COMPARATIVE GREEN PIT VIPER BEHAVIOR AND ACTIVITY PATTERNS

CURT HRAD BARNES

A Thesis Submitted in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy in Environmental Biology
Suranaree University of Technology
Academic Year 2021

รูปแบบการออกหาอาหารและกิจกรรมอื่น ๆ ของงูเขียวหางไหม้ ตลอดความชันของเส้นรุ้ง

เคิร์ท ฮแรด บาร์นส

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
สาขาวิชาชีววิทยาสิ่งแวดล้อม
มหาวิทยาลัยเทคโนโลยีสุรนารี
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Suranaree University of Technology has approved this thesis submitted in partial fulfillment of the requirements for a Degree of Doctor of Philosophy.

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ความชันของเส้นรุ้ง (COMPARATIVE GREEN PIT VIPER BEHAVIOR AND ACTIVITY PATTERNS)
อาจารย์ที่ปรึกษา : คอลิน โทมัส สไตรน, 207 หน้า.

คำสำคัญ: พฤติกรรม/การอนุรักษ์/งูเขียวหางไหม้

งูเขียวหางไหม้จัดอยู่ในกลุ่มวงศ์ย่อยงูหางกระดิ่งที่อาศัยอยู่บนต้นไม้เป็นหลัก ซึ่งมีสถิติการกัดสูงสุดในบรรดางูพิษทุกกลุ่มในภูมิภาคที่งูชนิดนี้อาศัยอยู่ มีการศึกษาแนวทางเพื่อแก้ไขปัญหาทางสังคมที่เกี่ยวกับสิ่งมีชีวิตเหล่านี้ในธรรมชาติยังมีอย่างจำกัด และงานวิจัยสำหรับการอนุรักษ์งูกลุ่มนี้มีไม่เพียงพอ แม้ว่าการศึกษาพฤติกรรมของงูเขียวหางไหม้มีศักยภาพในการแก้ไขปัญหาสำคัญ เช่น การจัดการปัญหางูกัดและการอนุรักษ์งู แต่จนถึงปัจจุบัน ยังไม่มีการศึกษาเกี่ยวกับงูเขียวหางไหม้มาประยุกต์ใช้เพื่อการจัดการหรือการอนุรักษ์อย่างแพร่หลาย

วัตถุประสงค์ของการศึกษาวิทยานิพนธ์นี้คือ 1) กำหนดและเปรียบเทียบสถานะพฤติกรรม (พฤติกรรมที่แสดงในช่วงเวลาที่ยาว) และเหตุการณ์ (พฤติกรรมที่เกิดขึ้นอย่างรวดเร็ว) และรูปแบบกิจกรรมที่สอดคล้องกัน เช่น เมื่องูเขียวหางไหม้มีการเคลื่อนไหวหรือไม่เคลื่อนไหว ต่องูเขียวหางไหม้ตัวอื่น 2) ประเมินความแตกต่างของพฤติกรรมและรูปแบบกิจกรรมระหว่างอายุและเพศของงูเขียวหางไหม้ 3) ประเมินอิทธิพลต่อพฤติกรรมและกิจกรรมของงูเขียวหางไหม้จากแหล่งที่อยู่อาศัยและสิ่งที่ไม่มีชีวิต 4) ประเมินภัยคุกคามต่องูเขียวหางไหม้จากมนุษย์ และจากงูเขียวหางไหม้ต่อมนุษย์ 5) เปรียบเทียบกลุ่มชนิดพันธุ์งูเขียวหางไหม้ต่างชนิดต่อพฤติกรรมและระยะเวลา 6) เปรียบเทียบความแตกต่างทางพฤติกรรมระหว่างประชากรที่แยกออกจากกัน (ประชากรย่อย) ภายในชนิดพันธุ์เดียวกัน 7) ประเมินประสิทธิภาพและความเป็นไปได้ของคอมพิวเตอร์วิทัศน์ (เช่น การเรียนรู้เชิงลึก) ต่อการศึกษาพฤติกรรมของงูเขียวหางไหม้ในธรรรมชาติ และ 8) ตรวจสอบปฏิสัมพันธ์ของงูเขียวหางไหม้ต่อสิ่งมีชีวิตอื่น ๆ และต่อสายพันธุ์เดียวกัน โดยการศึกษาภายในวิทยานิพนธ์ฉบับนี้ ได้รับการศึกษาแบบไม่รุกรานสิ่งมีชีวิต ไม่มีสัตว์ศึกษาถูกจับหรือสัมผัส และไม่ได้รับการรบกวนที่อยู่อาศัยของพวกมันโดยเจตนา

งูเขียวหางไหม้สองสายพันธุ์ ถูกศึกษาในสองพื้นที่ ณ จังหวัดนครราชสีมา ประเทศไทย *Trimeresurus albolabris* ในพื้นที่มหาวิทยาลัยเทคโนโลยีสุรนารี และ *T. macrops* ณ พื้นที่สงวนชีวมณฑลสะแกราช ผ่านการศึกษาด้วยการตั้งกล้องแบบต่อเนื่องเพื่อตรวจสอบรูปแบบและพฤติกรรมของงู

เขียวหางไหม้ ซึ่งรูปแบบกิจกรรมส่วนใหญ่บันทึกได้ในช่วงกลางคืน สำหรับเหตุการณ์พฤติกรรม (การอ้าปาก การสั่นหัว และ ยื่นหัวไปด้านหน้า) และพฤติกรรมเคลื่อนไหว (การหาอาหารและการเคลื่อนไหว) รวมถึงความหลากหลายของตัวแปรทั่วไป ถิ่นที่อยู่อาศัยย่อย ถิ่นที่อยู่อาศัยใหญ่ และสิ่งไม่มีชีวิต ซึ่งได้รับการเสนอว่าส่งผลต่อการแสดงออกของพฤติกรรมของงูเขียวหางไหม้

การศึกษานี้ได้ใช้คอมพิวเตอร์วิทัศน์ ซึ่งเป็นสาขาวิชาที่ก้าวหน้าอย่างรวดเร็ว โดยเฉพาะอย่างยิ่งกับการวิเคราะห์และทบทวนภาพ โดยการศึกษานี้ได้ใช้คอมพิวเตอร์วิทัศน์สองประเภทคือการตรวจจับการเปลี่ยนแปลงพิกเซลและการเรียนรู้เชิงลึกของรูปภาพและวิดีโอของงูเขียวหางไหม้และงูหางกระดิ่งที่ถูกบันทึกไว้ในธรรมชาติ สำหรับการตรวจจับการเปลี่ยนแปลงพิกเซล มักเกิดการประเมินเหตุการณ์พฤติกรรมที่มากเกินจริง แต่มีการใช้งานง่ายและทำงานได้รวดเร็ว ในขณะที่การเรียนรู้เชิงลึกนั้น ต้องใช้ความรู้ด้านเทคนิคและทักษะความเข้าใจอย่างมาก และใช้เวลาถึงหกชั่วโมงในการฝึกแต่ละแบบจำลอง แต่ทั้งนี้ การเรียนรู้เชิงลึกสามารถระบุสถานะพฤติกรรมได้อย่างมีประสิทธิภาพและสามารถทดสอบข้อมูลชุดใหม่ได้อย่างรวดเร็วเมื่อแบบจำลองเบื้องต้นได้รับการฝึกฝนเป็นที่เรียบร้อย

