionally, I want to thank Emilio Tan for assistance planning and helping carrying out many of my surveys during 2016, particularly those in the protected area of my study. My project would not have been possible without my field assistants Ana Pereira, Daphne Boulicault, Thomas Major, and William Farren who endured many long hours in the field straining their necks looking up in the forest canopy searching for vipers during surveys, listened to receiver beeps during radiotelemetry without losing their minds, suffered through dense thorn Moraceae patches while providing minimal threats of burning the forest down in retribution during habitat transects, and sat through hours of vipers anticipating their next meals on their computer screens. It was through their assistance and hard work my project became a reality. Also, I want to thank the multitude of SCSET volunteers who participated in my thesis at various stages and for moral support throughout.

I owe special thanks to Suranaree University of Technology for investing in my future through support and scholarship. I am grateful to the Thailand Institute of Scientific and Technological Research (TISTR) which recognized value in my research and chose to provide financial support as well as permissions. The National Research Council of Thailand (NRCT) provided funding for the human dominated area aspect of my project.

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LIST OF ABBREVIATIONS

AIC	=	Akaike's Information Criterion
DBH	=	Diameter at breast height
GLMM	=	Generalized linear mixed models
HDF	=	Heterogeneous disturbed forest
IUCN	=	International Union for Conservation of Nature
MCP	=	Minimum convex polygon
MDD	=	Mean daily displacement
SD	=	Standard deviation
SE	=	Standard Error
SERS	=	Sakaerat Environmental Research Station
SMI	=	Scaled mass index
SL	=	Supralabial
TISTR	=	Thailand Institute of Science and Technological Research
TRAL	=	*Trimeresurus albolabris*
TRMA	=	*Trimeresururs macrops*
TRVO	=	*Trimeresurus vogeli*
VES	=	Visual encounter survey

CHAPTER I

INTRODUCTION

1.1 Introduction

Over 18% of the 9,084 described reptile species are threatened with extinction worldwide (Böhm et al., 2013). Snake populations are thought to be in decline globally (Reading and Luiselli, 2010), highlighting the need for ecological study of this imperiled group. Snake populations face a wide array of extinction threats from a variety of anthropogenic activities. Species affected by anthropogenic habitat loss are particularly prevalent in Southeast Asia (Böhm et al., 2013). The impact of human-modified landscapes on snake space use, habitat selection, and behavior must be assessed to inform conservation action plans in the region.

Southeast Asia is a complex biodiversity hotspot which faces many threats, particularly deforestation and tree plantations, hunting and trade, mining, reservoir construction, wetland drainage, fire, pollution, invasive species, disease, and climate change (Hughes, 2017). Despite these threats, Southeast Asia is generally underrepresented in studies on faunal response to habitat loss and response to human-modified landscapes (Trimble and Aarde, 2012). Thailand is home to more than 142 species of amphibians and over 218 species of reptiles (IUCN, 2014), and has the smallest area of remnant forest cover in Southeast Asia (Sodhi et al., 2010). The herpetofaunal diversity and the level of human disruption make Thailand an ideal site to investigate the impacts of land-use change on tropical snake species. Green pit vipers (*Trimeresurus* sp.) are one of the most diverse and abundant obligate vertebrate predator groups in the Asian tropics, and are equipped to engage prey with advanced solenoglyphous fangs intricate in form capable of delivering a complex cocktail of hemotoxic and cytotoxic venom (Das, 2010; Strine, 2015). At least eight *Trimeresurus* species (Chanhome et al., 2011), likely more, are present in Thailand with new species being described as recently as 2011 (*T. phuketensis*, Sumontha et al., 2011). One species of green pit viper found in Thailand is listed as Endangered, *Trimeresurus kanburiensis*, due primarily to limited distribution and illegal harvest for the pet trade (IUCN, 2012). More than four species in Thailand have been labeled as Data Deficient (IUCN, 2016). Much confusion and inconsistency exists with the taxon *Trimeresurus*, making assessment and ultimately conservation of these snakes difficult (David et al., 2001, 2011).

Snakebite is a common and devastating environmental and occupation disease in rural developing countries in the tropics (Warrell, 2010a), and green pit vipers in particular are a medically important group of venomous snakes in Southeast Asia. In Thailand, *T. albolabris* and *T. macrops* accounted for 40 percent of total bites (307 bites by *T. albolabris* and 12 by *T. macrops*, Viravan et al., 1992); 95 percent for Bangkok (Meemano et al., 1987; Mahasandana and Jintakune, 1990); and 31.2 percent in Nakhon Ratchasima, Wang Nam Keaw, Pak Thong Chai regions (compilation of local hospital records). Snakebite preventative efforts should be focused on development of a basic understanding of snake behavior (Warrell, 2010b).

The United Nations Educational, Scientific, and Cultural Organization Man and the Biosphere Programme was developed to establish sustainable landscapes; balancing biodiversity conservation and sustainable human development. With a diverse landscape of protected forest and mixed agricultural matrix, the Sakaerat Biosphere Reserve is an ideal location to study herpetofauna and the impacts of rural community land-use on snake spatial ecology, habitat selection, and behavior. Three species of green pit viper have been documented within the Sakaerat Biosphere Reserve in Northeast Thailand, and previous research with this taxon specifically has previously been conducted within the core area of the reserve.

Recent snake research at the reserve has provided insight and deeper understanding into mortality of king cobras by ingestion of anthropogenic waste (Strine et al., 2014), nest attendance by Malayan pit vipers (Hill et al., 2006), and sexual dimorphism of green pit vipers (Strine, 2015; Strine et al., 2015). Comprehensive field studies of green pit viper ecology have been conducted in a wide array of natural and relatively pristine habitats, although published and unpublished works for this taxon in Sakaerat Biosphere Reserve have been conducted only in the core area. Despite presenting a serious occupational hazard in rural regions of East and Southeast Asia, basic ecology study of green pit vipers in anthropogenic landscapes has not previously been investigated. My study will be the first assessment of green pit viper spatial ecology, habitat selection, and behavior concurrently in both protected dry evergreen forest and also rural human-modified landscapes.

1.2 Research objectives

1) To investigate occupancy, detectability, and relative abundance of *T. macrops* within the Sakaerat Biosphere Reserve.

2) To compare home range and spatial movement patterns of *T. macrops* between human dominated and protected habitats and to investigate general home range and spatial movement patterns of multiple species of green pit viper (*T. albolabris*, *T. macrops*, and *T. vogeli*) in the Sakaerat Biosphere Reserve.

3) To compare habitat selection of *T. macrops* between human dominated and protected habitats and identify general habitat selection of multiple species of green pit vipers (*T. albolabris*, *T. macrops*, and *T. vogeli*) in the Sakaerat Biosphere Reserve.

4) To compare behavior patterns of *T. macrops* between human dominated and protected habitat and investigate general behavior of multiple species of green pit viper (*T. albolabris*, *T. macrops*, and *T. vogeli*) in the Sakaerat Biosphere Reserve.

1.3 Scope and limitations

Starting in November 2014 assessment of green pit viper spatial ecology, habitat selection, and behavior took place in the core, buffer, and transition areas of the Sakaerat Biosphere Reserve. The study area was confined to dry evergreen forest in the core area and a patchwork of mixed agricultural, natural forest, and small plantation habitats in the buffer and transition areas. Plantation forests are considered monoculture forest stands of eucalyptus or rubber, and fragments of natural forests with high levels of anthropogenic disturbance embedded in an agricultural matrix are described as heterogeneous disturbed forests (HDF).

Visual encounter survey (VES) method was utilized to investigate green pit viper occupancy, detection probability, and relative abundance during the night from September 2015 through November 2016. Surveys were conducted in human disturbed habitats throughout this entire period, and protected dry evergreen forest from July through November 2016.

Spatial ecology study was limited to two protected sites in the core area and three rural human disturbed sites in the transition and core areas of the Sakaerat Biosphere Reserve. Radiotelemetry study was conducted with the three species currently described in the reserve, including both males and females of two species, between 35 and 215 days in duration over the course of 3 sessions between November 2014 and January 2017.

Habitat selection methods were limited to comparison of utilized habitat from radio telemetry and visual encounter survey data to available habitat assessment survey data. Available habitat was assessed at two protected dry evergreen sites in the core area (cold season 2014) and one disturbed site in the buffer area of the reserve (cold season 2016).

Behavior was recorded for green pit vipers observed or captured during occupancy surveys and for every track a viper with a transmitter was visible. Trail cameras were opportunistically set to one minute intervals to capture behaviors of at least several minutes in duration for multiple days and nights when tracked vipers were visible.

CHAPTER II

LITERATURE REVIEW

2.1 Snake response to human disturbance

Behavior, habitat selection, and spatial ecology of snakes have previously been found to be influenced by anthropogenic disturbance (Pearson et al., 2005). Monocultures may provide suitable basking sites, favorable foraging opportunities, and reduced pressure from avian predators; thus providing at least temporary advantages over more natural habitats for certain species. Snakes may be able to persist in non-natural rural environments largely because of their inconspicuousness (due to sometimes cryptic, generalized habitat selection, and sedentary tendencies) and willingness to utilize non-natural prey types so long as they still maintain similar general characteristics as their natural counterparts (Shine and Fitzgerald, 1996).

Multiple studies have investigated habitat selection, and subsequently behavior in natural and human dominated areas. In Costa Rica Wasko et al. (2009) found that Fer- de- Lance (*Bothrops asper*) vipers preferred swamps and less disturbed areas over developed areas. However, in Australia Shine and Fitzgerald (1996) found carpet pythons (*Morelia spilota*) to be successful in disturbed, rural habitats with 31% of the snakes in the study using roofs as microhabitats at some point. Female grass snakes (*Natrix natrix helvetica*) in Switzerland were found to prefer edge habitat in another study, and utilized monoculture agricultural areas during their summer activity period (Wisler et al., 2008).

2.2 Study species

Approximately 30 species of green pit vipers have previously been described, but current taxonomy remains unclear (David et al., 2011). They inhabit a wide range of habitats, exhibit various levels of arboreal tendencies, and select a variety of prey species (Orlov et al., 2002). While not as toxic, green pit vipers inflict a far greater number of bites than more conspicuous species such as kraits and cobras in Thailand (Warrell, 1999, 2010a). Differences between green pit viper species present at the Sakaerat Biosphere Reserve in Northeast Thailand are summarized in Table 2.1 and visually presented in Figure 2.2. Previous work with green pit vipers has primarily focused on taxonomy and clinical effects (snakebite), with few ecological studies having been conducted with this taxon. Previous study with green pit vipers in the core area at the Sakaerat Biosphere Reserve revealed home range size of this group to be extremely small compared to study of other viper species, including the smallest viper in the world (Table 2.2). Despite the interesting ecological characteristics and strong local medical importance, field study of green pit viper basic biology in rural human dominated environments has not been conducted before this work.

The white- lipped green pit viper (*Trimeresurus* (*Cryptelytrops*) *albolabris*) is a medium sized species with a total length of 1,040 mm. The temporal scales of this species are generally smooth with 7-12 supralabials, the first of which is fused to the nasal. Breeding has been recorded in Thailand from September to November, and young are typically born from February to May (Chanhome, 2011). Devon- Song (2014) studied basic natural history of this species in South China; significant conclusions including sexual dimorphism and low translocation survival.

At a maximum total length of 710 mm, the big- eyed green pit viper (Trimeresururus (*Cryptelytrops*) macrops is the smallest species present at the Sakaerat Biosphere Reserve. Temporal scales of this species are strongly keeled and 9-12 supralabials are present which are separated from the orbit by a small row of scales. The big- eyed green pit viper was previously considered wide- ranging; however, a recent split resulted in three different species based primarily on molecular analyses (Malhotra et al., 2011). Natural history study of the big- eyed green pit viper was conducted in multiple habitat types in the core area of the Sakaerat Biosphere Reserve by Strine (2015). Spatial ecology ecology data obtained from this work also suggested extremely small home ranges (mean of 0.237 ha, MCP method) for the species.

The Vogel's green pit viper (*Trimeresurus* (*Viridovipera*) *vogeli*) is the largest green pit viper present at the Sakaerat Biosphere Reserve with a maximum total length of up to 1570 mm. Males of this species possess a striking white, red-edged ventrolateral stripe down the length of the body which is simply white in females. The Vogel's green pit viper is a relatively recently described species (David et al., 2001) which is currently known from the western Dongraek Mountains (Khao Yai National Park), the western edge of the Khorat Plateau (Sakaerat Biosphere Reserve), and small isolated south-eastern mountains (Khao Sai Dao Wildlife Sanctuary) in Thailand (Malhotra et al., 2004). The Sakaerat Biosphere Reserve is the lowest known elevation of the distribution of this species, at about 200 meters (Malhotra et al., 2004). Limited observation of Vogel's green pit viper suggested frogs, small mammals, and skinks to be the primary prey of this species (Malhotra et al., 2004).

Figure 2.1 Three distinct species of green pit vipers (*Trimeresurus*) from the Sakaerat Biosphere Reserve. A) female *T. albolabris*, B) female *T. macrops*, and C) male *T. vogeli*. Photographs A and C taken by author (C.H. Barnes), B was taken by B. Nadolski.

Table 2.1 Basic taxonomic differences between the 3 *Trimeresurus* species currently described from the Sakaerat Biosphere Reserve, summarized from Cox et al., 2012.

Trait	*T. albolabris*	*T. macrops*	*T. vogeli*
Dorsum	Bright/lime green	Pale green, sometimes a pale blue lateral stripe	Bright pale green (m) dark green (f)
Head	Long, distinct from neck	Distinct from neck	Large and distinct from neck
Supralabial (SL)	7-12 SL 1 fused to nasal	9-12 separate from orbite by small row of scales	10 SL 1 separated from nasal
Infralabial	10 to 13	10 to 13, pale blue-ish	12 to 13
Temporals	Smooth	Keeled	Weakly keeled or smooth
Postocular stripe	Absent	White (m), absent (f)	Thin white (m), absent (f)
Ventrals	149 to 186	160 to 177	157 to 173
Subcaudals	48 to 78	49 to 74	54 to 77

Table 2.2 Brief summary of previous viper spatial ecology literature. Minimum convex polygon (MCP) and fixed kernel (50% core and 99% activity areas) methods used to calculate home range and movement in hectares.

Species	Location	MCP	50% kernel	95% kernel	Reference
Agkistrodon contortrix	North America	9.9	-	-	Fitch, 1960
Agkistrodon contortrix	North America	18	-	-	Smith et al., 2009
Agkistrodon piscivorus	North America	1.2	-	3.05	Roth, 2005
Bitis schneideri	Southern Africa	0.1	-	-	Maritz and Alexander, 2012
Bothrops asper	Central America	5.95	0.37	3.71	Wasko et al., 2009
Crotalus atrox, C. molossus, and *C. tigris*	North America	5.42, 3.49, 3.48	-	-	Beck, 1995
Crotalus cerastes	North America	23.2		-	Secor, 1994
Crotalus oreganus	North America	3.09	0.37	3.065	Putnam et al., 2013
Gloydius shedaoensis	Asia	2.63	-	-	Shine et al., 2003
Montivipera raddei	Europe	24.59	-	-	Etling et al., 2013
Sistrurus catenatus	North America	4.03	0.04 – 5.5	0.15 – 24.48	Marshall Jr. et al., 2006
Vipera latastei	Europe	4.03	-	-	Brito, 2003

CHAPTER III

METHODS

3.1 Study area

The study was conducted within the Sakaerat Biosphere Reserve (SBR), located in Nakhon Ratchasima Province, Thailand (14.44–14.55°N, 101.88–101.95°E, Figure 3.1). The reserve has an 80 km^2 core area which is strictly protected to preserve and maintain species diversity, genetic variation, and landscapes and ecosystems. The buffer and transitional areas, which consist mostly of agricultural and settlement areas, comprise a combined 360 km^2. The core area predominately consists of primary growth dry evergreen forest (60%), dry dipterocarp forest (18%), and secondary plantation forest (<18%) (Tongyai, 1980). Dry evergreen forest is primarily characterized by tree species such as *Hopea adorata* interspersed with lianas and Moraceae thorn brush understory cover (Tongyai, 1980). Dry dipterocarp forest is endemic to South East Asia and is characterized by thick *Vietnamosasa pusilla* grass ground cover and dipterocarp trees such has *Shorea siamensis* and *Shorea obtusa* (Lamotte et al., 1998). The transition zone of SBR comprises nearly 82% of the total area and is characterized by isolated forest fragments in a patchwork of agricultural fields, small plantation forests, and human settlements. Sparse grassland and bamboo groves are interspersed between various habitat types, and human settlement and anthropogenic disturbed land accounts for 40% and agriculture for 2.98% of total reserve area (Ongsomwang and Suttivanich, 2013).

The intensive study area within Sakaerat includes the southeast portions of the core and buffer area with closely adjacent portions of transition area of the Sakaerat Biosphere Reserve with representative sites in the core, buffer, and transition areas within. Elevation for the area ranges from 250- 540 m. Mean annual precipitation was 87.4 ± 4.80 mm during the study period from 2014-2017, with peaks of rain in May and September with a short intermittent dry season in between (SERS, 2017). For consistency, May- end of October was considered the rain season. A cold dry season was observed between November- end of January and a hot dry season between February- end of April. Mean annual minimum temperature was 20.2 ± 0.35 °C, mean maximum temperature was 34.7 ± 0.78 °C, and mean humidity was 75.6 ± 2.28 %.

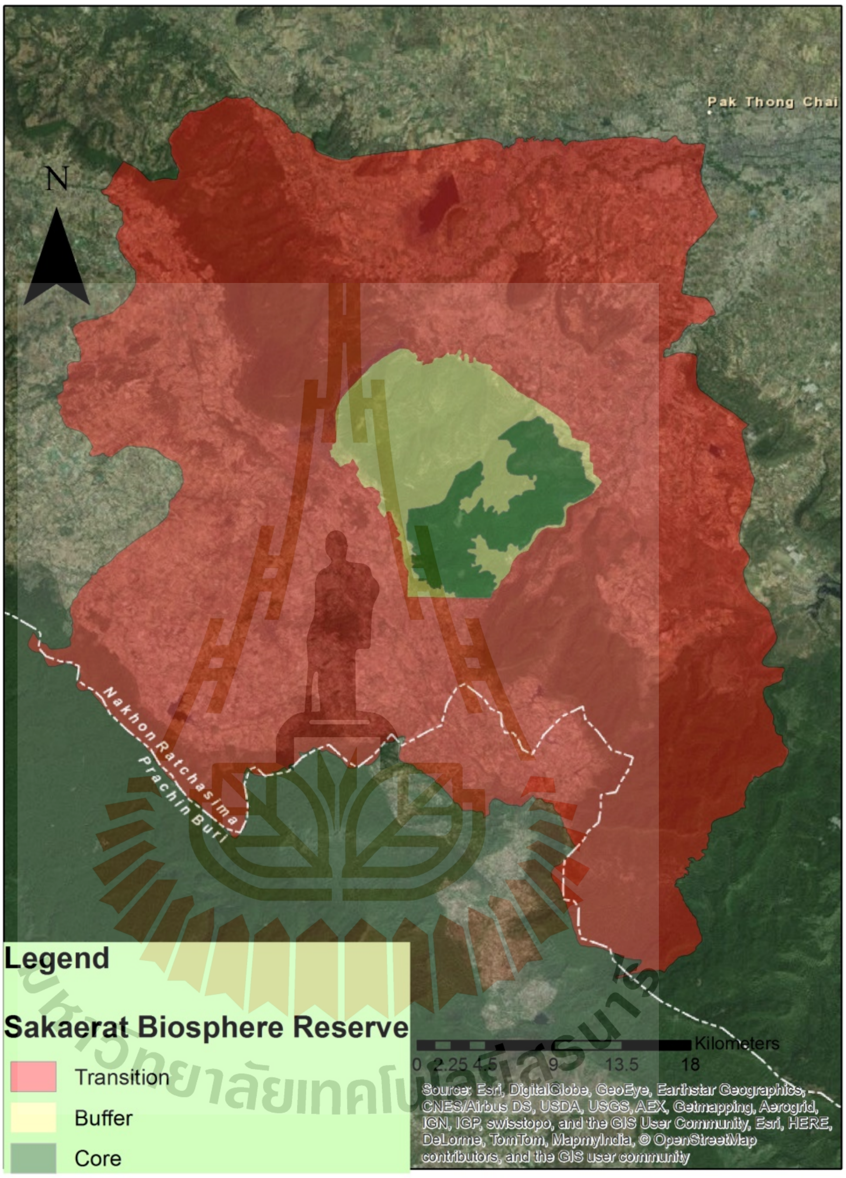

Figure 3.1 Map of the Sakaerat Biosphere Reserve with core (green), buffer (yellow), and transition (red) areas delineated (modified from Ongsomwang and Sutthivanich, 2014).

3.2 Occupancy, detectability, and relative abundance

3.2.1 Site selection

I assessed green pit viper occupancy, detection, and relative abundance in protected and human dominated areas of the Sakaerat Biosphere Reserve. A total of 18 sites were surveyed; 9 sites were selected as protected sites in the core area and another 9 human dominated sites were selected in the core, buffer, and transition areas (Figure 3.2).

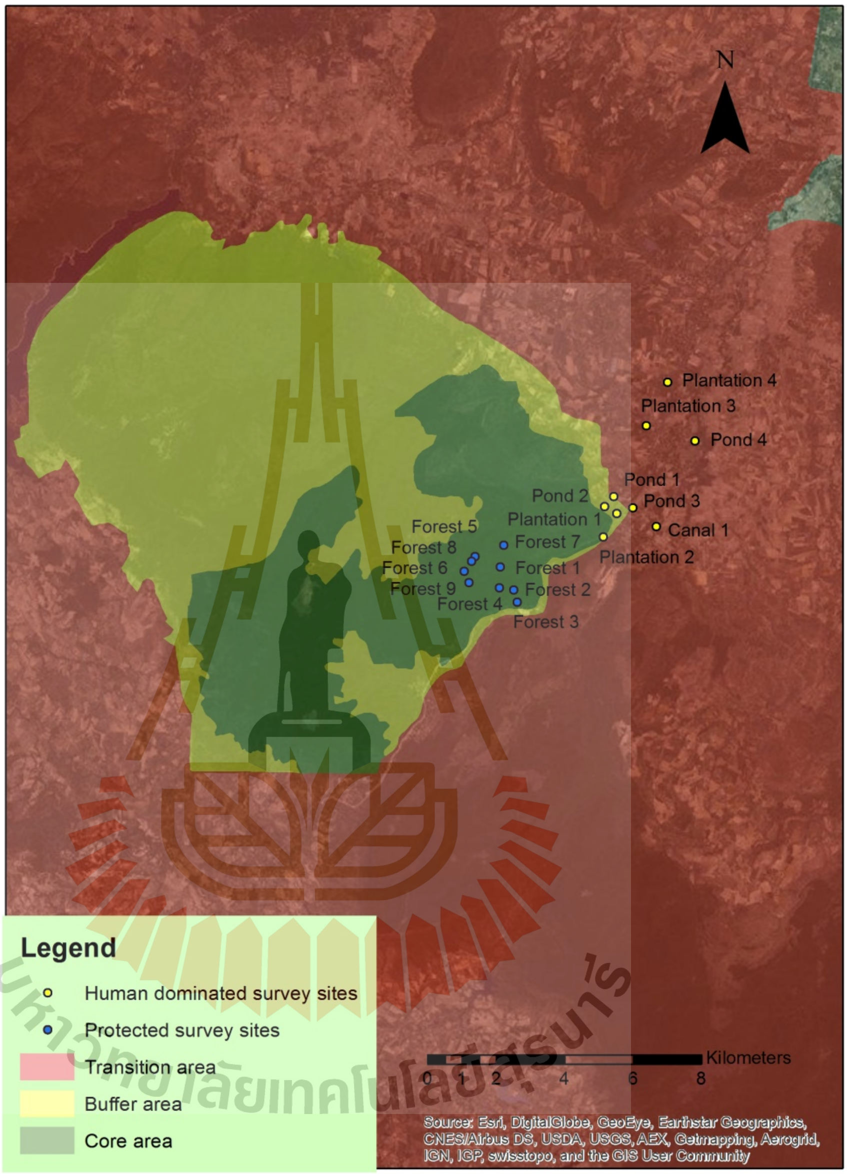

Figure 3.2 Map of 18 total human dominated and protected visual encounter survey sites for green pit vipers with Sakaerat Biosphere Reserve with core, buffer, and transition areas delineated.

The 9 sites in the core area to the north and west of the major highway (Highway 304) were selected as protected areas. All were dry evergreen dominant habitat type. The closest distance 2 sites were to another was 171 m, which was further than any single straight- line distance traveled by any radiotracked green pit viper in this or previous study by Strine (2015). This distance would require crossing and or stopping in highly undesirable habitat (roads, human settlements, etc.), which was unlikely and improbable. The first 3 protected sites were created as collaboration survey sites to study relative abundance of cat- eyed snakes (genus *Boiga*), which are significant avian nest predators in Northeast Thailand (Pierce and Pobrasert, 2013). These sites did not have prominent distinctive habitat features present (plantations, water sources, etc.), although they were created with the intent of comparing nest predation with distance to Highway 304. The first protected forest site, Forest 1 was the furthest from the major highway (Highway 304) at approximately 1,100 m, the next closest was Forest 2 at approximately 400 m from the highway, and the nearest site (Forest 3) to the major highway was approximately 50 m distance from the road. Sites Forest 4 and 5 were small ephemeral pond complexes, ponds being <20 m in diameter at longest point. These sites were sites utilized by flying frogs (*Rhacophorus kio*), with interesting habitat characteristics (Poo et al., 2016). The Forest 6 site was a radiotelemetry study area, and a location of many previous studies. This site was characterized by a medium sized artificial water body (“Upper dam pond”) of approximately 100 m longest distance between the dam and furthest pond edge, Forest sites 7 and 8 were within 10 meters of a small (<3 m wide) paved road between the Sakaerat Environmental Research Station and Forest 6 survey site. The last protected area survey site was located approximately 50 m from a small Buddhist forest retreat house. This site was part of the radiotelemetry portion of this study (and previous green pit viper study, Strine, 2015) before my surveys were conducted.