นอกเหนือจากพฤติกรรมของงูเขียวหางไหม้ นิเวศวิทยาพื้นฐานและธรรมชาติวิทยาได้รับการเก็บรวบรวมผ่านการตั้งกล้องแบบต่อเนื่องที่มหาวิทยาลัยเทคโนโลยีสุรนารี เขตสงวนชีวมณฑลสะแกราช และอุทยานแห่งชาติเขาแหลมด้วยเช่นกัน โดยมีการบันทึกการปรากฏของผู้ล่า เหยื่อ งูเขียวหางไหม้ตัวอื่นและมนุษย์ในพื้นที่อาศัยของงูเขียวหางไหม้ โดยเฉพาะอย่างยิ่งต่อการเก็บรวบรวมข้อมูลเชิงพฤติกรรมและเชิงนิเวศน์ของงูหางแฮ่มกาญจน์ ที่เป็นหนึ่งในตัวอย่างการศึกษา ได้รับการศึกษาอย่างครอบคลุมและเข้มข้น พร้อมกับการทบทวนในประเด็นเรื่องการค้าสัตว์เป็นเป็นปัจจัยที่ทำให้สายพันธุ์นี้ถูกคุกคามด้วยเช่นกัน

ทั้งนี้การระบาดใหญ่ของ COVID-19 ทั่วโลกส่งผลกระทบอย่างมีนัยสำคัญต่อการเดินทางและการศึกษาวิทยานิพนธ์ฉบับนี้ ในขณะที่การเก็บรวบรวมข้อมูลมีความยากลำบาก แต่ผลลัพธ์จากการศึกษาได้ให้ความรู้ทางนิเวศวิทยาและพฤติกรรมพื้นฐานที่ครอบคลุมมากขึ้นสำหรับงูเขียวหางไหม้ซึ่งสามารถใช้ในการจัดการปัญหางูกัดและการอนุรักษ์งู

สาขาวิชาชีววิทยา ลายมือชื่อนักศึกษา Curt H. Barnes

ปีการศึกษา 2564 ลายมือชื่ออาจารย์ที่ปรึกษา

CURT HRAD BARNES : COMPARATIVE GREEN PIT VIPER BEHAVIOR AND ACTIVITY PATTERNS. THESIS ADVISOR : COLIN T. STRIEN, Ph.D. 207 PP.

Keyword: Behavior/Conservation/Green Pit Viper

Green pit vipers are a primarily arboreal group of crotalid snakes which inflict the highest number of bites of any group of venomous snakes in the regions that they occur. Very little study of these organisms in the wild has been conducted to address this significant social issue, nor adequate research for their conservation. This dissertation utilized non- invasive field study and technology to investigate green pit viper behavior within the contexts of ecology, conservation, and snakebite.

Two species of green pit vipers at two study sites in Nakhon Ratchasima province, Thailand, *Trimeresurus albolabris* at Suranaree University of Technology and *T. macrops* at Sakaerat Biosphere Reserve, were studied using stationary continuous feed cameras to investigate activity patterns and behavior. Activity patterns were observed to be primarily nocturnal for behavior events (gape, headbob, and probe) and active behavior states (foraging and movement). A variety of general, microhabitat, macrohabitat, and abiotic variables were suggested to influence expression of those behaviors.

Computer vision is a rapidly advancing field, particularly with image analysis and review, and two types, pixel change detection and deep learning, were applied to pictures and videos of green pit vipers and rattlesnakes recorded in the field. Pixel change detection vastly overestimated behavior event presence but was simple to use and fast to run, while deep learning required much technical and conceptual knowledge and took up to six hours to train each model but showed promise for effectively identifying behavior states and testing new data once the initial models were trained was fast.

Basic ecology and natural history beyond behavior was collected using continuous feed cameras at Suranaree University of Technology, Sakaerat Biosphere Reserve, and Khao Laem National Park. Predators, prey, conspecifics, and humans observed in close proximity to vipers were documented from recordings. Comprehensive and intensive behavioral and ecological data was collected for a focal Kanchanaburi pit viper, and pet trade and presence topics were reviewed for this threatened species

The global pandemic COVID- 19 significantly impacted logistics and subsequent results of this dissertation. While data collection was challenging, results provided the most comprehensive behavioral and basic ecological knowledge yet for the green pit viper species studied in this dissertation.

School of Biology Student's signature Curt H. Barnes

Academic Year 2021 Advisor's signature

ACKNOWLEDGEMENT

I would like to sincerely thank my dissertation advisor, Dr. Colin Strine for all of his support throughout the course of this work. He was also my advisor for my MSc. and I am grateful for his continued assistance and tutorage. Additionally, I would like to extend my gratitude to my proposal and defense committee members: Drs. Alice Hughes, Duangkamol Maensiri, Santi Watana, and Rulon Clark. Input by each member was unique and vital.

Field data collection at the protected study areas would not have been possible without extensive collaboration by the directors and staff of Khao Laem National Park and Sakaerat Biosphere Reserve. While local outreach for this dissertation was severely limited due to the global COVID-19 pandemic, a park ranger was present for all work at Khao Laem National Park and students interning at Sakaerat Biosphere Reserve were able to be a part of most of data collection at this site. The exchange of ideas and knowledge during fieldwork with these groups was invaluable far beyond just collection of raw data.

Suranaree University of Technology graduate students greatly contributed to the success of this dissertation and growth of me individually. These humans who were going through similar experiences provided much-needed emotional support and advice. Their direct support during fieldwork and in the classroom is much appreciated.

Special thanks and gratitude are owed to my family. My parents, including my mother’s instillment of compassion and value of academia as well as my father’s interest in animals and push for ethical treatment of them have greatly influenced my perspectives on life, including this dissertation. I am lucky to have two younger sisters who are much more intelligent than me, and a brother born three minutes before me who shares similar interests and despite being half a world away today remains the same best friend I could never get rid of when we were growing up. I am still grappling to understand why another person would agree to spend their life with me, but I married at the beginning of this dissertation and am all the better student of ecology and human being for it. Living open and true to oneself, and approaching failures and limitations directly and honestly without shame but rather understanding and personal growth, while always striving for personal best are core values I have learned from my spouse. My in- laws were supportive throughout the dissertation, and I would like to extend my gratitude to them also.

Lastly, I owe special thanks and gratitude to Suranaree University of Technology for continuing to invest in my future through support and scholarship. Several organizations, the Society for the Study of Amphibians and Reptiles (SSAR) and the British Herpetological Society (BHS) saw fit to support our research with small green snakes half a world away, for which I am thankful. The National Research Council of Thailand (NRCT) and the Department of National Parks, Wildlife and Plant Conservation (DNP) of Thailand recognized value of our research and provided logistical support and permission to conduct study.

In light of the global biodiversity crisis, I do feel it worth extending gratitude to the study organisms themselves. Two graduate theses and more than seven years later, green pit vipers still intrigue and amaze me every single day. The more I learn about them, the more I realize there is still more yet to be learned. May green pit vipers continue to persist, and humans strive to appreciate and conserve them.

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LIST OF ABBREVIATIONS

DNP = Department of National Parks, Wildlife and Plant Conservation

IUCN = International Union for Conservation of Nature

NRCT = National Research Council of Thailand

KLNP = Khao Laem National Park

SBR = Sakaerat Biosphere Reserve

SERS = Sakaerat Environmental Research Station

SUT = Suranaree University of Technology

TRAL = *Trimeresurus albolabris*

TRKA = *Trimeresurus kanburiensis*

TRMA = *Trimeresurus macrops*

TRVO = *Trimeresurus vogeli*

CHAPTER I

INTRODUCTION

1.1 Introduction

Prominent naturalists as early as the 18th century (i.e- Buffon) proposed the importance of studying the behavior of wild animals, as opposed to domesticated animals or those in captivity. Comprehensive animal behavioral study, however, is fairly recent and Konrad Lorenz and Nikolaas Tinbergen are generally credited with laying the methodological and conceptual foundations for the discipline of ethology in the 1930's (Burkhardt, 1991). Understanding constraints on organisms has historically been a central theme in behavioral research (Schoener, 1971), with understanding the adaptive (suggesting increased reproductive success, "fitness") significance of behaviors a topic more recently explored (teleonomy; Thornhill, 1991). Concerningly, while non-squamate amniotic organisms have been historically well represented in behavior; learning, personality, individuality, and sociality study (Brattstrom, 1974; Bonnet et al., 2002; Pawar, 2003; Waters et al., 2011), squamate (lizards, snakes, and amphisbaenians) study of these themes are still lacking, particularly snakes (Ford, 1995; Doody et al., 2011; Schuett et al., 2017; Burghart, 2020). Behavioral ecology has the potential to assist in the development of effective interventions for wildlife; however, it has been argued that the subfield of conservation behavior continues to lag behind its promises of contributing to real-world application (Caro, 2007; Caro and Sherman, 2013).

Technology was defined by Berger- Tal and Lahoz-Monfort (2018) as having a "...broad meaning which encompasses practically any expression of human ingenuity applied to solving practical problems and thriving as a species" in their broad review of technological applications in conservation, although the Oxford Dictionary follows a more restriction definition- "Machinery and devices developed from scientific knowledge" (Oxford Living Dictionary Online, 2017). Even less than 30 years ago technology still elicited negative perception from some ecologists who viewed it as short-sighted and self-defeating, concentrating on treating the symptoms and not the big picture issues (Meffe, 1992), and often considered only as a last possible resort (Conway, 1986). Major global issues like rapid biodiversity decline and climate change and social factors including rapid advancement of technological application and decreased cost and increased availability of technology have made technological tools a common and indispensable aspect of conservation study today (Pimm et al., 2015; Snaddon et al. 2013). One of the most rapidly changing and becoming more applicable technology today is computer vision which has the potential to increase the breadth, duration, and repeatability of image-based ecological studies through automated image analysis (Kühl and Burghardt, 2013; Pennekamp and Schtickzelle, 2013; Dell et al. 2014).

Green pit vipers (*Trimeresurus* spp. *sensu lato*) are one of the most diverse and abundant predator groups in the Asian tropics (Uetz and Hallermann, 2015). They are equipped to subdue prey with a complex mix of hemotoxic and cytotoxic venom, delivered with evolutionarily advanced solenogyphous fangs (Das, 2010). Green pit vipers utilize a highly efficient and low-cost arboreal ambush mode of hunting which is aided by heat sensing pits on the front of their heads (characteristic of the subfamily Crotalinae). The taxonomy of the green pit viper group has undergone extensive revision, with the *Trimeresurus* genus recently split into seven genera or subgenera (David et al., 2011; Gumprecht et al., 2004; Malhotra and Thorpe, 2004) encompassing more than forty species (Uetz and Hallermann, 2015).

Previous research at the Sakaerat Biosphere Reserve (SBR) in Thailand suggests differences in habitat selection, occupancy and relative abundance, spatial ecology, and behavior of different green pit viper species (Strine, 2015; Barnes, 2017; Barnes et al., 2017; Barnes et al., 2018). Intraspecific differences by sex and fecundity have also been observed within green pit viper species (Strine et al., 2015; Barnes, 2017). Because co-occurring green pit vipers are inferred to occupy separate ecological niches, they provide a unique model in which to conduct in-depth comparative behavioral study.

Despite displaying radical diversity (>40 species), ecological study of green pit vipers remains scant and primarily limited to three species (*Trimeresurus/Cryptelytrops albolabris*, *Trimeresurus/Cryptelytrops macrops*, and *Trimeresurus/Viridovipera vogeli*). Additionally, previous study has observed significant microgeographic variation of morphological characters of the bamboo pit viper (*Trimeresurus stejnegeri*) across the island of Taiwan (Castellano et al., 1994), which could subsequently suggest interesting intra- specific (and perhaps inter- specific) behavioral differences within the green pit viper taxon. Occupation of separate ecological niches, coupled with extremely limited movement and small home ranges (< 10 moves in 90 days, minimum convex polygon home ranges of < 0.14 ha; Barnes et al., 2017; Strine et al., 2018; Barnes et al., 2019) suggest green pit vipers may serve as suitable models for comparative behavior and activity pattern study.

For this dissertation research I investigated the behavior of green pit vipers in Thailand. Specifically, I aimed to address the questions of how different green pit viper species behavior and how that is expressed temporally, how do behavior and activity patterns vary by age and sex, how do biotic and abiotic features factor into green pit viper behavior and activity patterns, what are threats to vipers from humans and from vipers to humans, are co- occurring green pit viper species behavior and activity patterns similar, are there behavioral differences between subpopulations, and do green pit vipers species and demographics interact with predators, prey, and conspecifics differently and do predators, prey, and conspecifics interact differently to green pit viper species and demographics. These questions were addressed non-invasively, without direct disturbance of focal individual vipers or their habitats, using fixed continuous feed cameras which were then reviewed manually, with computer vision, and deep learning. My findings will begin to reveal adaptations in their past and recent evolutionary history, and increase general understanding of ambush predation mode of foraging.