Human dominated sites were primarily water and/or plantation based in the Udom Sab subdistrict. These survey sites were located in the core, buffer, and transition areas of the Sakaerat Biosphere Reserve. Plantations consisted of monocultures of *Eucalyptus* (*Eucalyptus camaldulensis*) and or rubber (*Hevea brasiliensis*). *Eucalyptus* and rubber are planted in straight lines with between 2-5 m between rows. *Eucalyptus* stands are typically harvested every 2-5 years, with the trees being cut down to the base which is then allowed to regrow. The Plantation 1 site was a *Eucalyptus* plantation situated in the buffer area of the reserve between natural dry dipterocarp forest to the west and cassava fields to the east, and the major highway to the south. The Plantation 2 site was located at the southeast corner of the core area of the Sakaerat Biosphere Reserve, less than 100 m from the transition and buffer areas, and was a radiotelemetry site. This rubber plantation site was surrounded on 3 sides by an ephemeral stream and located to the south of Highway 304 (less than 50 m from the road), which splits the core area of the reserve. The third plantation site, Plantation 3, was a set of 2 adjacent rubber plantations in the transition area split by a small (<3 m wide) dirt road. Both plantations had small ponds within them. The Plantation 4 site was a *Eucalyptus* plantation located to the west of Highway 304 in the transition area, south of a small (<2 m wide) dirt road, and southeast of a small pond. A small community (<20 small houses) was located just to the north of the small dirt road. While not a permanent water body, this *Eucalyptus* site did retain water for some time after rains, likely due to the soil. Plantations 3 and 4 were situated in the buffer area of the reserve. The first water based human dominated survey site, Pond 1, was characterized by a small pond less than 20 m in diameter. This site was situated less than 20 m from natural dry dipterocarp forest, approximately 100 m from a small Buddhist temple, and approximately 30 m from several cassava fields and was located within the buffer area of the Sakaerat Biosphere Reserve. The second pond site, Pond 2, was characterized by a small pond of less than 30 m diameter surrounded by a patchwork of cassava fields and an island of remnant disturbed forest amongst it adjacent to a small house approximately 30 m from the site. The pond 3 site was characterized by a medium sized pond approximately 70 m in diameter in a complex of several smaller ponds. Only the one pond was surveyed due to logistics and complexity of emergent vegetation. This site was located within the buffer area of the reserve and there were less than 10 small households within 60 m (as close as 30 m proximity). The last pond based survey site was a small pond complex, with 3 ponds of 20, 30, and 100 m diameters with limited vegetative cover surrounding them. Directly adjacent to the ponds were a patchwork of agriculture, primarily flooded or drained (depending on the season) rice paddies. This site was a radiotelemetry study area for several banded kraits (*Bungarus fasciatus*) which were tracked on separate occasions as the surveys and located in the buffer area of the reserve. The last survey site, Canal 1, was characterized by an ephemeral creek less than 20 m at the widest point in the study area and located in the buffer area. This creek is downstream of a large dam and experiences letdowns at certain times due to local agriculture. Canal 1 was bordered by small households and a variety of agriculture practices including cassava, coconut, and corn. A small road (<3 m across) traverses the site with a bridge going over the creek itself.

3.2.2 Survey methods

Sites were surveyed opportunistically for an hour, although some sites did take longer or shorter depending on environmental or site specific characteristics. However, every site was surveyed for at least 0.5 hours and a maximum of 2.5 hours between 1800- 0300. Night was considered optimal survey time for green pit vipers by Strine (2015), and headlights and flashlights were used detect to them. Multiple visits during multiple seasons were attempted for each survey site. For logistic and safety purposes, 2 surveyors at minimum searched the different sites although guests were occasionally invited to participate. Number and names of surveyors were recorded for each survey. Time of most recent rain was recorded upon initial arrival at each site, and ambient temperature and humidity (approximately 1.2 m above ground level) were recorded both before and after each survey. Every time a snake was observed, survey time was paused and species and time was recorded. Certain snake species were captured during these surveys for the benefit of other snake research projects at the Sakaerat Biosphere Reserve, however all of these were returned to study sites within 24 hours. Habitat and behavior data were recorded for every green pit viper observed during these surveys (see sections 3.4.1 and 3.5.1 for further details), along with capture location. All green pit vipers were attempted to be captured by designated snake handlers using hooks, tongs, and bags made specifically for snake capture so as to provide basic morphometric information and compare recapture rates. Captured vipers were brought back to the lab at the Sakaerat Environmental Research Station where viper mass, body condition, and other morphometrics were recorded (see section 3.3 for further details). Vipers were released back to their site of capture within 24 hours. One night minimum was spaced between releases and site revisits so as not to influence detectability estimates. Radiotracked green pit vipers were not included in occupancy estimates, even though they were present and observed regularly during occupancy surveys, so as to prevent bias.

3.3 Spatial ecology and movement

Green pit vipers were selected through opportunistic searches and occupancy surveys at five study sites within the core, transition, and buffer zones of the Sakaerat Biosphere Reserve for radiotelemetry (Figure 3.3). Protected area radiotelemetry tracking sites included the Upper Dam Pond (Forest 6 site) and the Monk's House (Forest 9 site) within the core area of the reserve. These two dry deciduous forest were sites previously utilized for green pit viper spatial ecology study (Strine, 2015). Upper Dam Pond is ephemeral, although the water level was still high during the tracking period which immediately followed the rain season. Three sites were selected for radiotelemetry study in the transition and buffer areas of the Sakaerat Biosphere Reserve in Wang Nam Khieo village, within Udom Sap subdistrict. The three sites all displayed varying degrees of ephemerality, two were downstream from a dam and one was a pond.

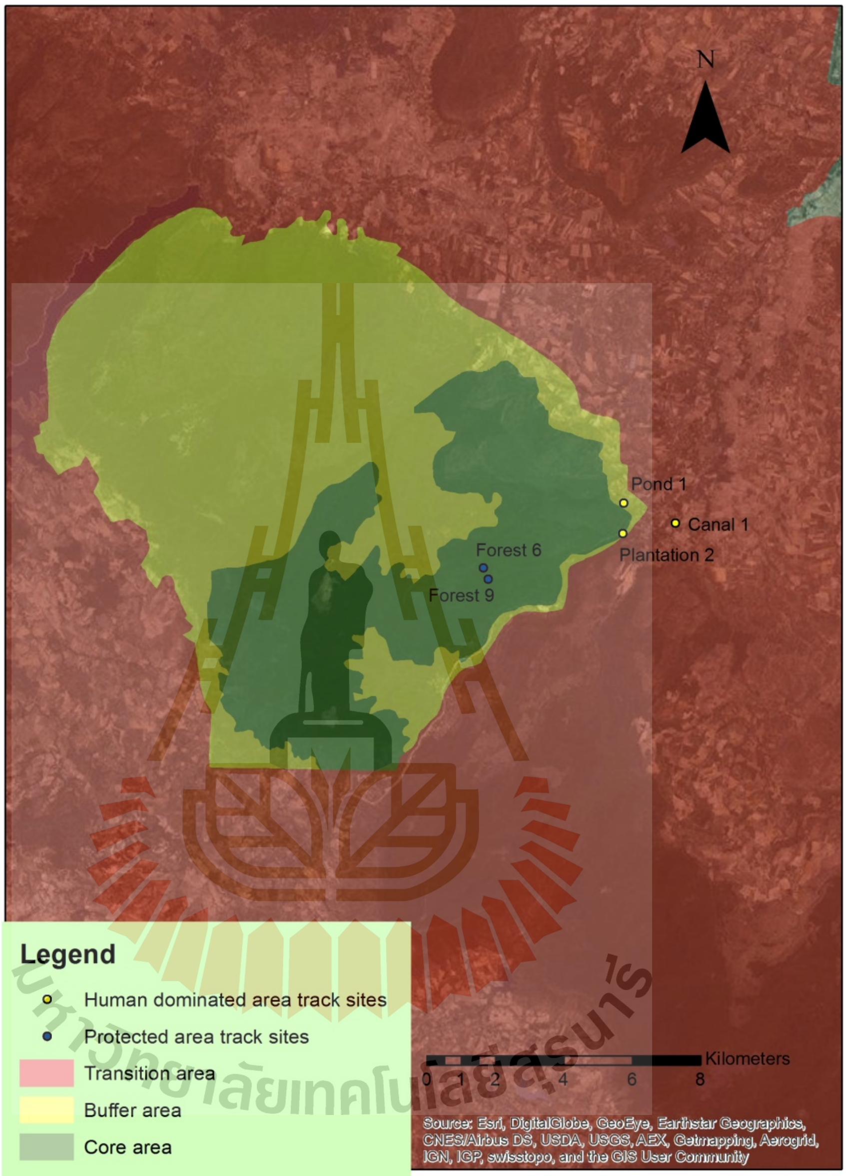

Figure 3.3 Map of radiotelemetry tracking sites with core, buffer, and transition areas of the Sakaerat Biosphere Reserve delineated.

After capture by designated handlers, vipers were housed in plastic boxes following (Llewelyn et al., 2009, 2011) at an outdoor lab at the Sakaerat Environmental Research Station. All tracked vipers were captured at night, and then morphometrics (snout- vent length, tail length, mass, etc.) were recorded the following day with the acrylic tube method utilized concurrently with isoflurane anesthesia (Wilkinson, 2014). Scaled mass index (SMI) was incorporated using previous data as a population (Strine et al., 2015) from which to assess body condition following Peig and Green (2009). Sex was determined through standard probing technique (Laszlo, 1975), and presence of vitellogenic follicles (gravidity) was determined through light palpation. Vipers were marked following the heat branding method of Winne et al. (2006) using portable subcautery units with replaceable batteries for clear subsequent observation in the field. Girth and mass were the primary factors influencing my decision to implant vipers with radio transmitters. While girth was an objective decision by the author and previous snake studies have collectively concluded that transmitters should not be more than 5% of the individual animal body mass (30 g for the transmitters in the study). Holohil BD-2, BD-2T, and BD-2THX model 1.8 g transmitters were used to track green pit vipers in this study, with battery life expectancy of between 1-6 months and signal range between 50-200 m. BD-2THX model transmitters have a helical antenna encased in ceramic which make for a shorter, more compact, but slightly wider transmitter (Figure 3.4A). BD-2 and BD-2T models possess a traditional long whip antenna, the only difference between the two models being BD-2T being temperature sensitive (Figure 3.4B). C. Barnes, M. Crane, Dr. C. Strine, and B. Nadolski performed all surgeries to ensure consistency and ethics following (Reinert and Cundall, 1982; Hardy and Greene, 2000, Figure 3.4C) methodology in which the transmitter is inserted into the coelomic cavity and the antennae is run laterally between the subcutaneous tissue and the peritoneum. Aseptic procedures were followed including boiling equipment for at least 15 minutes followed by an ethanol (95%) bath for at least 15 minutes prior to surgery. Equipment was stored in a sterile container with ethanol until surgery and was only handled by the surgeon who wore plastic gloves and avoided touching any non- aseptic surfaces throughout the surgery process. Vipers were retained for at least three hours following transmitter surgery and then were released the same night. Night is the period green pit vipers are most active (preliminary observation), and releasing a short period after the surgery enabled the vipers to heal and thermoregulate naturally. Transmitters were removed following the same surgical protocols. Surgical techniques were carried out in accordance with the Animal Care and Use Committee Guidelines (ACUCG) of Suranaree University of Technology. Several transmitters failed prematurely, some were retrieved and removed through visual (without tracking equipment) capture.

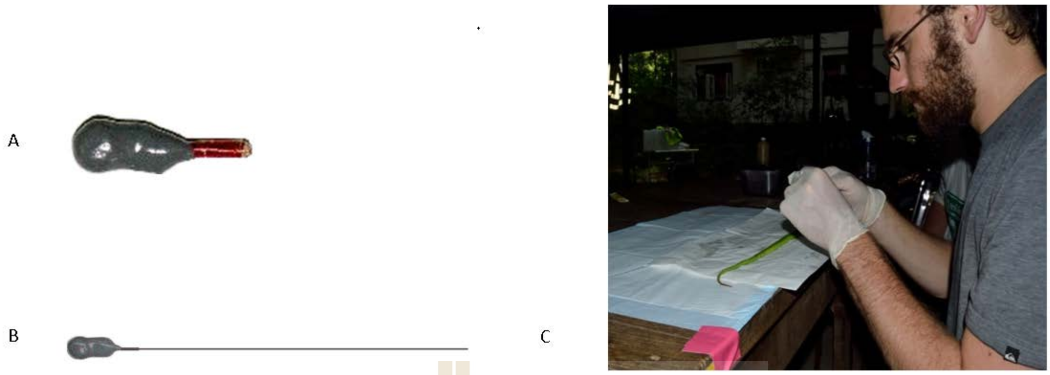

Figure 3.4 Radio transmitter (1.9 g) types utilized during this study (A and B) and author (C.H. Barnes) implanting radio transmitter in an adult *T. macrops* (C)

Following release, vipers were located once during the day and once at night, homing in and obtaining visual pinpoints (henceforth referred to as fixes) whenever possible with least disturbance. Global positioning system (GPS) points were recorded for viper relocations of greater than 10 meters. Shelter sites were not disturbed or manipulated, although visual inspection of these sites was conducted and observation of vipers within were still attempted if possible. Habitat and behavior data was assessed during every tracking session (see sections 3.4 and 3.5), with more in-depth data collected when visual observation of tracked vipers were obtained (i.e. microhabitat, ambush behavior, etc.) and when vipers moved more than 10 meters (meso- and macrohabitat). Ambient and ground temperature and humidity were recorded using a Kestrel™ 3000 Pocket Weather Meter. Because behavior was able to be analyzed through cameras and green pit vipers exhibited extreme sedentary nature, discontinuous radio tracking (Harris et al., 1990) was utilized for efficiency and to prevent intrusion of natural behavior and interactions of the study animals.

Disturbance during tracking, data recording, and leaving study sites was minimized and time spent in close proximity to the vipers was limited.

3.4 Habitat selection

3.4.1 Utilized habitat methods

Meso- and microhabitat were collected during VES for occupancy, detection, and relative abundance and also during radiotelemetry study. Meso- and microhabitat were both collected during every capture or observation during VES. Mesohabitat was assessed every fix a viper relocated more than 10 m from previous location during radio telemetry, microhabitat was assessed every fix a visual was obtained. Landscape level habitat features, macrohabitat, was collected every time a tracked viper in the human dominated area moved more than 10 m.

Macrohabitat was defined in this study as landscape level habitat features, including agriculture, bamboo forest, plantation, human settlement, wash, and heterogeneous disturbed forest (HDF). The landscape was relatively uniform and consistent in the protected study area (dry evergreen forest), so these features were only recorded in the human dominated study area. Dominant habitat was recorded as the primary habitat feature where a tracked viper was pinpointed. To get a sense of available habitat, and to understand ecotones and edge habitat dominant vegetative features were then assessed at 5 and 10 m intervals from the dominant habitat type assessed at the pinpoint. Wash was used to describe a landscape feature where water could collect and flow, although not necessarily at the time of tracking. Agriculture described rural farming practices including crop type and basic stage of rotation.

Pockets and matrices of remnant natural forest within the human dominated landscape were described as HDF.

Mesohabitat as used in the context of this study was defined as habitat features within 10 m of a green pit viper. Present/absence of paths, human settlements, fallen logs, large rocks, dense green (non-woody) vegetation, dense dead green vegetation, dense woody vegetation, dense dead woody vegetation, open canopy patch, dense lianas, thorn Moraceae, and water were mesohabitat habitat features recorded during all VES captures and radiotelemetry fixes when tracked vipers relocated more than 10 m.

Microhabitat was defined as habitat features within 1 meter or less of observed vipers either during VES or radiotelemetry. Presence/absence of green vegetation, small (<5 cm diameter) lianas and vines, large (>5 cm diameter) lianas and vines, saplings (<10 cm diameter at breast height at 1.37 m above ground level, DBH), trees (>10 cm DBH, diameter at breast height, 1.37 m above the ground), small (<1 m diameter) rocks, and large (>1 m diameter) rocks. Forest layer strata was defined as underground, on ground, groundstory (<1 m above the ground), understory (1-3 m), midstory (3-10 m), and abovestory (>10 m). Collectively, the midstory and abovestory were defined as "arboreal" (> 3m above ground) and underground, on ground, groundstory, and understory were defined as "not arboreal" (< 3 m).

3.4.2 Available habitat assessment methods

Three 100 m habitat transects 30 m apart were run at each radio telemetry study areas, within 3 study sites (Forest 6, Forest 9, and Canal 1, Figure 3.5) which were also VES sites, at 1, 5, and 10 m intervals. Available habitat was assessed through the same methodology as utilized habitat, but also more inclusive for overall study area general habitat comparison.

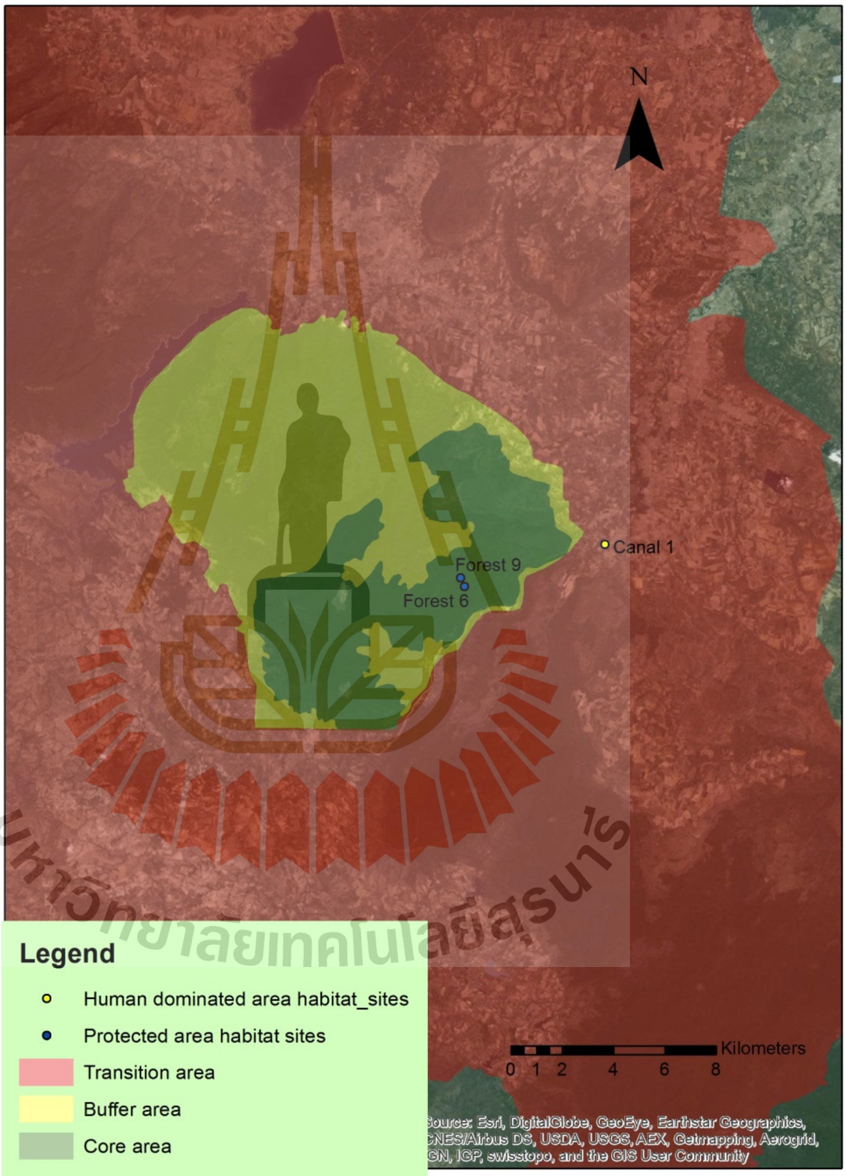

Figure 3.5 Map of available habitat sites with core, buffer, and transition areas of the Sakaerat Biosphere Reserve delineated.

At the 5 m interval, saplings, lianas and vines, rocks, fallen logs, termite mounds, anthropogenic waste, man-made structures, grassy vegetation, and leaf litter were recorded as none, very low, low, medium, high, and very high categories which were within 2 meters. Within 10 m of the 5 m interval, presence/absence data was recorded including paths, visible human structures, fallen logs, large rocks, dense green vegetation, dense dead green vegetation, dense woody vegetation, dense dead woody vegetation, open canopy patch, dense liana and vines, and water. The nearest tree was recorded, including nearest tree and its DBH (diameter at breast height, 1.3 m above the ground).

At the 10 m interval, the same categories within 2 meters were recorded as the 5 m interval. Also within 2 m, presence absence of trees and leaf litter were recorded. Number of trees between 10-30 cm and >30 cm DBH were recorded along with nearest tree to the interval and its DBH. Leaf litter was measured at the interval and the four cardinal points around it in a 1 m x 1 m quadrat, and then later averaged. Slope aspect was recorded and slope degree was assessed in categories as none (0%), slight (1-15%), light (16-25%), and medium (25-65%), and heavy (>65%) incline. Groundstory (<1 m above ground level), understory (1-3 m), midstory (3-10 m), and abovestory (>10 m) categories were recorded as none, very low, low, medium, high, and very high categories. Canopy cover percent was estimated using a hollowed out aluminum can pointed directly vertical. Within 10 m of the 10 m interval presence/absence of human structures and water was recorded. Presence/absence of green vegetation, small lianas (<5 cm diameter), large lianas (>5 cm in diameter), saplings (<10 m in diameter), trees, small rocks (<1 m in diameter), and large rocks (>1 m in diameter) were recorded within 1 m of the 10 m interval.

3.5 Behavior

3.5.1 Survey and radiotelemetry behavior assessment methods

Behavior was recorded during every green pit viper radiotelemetry fix and most observations and/or captures during VES, and were described similarly to state analysis for camera review (Section 3.5.2). These behaviors included "resting," "clear ambush," "ambiguous ambush," "moving," "predation event," "unknown," or "other." "Resting" behavior was defined as the focal viper having the head settled on the body. "Clear ambush" is defined as foraging behavior characterized by the head and neck extended a significant distance from the body towards a microhabitat feature. Preliminary study suggested vipers to be more active at night, with focal animals most commonly observed clearly ambushing during this time and resting during daytime hours. "Ambiguous ambush" was defined as the behavior when a viper was suspected to be ambushing, but the head was drawn in close to or on the body making clear distinction between resting and ambush states difficult. "Unknown" behavior was recorded for behaviors with unclear function also when the viper was not visible to observers during tracking, "Other" behavior was recorded for uncommonly observed behaviors. Whether or not a snake was in shelter and head angle were behavior characteristics recorded during radiotelemetry tracking and VES.

3.5.2 Camera utilization and review methods

Bushnell game cameras (Model X-8, 119327) with infrared night vision capability were placed approximately one meter away from tracked vipers on tripods and set to record behavior at one minute intervals (f/3, exposure time 1/20 sec, ISO 100, 35mm focal length). Care was taken when placing cameras not to disturb vipers. Small body size and an inability to activate temperature sensitive triggers can influence game camera performance (Jackson, 1999; Fitzgibbon, 2001; Pagnucco et al., 2011; Welbourne, 2013) and has limited previous game camera use with reptiles and other ectotherms. Sedentary and sit-and-wait ambush foraging species do not necessarily require triggering of sensors, and videography of these relatively sessile species can yield valuable behavioral data that would otherwise be challenging to obtain (Clark, 2006; Karlin and De la Paz, 2015).

Instantaneous focal scan sampling as described by Matin and Bateson (2007) was used to assess and quantify states and events. Scan sampling is generally more suited for determining percent of time spent during individual states of relatively long duration rather than discrete event observations (Altmann, 1974). Cross- validation study of this method with other behavior sampling methods including continuous and ad-libitum sampling have suggested scan sampling to be an unbiased and cost effective quantitative method to analyze behavior (Martin and Bateson, 2007). Remote camera recording was ideal for scan sampling analysis of the relatively sedentary green pit vipers in my study which primarily displayed clear and visible states, with few breaks of interesting events.

States were defined in this study as behaviors which were more than 1 scan (picture) in durations. Day time hours were categorized as 0600-1759 and night was defined as 1800-0559 for consistency. Behavior states were defined in my ethogram and classified into four categories; foraging, active, sedentary, indeterminate, and not visible for comprehensive understanding.

Active behavior states were further classified into “migrations” and “moves.” Migration was recorded when the focal viper shifted from one site to another, both sites being visible on the camera screen. A move was a complete transference and was recorded when the focal viper shifted from a site on the camera screen to another site not visible on the camera screen, or from a site not visible on the camera screen back into view on the camera screen.

Sedentary behavior was further classified into “resting” and “sheltering” behaviors. Resting was defined as having the head settled on the body or habitat in what could best be described as a relaxed position. Preliminary data suggested this to be the most prevalent state during daytime hours. Sheltering was the defined state only when the viper was not visible and other primary behaviors such as clear ambush were not observable due to obstruction by of a microhabitat feature.

Clear ambush, ambiguous ambush, and feeding were defined within the foraging behavior category. Clear ambush behavior was characterized by the neck and head of the focal viper extended outwards from the body towards a habitat feature. Ambiguous ambush was the defined behavior when the focal viper was suspected to be ambushing but the head was tucked in close to or settled on the body making clear distinction between resting and ambush state difficult.

Rarely observed states were described in the ethogram as “other” behavior and those which were indeterminable in function were recorded as “unclear” behavior. For understanding total time spent recording unsuccessful and to describe breaks in “moves,” the category “not visible” was recorded.

3.6 Data analysis

3.6.1 Occupancy, detectability, and relative abundance

I estimated detection probability and site occupancy across all sites using program PRESENCE (Version 2.4, Proteus Research and Consulting Ltd., Dunedin, New

Zealand). In PRESENCE, I used the single season model to estimate detection probability (*p*) and site occupancy (ψ). The estimate *p* is the probability of detecting a species of interest during a single survey given it is present at the site and the ψ is the proportion of sites, patches, or habitat units occupied by that species. Occupancy modeling assumes sites are closed to changes in site occupancy at the species level during the study, species are not detected if they are absent and may or may not be if they are actually present, and sites are independent (MacKenzie et al., 2002).

Site covariables (ψ), including whether or not the site was a plantation, if a pond was immediately present, if a canal was immediately present, if a stream was immediately present, size (ha) of study site, elevation, nearest human settlement distance, distance to closest water source, distance to closest forest patch, and distance to core area of the Sakaerat Biosphere Reserve were investigated in the modeling scheme to determine occupancy probability. Distances were calculated using ArcGIS 10.1. Survey specific sample covariates (*p*), variables which influenced detection probability, were recorded during VES and included rain within 6 hrs, rain within 24 hrs, temperature at start of survey, humidity at start of survey, and number of surveyors present during each survey. PRESENCE ranks models by Akaike's Information Criterion (AIC, Burnham and Anderson, 1998) in order of parsimony; ΔAIC is calculated in the program as relative differences in AIC values and the top ranked model. A difference of <2 ΔAIC suggests that while models below the top are not the best fit, there is still reasonable support for them. For comparison purposes, AIC_C, which adjusts for small sample sizes (Burnham and Anderson, 1998), were also presented. Input for AIC_C is arbitrary; I utilized the total number of vipers observed during surveys (n = 31) as a conservative measure. Different estimates were interpreted through the top AIC model, including naïve estimate, estimate of *p*, ψ, and ψ- hat. Naïve estimate is the proportion of sites which were surveyed where *T. macrops* was detected at least once without correcting for detection probability. The estimate ψ- hat derived parameter is the probability a site is occupied given that the species is never detected there during surveys.

3.6.2 Spatial ecology and movement

When appropriate, parametric statistical tests (Welch's t- tests and ANOVA) were run for spatial ecology and movement data. Assumptions of normality and homogeneity were tested in program R for home range and movement variables using the Shapiro- Wilk and Levene tests, respectively, and results presented. Independence was sought through temporal spacing of datapoints (1 fix during the day and 1 at night), during which time behavior of this group should be different (Strine, 2015). Welch's t- test does not assume equality of variance and adjusts the number of degrees of freedom accordingly. Mann- Whitney *U* and Kruskal- Wallace tests were utilized when assumptions were not met for similar parametrics.

Sample sizes for males, *T. albolabris*, and *T. vogeli* were small so statistical analyses were limited to female *T. macrops* unless noted. Few female *T. macrops* were tracked outside of the cold season (November to the end of January); I excluded those individuals from statistical analyses unless noted. Instead, basic descriptions of tracking of these periods and individuals are provided so as to maintain consistency.

As most of the *T. macrops* in the study were female, home range (MCP) and movement pattern (MDD) was compared through Mann- Whitney *U* tests with gravid and non- gravid individuals so as to determine its effect and proper assessment of sample size.

Body mass and snout- vent length were compared between human dominated and protected forest study areas using Welch’s t- tests and the 4 study sites using Kruskal-Wallace tests before analyses of spatial patterns were conducted. Similarly, number of fixes (each datapoint, or time a viper was located in the field), moves, and days tracked were compared between the 2 study areas through Mann- Whitney *U* tests and the 4 study sites through Kruskal- Wallace tests.

Number of fixes, days tracked, number of relocations, and home range size (MCP) at the Forest 6 site were compared using transmitters with helical antennas from my study to Strine (2015) previous results at the same site using transmitters with whip antennas using Mann- Whitney *U* tests. Both whip and helical antenna types were utilized in my study.

Home range was evaluated through minimum convex polygon (MCP) and kernel methods using the adehabitatHR, sp, maptools, and move packages in program R. Core (50% of all fixes) and activity (99%) areas were evaluated using fixed kernel density methods. Home range asymptotes were calculated for all individuals (including males, *T. albolabris*, and *T. vogeli*) using the hrBootstrap function in the sp package in R to compare estimated and realized MCP home range size. Linear regression was applied to determine if number of fixes or number of days tracked was better for predicting home range size (MCP) for all individuals (males, *T. albolabris*, and *T. vogeli*). MCP was compared with 50% and 99% kernel home ranges for all samples together using Welch’s t- tests.

Female *T. macrops* home ranges (MCP and fixed kernel) were compared during the cold season in the human dominated and protected study areas, and then broken down further when sample size was adequate to the site level using appropriate statistical tests previously mentioned. Observations of trends with home range size and characteristics of males, *T. albolabris*, and *T. vogeli* are also presented.

Movement was assessed through comparisons of numbers of moves, mean distance moved during those moves, and mean daily displacement (distance moved/days). A move was defined as a relocation of more than 5 m. Female *T. macrops* movement patterns were compared at the both the study area and site levels during the cold season. Movement trends for males, *T. albolabris*, and *T. vogeli* are also presented.

3.6.3 Habitat selection

Habitat availability, utilization, and selection was compiled and analyzed from transect, radio telemetry, and visual encounter survey methods. Data was primarily analyzed (unless otherwise noted) from the cold season (November to the end of January) as this was the period when most of the radiotelemetry study was conducted. When appropriate, parametric statistical tests (Welch's t- tests and ANOVA) were run for quantitative meso- and microhabitat (< 10 m and < 1 m from vipers, respectively) data. Assumptions of normality and homogeneity were tested in program R for home range and movement variables using the Shapiro- Wilk and Levene tests, respectively, and results presented. Mann- Whitney *U* and Kruskal- Wallace tests were utilized when assumptions were not met for similar parametrics in order to determine differences in quantitative available habitat variables between study areas and study sites. Chi- square tests were run in program R to distinguish proportion composition of available, utilized, and selected categorical habitat (meso and micro) variables in the protected and human dominated study areas.

Macrohabitat (landscape level features) in the human dominated study area (Canal 1 and Plantation 2 sites) was only assessed through radiotelemetry and presented as basic descriptions due to small sample size (only being recorded when tracked vipers moved more than 10 m). They were expressed as numbers of occasions or percent of total occasions.

Sample sizes for males, *T. albolabris*, and *T. vogeli* were small so meso- and microhabitat statistical analyses were limited to female *T. macrops* unless noted. Few female *T. macrops* were tracked outside of the cold season (November to the end of January); I excluded those individuals from statistical analyses unless noted. For comparison, only cold season available habitat data (obtained from transects) was used to determine and compare habitat utilization and selection between study areas and sites. Habitat utilization and selection of *T. macrops* captured during occupancy surveys in the cold season were included for comparison purposes. Habitat utilization and selection for males, *T. albolabris*, and *T. vogeli* was limited to basic descriptions unless noted.

3.6.4 Behavior

Green pit viper behavior was evaluated through observation during tracking, surveying, and review of Bushnell trail cameras which were set to observe radiotracked vipers. Because tracked viper behavior was expressed as proportions of time (fixes/datapoints), analyses were conducted with chi- square tests in program R with comparisons of behavior including between sexes, gravid or not gravid females, study area and site, and time of day as were vipers observed on the trail cameras (scans). General linear models (GLMM) were run in program R to understand the relationship between ground temperature, ground humidity, ambient temperature, and ambient humidity on ambush activity for tracked female *T. macrops* during the cold season. Unless noted, behavior during radiotelemetry and camera review was analyzed with female *T. macrops* only and during all seasons collectively. Behaviors of vipers observed or captured (after recording behavior data) during occupancy surveys were only presented descriptively. Behavior for males, *T. albolabris*, and *T. vogeli* was limited to basic descriptions unless noted.

CHAPTER IV

RESULTS AND DISCUSSION

4.1 Results

4.1.1 Occupancy, detectability, and relative abundance

I conducted a total of 174 visual encounter surveys at 18 sites (Tables 4.1- 4.4), between September 2015 through November 2016. Most sites were revisited multiple times. Total survey effort was 480.5 surveyor hours (calculated as observers x number of hours searched).

A total of 31 green pit vipers were detected during 24 of the 174 surveys at 4 of the 18 total sites. All green pit vipers detected were adult *T. macrops* and sex was determined later during processing if captured. They were detected at 2 human dominated and 2 protected study area sites, Canal 1, Plantation 2, Forest 2, and Forest 6. Three sites (Canal 1, Plantation 2, and Forest 6) had a water source present at least during part of the study period, while one site, Forest 2, did not. *T. macrops* were detected during 48% of the surveys at Plantation 2, 29% at Canal 1, 33% at Forest 2, and 8% at Forest 6. A total of 11 vipers observed were "recaptured" during the occupancy surveys; vipers were not brought in for various reasons including handler and snake safety, recapture of vipers which were already brought in and anesthetized within a month, and vipers which were currently part of the radiotelemetry portion of the study. However, if a viper did possess the characteristic heat brand utilized in this study or was observed within 1 m of previous sighting or was a tracked viper then it was recorded as a recapture.

Table 4.1 Summary of surveys for *T. macrops* in 18 protected and human dominated study sites in the Sakaerat Biosphere Reserve, Nakhon Ratchasima province, Northeast Thailand conducted during September 2015- November 2016.

Study site	Study area	Total visits	Hours surveyed	Surveyor hours	# of surveys vipers were detected	Number of vipers detected	Encounter rate
Canal 1	Human dominated	24	28.8	77.6	7	13	0.29
Plantation 1	Human dominated	5	3.9	7.9	0	0	0
Plantation 2	Human dominated	25	41.1	122.5	11	12	0.44
Plantation 3	Human dominated	11	19.6	47.3	0	0	0
Plantation 4	Human dominated	4	3.7	7.7	0	0	0
Pond 1	Human dominated	16	12.5	28.6	0	0	0
Pond 2	Human dominated	5	2.8	6.6	0	0	0
Pond 3	Human dominated	4	2.1	4.2	0	0	0
Pond 4	Human dominated	11	11.3	27.2	0	0	0
Forest 1	Protected	7	7.9	16.8	0	0	0
Forest 2	Protected	6	10.2	20.4	2	2	0.33
Forest 3	Protected	1	3.5	6.9	0	0	0
Forest 4	Protected	2	1.7	3.3	0	0	0
Forest 5	Protected	2	1.1	2.7	0	0	0
Forest 6	Protected	45	38.0	89.9	4	4	0.09
Forest 7	Protected	2	1.4	2.7	0	0	0
Forest 8	Protected	2	1.3	2.6	0	0	0
Forest 9	Protected	2	1.9	3.8	0	0	0
Total		174	192.6	478.6	24	31	

Table 4.2 Summary of surveys for *T. macrops* in 18 protected and human dominated study sites in the Sakaerat Biosphere Reserve, Nakhon Ratchasima province, Northeast Thailand conducted during the 2015 rain and cold seasons.

		Rain season 2015			Cold season 2015		
		Surveys	Detections	# detected	Surveys	Detections	# detected
Human dominated	Canal 1	1	0	0	6	3	6
	Plantation 1	2	0	0	0	0	0
	Plantation 2	5	2	2	12	7	7
	Plantation 3	2	0	0	5	0	0
	Plantation 4	1	0	0	0	0	0
	Pond 1	6	0	0	3	0	0
	Pond 2	2	0	0	0	0	0
	Pond 3	0	0	0	1	0	0
	Pond 4	3	0	0	3	0	0
Protected	Forest 1	0	0	0	0	0	0
	Forest 2	0	0	0	0	0	0
	Forest 3	0	0	0	0	0	0
	Forest 4	0	0	0	0	0	0
	Forest 5	0	0	0	0	0	0
	Forest 6	0	0	0	0	0	0
	Forest 7	0	0	0	0	0	0
	Forest 8	0	0	0	0	0	0
	Forest 9	0	0	0	0	0	0
	Sum	22	2	2	30	10	13

Table 4.3 Summary of surveys for *T. macrops* in 18 protected and human dominated study sites in the Sakaerat Biosphere Reserve, Nakhon Ratchasima province, Northeast Thailand conducted during the 2016 hot and rain seasons.

		Hot season 2016			Rain season 2016		
		Surveys	Detections	# detected	Surveys	Detections	# detected
Human dominated	Canal 1	5	2	5	7	2	2
	Plantation 1	0	0	0	2	0	0
	Plantation 2	4	2	3	4	0	0
	Plantation 3	1	0	0	2	0	0
	Plantation 4	0	0	0	2	0	0
	Pond 1	1	0	0	6	0	0
	Pond 2	0	0	0	2	0	0
	Pond 3	0	0	0	2	0	0
	Pond 4	1	0	0	2	0	0
Protected	Forest 1	0	0	0	7	0	0
	Forest 2	0	0	0	6	2	2
	Forest 3	0	0	0	1	0	0
	Forest 4	0	0	0	2	0	0
	Forest 5	0	0	0	2	0	0
	Forest 6	0	0	0	43	3	3
	Forest 7	0	0	0	2	0	0
	Forest 8	0	0	0	2	0	0
	Forest 9	0	0	0	2	0	0
	Sum	12	4	8	96	7	7

Table 4.4 Summary of surveys for *T. macrops* in 18 protected and human dominated study sites in the Sakaerat Biosphere Reserve, Nakhon Ratchasima province, Northeast Thailand conducted during the 2016 cold season.

		Cold season 2016		
		Surveys	Detections	# detected
Human dominated	Canal 1	5	0	0
	Plantation 1	1	0	0
	Plantation 2	0	0	0
	Plantation 3	1	0	0
	Plantation 4	1	0	0
	Pond 1	0	0	0
	Pond 2	1	0	0
	Pond 3	1	0	0
	Pond 4	2	0	0
Protected	Forest 1	0	0	0
	Forest 2	0	0	0
	Forest 3	0	0	0
	Forest 4	0	0	0
	Forest 5	0	0	0
	Forest 6	2	1	1
	Forest 7	0	0	0
	Forest 8	0	0	0
	Forest 9	0	0	0
	Sum	14	1	1

Site (ψ) and survey (p) specific models (55 total) were run in program PRESENCE and I sought to find the most parsimonious models. Between 2 and 46 parameters were input, with the lowest AIC and ΔAIC values having <4 (top 5 models are summarized in Table 4.1.1.5). The naïve estimate, or proportion of sites which were surveyed where *T. macrops* was detected at least once without correcting for detection probability, was 0.22. Proportion of sites occupied (ψ) was 0.34 ± 0.15 and overall detection probability (p) was 0.22 ± 0.04. The most parsimonious predicted AIC model with site detection probability not fixed, ψ(Plantation), p(Temp), provided estimates of p of the sites between 0.21 and 0.25 with a range of standard errors of 0.3- 0.04. Estimates of ψ for the sites were 0.5 except for Pond 1-4, with standard error of 0 for all. The ψ-hat estimates ranged at sites between 0.14 to 1.0, with standard errors between 0 and 0.04.

It is worth noting that AIC_C, which corrects for small sample sizes, produced dissimilar results to AIC results. The AIC_C method suggested ψ(Plantation), p(Temp) to be the best predictor with mixed results following thereafter (Table 4.5).

Table 4.5 Top 5 models of site occupancy (ψ) and detection probability (*p*) according to Akaike's Information Criterion for *T. macrops*.

Model	AIC	ΔAIC	w_i	AIC_c
ψ(plantation), *p*(.)	126.36	0	0.0801	126.76
ψ(plantation), *p*(temp)	126.68	0.32	0.0683	127.08
ψ(plantation, canal), *p*(.)	126.97	0.61	0.0591	127.80
ψ(plantation), *p*(humid)	127.01	0.65	0.0579	127.41
ψ(plantation, natfor), *p*(.)	127.08	0.72	0.05559	127.91
1 group, Constant P	129.71	3.35	0.015	130.11

4.1.2 Spatial ecology and movement

Between October 1 2014 and January 15 2017, I tracked 15 *T. macrops*, 2 *T. vogeli* and 2 *T. albolabris* (Table 4.6) for a mean of 96.10 ± 9.54 days (range= 35-190 days) and 97.79 ± 13.59 mean number of fixes (range= 10-202 fixes) through the course of three sampling sessions in five different sites (Canal 1, Pond 1, Plantation 2, Forest 6, and Forest 9). Only three male green pit vipers were tracked because of the strong sexual dimorphism of this taxon; males commonly being too small to meet the general 5% body mass rule for transmitter implantation. Male girth was also observed to rarely be adequate; non-natural behavior likely would have resulted if individuals captured opportunistically with low mass had been implanted with radio transmitters. Mean SMI for tracked vipers was 68.5 ± 3.79 (range 50.6- 109.3, Table 4.7). This study included gravid females (females with detectable ova during palpation; n = 1 *T. albolabris*, 10 *T. macrops*), either known from initial capture or after subsequent captures, at all of the radiotelemetry study sites. Minimum convex polygons of gravid female (n = 10) *T. macrops* were not statistically different than non- gravid females (n

= 3) in this study (W = 18, p = 0.6923) with data being non-normal (W = 0.9112, p = 0.1906) but having homogeneic variance (F = 0.5347, p = 0.4799); movement pattern was not significantly different either with the same samples (MDD, W = 18, p = 0.6923) with data being non- normal (W = 0.9489, p = 0.5816) but having homogeneic variance (F = 0.0315, p = 0.8624) so both gravid and non- gravid females were analyzed together (summarized in Table 4.8 and Table 4.9). All but 2 of the female *T. macrops* were tracked during the cold season; these were tracked from the end of the cold season until the end of the hot season. Other individual vipers were tracked during multiple seasons as well. Due to small sample size and to maintain consistency, these individuals were included in overall analyses but compared with basic descriptive statistics.

Table 4.6 Basic tracking information for green pit viper radiotelemetry study.

Viper ID	Study area	Site	Transmitter type	Start	End	Days tracked	Number of fixes
T. albolabris							
TRAL013	Human dominated	Pond 1	BD2T-HX	2015-10-01	2015-03-13	163	127
TRAL016	Human dominated	Plantation 2	BD2T-HX	2015-11-19	2015-12-24	35	10
T. macrops							
TRMA174	Protected	Forest 9	BD2, BD2T	2014-10-07	2015-01-27	110	188
TRMA178	Protected	Forest 9	BD2	2014-11-11	2015-02-13	92	153
TRMA186	Protected	Forest 9	BD2	2014-11-08	2015-02-12	94	139
TRMA211	Human dominated	Plantation 2	BD2T-HX	2015-11-17	2016-02-07	80	40
TRMA220	Human dominated	Canal 1	BD2T-HX	2015-12-05	2016-06-15	190	149
TRMA221	Human dominated	Canal 1	BD2T-HX	2015-12-02	2016-01-23	51	34
TRMA222	Human dominated	Plantation 2	BD2T-HX	2015-12-10	2016-02-28	78	48
TRMA229	Human dominated	Canal 1	BD2T-HX	2016-02-02	2016-06-16	134	84
TRMA231	Human dominated	Canal 1	BD2T-HX	2016-02-23	2016-06-16	110	98
TRMA232	Human dominated	Canal 1	BD2T-HX	2016-02-25	2016-05-03	88	64
TRMA270	Human dominated	Canal 1	BD2T-HX	2016-10-31	2017-01-08	90	69
TRMA271	Protected	Forest 6	BD2T-HX	2016-11-03	2017-01-07	64	86
TRMA273	Human dominated	Canal 1	BD2T-HX	2016-11-08	2016-01-03	55	67
TRMA274	Protected	Forest 6	BD2T-HX	2016-11-09	2017-01-07	85	58
TRMA282	Protected	Forest 6	BD2T-HX	2016-12-05	2017-01-11	36	42
T. vogeli							
TRVO002	Protected	Forest 9	BD2T	2014-10-01	2015-02-12	135	200
TRVO003	Protected	Forest 9	BD2, BD2T	2014-10-01	2015-02-13	136	202
					Mean	96.11	97.79
					SD	41.60	59.26
					SE	9.54	13.59

Table 4.7 Basic morphometric information for green pit viper radiotelemetry study.

Viper ID	Study area	Sex	SVL	Body mass	SMI	Gravid
T. albolabris						
TRAL013	Human dominated	Female	625	113.90	84.97	Yes
TRAL016	Human dominated	Male	501	40.20	59.83	Yes
T. macrops						
TRMA174	Protected	Female	535	43.70	69.69	Yes
TRMA178	Protected	Female	543	44.50	75.30	Yes
TRMA186	Protected	Female	594	44.80	66.59	Yes
TRMA211	Human dominated	Female	518	42.40	57.97	No
TRMA220	Human dominated	Female	580	91.30	88.56	Yes
TRMA221	Human dominated	Female	612	86.40	70.43	Yes
TRMA222	Human dominated	Male	500	33.00	50.59	No
TRMA229	Human dominated	Male	438	38.60	93.21	No
TRMA231	Human dominated	Female	520	47.00	69.84	Yes
TRMA232	Human dominated	Female	612	109.00	99.46	Yes
TRMA270	Human dominated	Female	590	83.50	93.46	No
TRMA271	Protected	Female	514	52.50	82.96	Yes
TRMA273	Human dominated	Female	593	73.90	82.89	Yes
TRMA274	Protected	Female	528	50.70	77.05	No
TRMA282	Protected	Female	610	94.70	95.20	Yes
T. vogeli						
TRVO002	Protected	Female	701	104.20	109.28	No
TRVO003	Protected	Female	722	106.80	106.80	No
		Mean	570.32	68.48	80.74	
		SD	70.38	28.53	16.52	
		SE	16.15	6.54	3.79	

Table 4.8 Basic movement information for green pit viper radiotelemetry study.

Viper ID	Study area	Number of moves	Mean distance between moves	MDD
T. albolabris				
TRAL013	Human dominated	21	28.75	0.18
TRAL016	Human dominated	3	25.12	0.72
T. macrops				
TRMA211	Protected	10	17.78	0.22
TRMA220	Protected	8	39.03	0.21
TRMA221	Protected	9	15.60	0.31
TRMA222	Human dominated	11	50.42	0.65
TRMA229	Human dominated	4	17.55	0.13
TRMA231	Human dominated	4	13.20	0.12
TRMA232	Human dominated	1	30.68	0.35
TRMA271	Human dominated	25	27.03	0.42
TRMA274	Human dominated	23	35.45	0.42
TRMA282	Human dominated	1	10.05	0.28
TRMA270	Human dominated	10	28.08	0.31
TRMA273	Protected	9	23.62	0.43
TRMA174	Human dominated	7	24.30	0.22
TRMA178	Protected	13	25.55	0.28
TRMA186	Protected	12	22.52	0.24
T. vogeli				
TRVO002	Protected	30	26.22	0.19
TRVO003	Protected	20	37.90	0.28
	Mean	11.63	26.25	0.31
	SD	8.42	9.77	0.16
	SE	1.93	2.24	0.04

Table 4.9 Basic spatial ecology information for green pit viper radiotelemetry study.

Viper ID	Study area	MCP (ha)	Kernel	
			50	99
T. albolabris				
TRAL013	Human dominated	0.36	0.21	1.35
TRAL016	Human dominated	0.06	0.08	0.55
T. macrops				
TRMA174	Human dominated	0.25	0.18	1.31
TRMA178	Protected	0.57	0.70	4.17
TRMA186	Protected	0.17	0.31	1.65
TRMA211	Protected	0.08	0.07	0.42
TRMA220	Protected	0.10	0.09	0.57
TRMA221	Protected	0.11	0.07	0.43
TRMA222	Human dominated	0.42	0.28	2.12
TRMA229	Human dominated	0.01	0.00	0.02
TRMA231	Human dominated	0.01	0.01	0.08
TRMA232	Human dominated	0.01	0.02	0.16
TRMA270	Human dominated	0.22	0.13	0.88
TRMA271	Human dominated	0.38	0.19	1.28
TRMA273	Protected	0.18	0.16	0.95
TRMA274	Human dominated	0.31	0.34	2.15
TRMA282	Human dominated	0.00	0.00	0.01
T. vogeli				
TRVO002	Protected	0.78	0.25	1.55
TRVO003	Protected	1.04	0.84	4.74
	Mean	0.27	0.21	1.29
	SD	0.28	0.23	1.30
	SE	0.06	0.05	0.30

Of the 19 vipers tracked, only 2 were *T. albolabris* and another 2 were *T. vogeli* due to the extremely low encounter rate in the study areas. Male individuals (n= 2 *T. macrops*, 1 *T. albolabris*) and the single female *T. albolabris* were excluded from statistical comparison between the study sites due to small sample size, however, these animals were treated as focal animals and general observation between them and the female *T. macrops* (n= 13) and female *T. vogeli* (n= 2) have been included. The male *T. macrops* (n=2) were tracked between different seasons, so direct statistical comparison between each other or females was not possible. The one female *T. macrops* from the plantation study site was excluded from site specific analyses, but included in comparisons between disturbed and forest study areas. Both *T. vogeli* were tracked before this study began (initially implanted 07 and 09 July, 2014 for TRVO002 and TRVO003, respectively) and removed (23 April, 2015, TRVO003) or lost signal (04 April, 2015, TRVO02) after the three female *T. macrops* in the study site were removed; this data was not included in analyses. Number of fixes was a better predictor for MCP (R^2 = 0.4352) than number of days tracked (R^2 = 0.0912) overall for all individuals tracked (n = 19). Home range MCP bootstrap results varied with tracked green pit vipers. Asymptotes were clearly achieved by 1 of the *T. albolabris* (TRAL013), some of the *T. macrops* (TRMA211, 222, 232, and 274), and both of the *T. vogeli* (TRV002 and 003) tracked. The second *T. albolabris* tracked and some of the *T. macrops* bootstrap estimates displayed lines which were moving towards the asymptote. Figure 4.1 displays examples of tracked vipers with A) limited movemement, B) limited sample time, and C) asymptote attained. Comparison of home range analysis methods produced similar results for MCP and 50% kernels (t = - 0.72, df = 34.4, p = 0.4764) for all tracked vipers (n = 19), however, 99% kernels produced significantly larger home range estimates than the MCP method (t = 3.3217, df = 19.662, $p < 0.005$). Data from 50% kernel and MCP comparison data was normal (W = 0.8189, $p < 0.001$) and exhibited homogenous variance (F = 0.9683, p = 0.3317); 99% kernel and MCP comparison data was normal (W = 0.7005, $p < 0.001$) but displayed heterogeneic variance (F = 11.556, $p < 0.005$).