Applied significance of this dissertation includes snakebite management and conservation for different green pit viper species. When are vipers more likely to be active and what human activities might viper behaviors and activity patterns overlap are several questions I would like to begin to address. Similarly, at least one of the proposed species is threatened with extinction and the rest of the species are listed as categories of lowest concern despite no population work and less than five comprehensive ecological studies having been conducted for any of them. Theoretical significance to my study includes addressing that general ecology and natural history knowledge gap, further increasing knowledge about ambush foraging predators, and building on the recently shifting paradigm of understanding sociality and behavioral ecology of vipers. Green pit vipers inflict a high proportion of snakebites in East and Southeast Asia (Warrell, 1999, 2010), inhabit a variety of habitat types, and vary in population status from Data Deficient to Endangered by the International Union for Conservation of Nature (IUCN), justifying conservation application of my research.

1.2 Objectives and hypotheses

The objectives of this study are:

1. Determine and compare behavior states (behavior displayed in relatively long durations) and events (spontaneous behavior) and corresponding activity patterns (when are vipers most active or inactive) of multiple green pit viper species.
2. Assess behavior and activity pattern differences between different ages and sexes of vipers.
3. Assess how habitat and abiotic traits influence behavior and activity of green pit vipers and co- occurring species.
4. Assess threats to vipers from humans, and from vipers to humans.
5. Compare sympatric green pit viper and other viper species behavior and activity periods.
6. Compare behavioral differences between isolated populations (subpopulations) within species.
7. Assess effectiveness and feasibility of computer vision (such as deep learning) to behavioral study with wild green pit vipers.
8. Investigate interactions (predator-prey, conspecific, etc.) green pit vipers and sympatric viper species experience.

The corresponding hypotheses are:

1. I predict behavior and activity patterns of green pit vipers will differ across sites and species. I believe that this will be due to the increased anthropogenic disturbance at SUT compared to the protected and more forested SBR. Alternatively, vipers at SBR and SUT may display similar behavior and activity patterns due to their close proximity to each other and evolutionarily similar (both members of the *Cryptelytrops* clade) most common species, the big- eyed and white- lipped pit vipers.

2. I predict adult females will likely spend less time foraging due to potential for body cavity space being taken up by young, and more time thermoregulating (resting) to prepare for young. I hypothesize that neonate/juvenile and male vipers will spend more time foraging and active (ambushing and moving) than adult females of the same species, due to their smaller size and more limited prey options. Alternatively, neonate/juvenile and male vipers may devote more time thermoregulating (resting) than females of the same species due to their smaller body size, which should make them more susceptible to heat loss and gain. Additionally, while reproductive study has been conducted in captivity, very little has been conducted in the wild- perhaps not all females mate every year. Females may spend more time higher above the ground to lose radiation reflected from the ground.

3. I hypothesize that vipers at SUT will spend more time ambushing during the cold season due to higher temperatures aided by less canopy cover compared to SBR. The temperatures combined with less canopy cover during the hot season may prove detrimental for vipers at SUT, and during this time they may spend more time resting than vipers at SBR. Alternatively, denser forests at SBR may hold moisture and temperature better than SUT, and vipers may instead move and ambush more frequently during the cold season (and less during the hot season) than those found at SUT. Within the daily activity period, vipers at both sites may increase crepuscular and daytime activity during the cold season to take advantage of thermoregulation opportunities; alternatively, temperatures may be low enough and prey so infrequently encountered also that foraging and movement activities may drastically decrease temporally, and I may instead observe consistent inactive activity patterns both during the day and night.

4. I hypothesize that vipers near human settlements or human influence (trails, roads, buildings, etc.) will spend more time resting due to threat of mortality. They will use different habitat features and ambush and rest in different sites than less disturbed vipers of the same species, consume prey and interact with species directly more frequently than less disturbed vipers. Adult females in human dominated or used areas may spend more time arboreal or resting than males or juveniles of the same species, so as to reduce threat to their young.

5. I predict niche partitioning to be readily observed- different strata and behavioral adaptations will be displayed by different species and gender. Vipers will forage and rest at different time and heights, while consuming different prey. Closely related species and species which occupy similar niches will display similar behavior patterns.

6. I predict comparatively minor differences for behavior states and activity patterns, but significant variation in events observed for isolated populations (subpopulations). These may be due to slightly different habitat use and abiotic factors. Differences in general behavior and activity patterns of subpopulations within study sites will vary less than populations at completely different sites or different species (same or different sites).

7. I anticipate deep learning will require large numbers (> 10 videos of different vipers) of training samples for computationally intensive (> 6 hours to run) models which will prove effective at small scale (for a single species at a single site), which will then prove less effective as scale increases (adding additional species and sites). Simple pixel change detection software will be much less computationally intensive, but will have significantly higher false positive observations.

8. Finally, I predict prey species will demonstrate clear anti-predator behavior (tail flagging, mobbing, attacking, etc.) towards vipers. Prey species will respond differently to different species of viper due to threat differences. Vipers will respond towards potential predators through crypsis (blending in to their environment), fleeing, and active (striking) defense mechanisms. Different species of green pit vipers will respond differently, some may rely more on crypsis, others active defense. I predict direct confrontation with conspecifics, predators, and prey will vary within and between species, and will favor larger individuals (females) and species due to increased visibility. I predict direct confrontation between conspecifics will be more frequently observed between closely related species and within sexes due to competition for resources.

1.3 Scope and limitations of study

Field research began in July 2020 and continued through July 2021 at three sites in Thailand. Up to five vipers of multiple species, age, and sex were recorded on camera at one time at each of the study areas during each field season for at least one hour. Non- invasive methods were utilized for this dissertation and no vipers were captured, habitats and organisms in close proximity were not intentionally disturbed, were any samples (tissue, genetics, etc.) collected, so as to expedite research permission and license acceptance. Research permissions and licensing for the 4 sites (originally had an additional site in China) selected took > 1 year to be approved by Suranaree University of Technology, Chinese Academy of Science, National Research Council of Thailand, Institute for Animals for Scientific Purpose Development, and Department of National Parks of Thailand; requiring > 50 emails and significant assistance from Wanrawee Tipprapatkul, Plamjet Kangtrakul (SUT Biology Department), Kamonphon Montaphong (SUT Biology Department), Dr. Alongkot Chukaew (Thai Elephants Conservation Centre), Dr. Alice Hughes (external committee member, Chinese Academy of Sciences), and Dr. Colin Strine (advisor, SUT Biology Department). Thus, data requiring viper capture (mass, fecundity, presence of food boli, etc.) were not collected for this study and it was not possible to directly investigate the adaptive role (fitness) of the behaviors which would require cognition and learning experiments and genetic sampling.