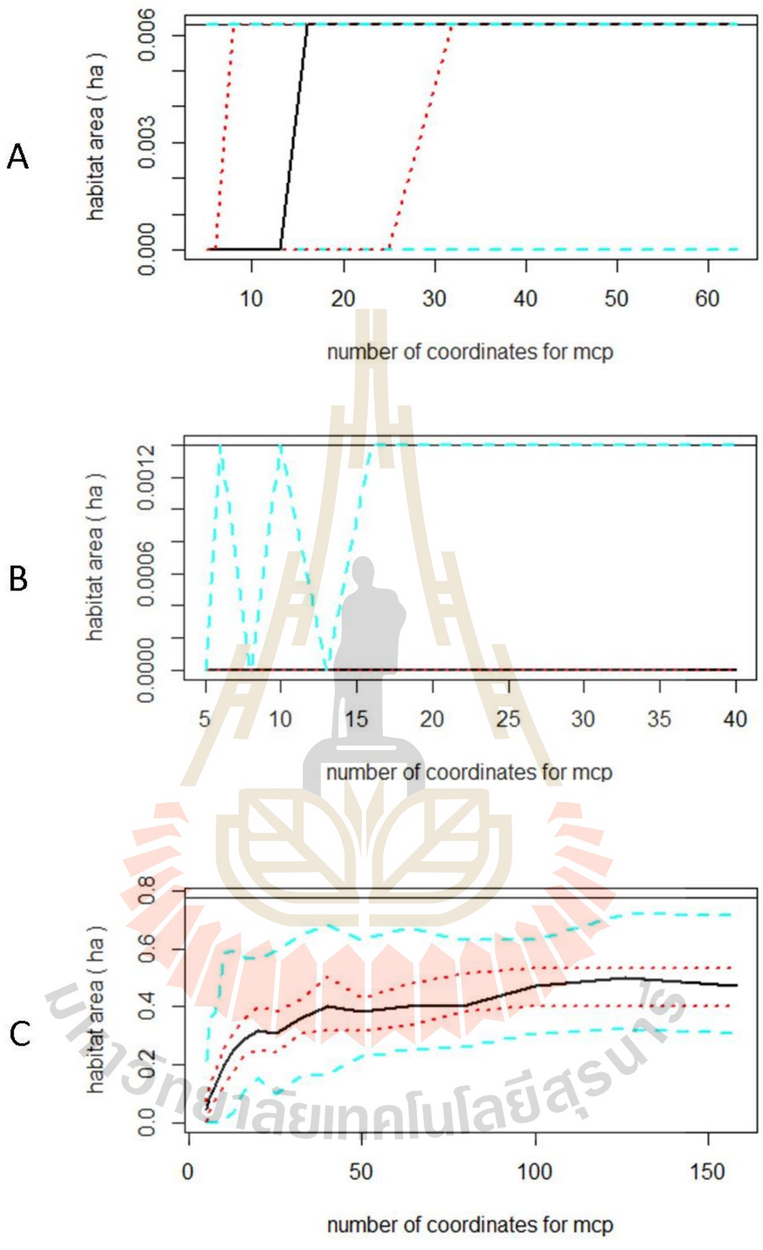

Figure 4.1 MCP bootstrap home range asymptotes created from tracked green pit vipers at the Sakaerat Biosphere Reserve. Shown are A) limited movement (TRMA232), B) limited sample time and movement (TRMA282), and C) asymptote attained (TRVO002).

The mean body mass of female *T. macrops* did not differ significantly (t = 1.7363, df = 10.991, p = 0.1104) between the human dominated (n = 7) and protected forest (n = 6) study areas. Similarly, snout- vent length did not differ significantly between the areas (t = 0.9605, df = 10.799, p = 0.3578). Body mass data was homogenous (F = 0.5566, p = 0.4713) and normal (W = 0.8515, p < 0.05), and SVL data was homogenous (F = 0, p = 1.0) and normal (W = 0.8533, p < 0.05). Because morphometric data did not differ significantly between human dominated and protected forest study areas, comparison of spatial patterns were possible.

I utilized several 1.9 g transmitter types for my study, including BD- 2, BD- 2T, and BD- 2THX. The BD-2 and BD-2T are identical traditional whip antenna transmitters, the only difference being function (BD-2T is calibrated for temperature sensitivity). The BD- 2THX has this antenna coiled into a short portion of potting material which just extends out from the transmitter, and has been called a helical transmitter by the manufacturer, Holohil Ltd. Whip antennas (both BD- 2 and 2T) were utilized for 3 female *T. macrops* and 2 *T. vogeli* in the Forest 9 protected study site, however they were not utilized in any other area nor were transmitters with helical antennas utilized again in the Forest 9 study area. However, previous study at the Forest 6 (Strine 2015) study site utilized whip antennas with female *T. macrops* (n = 9), which I compared females of this species with helical antenna transmitters (n = 3). Although number of vipers tracked was greater from the previous study, days tracked and number of fixes were not significantly different (W = 17, p = 0.6; and W = 12, p = 0.8636, respectively) between the 2 studies. Overall MCP home range and number of moves did not differ between the two studies and transmitter types (W =

12, p = 0.8333; and W = 16, p = 0.7106, respectively). Data for days tracked by transmitter type by the two studies was homogenous (F = 0.0619, p = 0.8085) but not normal (W = 0.9592, p = 0.7718), number of fixes was homogenous (F = 0.8023, p = 0.3915) but not normal (W = 0.8953, p = 0.138), MCP was homogenous (F = 1.7012, p = 0.2284) but not normal (W = 0.9645, p = 0.8352), and number of moves was homogenous (F = 1.6882, p = 0.223) but not normal (W = 0.9438, p = 0.5485).

The number of days and tracks was not significantly different (t = 0.7111, df = 9.671, p = 0.4938; and W = 13, p = 0.2949, respectively) between female *T. macrops* tracked in the protected (n= 6) and human dominated study areas (n= 7) in my study. Number of days females were tracked at the three sites (Canal 1 n= 6, Forest 6 n= 3, Forest 9 n= 3) which were compared were not significantly different (Kruskal-Wallace chi- square = 3.998, df= 2, p = 0.1355), however, number of fixes were almost statistically significant different (Kruskal- Wallace chi- square = 5.7692, df= 2, p= 0.055). Data for number of days tracked in each study area was homogenous (F = 0.6445, p = 0.4391) and normal (W = 0.8649, p < 0.05), and number of tracks was homogenous (F = 2.6498, p = 0.1318) and normal (W = 0.8982, p = 0.1263). Data for number of days tracked in each study site was homogenous (F = 1.3174, p = 0.3149) but not normal (W = 0.8712, p = 0.06772), and number of tracks was homogenous (F = 0.5798, p = 0.5796) and also not normal (W = 0.9138, p = 0.2385). Because number of fixes and the number of days female *T. macrops* tracked did not vary significantly statistically between the study areas and sites, comparison of spatial patterns were possible at those levels.

Female *T. macrops* (n = 13) were tracked for a mean of 90.5 ± 9.6 days and 87.9 ± 12.3 fixes. Overall mean female *T. macrops* home range was estimated to be 0.19 ±

0.4 ha for minimum convex polygon (MCP) and 0.17 ± 0.05 ha for core area (50% fixed kernel) and 1.08 ± 0.29 ha for activity areas (99% fixed kernel). Individuals moved a mean of 9.8 ± 1.8 times for a mean distance of 25.4 ± 2.7 m during the duration they were tracked. Mean daily displacement was a mean of 0.29 ± 0.026 m/day for all female *T. macrops*.

Spatial ecology of the tracked female *T. macrops* was not significantly different between the protected (n = 6) and human dominated (n = 7) study areas. Home range MCP was not significantly different for tracked vipers in the areas ($W = 9$, $p = 0.1014$), as were core ($t = -2.1202$, $df = 5.462$, $p = 0.08279$) and activity kernel areas ($t = -2.191$, $df = 5.493$, $p = 0.07513$). Home range MCP data was homogenous ($F = 4.3515$, $p = 0.06$) but not normal ($W = 0.8892$, $p = 0.09$), 50% kernel was not homogenous ($F = 4.0877$, $p = 0.0682$) but was normal ($W = 0.8043$, $p = 0.007668$), and 99% kernel was both homogenous ($F = 3.6518$, $p = 0.0824$) and normal ($W = 0.8214$, $p = 0.01239$). Number of moves ($W = 11.5$, $p = 0.1967$), mean distance moved ($W = 21$, $p = 1$), and MDD ($t = 0.8273$, $df = 7.398$, $p = 0.4339$) suggested movement patterns to be similar between the study areas. Data for area comparison of number of moves was homogenous ($F = 4.3515$, $p = 0.06$) but not normal ($W = 0.8892$, $p = 0.09$); mean distance moved was also homogenous ($F = 0.521$, $p = 0.48$) but not normal ($W = 0.981$, $p = 0.98$), and MDD was both homogenous ($F = 1.9616$, $p = 0.19$) and normal ($W = 0.5181$, $p < 0.05$).

Similarly, movement and space use by the tracked female *T. macrops* did not differ significantly between the 3 study sites (n = 6 Canal 1, n = 3 Forest 6, n = 3 Forest 9). Data at the site level was homogenous ($F = 3.01$, $p = 0.10$) but not normal ($W = 0.9209$, $p = 0.29$) for MCP, homogenous ($F = 5.0891$, $p = 0.03$) but not normal

(*W* = 0.8217, *p* = 0.02) for core area, homogenous (*F* = 5.752, *p* = 0.02) but not normal (W = 0.8384, *p* = 0.03) for activity area. Data was homogenous (*F* = 10.029, *p* = 0.005) but not normal (W = 0.8946, *p* = 0.13) for number of moves, homogenous (*F* = 2.7831, *p* = 0.11) but not normal (W = 0.9706, *p* = 0.92) for mean distance moved, and homogenous (*F* = 1.5667, *p* = 0.26) and normal (W = 0.5383, *p* < 0.001) for MDD. Home range was not significant with the MCP (Kruskal- Wallace chi- square = 2.8846, *df* = 2, *p* = 0.2364), core area kernel (Kruskal- Wallace chi- square = 4.7308, *df* = 2, *p* = 0.09391) and activity area kernel (Kruskal- Wallace chi- square = 5.2436, *df*= 2, *p* = 0.07267) methods. Similarly, movement was also very similar between the sites including number of moves (Kruskal- Wallace chi- square = 1.8947, *df* = 2, *p* = 0.3878), mean distance moved (Kruskal- Wallace chi- square = 1.4615, *df* = 2, *p* = 0.8968), and MDD (*F* = 0.398, *df* = 2, *p* = 0.683). Broken down further, home range was not significantly different between the two forest sites (n = 3 Forest 6, n = 3 Forest 9) with MCP (*W* = 5, *p* = 1), core area kernel (*W* = 6, *p* = 0.7), and activity area kernel (*W* = 7, *p* = 0.4). Number of moves between the two forest sites was also not significantly different (*W* = 7, *p* = 0.3758). Forest site MCP data was homogenous (*F* = 0.0153, *p* = 0.9075) but not normal (*W* = 0.9945, *p* = 0.9973); core area kernel was homogenous (*F* = 1.0988, *p* = 0.3537) but not normal (*W* = 0.9217, *p* = 0.518); activity area kernel was homogenous (*F* = 0.9638, *p* = 0.3818) but not normal (*W* = 0.9189, *p* = 0.4973); and moves was homogenous (*F* = 0.622, *p* = 0.4744) but not normal (*W* = 0.9518, *p* = 0.7549).

Sample size was limited for males (n= 3), *T. albolabris* (n = 2), and *T. vogeli* (n = 2) for this study. Basic spatial ecology and movement data for these individuals are presented in Table 4.1.2.3 and Table 4.1.2.4. Both female *T. vogeli* displayed larger home ranges (MCP, activity area, core area) than any of the *T. macrops*, and the gravid female *T. albolabris* was larger than all but 2. Home range, MCP, and kernels (50 and 99%), are visualized by study site (not by study period) in Figures 4.2 - 4.11.

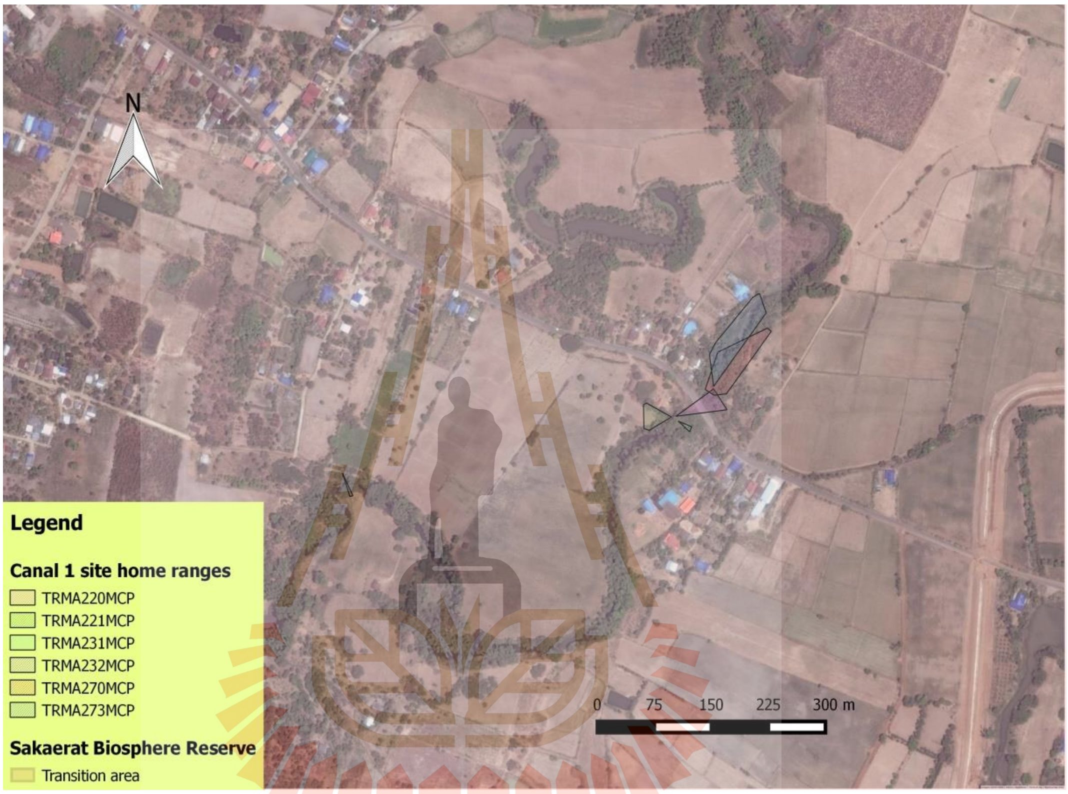

Figure 4.2 Map of home ranges (minimum convex polygon, MCP) for 6 adult female *T. macrops* radiotracked at a water based site (Canal 1) within the Sakaerat Biosphere Reserve, with the transition area of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand. An additional male *T. macrops* was tracked at this site, but displayed limited movement.

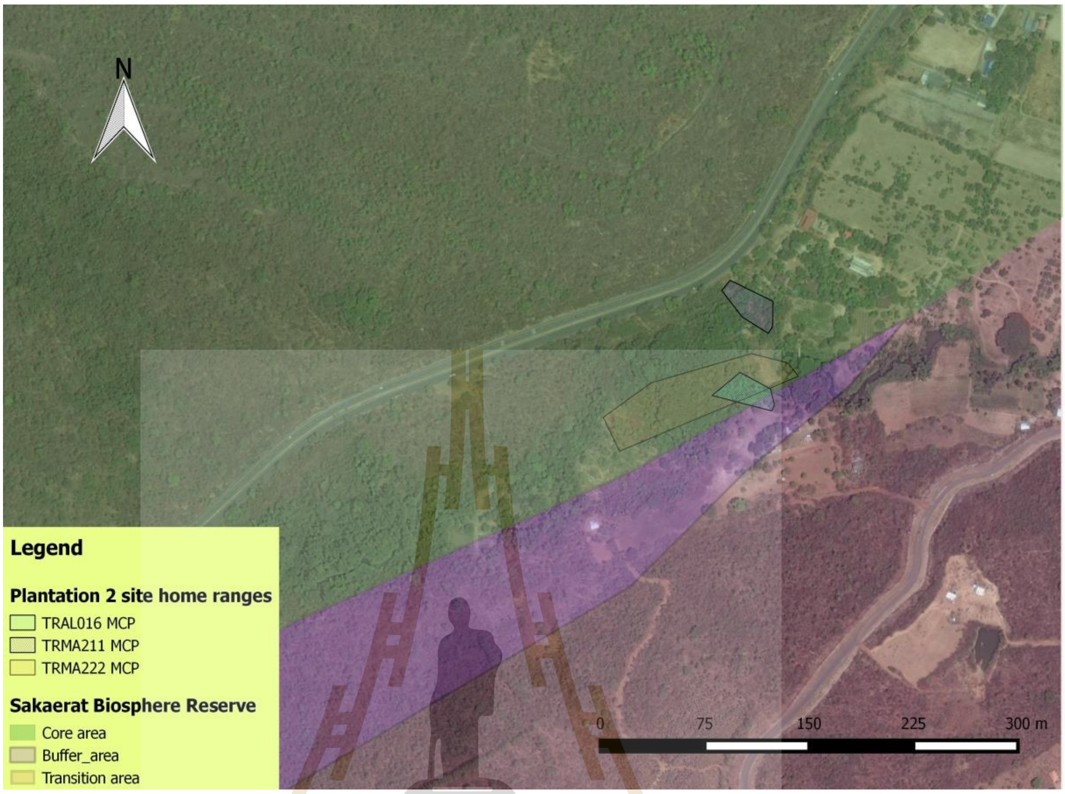

Figure 4.3 Map of home ranges (minimum convex polygon, MCP) for 1 adult male *T. albolabris*, 1 adult female *T. macrops*, and 1 adult male *T. macrops* radiotracked at a plantation based site (Plantation 2) within the Sakaerat Biosphere Reserve, with the core, buffer, and transition areas of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand.

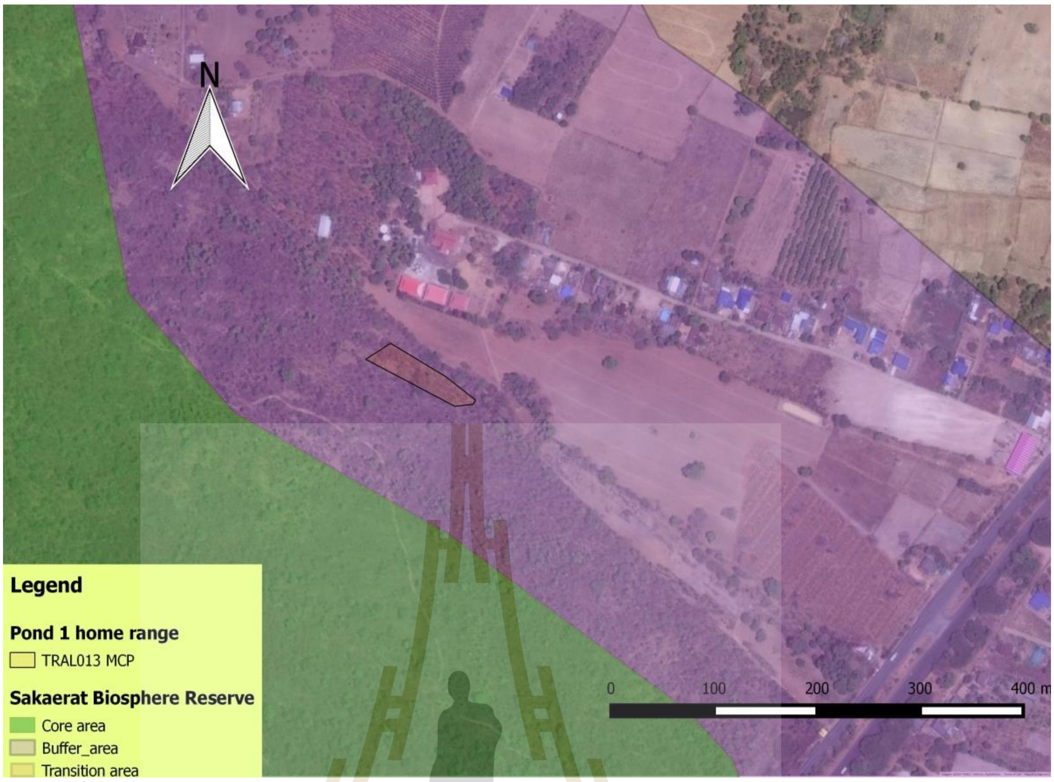

Figure 4.4 Map of a home range (minimum convex polygon, MCP) for 1 adult female *T. albolabris* radiotracked at a water based site (Pond 1) within the Sakaerat Biosphere Reserve, with the core, buffer, and transition areas of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand.

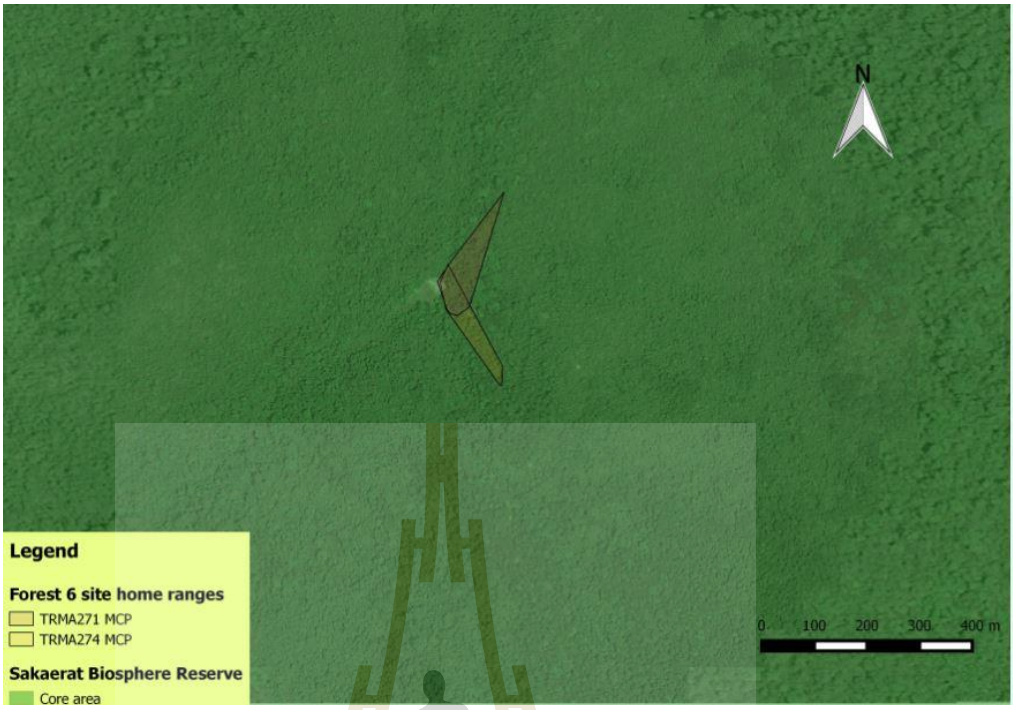

Figure 4.5 Map of home ranges (minimum convex polygon, MCP) for 2 adult female *T. macrops* radiotracked at a water based site (Forest 6) within the Sakaerat Biosphere Reserve, with the core area of the reserve delineated. This study site was part of the protected study area. An additional female *T. macrops* was tracked at this site, but displayed limited movement.

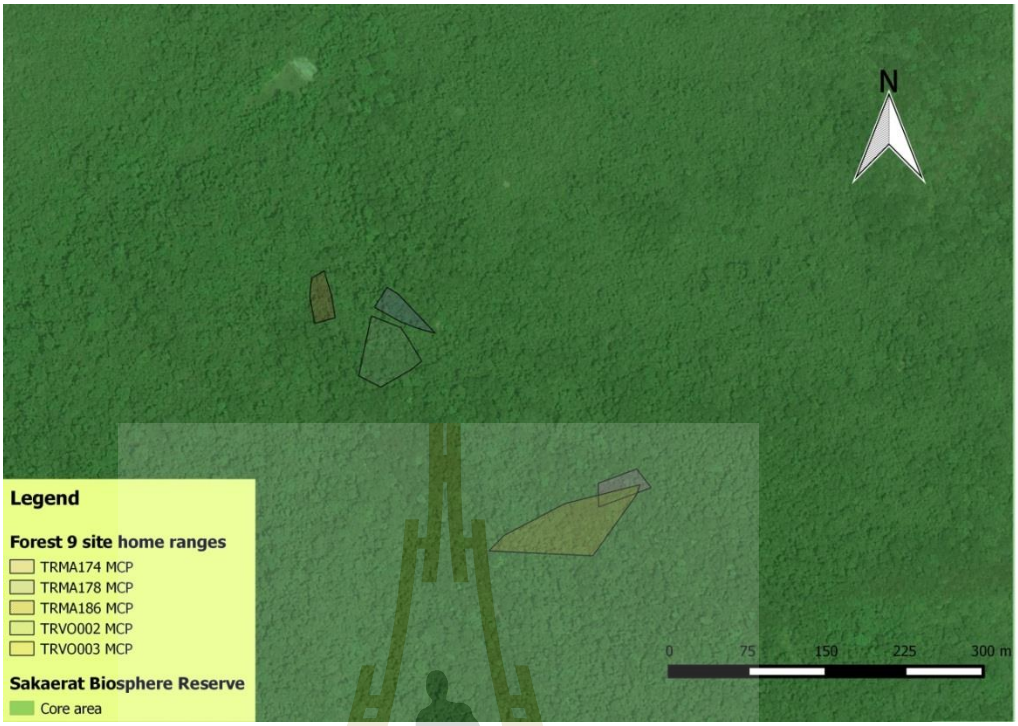

Figure 4.6 Map of home ranges (minimum convex polygon, MCP) for 3 adult female *T. macrops* and 2 adult female *T. vogeli* radiotracked at a forest based site (Forest 9) within the Sakaerat Biosphere Reserve, with the core area of the reserve delineated. This study site was part of the protected study area.

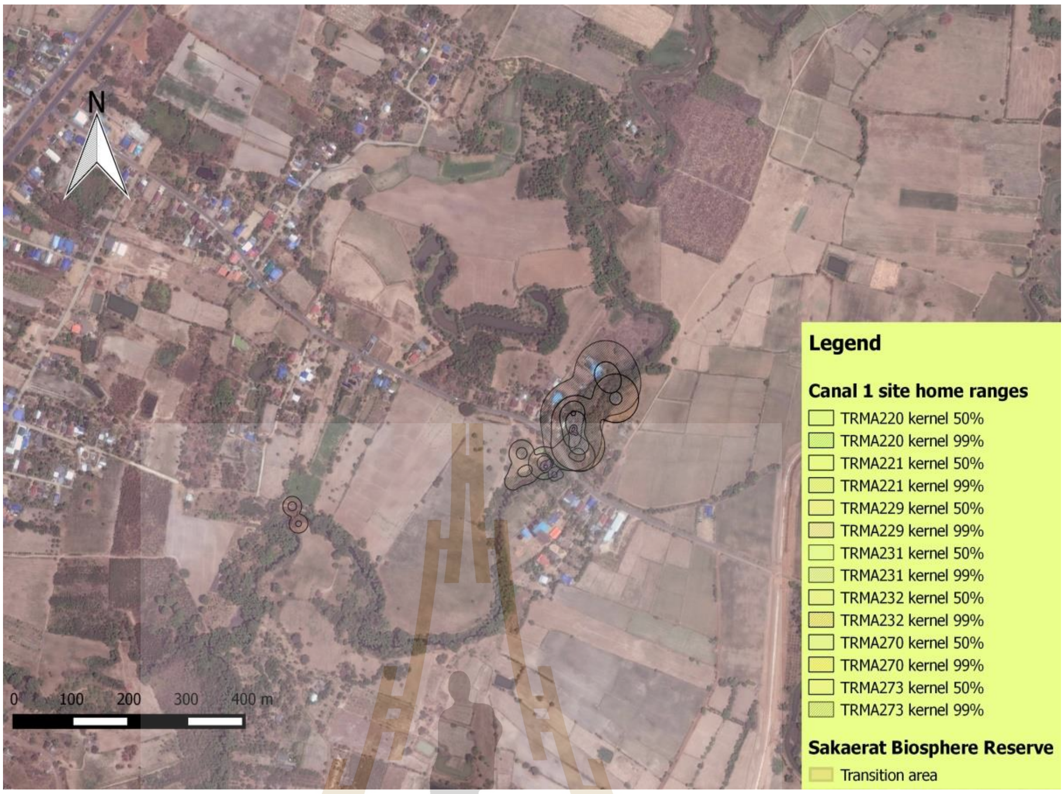

Figure 4.7 Map of home ranges (fixed kernel, 50 and 99%) for 6 adult female and 1 adult male *T. macrops* radiotracked at a water based site (Canal 1) within the Sakaerat Biosphere Reserve, with the transition area of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand.

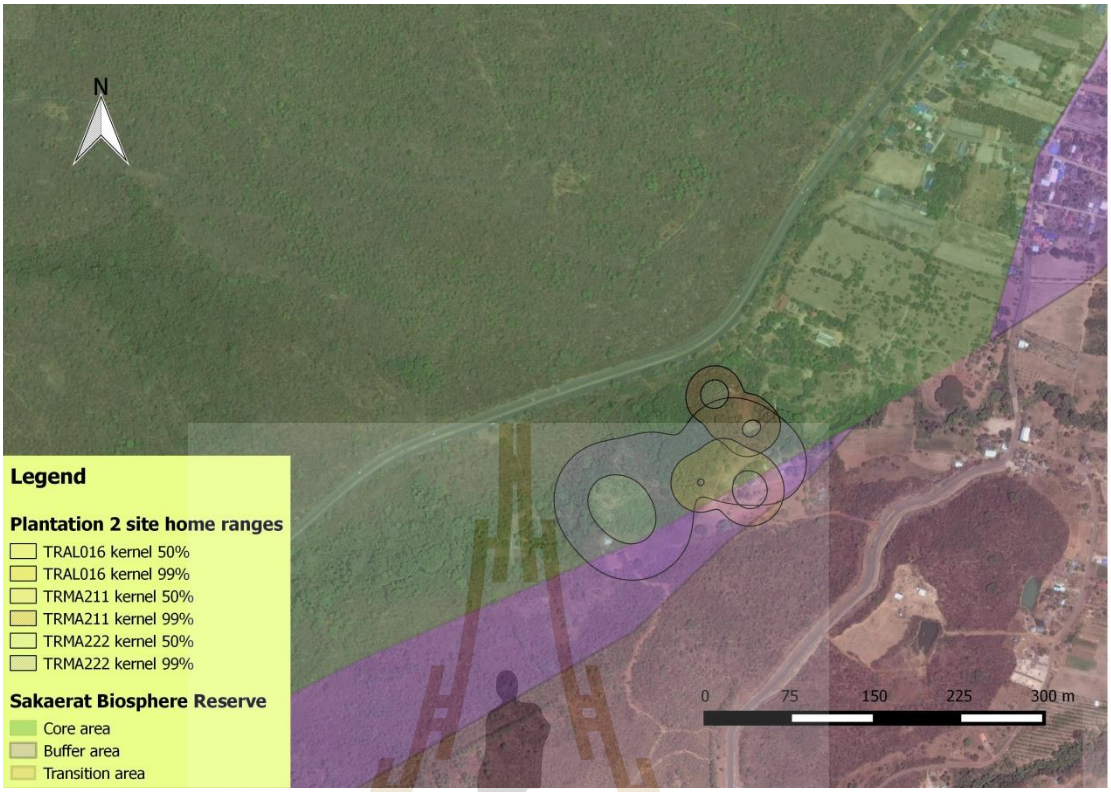

Figure 4.8 Map of home ranges (fixed kernel, 50 and 99%) for 1 adult male *T. albolabris*, 1 adult female *T. macrops*, and 1 adult male *T. macrops* radiotracked at a plantation based site (Plantation 2) within the Sakaerat Biosphere Reserve, with the core, buffer, and transition areas of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand.

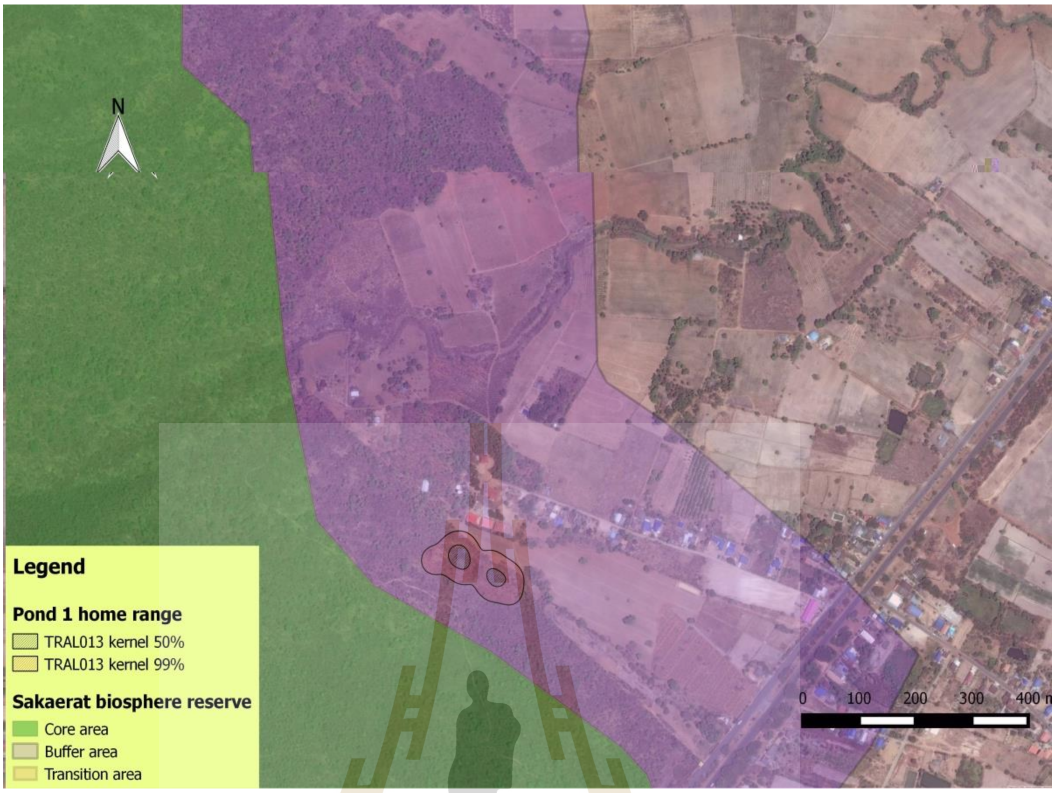

Figure 4.9 Map of a home range (fixed kernel, 50 and 99%) for 1 adult female *T. albolabris* radiotracked at a water based site (Pond 1) within the Sakaerat Biosphere Reserve, with the core, buffer, and transition areas of the reserve delineated. This study site was part of the human dominated study area, which was conducted in the Udom Sab subdistrict, Nakhon Ratchasima district, Northeast Thailand.

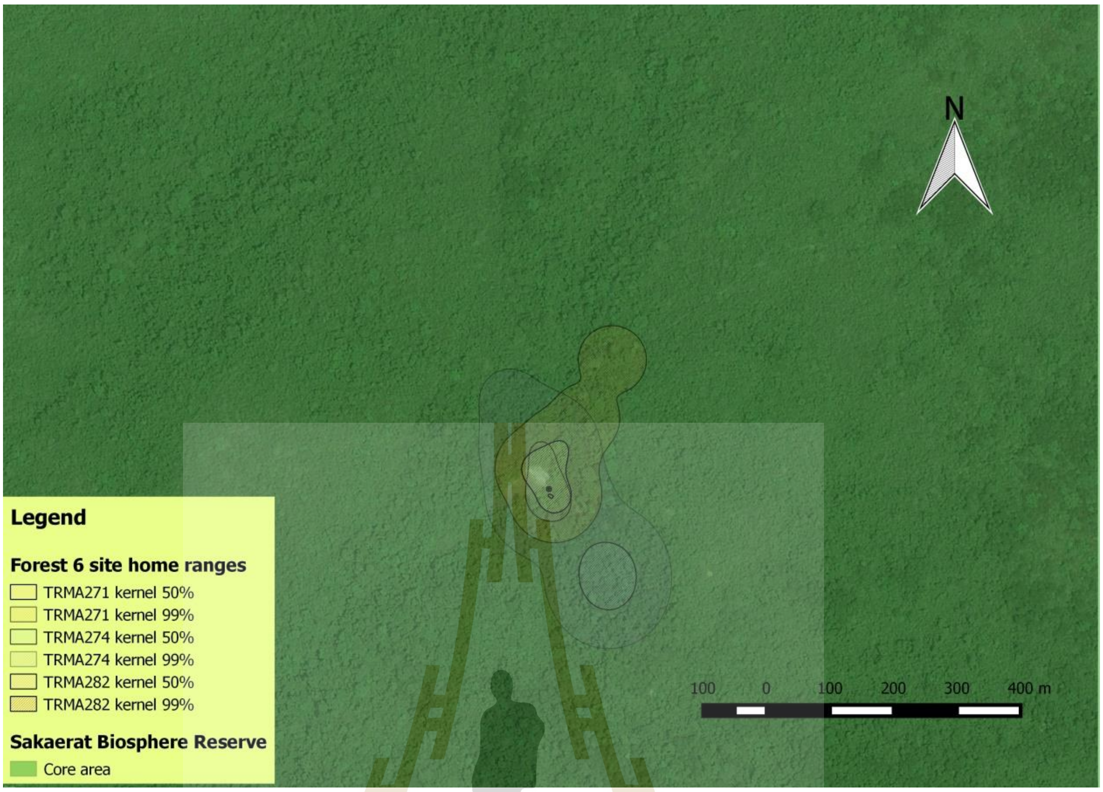

Figure 4.10 Map of home ranges (fixed kernel, 50 and 99%) for 3 adult female *T. macrops* radiotracked at a water based site (Forest 6) within the Sakaerat Biosphere Reserve, with the core area of the reserve delineated. This study site was part of the protected study area.

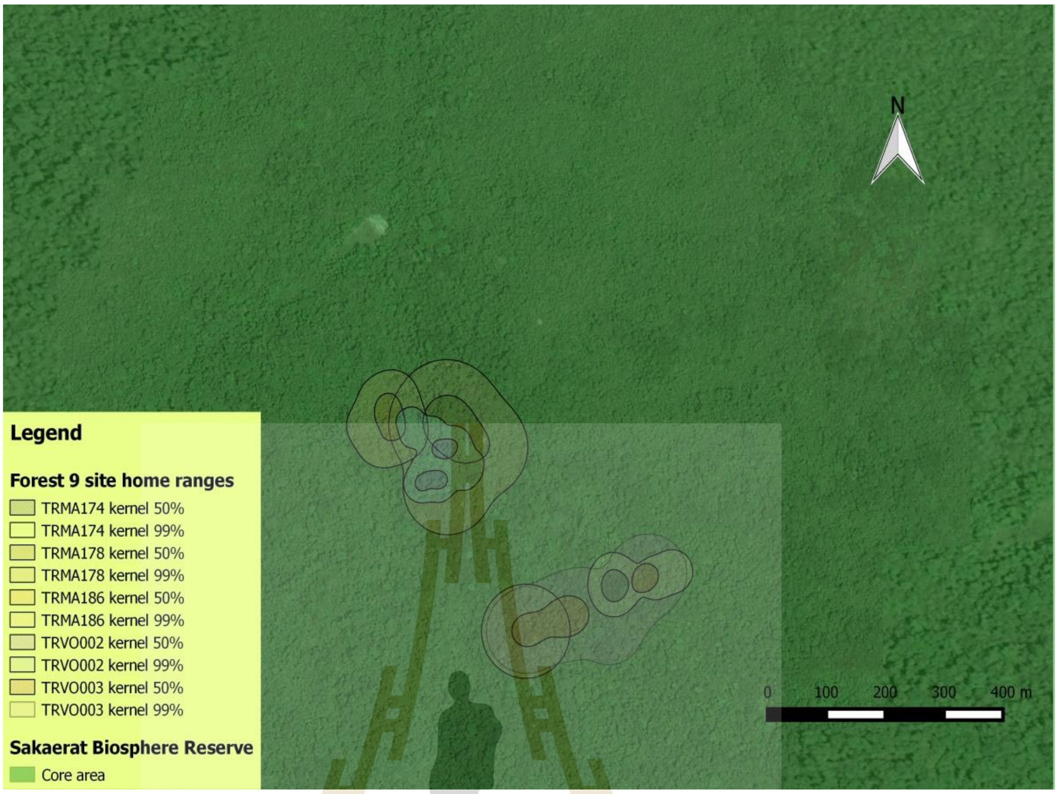

Figure 4.11 Map of home ranges (fixed kernel, 50 and 99%) for 3 adult female *T. macrops* and 2 adult female *T. vogeli* radiotracked at a forest based site (Forest 9) within the Sakaerat Biosphere Reserve, with the core area of the reserve delineated. This study site was part of the protected study area.

4.1.3 Habitat selection

Habitat transects were conducted at three sites which were also utilized for radiotelemetry and survey portions of this study during the cold season (November-February) in 2014 and 2016. Microhabitat (habitat within 1 m) and mesohabitat (within 10 m) transect data were directly comparable, i.e. data was collected in the same manner and season, to the tracking and survey portions of the study. Because only 1 male *T. albolabris* and 2 male *T. macrops* were part of the radiotelemetry study (and only 1 *T. macrops* male was tracked in an area where transects were conducted), observations were made but statistical analyses were not conducted. Visual encounter surveys were conducted between September 2015 through November 2016, and habitat observations were made at nearly all captures or observations. Vipers (n = 33) were observed at 4 survey sites, however, sample size was small (n = 2) and habitat data was not sufficient at 1 of the protected sites (Forest 2). Several (n = 4) vipers were detected during the rain season at the protected Forest 6 site, however, available habitat transects were not run during this season so these vipers were excluded from habitat analyses. Vipers were also detected at the human dominated Plantation 2 site, although available habitat transects were not previously conducted at this location. Thus, habitat selection analyses for survey detections were only able to be carried out for vipers (n= 6) observed during the cold season at the Canal 1 human dominated site.

Landscape level habitat features (macrohabitat) were ubiquitous in the protected study area (dry evergreen habitat). However, macrohabitat was fairly static in the human dominated areas. Agriculture, bamboo, plantation forest, human settlement, wash, and heterogeneous disturbed forest (HDF) were landscape level habitat features recorded during tracking of male (n = 2) and female (n = 7) *T. macrops* in the human dominated study area (Table 4.10). Dominant utilized habitat recorded in the human dominated study area was HDF (63.0%) followed by human settlement (14.8%) and wash (8.64%). Macrohabitat features available within 5m of the dominant habitat utilized were primarily HDF (48.6%) and then agriculture (19.3%) and wash (11.9%) and human settlement (11.0%). Primary macrohabitat features utilized within 10m of tracked vipers in the human dominated area included HDF (63.5%), agriculture (14.0%), and wash (11.2%). Fallow field was the agriculture feature used as dominant habitat (1 occasion) and *Eucalyptus* and rubber (2 occasions each) were the plantation types. Fallow field (20 occasions) and cassava edge (1 occasion) were agriculture types and rubber (4 occasions) and *Eucalyptus* (1 occasion) were plantation types available within 5m of the dominant habitat utilized. Within 10 m of utilized macrohabitat, fallow field (11 occasions), cassava (2 occasions), recently plowed field (2 occasions), and pepper (1 occasion) were agriculture types available and *Eucalyptus* was available plantation within 10m of the dominant habitat utilized on 2 occasions.

Protected and human dominated study areas differed significantly in availability proportions of mesohabitat (chi- squared = 89.87, $df = 9$, $p < 0.001$). Open canopy, lianas and vines, and fallen logs logs made up the highest proportions of available protected study area mesohabitat features, while open canopy, green vegetation, and fallen logs were mesohabitat features most present in human dominated (Canal 1) habitat transects. At the Forest 6 site open canopy, lianas and vines, and fallen logs were the most available habitat features. Open canopy, woody vegetation, and fallen logs were most available at the Forest 9 site.

Female *T. macrops* were observed to utilize mesohabitat features significantly different in the protected (n = 5) compared to the human dominated (n = 4) study area during radiotelemetry study (x- squared = 46.2142, $df = 9$, $p < 0.001$). Tracked vipers in the protected study area used sites with green vegetation, woody vegetation, and fallen logs within 10 m most frequently, while vipers tracked in the human dominated study area were within 10 m of features with open canopy, green vegetation, and human settlements most frequently. Mesohabitat features utilized by tracked vipers were significantly different than available mesohabitat features in both the protected (x- squared = 62.1745, df= 9, p< 0.001) and human dominated study areas (x-squared= 16.3804, *df* = 9, *p* = 0.05), indicating habitat selection. Further investigation of the Forest 6 (n = 2, x- squared = 55.8271, *df* = 9, *p* < 0.001) and Forest 9 (n = 3, x-squared = 43.2054, *df* = 9, *p* < 0.001) sites also suggested habitat selection within those sites themselves. Mesohabitat use observed during surveys at the Canal 1 site, however, were not significantly different than available habitat at the same area (n = 4, x- squared = 7.6714, *df* = 9, *p* = 0.576). Mesohabitat was observed being utilized in similar proportions by vipers during tracking and surveys (n = 4 and n = 4, x- squared = 12.3927, *df* = 9, *p* = 0.1921) at the Canal 1 site.

Protected and human dominated study areas differed significantly in availability proportions of microhabitat (x- squared = 135.0518, *df* = 6, *p* < 0.001) during radiotelemetry study. Saplings, small lianas, and small rocks made up the highest proportions of available protected study area microhabitat features, while green vegetation, saplings, and large rocks were microhabitat features most present in human dominated habitat transects.

Female *T. macrops* were observed to utilize microhabitat features significantly different during radiotelemetry in the protected (n = 6) and human dominated study areas (n = 4, x- squared = 30.2933, *df* = 6, *p* < 0.001). Tracked vipers in the protected study area used small lianas, saplings, and green vegetation most frequently, while vipers tracked in the human dominated study area were observed utilizing trees, green vegetation, and small lianas most frequently. Vipers did not use habitats with different slope percent categories during radiotelemetry study in the protected and human dominated habitats, although they were very similar (x- squared = 9, *df* = 4, *p* = 0.06; primarily utilizing slight slopes between 1-15% inclines). Tracked vipers at the protected study area did exhibit habitat selection with regards to slope (x- squared = 138.1429, *df* = 4, $p < 0.001$), however, human dominated area viper utilization was very similar to available slope (x- squared= 9, *df* = 4, $p = 0.06$).

Tracked female *T. macrops* utilized microhabitat significantly differently than what was available at the Forest 6 (n = 3, x- squared = 44.3782, *df* = 6, $p < 0.001$), Forest 9 (n = 3, x- squared = 110.0229, *df* = 6, $p < 0.001$), and Canal 1 (n = 4, x- squared = 23.5346, *df* = 6, $p < 0.001$) habitat sites. Small lianas, saplings, and trees were utilized most by tracked *T. macrops* at the Forest 6 study site while saplings, small lianas, and rocks were microhabitat features most present. Saplings, small lianas, and green vegetation were utilized most by tracked *T. macrops* at the Forest 9 study site, but saplings, small lianas, and small rocks were most present. Trees, green vegetation, and small lianas were used most as microhabitat by tracked *T. macrops* at the Canal 1 study site, while green vegetation, saplings, and large rocks were most available. Green pit vipers were also observed during surveys (n = 4) to primarily utilize trees, green vegetation, and small lianas as microhabitat which differed significantly from measured available habitat, suggesting habitat selection area (x- squared = 22.5465, *df* = 6, $p < 0.001$). Microhabitat was observed being utilized in similar proportions by vipers during tracking and surveys (n = 4 and n = 4, x- squared = 4.6985, *df* = 6, $p = 0.583$) at the Canal 1 site.

Canopy cover, leaf litter depth, distance to nearest path, number of trees between 10-30 cm diameter at breast height (DBH) within 10 m, number of trees >30 cm DBH within 10 m, distance to the nearest tree, and DBH of nearest trees were measured during transects at the Canal 1, Forest 6, and Forest 9 study sites. Canopy cover was highest in the protected study areas ($W = 616.5$, $p < 0.001$), with the most at the Forest

9 site (Kruskal- Wallace chi-square = 22.06, *df* = 6, $p < 0.001$). Similarly, leaf litter was highest in the protected study areas ($W = 474$, $p < 0.001$), particularly at the Forest 9 site (Kruskal- Wallace chi-square = 28.44, *df* = 2, $p < 0.001$; although Forest 6 was very similar in depth). Path distance and number of trees 10-30 cm were not significantly different at either the area or the site level. There were significantly more trees greater than 30 cm dbh at the human dominated area ($W = 253.5$, $p < 0.001$); at the site level Canal 1 had significantly more larger trees (Kruskal- Wallace chi-square = 31.62, *df* = 2, $p = 0.002$) than the two forest sites which were very similar. Trees were significantly farther at the human dominated study area ($W = 616.5$, $p < 0.001$), and was also farther at the site level (Kruskal- Wallace chi-square = 28.00, *df* = 2, $p < 0.001$). The DBH of trees closest to the transect intervals were significantly larger at the human dominated study area ($W = 3396.5$, $p < 0.001$), at the site level it was also significantly larger than either of the 2 forest areas (Kruskal- Wallace chi-square= 31.62, *df* = 2, $p < 0.001$).

Forest layer vegetative cover was significantly different between the 3 sites assessed during habitat surveys (x- squared = 39.3507, *df* = 6, $p < 0.001$) and is summarized in Table 4.10. Groundstory vegetative cover was the densest layer at the Canal 1 site (41.7%), while the abovestory layer was the densest at the protected sites (31.9% at Forest 6, 32.4% at Forest 9).

Table 4.10 Forest layer availability (%) assessed as abundance categories during habitat transects during 2014 and 2016 cold seasons.