The COVID- 19 pandemic presented significant challenges for fieldwork. While permission was obtained to conduct study in China (Xishuangbanna Tropical Botanical Gardens, XTBG), travel was banned for most of 2020 and 2021. During periods when travel restrictions eased up, Thailand has maintained a strict quarantine policy for returning to the country which is expensive and time consuming. As such, XTBG was removed from this dissertation as a field site. Travel has been a challenge for another proposed study site, Khao Laem National Park, as provincial travel within Thailand has also been restricted at various times during 2020 and 2021. Vipers were also difficult to find at this site, so behavior, activity patterns, and natural history of vipers at this site have been relegated to a section independent of the Sakaerat Biosphere Reserve and Suranaree University sites for which primary analyses were run.

Research and ethics permissions allowed for non - invasive photographic viper individual identification and morphometric measurements, but white- lipped vipers (*T. albolabris*) at SUT appeared sensitive to light both from camera flashes and prolonged exposure to headlights (no vipers at this site were found during the day which could mitigate this stressor), so these techniques were not used for comparative analyses (SUT and SBR). Prior limited observation of Kanchanaburi pit vipers (*T. kanburiensis*) suggested the species to be resilient to limited light disturbance, which was confirmed by the first individual observed at the Khao Laem site. Thus, since this area is not being compared directly and there are less than 10 notes and publications on the species it was decided to utilize cautiously (monitoring viper response, limiting time and disturbance near them) non- invasive photographic viper individual identification with *T. kanburiensis*. This dissertation proposal has been uploaded and updated on the Open Science Framework (OSF) website so changes can be tracked (versions uploaded on August 14, 2020 osf.io/x567f; April 12, 2021 osf.io/5a78m; and May 09, 2021 osf.io/qdb59; see Nosek et al. (2019) for benefits of pre- registration).

This study originally planned to look at maximum likelihood estimates of observed total population size, relative abundance, and detection probability derived from area-time constrained searches via n- mixture models (Royle, 2004; Kery, and Royle, 2015), with the hypothesis that behaviors could be conspecific density dependent as a unique chapter in my dissertation. The “occuPcount” function in the “unmarked” R package was going to be used to obtain estimates of site-specific abundance and to identify the significant environmental parameters affecting it. Functions (ranef) and (bup) in the “unmarked” R package were planned to be used to report the empirical unbiased abundance estimates (λ) of vipers. N-mixture models with covariates affecting abundance were planned to be assessed by comparing (AICc) values. Goodness of- fit tests in the “unmarked” package were planned to be performed with 200 bootstraps (Fiske and Chandler, 2011) in R. Justification for not estimating population parameters were that vipers were more difficult to locate than anticipated at all study areas and white- lipped vipers (*T. albolabris*) at SUT specifically appeared sensitive to light disturbance at night when setting cameras. This would have violated research and ethics permissions which did not allow for disturbance of vipers, their habitats, or other organisms within those habitats. Prior work had not been conducted at that study site, and the three species at SBR (*T. albolabris*, *T. macrops*, *T. vogeli*) appeared resilient to the same disturbance.

1.4 Applied and theoretical applications of study

Findings from this dissertation pose multiple applied and theoretical implications. Understanding green pit viper activity patterns, behavior, and basic natural history as well as technological tools which could aid in the understanding of them are carry significant applied consequences for understanding of venomous snakebite management conservation. Where do vipers come into contact with humans, what actions can humans take to reduce defensive bites to them by vipers, and how do human activities influence viper ecology are topics explored peripherally in this dissertation which have only just begun to be explored through investigation of these organisms in the wild (i.e.- moving beyond review of hospital records). Those same dissertation questions- activity pattern, behavior, natural history, and technological tools also carry broad theoretical benefits including simply understanding the natural world around humans better, assisting with understanding other ambush foraging vertebrates which may be more difficult to study, and further advancing the relatively recent paradigm that snakes do possess and exhibit interesting behaviors worth investing in as much as for any other organism.

1.5 References

Barnes, C. (2017). The spatial ecology, habitat selection, and behavior of big- eye green pit vipers (*Trimeresurus macrops*) in human dominated and protected areas in the Sakaerat Biosphere Reserve. Master's Thesis, Suranaree University of Technology, Thailand.

Barnes, C.H. and Knierim, T.K. (2019). Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus* (*Cryptelytrops*) *albolabris* (Reptilia: Squamata: Viperidae) vipers in Bangkok, Thailand. *Journal of Threatened Taxa 11*(12): 14503-14510.

Barnes, C.H., Strine, C.T., Suwanwaree, P., and Hill III, Jacques. (2017). Movement and home range of green pit vipers (*Trimeresurus* spp.) in a rural landscape in Northeast Thailand. *Herpetological Bulletin 142*: 19-28

Barnes, C.H., Strine, C.T., Suwanwaree, P., and Major, T. (2018). *Cryptelytrops albolabris*: behavior. Herpetological Review *49*(1): 129-130.

Berger-Tal, O., and Lahoz-Monfort, J.J. (2018). Conservation technology: The next generation. *Conservation Letters 11*(6): p.e12458.

Bonnet, X., Shine, R., and Lourdais, O. (2002). Taxonomic chauvinism. *Trends in Ecology and Evolution 17*: 1-3.

Brattstrom, B.H. (1974). The evolution of reptilian social behavior. *American Journal of Zoology 14*: 35-49.

Burghart, G.M. (2020). The learning repertoire of reptiles. In: Zoo Animal Learning and Training, First Edition. Edited by Melfi, V.A., Dorey, N.R., and Ward. S.M. pp. 227-230. John Wiley & Sons Ltd.

Burkhardt, R.W. (1991). Theory and practice in naturalistic studies of behavior prior to ethology's establishment as a scientific discipline. In: Interpretation and explanation in the study of behavior. Eds. Beckoff, M., and Jamieson, D. Boulder, CO: Westview Press.

Caro, T., and Sherman, P.W. (2013). Eighteen reasons animal behaviourists avoid involvement in conservation. *Animal Behaviour 85*: 305-312.

Castellano, S., Malhotra, A., and Thorpe, R.S. (1994). Within- island geographic variation of the dangerous Taiwanese snake, *Trimeresurus stejnegeri*, in relation to ecology. *Biological Journal of the Linnean Society 52*: 365-375.

Conway, W. (1986). Can technology aid species preservation? In: Biodiversity, E.O. Wilson (Ed.). pp. 263-268. Washington DC, USA: National Academic Press.

Das, I. (2010). A Field Guide to the Reptiles of South-East Asia. New Holland Publishers, London, UK.