	Canal 1	Forest 6	Forest 9
Groundstory	41.7	20.7	21.5
Understory	20.6	19.5	19.3
Midstory	13.1	27.9	26.8
Abovestory	24.6	31.9	32.4

Tracked *T. macrops* utilized forest layers differently in protected than in human dominated areas. Female vipers in the human dominated study area were observed higher proportion of fixes arboreal (in the mid- and abovestory forest levels) than terrestrial (underground, on ground, groundstory, and understory levels) during the cold season (x- squared = 26.6145, *df* = 1, *p* < 0.001). Tracked female T. macrops utilized forest layers differently in the cold season than during the hot season in the protected area (x- squared = 390.9275, *df* = 5, *p* < 0.001). During the cold season, female vipers in the protected area were primarily in the groundstory, followed by understory and midstory in proportions; in the hot season most viper fixes were in the groundstory, underground, and on the ground. In the human dominated study area, both investigations of females only (x- squared = 28.1084, *df* = 5, *p* < 0.001) and also males and females combined (x- squared = 37.1895, *df* = 5, *p* < 0.001) revealed significant differences in forest layer use between seasons. Male and female vipers utilized the understory in greatest proportion to other forest layers in the human dominated study area, however the next highest proportion used during the cold season was the groundstory followed by the midstory whereas vipers used the midstory with slightly less use of the groundstory during the hot season. Females specifically used the understory in the highest proportion during the cold season, followed by groundstory and then midstory, compared to the same highest use of the groundstory and underground followed by the midstory during the hot season. Gravid females were barely significantly different than non- gravid female *T. macrops* in the human dominated study area (x- squared = 11, *df* = 5, *p* = 0.05). Gravid female *T. macrops* utilized the understory in the highest proportion, followed by the groundstory and then the midstory while non- gravid females used understory and underground equally in the highest proportion followed by groundstory and midstory equally the next highest. Forest layer use was significantly different within the human dominated (x- squared = 35.6216, *df* = 5, *p* < 0.001) and protected (x- squared = 192.7586, *df* = 5, *p* < 0.001) study areas during the day and night. Although vipers were observed to be utilizing lower forest layers for both study areas (not arboreal), they were observed in higher proportions arboreal to not arboreal in the human dominated compared to the protected study area during the day (x- squared = 23.8378, *df* = 1, *p* < 0.001) and night (x- squared = 23.2105, *df* = 1, *p* < 0.001).

Viper observations during surveys were limited (n = 26 layer observations), but vipers were found arboreal less frequently (n = 9) than arboreal (n = 17). This generalization followed for both the protected (n = 3 not arboreal, n= 0 arboreal) and human dominated (n= 14 not arboreal, n = 9 arboreal) study areas. During the cold season, *T. macrops* were observed and/or captured most frequently in the midstory followed by the understory and then groundstory and on the ground equally; in the hot season the understory and groundstory were equally the most frequent followed by equal observations/captures in the midstory and on the ground; vipers were most frequently observed/captured in the understory followed equally by the groundstory and on the ground during the rain season.

Comparison of forest layer observation revealed differences between surveys (n = 26) and tracking (n = 15) for *T. macrops*. While more *T. macrops* were observed to be not arboreal (< 3m above ground level) than arboreal (> 3m above ground level) for both methods, a significantly higher proportion (x- squared = 298.0662, $df = 1$, $p < 0.001$) of vipers were observed to be arboreal during surveys (34.6% of observations) than during tracking (14.4%). Vipers were most frequently observed to be in the groundstory (40.9%), followed by understory (27.5%), and then midstory (14.1%) during tracking; vipers were observed to be in the understory (34.6%) most frequently, followed by the midstory (26.9%) and then the groundstory (23.1%) during surveys which was significantly different than tracking (x- squared= 394.8676, $df = 5$, $p < 0.001$).

Sample size was limited for *T. albolabris* (n = 1) and *T. vogeli* (n = 2), however, basic habitat observations during cold seasons during radiotelemetry are reported in Table 4.11 (microhabitat) and Table 4.12 (mesohabitat) with female *T. macrops* (n = 11) included for reference in comparison. The single female *T. albolabris* utilized habitats with green vegetation microhabitat features most frequently, followed by small lianas and saplings, then large lianas and trees. Two female *T. vogeli* utilized small lianas most frequently as microhabitat features, followed by green vegetation, and then saplings. The single female *T. albolabris* utilized green vegetation, open canopy, and lianas and vines equally most frequently as mesohabitat features. The 2 female *T. vogeli* utilized woody vegetation most frequently and open canopy and lianas and vines equally slightly less most often. Females of the 3 green pit viper species were observed to utilize forest layers differently (x- squared= 55.4121, *df* = 10, $p < 0.001$) during radiotelemetry during the cold season (n = 1 *T. alblolabris*, n = 11 *T. macrops*, n = 2 *T. vogli*). They were also observed arboreal for different proportions of tracks (x- squared = 30.2347, *df* = 2, $p < 0.001$), with *T. vogeli* observed most frequently arboreal compared to the lower forest layers (45% of tracks), *T. macrops* much less frequently (23%), and the single female *T. albolabris* was never observed to be arboreal.

Table 4.11 Basic microhabitat utilization (# of fixes) of female green pit vipers tracked during radiotelemetry study during cold seasons between 2014-2016.

	T. albolabris	*T. macrops*	*T. vogeli*
Green veg	5	304	99
Small lianas	4	326	114
Large lianas	1	193	47
Saplings	4	307	87
Trees	1	235	72
Small rocks	0	40	1
Large rocks	0	19	2

Table 4.12 Basic mesohabitat utilization (# of fixes) of female green pit vipers tracked during radiotelemetry study during cold seasons between 2014-2016.

	T. albolabris	*T. macrops*	*T. vogeli*
Path	1	48	4
Human structure	0	44	0
Fallen logs	1	63	6
Large rocks	0	28	1
Green veg	2	95	3
Woody veg	1	71	8
Dead woody veg	1	42	6
Open canopy	2	84	7
Lianas and vines	2	59	7
Water	0	30	0

The 2 female *T. vogeli* appeared to exhibit both microhabitat (x- squared= 204.4171, *df* = 6, *p* < 0.001) and mesohabitat (x- squared = 19.9048, *df* = 9, *p* = 0.02) selection. While saplings were the most frequently observed available microhabitat features, followed by small lianas, and then small rocks at the Forest 9 site where the 2 *T. vogeli* were tracked, the vipers utilized small lianas most frequently, followed by green vegetation, and then saplings most often as microhabitat. Open canopy was the most available mesohabitat feature at the Forest 9 site followed by fallen logs and lianas and vines equally, but the 2 *T. vogeli* instead utilized woody vegetation most frequently and then open canopy and lianas and vines for mesohabitat.

4.1.4 Behavior

Behavior data was recorded from surveys, (n = 28 available observations), tracking (n = 13), and Bushnell trail camera recordings (n = 23). Behavior data was collected from 28 of the 31 total *T. macrops*, observed during surveys, before and regardless of the decision to capture them. Dominant behavior was recorded during every track for all of the vipers tracked during the telemetry portion of this study, particularly when vipers were visible. Sample size was a limiting factor for males and *T. albolabris* and *T. vogeli* green pit viper species during tracking and surveys, so statistics were primarily limited to female *T. macrops*.

Tracked gravid (n = 10) and non-gravid female (n = 3) *T. macrops* displayed statistically significant different proportions of time in active (ambush and moving) and sedentary (resting and sheltering) behavior (x- squared = 13.7168, *df* = 1, $p < 0.001$). Gravid females (n = 10) were observed moving significantly less proportion of fixes than non- gravid females (n = 3, x- squared = 6.538, *df* = 1, $p = 0.01$). However, tracked gravid female *T. macrops* (n = 10) did not spend more or less time ambushing than non- gravid females (n = 3, x- squared = 1.44, *df* = 1, $p = 0.2301$). Female tracked *T. macrops* in the human dominated area (n = 7) were visible displaying active behavior a higher proportion of fixes compared to sedentary behavior than female vipers in the protected (n = 6, x- squared = 4.0382, *df* = 1, $p = 0.04$). Male (n = 2) and female (n= 13) active and sedentary behavior did not differ significantly (x-squared= 2.78, df= 1, p = 0.09558). However, ambush behavior between males (n = 2) and females (n = 13) was significantly different (x- squared = 18.0625, *df* = 1, $p < 0.001$), with males spending more time ambushing and females spending more time not ambushing. When models of ground temperature, ground humidity, ambient temperature, and ambient humidity were run, ambient temperature ($p = 0.01$) with ambient humidity ($p = 0.04$) as an additive effect appeared to be the best predictors of ambush activity for tracked female *T. macrops* (n = 13) during the cold season (*df* = 1, AIC = 757.33).

Survey data was not sufficient for area and site comparison (n = 25 for human dominated, n = 3 for protected). Of the survey observations, 15 vipers were clearly ambushing, 3 were ambiguously ambushing, 5 were moving, 2 were resting, and 2 displayed behavior which was not determinable. While vipers observed during tracking and surveys were primarily observed displaying active behaviors than inactive, a higher proportion was observed to be active during tracking than during surveys.

Clear recordings from Bushnell trail cameras were analyzed for 7 radiotracked female *T. macrops* in protected (n = 4) and human dominated (n = 3) study areas for a total of 14, 293 1 minute scans (n = 4507 scans in the protected area, n = 9787 human dominated) during the rain, cold, and hot seasons between 2014- 2017 at the Forest 6, Forest 9, Canal 1, and Plantation 2 study sites. Gravid females (n= 6) were observed a higher proportion of scans displaying sedentary behavior compared to active behavior than non- gravid females (n = 1; x- squared = 369.5218, *df* = 1, $p < 0.001$). However, gravid females were observed migrating and moving more frequently than non-gravid females (x- squared = 2800.645, *df* = 1, $p < 0.001$). Overall behavior differed significantly between the protected (n = 3) and human dominated (n = 4) study areas (x- squared = 1069.217, *df* = 7, $p < 0.001$; Table 4.13). While individuals in the protected and human dominated study areas were observed ambushing more frequently than not ambushing, vipers in the human dominated area were observed significantly more often ambushing than protected area vipers (x- squared = 308.3468, *df* = 1, $p < 0.001$). Protected area individuals were observed for more scans clearly ambushing (n= 1324 scans) than ambiguously ambushing (n = 355), which was significantly different (x- squared = 559.2382, *df* = 1, $p < 0.001$) than human dominated area individuals which were observed clearly ambushing for less scans (n = 1308) than ambiguously ambushing (n = 1561). Behavior was also observed to be significantly different (x- squared = 953.4601, *df* = 7, *p* < 0.001) during the day and night overall (Table 4.14). Ambiguous ambush was most the frequently observed behavior during the day, followed by sheltering, and then resting. Clear ambush was the most frequently observed behavior during the night, followed by ambiguous ambush, and then sheltering.

Table 4.13 Overall behavior of 7 female *T. macrops* in human dominated and protected study areas recorded at 1 minute scan intervals from Bushnell trail cameras.

Behavior	Human dominated	Protected
Ambiguous ambush	1561	355
Clear ambush	1308	1324
Resting	886	0
Migration	83	69
Move	37	60
Feeding	21	0
Sheltering	1031	675
Other state	23	0

Table 4.14 Comparison of behavior of 7 female *T. macrops* in human dominated and protected study areas during the day (0600- 1759) and night (1800- 0559) recorded at 1 minute scan intervals from Bushnell trail cameras.

Behavior	Day	Night
Ambiguous ambush	823	1093
Clear ambush	426	2206
Resting	603	283
Migration	68	84
Move	18	79
Feeding	15	6
Sheltering	705	1001
Other state	0	29

Behavior was observed to be significantly different during the night time (1800- 0559) in the protected (n = 4) and human dominated study areas (n = 3, x-squared = 658.5979, *df* = 7, $p < 0.001$; Table 4.15) during camera review. Female *T. macrops* in the protected area were observed significantly more frequently during scans ambushing than not ambushing compared to vipers in the human dominated area (x- squared = 345.4697, *df* = 1, $p < 0.001$) during the night. Green pit vipers in the protected study area were observed clearly ambushing (n = 1286) more frequently than ambiguously ambushing (n = 355), which was significantly different (x- squared = 528.1907, *df* = 1, p < 0.001) at night than vipers in the human dominated area which were observed clearly ambushing (n = 920) only marginally more than ambiguously ambushing (n = 738).

Table 4.15 Behavior of 7 female *T. macrops* in human dominated and protected study areas recorded at 1 minute scan intervals from Bushnell trail cameras during night (between 1800- 0559).

Behavior	Human dominated	Protected
Ambiguous ambush	738	355
Clear ambush	920	1286
Resting	283	0
Migration	72	12
Move	37	42
Feeding	6	0
Sheltering	326	675
Other state	23	6

Multiple behavior types were not observed on camera for protected area vipers (n = 4) during the day time (0600- 1759), which prevented chi-square analysis comparison between female *T. macrops* in the 2 study areas (Table 4.16). However, female *T. macrops* in the protected area were observed significantly more frequently during scans ambushing than not ambushing compared to vipers in the human dominated area (x- squared = 12.115, df = 1, $p < 0.001$). Vipers in the protected study area were observed clearly ambushing more frequently than ambiguously ambushing during the day, which differed significantly (x- squared = 38, df = 1, $p < 0.001$) from human dominated area vipers which were observed clearly ambushing less frequently than ambiguously ambushing during day time hours.

Table 4.16 Behavior of 7 female *T. macrops* in human dominated and protected study areas recorded at 1 minute scan intervals from Bushnell trail cameras during day (between 0600- 1759).

Behavior	Human dominated	Protected
Ambiguous ambush	823	0
Clear ambush	388	38
Resting	603	0
Migration	11	57
Move	0	18
Feeding	15	0
Sheltering	705	0
Other state	0	0

Behavior was recorded on trail cameras for the tracked female (n = 1) *T. albolabris* (n = 1418 scans) and both (n = 2) *T. vogeli* (n = 1873 scans). Both species were primarily observed clearly ambushing (summarized in Table 4.17). Behavior was difficult to record for these individuals due to the secretive nature of the *T. albolabris* which primarily utilized dense green vegetation as microhabitat and arboreal behavior of both *T. vogeli*. Continual recording was difficult for *T. vogeli*, as they utilized a unique form of ambush behavior and were rarely observed utilizing the same shelter site as an ambush site. This species primarily utilized ambush sites about 1 m away from resting sites, shifting between the sites every day (resting) and night (to ambush site).

Table 4.17 General behavior observations of 1 female *T. albolabris*, 7 female *T. macrops*, and 2 female *T. vogeli* in human dominated and protected study areas recorded at 1 minute scan intervals from Bushnell trail cameras.

Behavior	*T. albolabris*	*T. macrops*	*T. vogeli*
Ambiguous ambush	292	1916	0
Clear ambush	668	2632	1708
Resting	406	886	148
Migration	47	152	8
Move	0	97	3
Feeding	0	21	0
Sheltering	0	1706	0
Other state	5	23	6

4.2 Discussion

4.2.1 Occupancy, detectability, and relative abundance

Even though occupancy modeling seeks the most parsimonious models, strong support for presence of canal as well as distance to natural forest was evident. Snakes can select habitat at different landscape scales, which may be reflected with occupancy modeling (Steen et al., 2012). Similarly, strong support was exhibited for multiple survey covariables within the top models, including temperature and humidity.

Green pit vipers may be able to persist in human dominated habitats other than those I assessed. Rural environments are a complex heterogeneous matrix of habitat at multiple biologically significant scales (micro, meso, and macrohabitat). For modeling site occupancy (ψ), I sought to classify survey sites by what I observed to potentially be the simplest but most likely relevant features. However, insufficient detection probability (*p*) complexity has been suggested to produce negative bias in occupancy estimates for amphibians (Baily et al., 2007).

Adequately modeling occupancy for green pit vipers proved challenging due to their sedentary and cryptic nature. Radiotelemetry study (Section 4.1.2) revealed that this group spends a significant amount of time sheltering and relatively sessile. While primarily a relatively arboreal species, it is worth noting that *T. macrops* were observed during radio telemetry spending time underground, particularly gravid females, and this in turn could affect detection. Arboreal vipers were detected during surveys, however this vertical dimension could still have presented additional challenges.

Habitat complexity proved challenging for occupancy modeling surveys. Dry evergreen forest was heterogeneous at most forest layers, while certain human dominated sites (namely plantations) could be very uniform. Typically, human dominated sites were very easy to walk due to limited vegetative undergrowth and visibility for most forest layers was high. In contrast, protected forest sites were much more physically challenging to survey due to undergrowth complexity (namely lianas and thorn Moraceae) and visibility in vegetatively dense patches of the protected sites could be limited to several meters. However, the Pond 1 site in the human dominated study area had very dense undergrowth (primarily bamboo grass, *Vietnamosasa pusilla*) present during surveys, except during the hot season when fires cleared the lower forest layer of vegetation. The dense undergrowth may have biased detection (0 vipers during my surveys) at this site, as 2 *T. albolabris* were captured within the boundaries of this site, 1 of which was even radiotracked concurrently during surveys.

Inclusion of radiotracked vipers could potentially have reflected true occupancy, particularly of *T. albolabris* and *T. vogeli*, however, knowledge of these individuals and their habits could have in turn biased estimates. Not including these individuals should not have influenced occupancy estimates, as estimation of site occupancy and detection probability requires that sites only be closed to species occupancy and not individual occupancy (MacKenzie et al., 2002).

No neonate or juvenile green pit vipers were observed during surveys. These age classes may be especially difficult to detect due to their small size. Previous study of the habits of neonate and juvenile green pit vipers is nonexistent; however, previous study in North America described ontogenetic shifts of food habits, foraging behavior, and habitat use in snakes (Lind and Welsh, 1994; Law and Dickman, 1998; Clark et al., 2016). Neonate and juvenile green pit vipers may utilize habitat or display behavior which may make these cohorts more difficult to detect during surveys than adults.

Even though not all green pit vipers were brought in due to safety and logistical reasons, identification of species was likely not an issue. All 3 species had previously been captured at the Sakaerat Biosphere Reserve, and no cases of mis-identification were confirmed for individual vipers which were brought in during the occupancy surveys. Even at higher forest layers, body characteristics (head shape, overall size, etc.) and general coloration were distinctive enough for species identification.

Detection rates (*p*) observed in my study (0.21-0.25) were comparable to studies of terrestrial snakes and vipers in North America (*Sistrurus catenatus*, 0.14-0.25, Harvey, 2005; and 0.00-0.17 for forest multiple forest species, Steen et al., 2012). My estimates were much lower, however, than those produced for 2 large bodied sympatric terrestrial true vipers in Africa which estimated detection rates as high as 0.7 (Luiselli,, 2006) although this study encountered far more individuals than my study. Besides snakes, detection rates from my study are similar to results from previous studies of fossorial or nocturnal bird and mammal species (O'Connell et al., 2006; Wintle et al., 2005). It is also worth noting that interspecific variation in detectability has been observed in multiple taxonomic groups (Magurran and Henderson, 2003).

Temperature and humidity were found to strongly influence detection as indicated by their presence in the top 5 models. Temperature in particular has previously been established as an important estimate of detection and crucial for occupancy estimation for snake study (Bauder et al., 2017), although previous application of detection probability remains scarce for occupancy modeling of this taxon (Durso and Seigel, 2015). Temperature and humidity (often with rainfall) have previously been found to strongly influence amphibians (MacKenzie et al., 2002; Cook et al., 2011; Roloff et al., 2011; Canessa et al., 2012), and this may in part play a role for green pit vipers which may be anurophagus and also prefer to be located near water (Strine, 2015).

Interestingly, 2 human dominated and 2 protected area sites were found to be occupied by green pit vipers (*T. macrops*) during surveys. Encounter rate varied from 9% to 54% for surveys where vipers were detected. Both human dominated sites, and one protected area site were characterized by a water body. This could suggest preference for water sites by *T. macrops*, potentially due to anuran prey, as proposed by Strine (2015). However, none of the water variables (distance to water or the various types of water) plantation and distance to natural forest were the primary site occupancy variables in the top models. The Plantation 2 site was the second most frequently surveyed of all the sites and had the highest amount of effort (hours and surveyor hours) while still having the second highest encounter rate (44% of all surveys) of all the sites, which likely had a strong influence in the model and was the reason the variable "Plantation" ranked highly. Distance to natural forest was included as a site variable in one of the top models, which may be explained by the highest distance to natural forest with vipers detected being very low (55 m) compared to sites where vipers were not detected (up to 1,870 m distance from natural forest).

General reptile and amphibian surveys (not for occupancy modeling) conducted by Inger and Colwell (1977) at the Sakaerat Biosphere Reserve produced different results than those observed during my study. Two species of green pit viper were detected, and "center of distribution" was described as dry evergreen forest. Far more individuals of both species were discovered in the protected forest (n = 32) than in agriculture (n = 5).

4.2.2 Spatial ecology and movement

Results from the spatial ecology portion of my study suggested female *T. macrops* home range and movement are not significantly affected by rural human disturbance, as they were not significantly different between study areas. Findings between the study sites also produced similar home range and movement results. Similar findings were observed by Strine (2015) at SERS with female *T. macrops*, with larger home ranges and increased movement in sites with limited human disturbance compared to those with more disturbance, although statistical significance did not detect a difference. A previous study of rattlesnakes (*Sistrurus catenatus*

catenatus) suggested similar findings in a natural park in Canada, with snakes being less visible to observers, moving less frequently, and moving less distance as human disturbance increased (Parent and Weatherhead, 2000).

No significant difference was observed for gravid and non-gravid females for movement or spatial estimates. Most previous studies have found gravid female snakes/vipers to move less frequently and smaller distances than non- gravid females (Johnson, 2000). Gravidity can pose significant locomotor challenges for snakes, which may or may not be reflected in movement and spatial patterns (Seigel et al., 1987). Further understanding of the benefits (and mitigation of costs) of utilization of similar space and movement patterns of gravid to non- gravid female green pit vipers is required.

Overall, adult male and females face different challenges which can be reflected in behavior, movement, and space use (Madsen, 1987). However, in my study male and green pit vipers appeared to display similar movement and home range characteristics. Males were not tracked during the peak of what has been described for the green pit viper breeding season, September- November (Chanhome et al., 2011), which may have influenced effective overall home range size and movement patterns.

Although sample size was limited, both *T. vogeli* in my study exhibited larger home ranges than any of the tracked *T. macrops*, and the female *T. albolabris* also displayed larger home ranges than all but 2 of the tracked *T. macrops*. Mean distance between moves and MDD were similar between species, however, tracked female *T. albolabris* and *T. vogeli* had more numbers of moves than all but 2 *T. macrops*. The female *T. albolabris* tracked during my study displayed different home range and movement patterns than the one tracked at the Sakaerat Biosphere Reserve by Strine (2015). The *T. albolabris* in the other study moved less (14 moves) than the one in my study (21 moves), and the home range (MCP) was estimated to be smaller (0.235 ha) than the *T. albolabris* in my study (0.36 ha) even though the other individual was tracked for a longer period of time.

Similar to Strine (2015), male green pit vipers of appropriate size were difficult to obtain for radiotelemetry study. I was fortunate, however, to track 3 males of 2 species. Signal was lost prematurely (< 90 days) for the male *T. albolabris* and 1 of the male *T. macrops*. The *T. macrops* was located visually during the evening check immediately preceding the morning check for that day, indicating the transmitter failed within a very short period of time with no notice such as irregular signal strength. This viper lost mass (from 33 to 28 g) and substantial girth, and the decision was made to remove the transmitter but not implant another. I suspect the stress of the transmitter surgery and unsuccessful adequate ambush site selection (suggested by relatively high number of moves, 11, and exhibiting the highest mean distance between moves, 50.42, of all tracked snakes) during time when prey (amphibians) was likely limited may have played a role. This viper was tracked outside of the observed breeding season for this species (Chanhome et al., 2011; personal observation by author), so mate- searching was not likely a reason for body condition decline. Serious consideration to body condition, including mass and girth, should be taken into account when implanting arboreal snakes with radiotransmitters. The general minimum mass rule suggested for snakes may not be ethical for arboreal snakes which have evolved slender bodies, which may be more ideal for locomotion (Crotty and Jane, 2014); particularly going into what is generally considered inactive periods. Negative effects were not observed for gravid females (similar to Reinert and Cundall, 1982), and individuals appeared to experience no problems while birthing towards the end of the cold season/beginning of the hot season.

It is worth noting that signal was also lost prematurely for multiple females implanted with BD-2THX transmitters. These individuals may have been predated, with the transmitter being carried a substantial distance further than the maximum distance of transmitter signal strength (> 200 m). Intensive searches were conducted for these vipers, however, and the male *T. macrops* which was visually located immediately following transmitter failure suggest this may not necessarily be the case. Only 1 confirmed case of predation was confirmed in the study (TRMA231), and the transmitter was located less than 200 m from the last known location. Interestingly, the last known location of this viper was <10 m from a human settlement and most likely predator was a snake based off the scat the transmitter was found in. This would not be unusual, as a subadult king cobra (*Ophiophagus hannah*) was captured much later after this event less than 200 m from the house and scat (actually <10 m from TRMA229) in a fish trap by local villagers.

Human inflicted viper mortality was not observed in my study, despite the snakes spending relatively long periods of time (> 2 weeks) near human settlements and agriculture fields. Interestingly, the Canal 1 human dominated study area was directly utilized by both permanent (landholders) and temporary (fishermen and seasonal farmhands) who reported regularly coming into contact with green pit vipers. Previous radiotelemetry studies (Durbian, 2006; Wittenberg, 2012) have reported direct human inflicted viper morality in rural communities (*Sistrurus catenatus* and *Crotalus horridus*; agriculture practices, farm implements, cars, etc.). Adult timber rattlesnakes (*C. horridus*) in mature forests have previously been reported to have annual survival rates of approximately 90% (Brown et al., 2007), however, radiotelemetry study by Wittenberg (2012) observed mortality of this species within the 2 year study period in a rural community to be 34% with a majority (75%) of those being attributed to anthropogenic causes.

Tracked female *T. macrops* from my study displayed similar movement and home range size (MCP) as previous study from the Sakaerat Biosphere Reserve (Strine , 2015), although averages were slightly lower for my study. Females from the Strine (2015) averaged 14.6 moves per viper, while females in my study averaged 9.8 moves. Home range size, as measured by MCP, was 0.237 ha for Strine (2015), while females in my study averaged 0.19 ha. These home range and movement patterns were very similar, despite the difference of transmitter types of most vipers tracked during my study. This was confirmed through comparison of individuals at the Forest 6 (Upper Dam Pond) study site, which found no significant difference between home range or movement pattern of vipers between the studies. However, vipers from both studies were not tracked concurrently (several years in between tracking) which may have influenced results. Similarly, detecting differences in home range and movement is difficult due to the sedentary nature of *T. macrops*.

Limited movement and miniscule home ranges observed in my study provided further evidence for extreme sedentary tendencies of the green pit viper group as suggested by Strine (2015). Previous study of ambush vipers have produced MCP home range estimates such as 1.2 ha for the North American *Agkistrodon pisciverus* (Roth, 2005), 5.95 ha for the Central American *Bothrops asper* (Wasko and Sasa, 2009), 24.59 ha for the European *Montivipera raddei* (Etling et al., 2013), and

2.63 ha for the Asian *Gloydius shedaoensis* (Shine et al., 2003). Even the smallest viper in the world, *Bitis schneideri,* was estimated to exhibit MCP home range sizes of 0.10 ha for adult females (Maritz and Alexander, 2012).

Green pit vipers (both *T. macrops* and *T. vogeli*) tracked in the protected area were observed between fixes on opposite sides of a dirt road on multiple occasions. At the Canal 1 site, vipers were observed on opposite sides of a two- lane road although a bridge also spanned the distance of the canal. How the vipers moved across these barriers, or if the canal vipers went under the bridge which had exposed concrete only underneath requires further study. One of the female *T. vogeli* (TRVO002) was observed visually on multiple occasions crossing sides of the road through connections in vines, tree branches, and overhanging vegetation. At the Plantation 2 site the male *T. albolabris* was also observed on a single occasion crossing the stream via overhanging trees and branches. Interestingly, a tracked female green pit viper (TRMA174) was observed regularly ambushing a dirt road at the Forest 9 site even though trail cameras captured multiple vehicles and people (including poachers) consistently using that path. While many vipers were found on roads by the author throughout the study, none of the tracked green pit vipers were observed physically crossing roads and further understanding of movement between and across these potential barriers is required. Previous study by Shepard et al. (2008) found that not only did roads present negative genetic and demographic consequences as has been suggested by other taxonomic groups, but Eastern massassaugas (*Sistrurus catenatus*) actively avoided crossing roads and thus suggested a behavioral response created by the potential barrier.

As suggested by Strine (2015), MCP and kernel methods are imperfect estimators for home range size for green pit vipers. The MCP method does not take into account occurrence of movement (highly versus rarely utilized areas) and can cause bias for limited movement (Nilsen et al., 2008). Previous study has shown kernels can produce estimates larger than polygons (Row and Blouin- Demers, 2006), however MCP and 50% kernels (but not 99%) were similar in my study. Both kernel and MCP methods include large areas of unused space due to limited movement. Because of these factors, current home range estimators (MCP and fixed kernels) are imperfect methods for fully understanding space use by green pit vipers. Were more moves observed (potentially through tracking longer), incorporating multiple dimensions to home range analysis would provide more biologically relevant estimates. While home range by itself was not significantly different between the protected and human dominated study area, habitat selection at multiple levels was and incorporating habitat usage into home range estimates could prove significant. Previous study of the vertical strata has already been incorporated into avian home range research and could be used for green pit vipers provided enough (>40) vertical location fixes were attained.

4.2.3 Habitat selection

Landscape level habitat utilization as observed by tracked male and female *T. macrops* in the human dominated area of my study can be interpreted several ways. The feature primarily utilized at all scales (0, 5, and 10m distance to vipers), HDF, could be influenced by size or type of this remnant “ideal” habitat. HDF may be strongly influenced by the third most frequently utilized macrohabitat feature immediately adjacent (0 m) to vipers, wash. Natural vegetation may have been retained in washes for erosion control or due to difficulty of removal due to higher slopes and presence of boulders in these features. Regardless of purpose for retention, HDF was the primary dominant macrohabitat type utilized by *T. macrops* in the human dominated study area and as such retention of natural habitat could be crucial for persistence of this species.

Human settlement was the second most frequently utilized macrohabitat feature immediately (0 m) present near vipers. Human settlements may have been used due to retention of vegetation, albeit not natural, of the rural households as well as close proximity (<10 m) to HDF and washes. The 3 households were aware of the tracked vipers' presence and were accommodating, which may or may not have been representative of many other households. Similarly, 1 of those settlements served as a vacation home (weekends) and housing for field workers (seasonal) so that household likely experienced minimal disturbance.

Agriculture was the second most frequently utilized landscape level habitat type within 5 and 10 m of tracked vipers, with fallow fields being used most frequently at these distances. Cassava was only utilized on 1 occasion less than 5m and 2 less than 10m and plantations (rubber and *Eucalyptus*) were similarly rarely utilized at all distances to vipers. Recently plowed fields and peppers were observed within 10m of tracked vipers on few occasions also. Agriculture was perhaps the most difficult habitat type to assess and quantify throughout the study due to the number and method of land alterations. For instance, 1 section which was utilized by a viper (TRMA231) as dominant and edge habitat changed crop types 3 times within 2016. Each of the crop types and subsequent planting, treatment, maintenance, harvest, and other agriculture methods could have influenced utilization of the viper. Size and timing of crops or factors associated may have also played an important role. Female grass snakes (*Natrix natrix helvetica*) were found to prefer agriculture edge habitat and utilize monocultures during their summer activity periods potentially due to suitable basking sites, favorable foraging opportunities, and reduced avian predation risk compared to more natural habitats (Wisler et al., 2008).

Surprisingly, one of the natural habitats in the human disturbed area also experienced drastic and likely anthropogenic alteration. The dry dipterocarp forest directly adjacent to the Pond 1 tracking and survey site experienced at least 2 separate fires while TRAL013 was radiotracked. Interestingly for what has traditionally been described as an arboreal snake species, the tracked female *T. albolabris* survived one of the fires in a termite mound and another in a fallen log. Being heavily gravid at the time of these fires (February and March), this viper may have been in fact taking advantage of elevated temperatures produced by the flames instead of choosing to escape up into the branches of adjacent dipterocarp trees. By utilizing edge habitat and microhabitat which were potentially higher in temperature than surrounding environments, the female *T. albolabris* in my study may have been actively thermoregulating in response to gravidity. Reinert and Zappalorti (1988) observed that gravid female timber rattlesnakes (*Crotalus horridus*) utilized less dense forested sites with warmer climactic conditions than male and non-gravid female rattlesnakes, even though these habitats were limited and primarily restricted to the edge of sand roads. Previous studies have reported mixed results with fire and the impacts on reptile behavior, populations, and community dynamics (Cavitt, 2000), and more work is needed to understand the role of fire disturbance on green pit vipers.

Habitat was utilized during radiotelemetry in different proportions than what was available at both the meso- and microhabitat levels during radiotelemetry by *T. macrops* within both the protected and the human dominated study areas. At the mesohabitat level, *T. macrops* primarily selected green vegetation, woody vegetation, and fallen logs in the protected area; in the human dominated area they primarily selected open canopy, green vegetation, and human structures. At the microhabitat level, *T. macrops* primarily selected saplings, small lianas, and green vegetation in the protected study area; in the human dominated study area they primarily selected trees, green vegetation, and small lianas. Green vegetation was selected by *T. macrops* at both the meso- and microhabitat levels in both protected and human disturbed habitats, and small lianas were also selected by *T. macrops* both in protected and human disturbed habitats at the microhabitat level. From a comparative standpoint, as would be expected natural mesohabitat features which were selected by *T. macrops* in protected areas such as woody vegetation and fallen logs were available in lower proportions in the human dominated area. Interestingly, trees were limited in the human dominated study area (7% of available microhabitat); however, they were strongly utilized by *T. macrops* (15% of radiotelemetry datapoints). While *T. macrops* was not observed to spend as much time arboreal as other green pit viper species (*T. albolabris* and *T. vogeli*) in the study, *T. macrops* may still require trees for their basic life history.

Previous habitat investigation with green pit vipers has been limited, particularly with field observation and assessment. Personal observation and generalizations by authors such as Orlov (2002) and Chanhome (2011) have provided limited descriptions for green pit viper habitat utilization. Inger and Colwell (1977) provided limited habitat utilization observations from the Sakaerat Biosphere Reserve, and suggested that seedlings, tall grass, and shrubs were more frequently used than trees. Strine (2015) provided perhaps the most in- depth investigation of green pit viper habitat selection, and suggested canopy cover was an important variable for *T. macrops* ambush site selection in relatively undisturbed areas of the Sakaerat Biosphere Reserve.

4.2.4 Behavior

Female *T. macrops* in the human dominated area displayed active behavior a higher proportion of fixes compared to sedentary behavior than female vipers in the protected area during radiotelemetry fixes. Similarly, female *T. macrops* were observed on trail cameras in the human dominated study area to spend a significantly higher proportion of time ambushing than vipers in the protected area. However, female *T. macrops* in the protected study area were observed on trail cameras to spend higher proportions of time clearly ambushing than ambiguously ambushing, which was not observed for vipers in the human dominated study area. Previous study has not cross-validated camera and radiotelemetry methods with snakes, however, Wittenberg and Beaupre (2014) did find increased growth rates for the timber rattlesnake (*Crotalus horridus*) in an agricultural landscape compared to forest individuals which they attributed to more stable food sources for prey species. This could explain radiotracked vipers needing to spend less time ambushing in the human dominated study area of my study compared to their protected forest counterparts.

Interestingly, while gravid and non-gravid females were not observed to exhibit significantly different spatial or relatively large scale movement patterns they were observed displaying statistically significantly different proportions of time in active (ambush and moving) and sedentary (resting and sheltering) behavior during fixes during radiotelemetry study. Specifically, gravid females were observed moving significantly less proportions of those fixes than non-gravid females. Bushnell trail camera review, however, produced different results; gravid *T. macrops* were observed migrating and moving more frequently than non- gravid females. This could be due to the difference of scale of observation for the 2 methods, and infrequent radiotelemetry observation (1 fix every night) and recording of movement > 5m between fixes which may not adequately describe movement and activity even for a sedentary snake species such as *T. macrops*. Previous studies have suggested gravid females move differently and less (Shine, 1999; Johnson, 2000; Blouin- Demers, 2001), while also primarily displaying inactive behavior due to constraints of body girth and gravidity associated with feeding (Slip and Shine, 1988; Reinert et al., 1984; Gregory et al., 1999). While previous study of snakes have strongly suggested decreased foraging time and food intake, a field and laboratory study of female Australian skinks suggested this is not necessarily the case for all reptiles (at least with food intake) and even the nature of reproductive costs of even closely related species may differ (Shine, 1980). Camera and tracking results of active behavior of green pit vipers from my study, specifically movement and foraging, requires further study.

Ambient temperature with ambient humidity as an additive effect was the best model for predicting ambush behavior of tracked female *T. macrops* during the cold season. That is intuitive for arboreal viper species which were tracked when temperature may have been a key influence on life history patterns. This differed with Strine (2015), which suggested that ground humidity (not ambient temperature or humidity) played the most important role in ambush behavior. However, that study assessed weather during multiple seasons, of which temperature may not have been the most important factor (i.e. rain season). Tsai and Tu (2005) compared multiple laboratory methods for studying green pit viper behavior, while also suggesting the preferred temperature (T_b) of the study species (*Trimeresurus s. stejnegeri*) to be lower (22.5 ˚C) than most other species of snakes (28- 34 ˚C).

The use of trail cameras to intensely, but not invasively, assess behavior confirmed previous observations of the green pit vipers while also describing in detail their life history. Strine (2015) suggested *T. macrops* to be a primarily nocturnal ambush predator through radiotelemetry, trail camera use by my study confirmed this observation and quantitatively assessed in finer detail proportion of time spent sedentary and active and activity periods. Two separate feeding instances of anuran prey were observed for a *T. macrops* in the human dominated study area (TRMA211), both instances taking more than 5 minutes for ingestion to be complete. Anurans have previously been suggested to be major prey items for green pit vipers (Chanhome et al., 2011; Strine, 2015), which were at least partially confirmed by the 2 predation events in my study. While live feed or continuous recording video cameras would have provided even finer detail for these observations, trail cameras proved more than adequate to capture states of relatively long periods (>1 minute in duration) including feeding. Thus, trail cameras may provide a cost effective and logistically feasible method for assessing green pit viper behavior.

CHAPTER V

CONCLUSION

As a preliminary work, this study provides insight and useful results to promote continued field research on green pit vipers within the Sakaerat Biosphere Reserve and elsewhere. Sample sizes were limited for all aspects of my study, and analysis of spatial ecology in particular requires large sample sizes to adequately provide reliable conclusions (Kernohan et al., 2001). Strine (2015) studied green pit vipers in relatively pristine habitats and I investigated them in rural environments in which patches of natural habitat was still present; study of green pit vipers in urban environments has still yet to be conducted. Green pit vipers, particularly *T. albolabris* and *T. macrops* in Bangkok, Thailand (Meemano et al., 1987; Mahasandana and Jintakune, 1990), still present a very serious venomous snakebite hazard in tropical Southeast Asian urban communities.

Although logistically challenging (increased drive time and gasoline expense), more sites would prove beneficial for understanding occupancy and detectability of green pit vipers. Sites were visited on many sampling occasions for my study to obtain preliminary understanding of detectability, however vipers were detected fairly consistently at occupied sites so fewer site visits could prove beneficial. More sites could prove useful for understanding and quantifying site characteristics (more habitat types, and subsampling within them), while still potentially being logistically feasible (MacKenzie and Royle, 2005). I utilized area as a constraint for surveys, crossvalidation with transect methods (i.e. Luiselli, 2006b) should also be tested. Comparison of habitat characteristics could also be compared using a presence only model (i.e. MaxEnt, Elith et al., 2011), particularly for species and life history groups which may be particularly difficult to detect.

Results from my study confirmed that home range and relatively large scale (> 5m) movement by vipers is largely not influenced by human disturbance, similar to Strine (2015). Caution should be drawn, as the green pit vipers which were tracked in the human dominated study area of my study utilized both anthropogenic disturbed areas within their home range as well as natural (HDF) areas. The space used by vipers in my study was heterogeneous, and vipers moved across a variety of habitat types within their home ranges. Maintaining natural habitat and habitat complexity may be crucial for viper movement and home range use. Thus, caution should be expressed before extrapolating conclusions of limited difference of spatial ecology and movement of green pit vipers in protected and human dominated habitats suggested in my work to other disturbed environments.

Much of the recommendations from the spatial ecology and movement pattern portions of my study are similar to those suggested by Strine (2015) which studied green pit vipers in protected and mildly disturbed habitats. More work is required for *T. albolabris* and *T. vogeli*, as well as male *T. macrops*. Larger sample sizes of individuals other than female *T. macrops*, and assessment during multiple seasons is necessary. Quantification of how vipers move, particularly across potential barriers such as road is also needed.

More work, particularly descriptive and quantitative study, is required for better understanding green pit viper habitat utilization in protected and human dominated areas as is potential benefits, costs, and consequences of habitat selection. Thermoregulation and prey availability in particular have been identified by previous studies of snakes in rural environments to influence habitat use (Durner and Gates, 1993; Shine and Fitzgerald, 1996; Wisler et al., 2008). More intensive quantification of remnant natural habitat and agricultural practices is needed for comprehensive understanding of green pit viper habitat selection in rural areas. Assessing HDF patch vegetative species diversity, estimating size of remnant HDF patches and distance between those patches, and calculating edge ratio may provide valuable information as to habitat utilization and selection of green pit vipers in rural communities. Communication with local farmers and agriculture workers and assessing habitat correspondingly (measuring growth of crops, understanding crop rotations, assessing potential effects of planting and harvesting, etc.) may provide a more inclusive understanding of green pit viper habitat utilization and selection in and near fields and plantations.

My study provided the first in-depth look at “a day in the life of a green pit viper” through intensive, but only mildly invasive, camera monitoring of radiotracked focal animals. Future work should include more individuals of different sex and species. More comprehensive understanding of green pit viper behavior could be obtained through live feed or continuous recording camera methodology, which has already be utilized for New World vipers (Clark, 2006). However, increased cost and decreased logistic feasibility would have to be taken into account. Large and more expensive and complex setups would be required for those methods; however, intimate knowledge could be gained for green pit viper activity, particularly events. The benefits of utilizing trail cameras are worth mentioning, despite the limitations of more in-depth quantification of behavior.

Trail cameras are widely available, fairly cost effective, and are utilized by many groups of laymen already (summarized in Trolliet et al., 2014).

While some of the results suggest that there are not significant differences between the studied anthropogenic disturbance types, the study did not provide enough conclusive evidence to fully describe how green pit vipers are affected by rural habitat disturbance in the Sakaerat Biosphere Reserve. Continued use, detection, and survival of green pit vipers in agriculturally dominated landscapes within the reserve indicates at least an element of tolerance of disturbance by the vipers, however further work with larger sample sizes including all life history classes and species present is required. Caution should be expressed of this persistence of green pit vipers in rural habitat communities, and results of my study should not be hastily extrapolated to other disturbed areas. I suggest that future studies focus more intensively on a single response factor (occupancy, spatial ecology and movement, habitat selection, or behavior) and then seek to better quantify factors in rural areas such as patch size, management activities, and size and attributes of human settlements, which could potentially influence green pit viper communities.

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APPENDICES

APPENDIX A

OCCUPANCY MODELING DATA

Table A-1 Number of surveyors (sample covariable, *p*) used in program PRESENCE for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016.

	Visit																																												
Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Canal_1	2	4	2	2	2	2	4	2	4	4	2	3	2	2	2	2	2	2	2	2	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_1	2	2	2	2	2	2	2	3	2	3	3	2	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_2	2	2	3	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_3	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_4	2	2	2	2	2	2	5	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_1	2	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_2	2	2	5	2	2	2	2	4	2	4	4	2	3	2	2	3	6	5	4	4	5	2	4	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_3	2	2	2	2	2	3	2	2	2	2	2	4	2	7	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_4	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_1	2	2	2	2	3	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_2	2	2	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	4	2	2	2	2	3	2	2	3	2	2	2	2	2	2	2	3	6	4	2	2	2	2	2	2	3	2	2	2
Forest_7	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A-2 Humidity (sample covariable, *p*) used in program PRESENCE for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016.

Visit

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Canal_1	76.0	76.0	92.0	84.3	87.1	88.6	83.5	68.0	71.3	60.6	76.0	76.0	71.0	81.3	87.3
Pond_1	92.5	95.3	95.3	95.3	96.5	92.7	95.3	100.0	100.0	95.3	93.2	94.0	100.0	90.2	93.4
Pond_2	95.5	95.5	94.0	100.0	92.4	-	.	.	.	.	.	.	.	.	.
Pond_3	86.3	86.1	82.5	85.0	-	.	.	.	.	.	.	.	.	.	.
Pond_4	84.8	92.5	98.0	83.0	95.4	95.4	65.0	84.8	78.3	83.0	94.0	119.3	-	.	.
Plantation_1	90.4	94.4	80.2	94.7	92.1	-	.	.	.	.	.	.	.	.	.
Plantation_2	96.4	95.6	95.0	100.0	92.6	91.7	99.7	100.0	84.0	100.0	100.0	100.0	98.3	98.2	91.3
Plantation_3	88.1	91.1	98.1	98.5	99.8	81.5	84.5	98.2	100.0	92.0	98.5	98.5	98.5	67.1	81.0
Plantation_4	86.7	85.8	94.0	95.9	-	.	.	.	.	.	.	.	.	.	.
Forest_1	88.9	88.5	100.0	98.5	79.3	81.5	85.5	-	.	.	.	.	.	.	.
Forest_2	89.0	84.2	89.4	75.5	81.6	96.6	-	.	.	.	.	.	.	.	.
Forest_3	100.0	-	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	96.8	96.8	-	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	93.0	91.2	-	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	85.2	88.4	99.9	80.7	84.4	82.2	81.0	87.0	87.7	82.5	88.7	83.0	67.1	82.4	94.6
Forest_7	100.0	75.9	-	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	80.0	100.0	-	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	100.0	100.0	-	.	.	.	.	.	.	.	.	.	.	.	.

Site	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Canal_1	94.3	100.0	89.0	87.8	87.3	83.4	85.3	87.9	81.9	-	.	.	.	.	.
Pond_1	95.3	-	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_2	91.3	99.6	66.6	68.9	67.4	63.0	92.2	100.0	90.2	99.9	-	.	.	.	.
Plantation_3	100.0	99.4	100.0	-	.	.	.	.	.	.	.	.	.	.	.
Plantation_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	100.0	100.0	100.0	100.0	90.5	85.4	84.9	86.8	96.3	100.0	96.9	83.6	82.8	90.5	90.5
Forest_7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Site	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Canal_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	83.2	79.1	78.3	78.0	91.9	87.7	77.4	98.0	83.6	81.4	100.0	100.0	97.0	100.0	85.3
Forest_7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A-3 Temperature (sample covariable, *p*) used in program PRESENCE for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016.

	Visit																																												
Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Canal_1	27.0	27.0	25.0	25.8	26.8	27.8	26.7	27.2	26.0	29.9	27.0	27.0	30.7	28.1	27.6	26.8	24.9	28.0	27.6	24.6	26.7	27.0	26.4	25.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_1	26.9	26.4	26.4	26.4	24.5	27.1	26.4	26.0	24.8	26.4	25.6	27.9	26.1	27.8	27.1	26.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_2	26.7	26.7	26.4	27.4	26.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_3	26.3	28.7	28.6	27.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_4	26.4	24.9	26.0	27.6	29.6	29.6	22.5	27.6	29.2	26.8	26.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_1	21.5	26.8	26.8	26.2	27.8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_2	24.8	27.3	26.0	25.4	26.8	25.5	26.2	25.3	25.0	26.4	26.3	26.1	25.8	25.3	25.8	25.8	24.1	24.0	21.9	28.1	29.6	26.7	25.5	22.5	80.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_3	23.4	24.7	24.1	24.5	24.8	26.7	23.0	25.9	26.7	25.6	25.6	25.6	25.6	27.6	27.8	27.4	25.3	25.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_4	26.1	24.5	26.6	26.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_1	22.8	27.6	24.2	23.5	28.4	28.2	27.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_2	27.4	28.4	26.3	28.1	28.2	26.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_3	23.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	24.1	24.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	26.0	27.8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	26.3	24.3	23.6	26.1	26.3	26.9	27.0	26.9	26.8	27.6	26.4	26.9	28.2	27.0	24.8	24.6	24.6	24.1	24.8	24.5	27.5	26.8	26.8	25.7	24.7	25.8	27.6	27.4	26.4	26.7	26.4	26.7	26.4	27.8	24.8	26.0	27.0	25.7	26.5	27.8	24.6	25.1	24.6	25.7	22.9
Forest_7	26.0	28.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	27.7	24.7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	22.5	23.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A-4 Rain within 6 hours (sample covariable, *p*) yes (1) or no (0) used in program PRESENCE for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016.

Site	Visit 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Canal_1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond 2	0	0	1	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_3	0	0	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond_4	0	0	0	0	0	0	0	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_1	0	0	0	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_3	0	1	0	0	1	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantation_4	0	0	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_1	1	0	1	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_2	1	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_4	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_5	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	1	0	0
Forest_7	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_8	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Forest_9	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A-5 Rain within 24 hours (sample covariable, *p*) yes (1) or no (0) used for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016.

																								Visit																						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
	Canal_1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pond_1	0	0	0	0	1	0	1	1	1	0	0	0	1				.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pond 2	0	0	1	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pond_3	0	0	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pond_4	0	0	1	0	1	0	0	1	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Plantation_1	0	1	0	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Plantation_2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Plantation_3	0	1	0	0	1	0	0	0	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Site	Plantation_4	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_1	1	0	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_2	0	0	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_4	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_5	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_6	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	0
	Forest_7	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_8	1	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Forest_9	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A-6 Sample covariables (ψ) used in program PRESENCE for occupancy modelling of surveys (*n* = 174) at sites (*n*= 18) during the study period from September 2015 through November 2016. Plantation_site, pond_closest, canal_closest, and stream_closest variables yes (1) or no (0); area in ha, elevation in m, house_dist is m distance to closest house, water_dist is m distance to closest water source, nat_forest_dist is m distance to closest patch of forest, core_area_dist is m distance to the core area of the Sakaerat Biosphere Reserve.