David, P., Vogel, G., and Dubois, A. (2011). On the need to follow rigorously the Rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: The case of the nominal genus *Trimeresurus* Lacipede, 1804 (Reptilia: Squamata: Viperidae). *Zootaxa 2992*: 1-51.

Dell, A.I., Bender, J.A., Branson, K., Couzin, I.D., de Polavieja, G.G., Noldus, L.P., and Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends in Ecology and Evolution 29*: 417-428.

Doody, J.S., Burghardt, G.M., and Dinets, V. (2013). Breaking the social-non-social dichotomy: a role for reptiles in vertebrate social behavior research? *Ethology 199*: 1-9.

Fiske, I. and Chandler, R. (2011). Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software 43*: 1-23.

Ford, N. (1995). Experimental design in studies of snake behavior. *Herpetological Monographs 9*: 130-139.

Gumprecht, A., Tillack, F., Orlov, N. L., Captain, A., and Ryabov, S. (2004) Asian Pitvipers. Geitje Books, Berlin, 368 pp.

Kéry, M. and Royle, J.A. (2015). Modeling abundance using multinomial N-mixture models. *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS*. p. 393-461.

Kuhl, H.S., and Burghardt, T. (2013). Animal biometrics: Quantifying and detecting phenotypic appearance. *Trends in Ecology and Evolution 28*: 432-441.

LeCun, Y., Bengio, Y., and Hinton, G. (2015). Deep learning. *Nature 521*(7553): 436-444.

Malhotra, A., and Thorpe, R. S. (2004). A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pit vipers *Trimeresurus* and *Ovophis*. *Molecular Phylogenetics and Evolution 32*: 83-100.

Meffe, G. K. (1992). Techno-arrogance and halfway technologies: Salmon Hatcheries on the Pacific Coast of North America. *Conservation Biology 6*: 350-354.

Nosek, B.A., Beck, E.D., Campbell, L., Flake, J.K., Hardwicke, T.E., Mellor, D.T., van't Veer, A.E., and Vazire, S. (2019). Preregistration is hard, and worthwhile. *Trends in Cognitive Sciences 23*: 815-818.

Oxford Living Dictionary Online. (2017). "technology, n." Oxford University Press. Retrieved from https://en.oxforddictionaries.com/definition/technology.

Pawar, S. (2003). Taxonomic chauvinism and the methodological challenged. *Bioscience 53*: 861- 864.

Pennekamp, F., and Schtickzelle, N. (2013). Implementing image analysis in laboratory-based experimental systems for ecology and evolution: a hands-on guide. *Methods in Ecology and Evolution 4*: 483-492.

Pimm, S.L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z, and Loarie, S. (2015). Emerging technologies to conserve biodiversity. *Trends in Ecology & Evolution 30*: 685-696.

Royle, J.A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics 60*(1): 108-115.

Schoener, T.W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics 2*: 369-404.

Schuett, G.W., Clark, R.W., Repp, R.A., Amarello, M., Smith, C.F., and Greene, H.W. (2017). Social behavior of rattlesnakes: a shifting paradigm. In: Schuett, G.W., Feldner, M.J., Smith, C.F., and Reiserer, R.S. (eds.). Rattlesnakes of Arizona, vol. 2. Eco Publishing, Rodeo, NM, USA. p. 161-244.

Snaddon, J., Petrokofsky, G., Jepson, P., and Willis, K. J. (2013). Biodiversity technologies: Tools as change agents. *Biology Letters 9*: 20121029.

Strine, C. (2015). The ecological study of green pit vipers in Sakaerat Environmental Research Station, Nakhon Ratchasima. Doctoral Thesis, Suranaree University of Technology, Thailand.

Strine, C., Silva, I., Barnes, C.H., Marshall, B.M., Artchawakom, T., Hill III, J., and Suwanwaree, P. (2018). Spatial ecology of a small arboreal ambush predator, *Trimeresurus macrops* Kramer, 1977, in Northeast Thailand. *Amphibia- Reptilia 39*(2018): 335-345.

Strine, C., Silva, I., Nadolski, B., Crane, M., Barnes, C., Artchawakom, T., Hill, J., and Suwanwaree, P. (2015). Sexual dimorphism of tropical green pit viper *Trimeresurus* (*Cryptelytrops*) *macrops* in Northeast Thailand. *Amphibia-Reptilia 36*: 1-12.

Thornhill, R. (1991). The study of adaptation. In: Interpretation and explanation in the study of behavior. Eds. Beckoff, M., & Jamieson, D. Boulder, CO: Westview Press.

Uetz, P., and Hallermann, J. (2015). Reptile database. http://reptile-database.reptarium.cz. Accessed on March 01, 2015.

Valletta, J.J., Torney, C., Kings, M., Thornton, A., and Madden, J. (2017). Applications of machine learning in animal behaviour studies. *Animal Behaviour 124*: 203-220.

Warrell, D.A. (1999). Guidelines for the clinical management of snake-bites in the south-east Asia region. *Asian Journal of Tropical Medicine & Public Health 30*: 1-20.

Warrell, D.A. (2010). Guidelines for the clinical management of snake-bites in the south-east Asia region. World Health Organization, Regional Office for South East Asia, New Delhi, pp. 1-67.

Waters, R.M., Bowers, B.B., and Burghardt, G.M. (2017). Personality and individuality in reptile behavior. In: Personality in Non- human Animals (eds. Vonk, J., Weiss, A., and Kuczaj, S.), pp. 153-184. New York, NY: Springer.

CHAPTER II

LITERATURE REVIEW

2.1 Animal behavior

Foraging and predation study is essential for ecological and evolutionary research and is central to our understanding of ecological physiology (Beaupre and Duvall, 1998), coevolutionary arms races (Brodie and Brodie, 1999), and ecosystem dynamics (Duffy, 2003). Ecologists have long been intrigued by the question "how do animals balance the costs and benefits of foraging?" Foraging predators should attempt to maximize energy intake while concurrently minimizing energy loss (Hamilton, 2010), with factors such as prey biomass, vulnerability, and encounter rate significantly influencing diet choice.

Study of crotaline snakes, members of the family Viperidae, subfamily Crotalinae, have provided valuable insight into ecological theory, including bioenergetics (Beaupre, 1993; Secor and Nagy, 1994), habitat selection (Reinert, 1984), life history (Brown, 1991), mating systems (Duvall et al., 1992), and foraging behavior (Clark, 2016). Vipers employ an energetically minimal ambushing foraging mode ideal for behavioral study. Study by Reinert et al. (2011) has suggested elasticity of foraging behavior for the timber rattlesnake (*Crotalus horridus*) due to prey availability and characteristics of the local environment. Behavioral investigation of the medically important and ecologically diverse green pit viper taxon may further elucidate foraging and activity patterns of crotaline snakes and other ambush predators.