		Site covariate									
		Plantation_site	Pond_closest	Canal_closest	Stream_closest	Area	Elevation	House_dist	Water_dist	Nat_forest_dist	Core_area_dist
Site	Canal_1	0	0	1	0	0.87	246	7	0	0	1257
	Pond_1	0	1	0	0	0.3	249	101	0	13.13	134
	Pond 2	0	1	0	0	0.1	242	20	0	370	536
	Pond_3	0	1	0	0	0.46	235	10	0	0	665
	Pond_4	0	1	0	0	1	232	0	0	0	3328
	Plantation_1	1	0	0	0	1.79	242	15	180	55	212
	Plantation_2	1	0	0	0	3.67	254	32	0	52	0
	Plantation_3	1	1	0	0	2.78	235	12	0	270	2153
	Plantation_4	1	0	0	0	1.77	232	14	63	1,870	3104
	Forest_1	0	0	0	1	0.25	439	990	473	0	0
	Forest_2	0	0	0	1	0.25	354	1292	541	0	0
	Forest_3	0	0	0	1	0.25	354	132	196	0	0
	Forest_4	0	1	0	0	0.34	439	883	0	0	0
	Forest_5	0	1	0	0	0.27	494	780	0	0	0
	Forest_6	0	1	0	0	0.43	494	355	0	0	0
	Forest_7	0	0	0	1	0.25	421	830	439	0	0
	Forest_8	0	0	0	1	0.25	494	617	122	0	0
	Forest_9	0	0	0	1	0.25	494	0	218	0	0

APPENDIX B

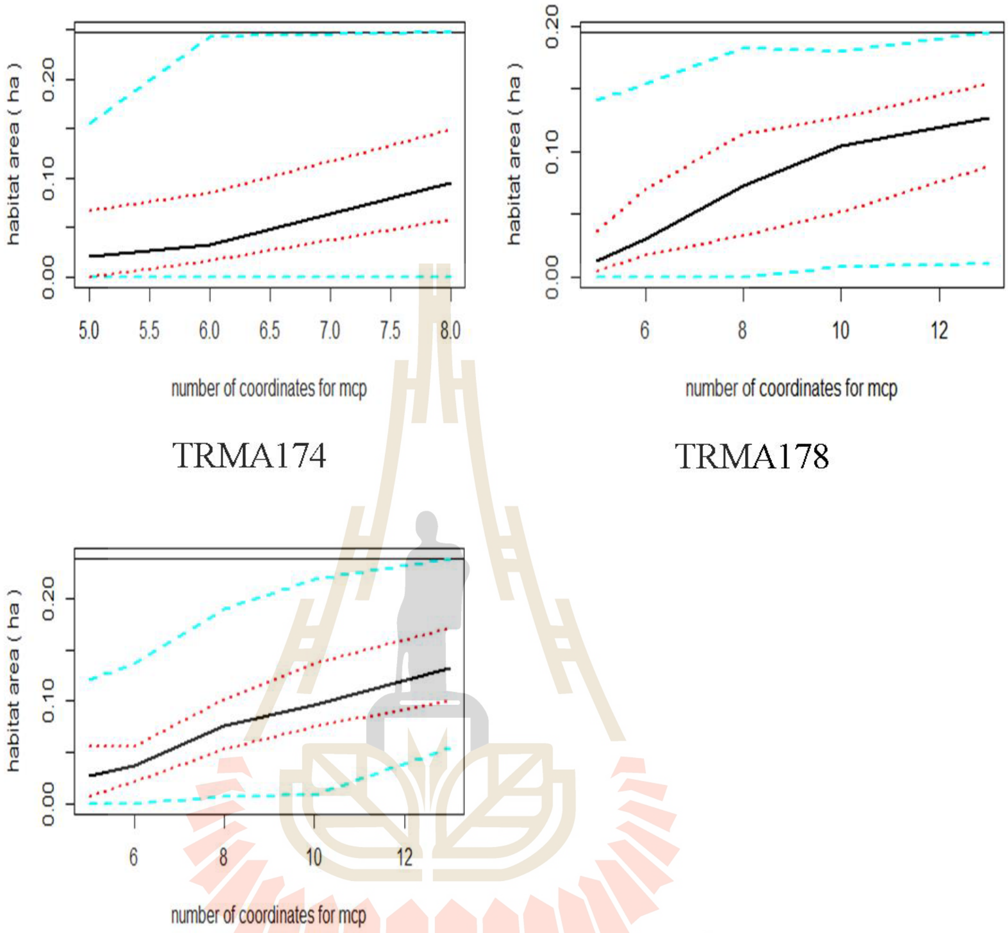
SPATIAL ECOLOGY AND MOVEMENT DATA

Table B-1 All female *Trimeresurus sp*. used for radiotelemetry (*n*= 16) during the study period from November 2014 to January 2017.

	Morphometrics				Tracking information						
Snake ID	**SVL (mm)**	**Mass (g)**	**SMI**	**Gravid**	**Transmitter type**	**First track**	**Area**	**Site**	**Final track**	**Track days**	**Fate**
T. albolabris											
TRAL013	625	113.9	85	Y	BD2T-HX	01.10.15	HD	Pond 1	13.03.15	163	TF
T. macrops											
TRMA174	535	43.7	69.7	Y	BD2, BD2T	07.10.14	Protected	Forest 9	27.01.15	110	Released
TRMA178	543	44.5	75.3	Y	BD2	11.11.14	Protected	Forest 9	13.02.15	92	Released
TRMA186	594	44.8	66.6	Y	BD2	08.11.14	Protected	Forest 9	12.02.15	94	Released
TRMA211	518	42.4	58.0	N	BD2T-HX	17.11.15	HD	Plantation 2	07.02.16	80	TF
TRMA220	580	91.3	88.6	Y	BD2T-HX	05.12.15	HD	Canal 1	15.06.16	190	Released
TRMA221	612	86.4	70.4	Y	BD2T-HX	02.12.15	HD	Canal 1	23.01.16	51	TF
TRMA231	520	47	69.8	Y	BD2T-HX	23.02.16	HD	Canal 1	16.06.16	110	Mortality
TRMA232	612	109	99.5	Y	BD2T-HX	25.02.16	HD	Canal 1	03.05.16	88	Unknown
TRMA270	590	83.5	93.5	N	BD2T-HX	31.10.16	HD	Canal 1	08.01.17	90	Released
TRMA271	514	52.5	83.0	Y	BD2T-HX	03.11.16	Protected	Forest 6	07.01.17	64	Released
TRMA273	593	73.9	82.9	Y	BD2T-HX	08.11.16	HD	Canal 1	03.01.16	55	Released
TRMA274	528	50.7	77.1	N	BD2T-HX	09.11.16	Protected	Forest 6	07.01.17	85	Released
TRMA282	610	94.7	95.2	Y	BD2T-HX	05.12.16	Protected	Forest 6	11.01.17	36	Released
MEAN	565.3	66.5	78.2							88.1	
SE	10.6	6.6	4.0		n = 13					10.5	
T. vogeli											
TRVO002	701	104.2	109.3	N	BD2T	01.11.14	Protected	Forest 9	12.02.15	135	TF
TRVO003	722	106.8	106.8	N	BD2, BD2T	01.11.14	Protected	Forest 9	13.02.15	136	Released
MEAN	711.5	105.5	108							135.5	
SE	10.5	1.3	1.2		n = 2					0.5	

Table B-2 All male *Trimeresurus sp*. used for radiotelemetry (*n*= 3) during the study period from November 2014 to January 2017.

	Morphometrics			Tracking information						
Snake ID	**SVL (mm)**	**Mass (g)**	**SMI**	**Transmitter type**	**First track**	**Area**	**Site**	**Final track**	**Track days**	**Fate**
T. albolabris										
TRAL016	501	40.2	59.8	BD2T-HX	19.11.15	HD	Pond 1	24.12.15	35	TF
T. macrops										
TRMA222	500	33.0	50.6	BD2T-HX	10.12.15	HD	Plantation 2	28.02.16	78	Released
TRMA229	438	38.6	93.2	BD2T-HX	02.02.16	HD	Canal 1	16.06.16	134	TF
MEAN	469	35.8	71.9						106.0	
SE	31	2.8	21.3		n = 2				28.0	

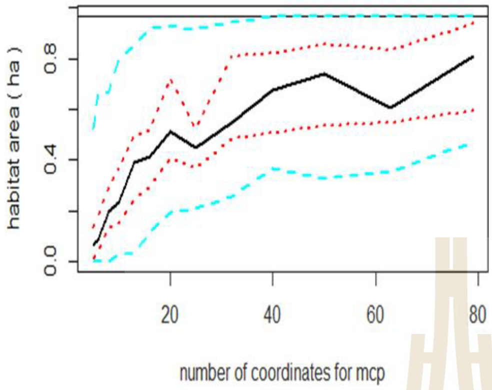


TRMA174

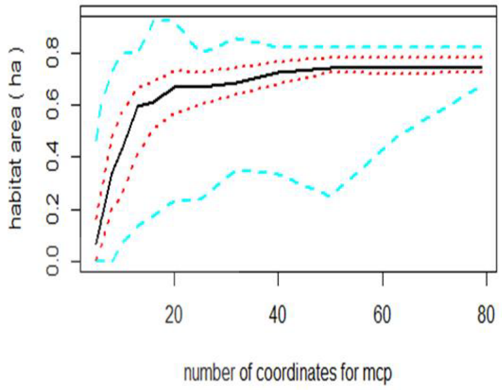
TRMA178

TRMA186

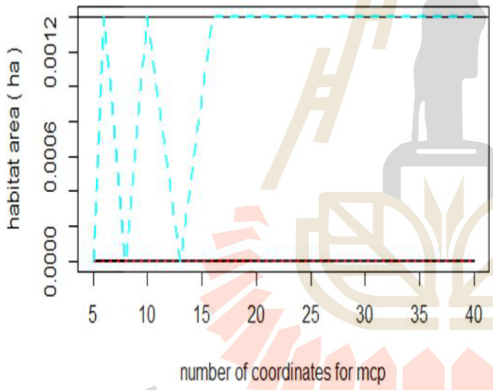
Appendix B-3 MCP home range bootstrap for female *Trimeresurus macrops* radiotracked in the protected area Forest 9 site.



TRMA271

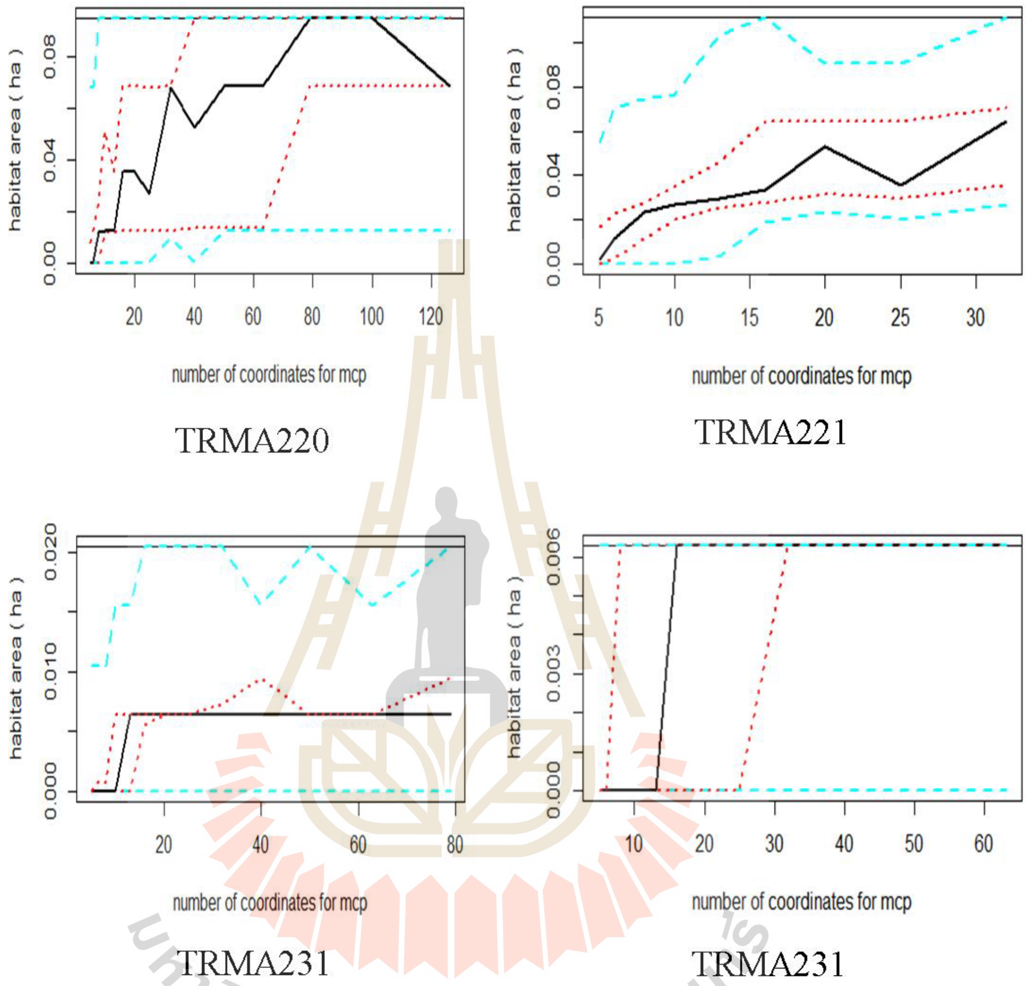


TRMA274

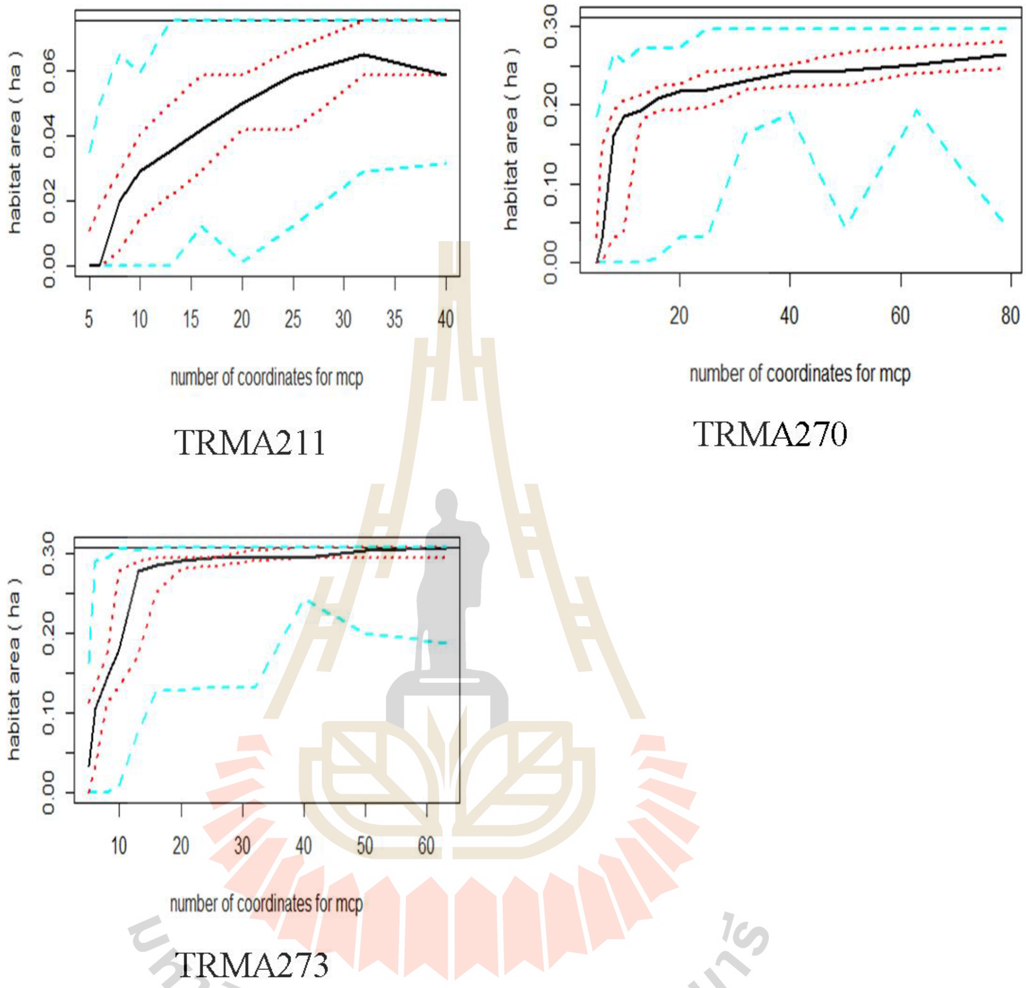


TRMA282

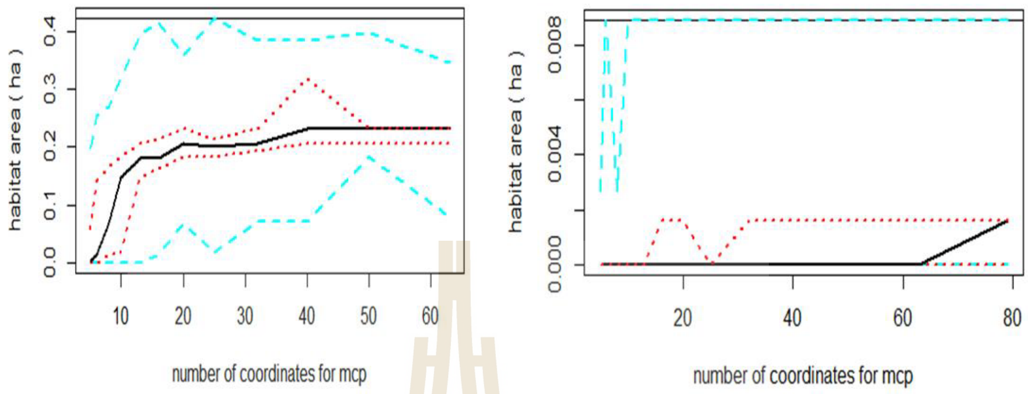
Appendix B-4 MCP home range bootstrap for female *Trimeresurus macrops* radiotracked in the protected area Forest 6 site.



Appendix B-5 MCP home range bootstrap for female *Trimeresurus macrops* radiotracked in the human disturbed area Canal 1 site.

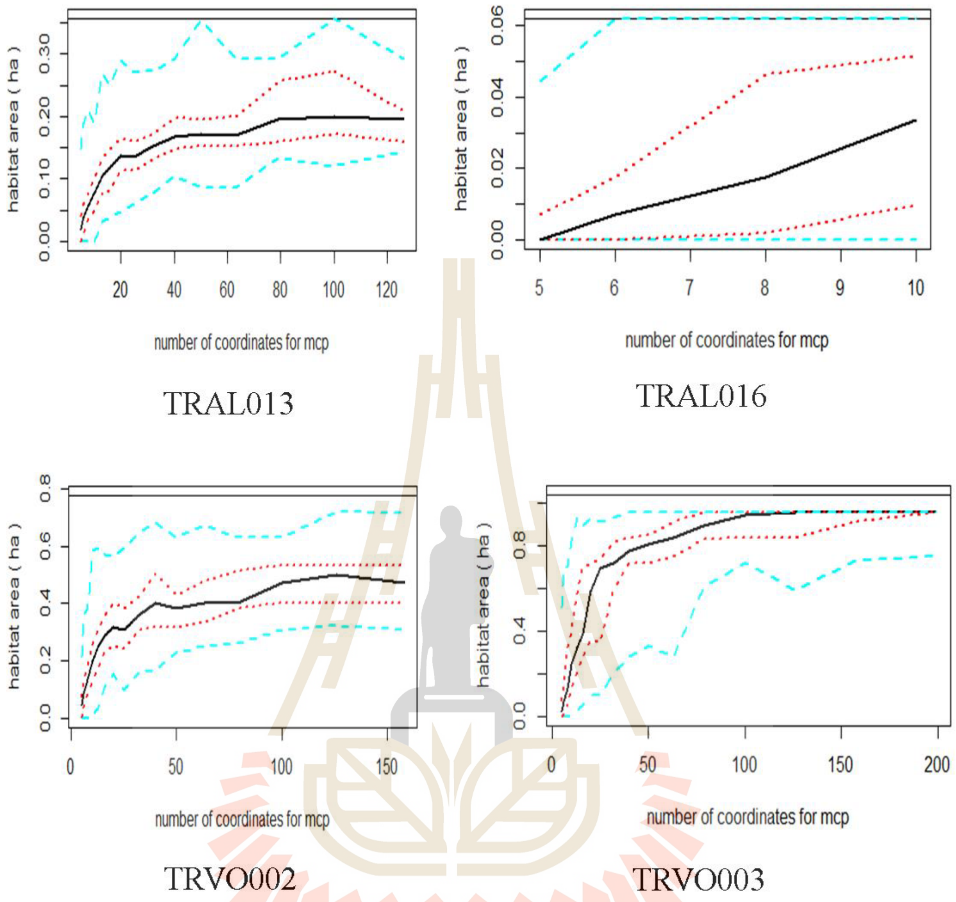


Appendix B-6 MCP home range bootstrap for female *Trimeresurus macrops* radiotracked in the human disturbed area Canal 1 (TRMA20 and 273) and Plantation 2 (TRMA211) sites.



TRMA222 TRMA229

Appendix B-7 MCP home range bootstrap for male *Trimeresurus macrops* radiotracked in the human disturbed area Canal 1 (TRMA229) and Plantation 2 (TRMA222) sites.



Appendix B-8 MCP home range bootstrap for *Trimeresurus albolabris* female (TRAL013) and male (TRAL016) and female *T. vogeli* (TRVO002 and 003) radiotracked in the Forest 9 (TRVO002 and 003), Plantation 2 (TRAL016), and Pond 1 (TRAL013) sites.

APPENDIX C

HABITAT ASSESSMENT DATA

Table C-1 Available mesohabitat features within 100 m habitat transects (*n*= 3 at each site) conducted during the study period from 2014 through 2016 during cold seasons (November- February).

	Mesohabitat										Area
Site ID	Human settlement	Path	Fallen logs	Large rocks	Green vegetation	Woody vegetation	Dead woody vegetation	Open canopy	Lianas/vines	Water	
Canal 1	16	18	25	18	27	15	8	30	16	21	HD
Forest 6	0	8	51	37	32	40	28	59	57	0	Protected
Forest 9	0	4	27	12	2	16	9	29	27	0	Protected

Table C-2 Available microhabitat features within 100 m habitat transects (*n*= 3 at each site) conducted during the study period from 2014 through 2016 during cold seasons (November- February).

	Microhabitat							Area
Site ID	Green vegetation	Small lianas	Large lianas	Saplings	Trees	Small rocks	Large rocks	
Canal 1	24	11	1	14	18	12	13	HD
Forest 6	3	57	17	59	21	32	7	Protected
Forest 9	3	43	13	45	9	23	4	Protected

Table C-3 Utilized mesohabitat features from radiotracked female *Trimeresurus* spp. collected every fix which was a 10m or greater move during the study period from 2014 through 2016 during cold seasons (November- February) which were later compared to available transects to determine habitat selection.

	Mesohabitat										Site	Area
Snake ID	Human settlement	Path	Fallen logs	Large rocks	Green vegetation	Woody vegetation	Dead woody vegetation	Open canopy	Lianas/vines	Water		
T. macrops												
TRMA174	0	9	10	4	8	7	6	10	7	0	Forest 9	Protected
TRMA178	0	6	8	1	1	7	6	6	6	0	Forest 9	Protected
TRMA186	0	7	10	3	8	11	6	9	11	0	Forest 9	Protected
TRMA220	0	0	0	1	0	1	1	1	1	0	Canal 1	HD
TRMA221	17	17	8	2	33	12	7	33	12	12	Canal 1	HD
TRMA270	4	2	4	3	5	4	2	5	3	5	Canal 1	HD
TRMA271	5	5	17	11	17	17	4	7	12	5	Forest 6	Protected
TRMA273	2	1	0	0	1	0	0	2	1	2	Canal 1	HD
TRMA274	7	8	12	3	15	14	11	11	12	4	Forest 6	Protected
T. vogeli												
TRVO002	0	1	3	1	3	3	3	2	2	0	Forest 9	Protected
TRVO003	0	3	3	0	0	5	3	5	5	0	Forest 9	Protected

Table C-4 Utilized microhabitat features from radiotracked female *Trimeresurus* spp. collected during every visual observation during the study period from 2014 through 2016 during cold seasons (November- February) which were later compared to available transects to determine habitat selection.

Snake ID	Microhabitat							Site	Area
	Green vegetation	Small lianas	Large lianas	Saplings	Trees	Small rocks	Large rocks		
T. macrops									
TRMA174	67	44	41	67	68	9	2	Forest 9	Protected
TRMA178	78	90	64	87	44	6	1	Forest 9	Protected
TRMA186	27	43	36	39	12	3	0	Forest 9	Protected
TRMA220	5	3	0	1	5	1	1	Canal 1	HD
TRMA221	2	3	0	5	5	3	0	Canal 1	HD
TRMA270	6	3	2	0	5	2	2	Canal 1	HD
TRMA271	11	12	3	11	11	8	8	Forest 6	Protected
TRMA273	4	4	1	3	3	1	0	Canal 1	HD
TRMA274	9	13	1	11	9	6	3	Forest 6	Protected
TRMA282	9	14	1	11	10	6	3	Forest 6	Protected
T. vogeli									
TRVO002	31	27	6	18	23	1	0	Forest 9	Protected
TRVO003	68	87	41	69	49	0	2	Forest 9	Protected

APPENDIX D

BEHAVIOR ASSESSMENT DATA

Table D-1 All radiotracked female *Trimeresurus* spp. used for camera analysis (*n*= 10) with number of scans observed in each behaviour.

	Reproductive status		Active behaviors		Foraging behaviors			Sedentary behaviors		Miscellaneous			Total scans	Location	
Snake ID	Sex	Gravid	Migration	Move	Ambiguous ambush	Clear ambush	Feeding	Resting	Sheltering	Not visible	Other	Unclear		Area	Site
T. albolabris															
TRAL013	F	Y	47	0	292	668	0	406	0	0	5	0	1419	HD	Pond 1
T. macrops															
TRMA174	F	Y	0	0	0	0	0	0	0	0	0	620	624	Protected	Forest 9
TRMA178	F	Y	6	37	0	652	0	0	0	204	1	0	901	Protected	Forest 9
TRMA186	F	Y	0	0	0	0	0	0	675	0	0	0	676	Protected	Forest 9
TRMA211	F	N	55	20	1027	639	21	0	1031	3446	9	311	6560	HD	Plantation 2
TRMA220	F	Y	28	1	448	236	0	603	0	1079	14	0	2410	HD	Canal 1
TRMA232	F	Y	0	16	86	433	0	283	0	0	0	0	575	HD	Canal 1
TRMA271	F	Y	63	23	35	672	0	0	0	565	5	625	2308	Protected	Forest 6
MEAN			21.7	13.9	228.0	376.0	3.0	126.6	243.7	756.3	4.1	222.3	2007.7		
SE			10.4	5.5	10.4	113.2	3.0	88.8	162.0	473.0	2.1	112.0			
T. vogeli															
TRVO002	F	N	0	3	0	568	0	0	0	0	4	0	575	Protected	Forest 9
TRVO003	F	N	8	0	0	510	0	148	0	0	2	0	668	Protected	Forest 9
MEAN			4.0	1.5	0	539.0	0	74.0	0	0	3.0	0	621.5		
SE			4.0	1.5	0	29.0	0	74.0	0	0	1.0	0	46.5		

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Publications

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