2.1.1 Comparative ethology

Comprehensive review of comparative ethology is provided by Burghardt and Gitterman (1990). They define comparative ethology as "the use of behavior patterns in the analysis of behavior evolution emphasizing the processes underlying the mechanisms and evolution of behavior, adaptive function, and phylogenetic reconstruction." Burghardt and Gitterman (1990) make the case that "...

to be comparative is to adopt a taxonomically oriented evolutionary framework based on characters with common origins." Some early ethologists considered stereotyped behaviors as on par with morphological characters (Beckoff, 1977), looking to species differences through naturalistic behavior patterns (Burghardt, 1985; Barlow, 1989).

Although severely lacking, significant insights and methodologies have arisen from comparative ethological studies with snakes. Much of this has been derived from work by Gordon M. Burghardt, who has effectively sought to address Tinbergen's four foundations of ethological study (physiological causation, individual development, evolutionary history, and function; Tinbergen, 1963) within a comparative behavior approach. Study of garter snakes (genus *Thamnophis*) has illuminated that species, populations, litters, and individual differences exist and arc important at different levels of comparative ethological analysis (Burghardt, 1993). Such insight into comparative analyses of *Thamnophis* was possible due to the specious nature of the genus (25-30 species), and Burghardt (1993) made the bold claim that "looking at only one convenient species is to place self-imposed blinders on oneself, conceptually and empirically, or even risk being seriously misled." Like garter snakes, green pit vipers are incredibly specious and display interesting characteristic innate discrete behavior patterns.

2.1.2 Camera applications to animal behavir, prey selection, and community ecology

Camera technology has recently become an innovative method in conservation biology. Research objectives from many disciplines including entomology, avian ecology, animal behavior, and wildlife management have been addressed through remote fixed cameras (Cutler and Swann, 1999). Recent development in computer vision has the potential for reduced time for reviewing video data and increasing oversight (reviewed by Weinsten, 2017). Vipers specifically are uniquely well suited for camera studies due to their sit-and-wait ambush foraging mode (Clark, 2006; Dorcas and Willson, 2009), and subsequently a variety of species have been studied using this method. Until early 2000, most previous knowledge of viper foraging was obtained from laboratory study, anecdotes, and dietary and morphological analyses (Cundall and Greene, 2000).

Fixed cameras provide a uniquely relatively non- invasive alternative for quantifying foraging behavior and activity patterns for vipers. Cameras have primarily been utilized for predator- prey study of New World viperids (rattlesnakes, genus *Crotalus*). Innovative foraging and behavioral research using camera technology has been published for red diamond (*Crotalus ruber*, Barbour and Clark, 2012), northern pacific (*C. oreganus*, Barbour and Clark, 2012; Putman et al., 2016), timber (*C. horridus*, Clark, 2006), and sidewinder (*C. cerastes*, Clark et al., 2016) rattlesnakes. Behavioral research for wild sit-and-wait foraging snakes with cameras has expanded little outside of this region (North America), however, Glaudas et al. (2017) was able to reveal potential biases of using museum specimens alone for determining diet for the South African puff adder (*Bitis arietans*) through fixed videography.

Preliminary research and previous study with cameras and green pit vipers at SBR by Barnes (2017) has revealed insight into activity period, prey selection, inter- and intraspecific interaction, general behavior, and natural history of this interesting group of snakes (Figure 2.1). Use of camera technology was additionally able to confirm thermal ecology of a white- lipped viper (*T. albolabris*) during a fire event in a rural landscape at SBR (Barnes et al., 2018), social behavior of big- eyed vipers (*T. macrops*) in forested areas of SBR (Barnes et al., 2020), and behavior, activity patterns and interspecific interactions of *T. albolabris* in Bangkok, Thailand (Barnes and Knierim, 2019). Displaying limited movement and small home range sizes, as miniscule as 0.14 ha (minimum convex polygon; Barnes et al., 2017; Strine et al., 2018; Barnes et al., 2019), green pit vipers are ideal models for behavior research of sit- and- wait ambush foraging mode predators.

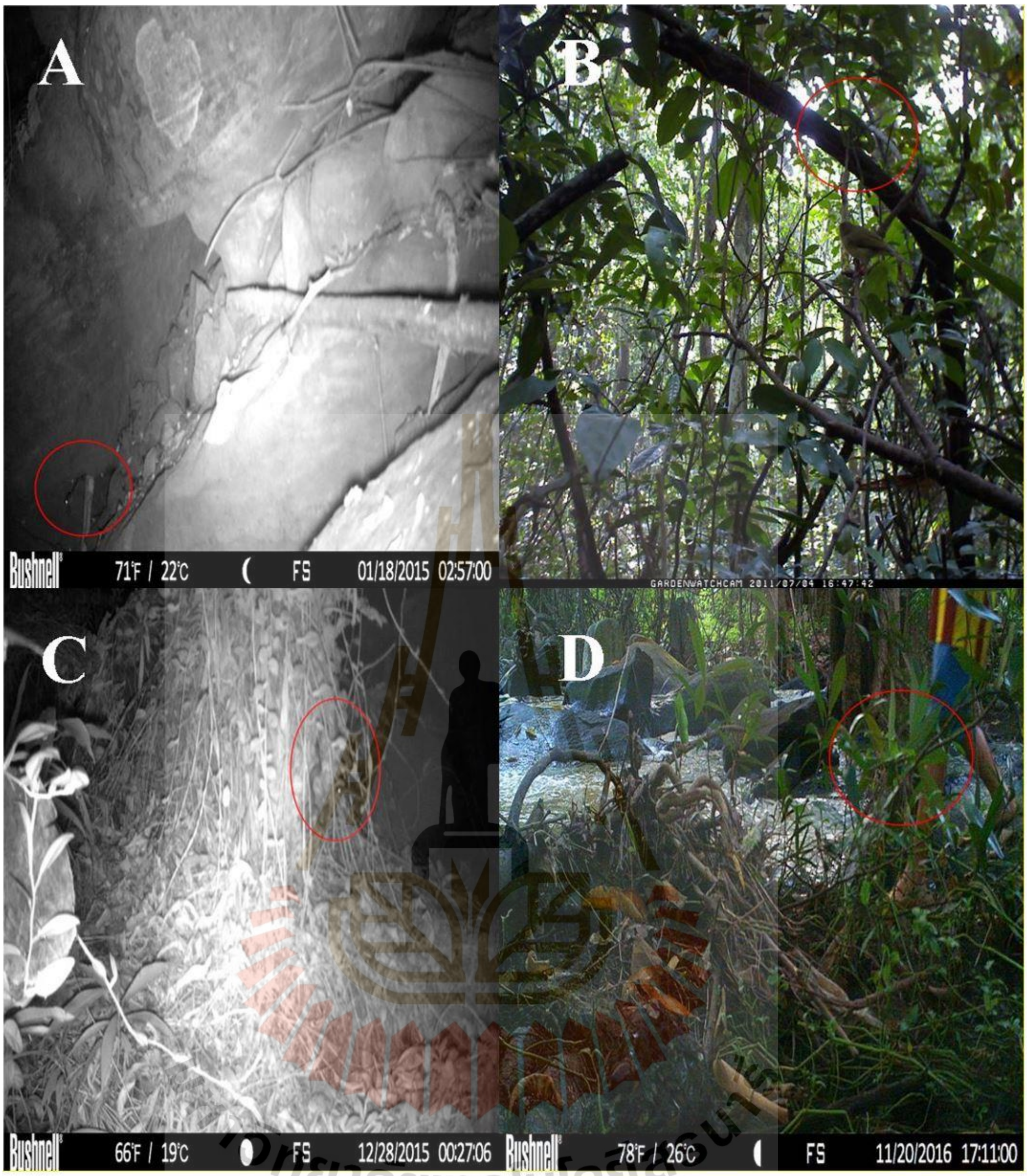

Figure 2.1 Interesting green pit viper (*Trimeresurus* spp. *sensu lato*) behavior observed previously by C.H. Barnes during study at Sakaerat Biosphere Reserve in northeast Thailand using time- lapse cameras with focal vipers circled in red for clarity; predation of anuran prey A), interaction between viper and previously banded passerine bird B), intraspecific interaction between two vipers C), and interaction between a resting viper and villager in rural habitat D).

2.2 Computer vision

Most broadly, computer vision is a form of image-based artificial intelligence that mimics human vision by generating rules for the form, grouping and, changes of image pixels (Weinstein, 2017). Computer vision evolved from multiple disciplines, with contributions from computer science (Branson et al. 2014), astronomy (Arzoumanian et al. 2005), and remote sensing (LaRue et al. 2016). Review of computer vision and applications of image analyses to ecology and conservation questions is presented by (Weinstein, 2017). Within this over- arching field fall artificial intelligence (AI), machine learning, neural networks, and deep learning (Figure 2.2).

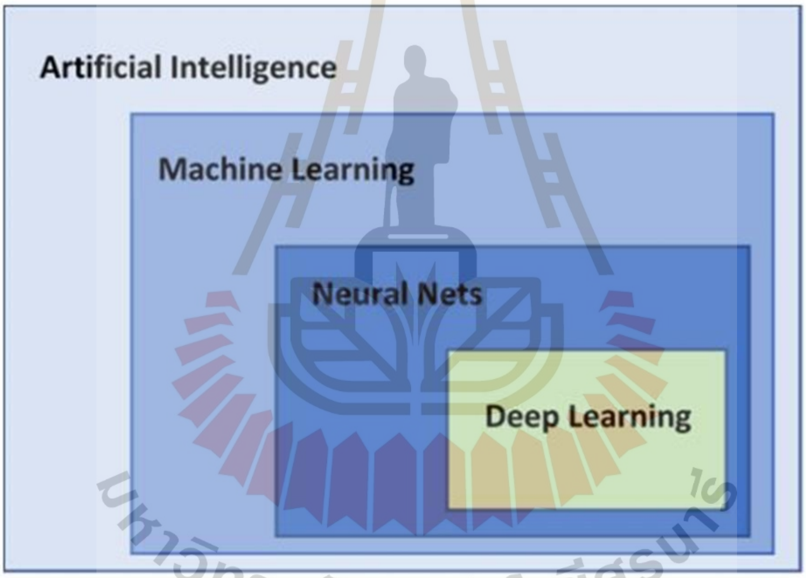

Figure 2.2 Different aspects of computer vision, and how they are related to each other, from Islam (2020).

Most succinctly, AI is a general concept comprised of intelligent programs and machines that can creatively solve problems (Islam, 2020). Within AI, machine learning is a subfield providing a system to learn and improve automatically from experience through an explicit program with minimal human interaction (Islam, 2020). The goal of these algorithms is to seek to recognize relationships between input-output data and predict the value or the class when a new data point is given (Islam, 2020). Neural networks are a subfield of machine learning which excels with massive volumes of data, including number of variables or diversity of the data (Islam, 2020). Basically, neural networks depict associations and discover consistencies within a set of patterns from data. Lastly, deep learning is a richer structure of neural networks. Deep learning is particularly attractive to ecologists because image features are not a priori designed, but rather learned from existing labelled images (Marburg and Bigham, 2016; Wilf et al., 2016; see Figure 2.3 for illustration of basic conceptual design).

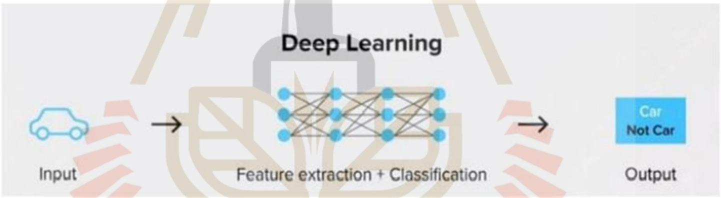

Figure 2.3 Conceptual design of deep learning method. Deep learning involves stacking layers that automatically learn complex, abstract, and discriminating features. Figure modified from Islam (2020).

Computer vision has been applied to a variety of subfields within general ecology including but not limited to camera traps, GIS, and spatial ecology (summarized in Weinstein, 2017). Computer vision has been applied specifically with snakes to identify species from images (Durso et al., 2021), viper movement patterns (DeSantis et al., 2020), presence at a location using camera traps (Islam, 2020), and for understanding mimicry among snake species (Solan et al., 2020).

2.3 Vipers (family Viperidae)

The snake family Viperidae is currently (extant) found on all continents except for Australia and Antarctica (cosmopolitan distribution), inhabit nearly all terrestrial ecosystem types, and are vulnerable to a variety of anthropogenic threats (Maritz et al., 2016; Figure 2.4 and Figure 2.5). Vipers reach the highest elevations (up to 4800 m above sea level, *Gloydius himalayanus*), and both the highest and lowest latitudes (over 65° north and 47° south, *Vipera berus* and *Bothrops ammodytoides*, respectively) among all snakes (Greene, 1997). The adder (*V. Berus*) also displays the widest distribution of any terrestrial snake (Smith, 1973). More than 342 species of vipers are extant, arranged in more than 35 genera, and belonging to three subfamilies (Alencar et al., 2016). Crotalinae (or "pit vipers") are the most diverse and widely distributed subfamily, comprising around 232 species currently distributed in the Old and New World (Alencar et al., 2016).

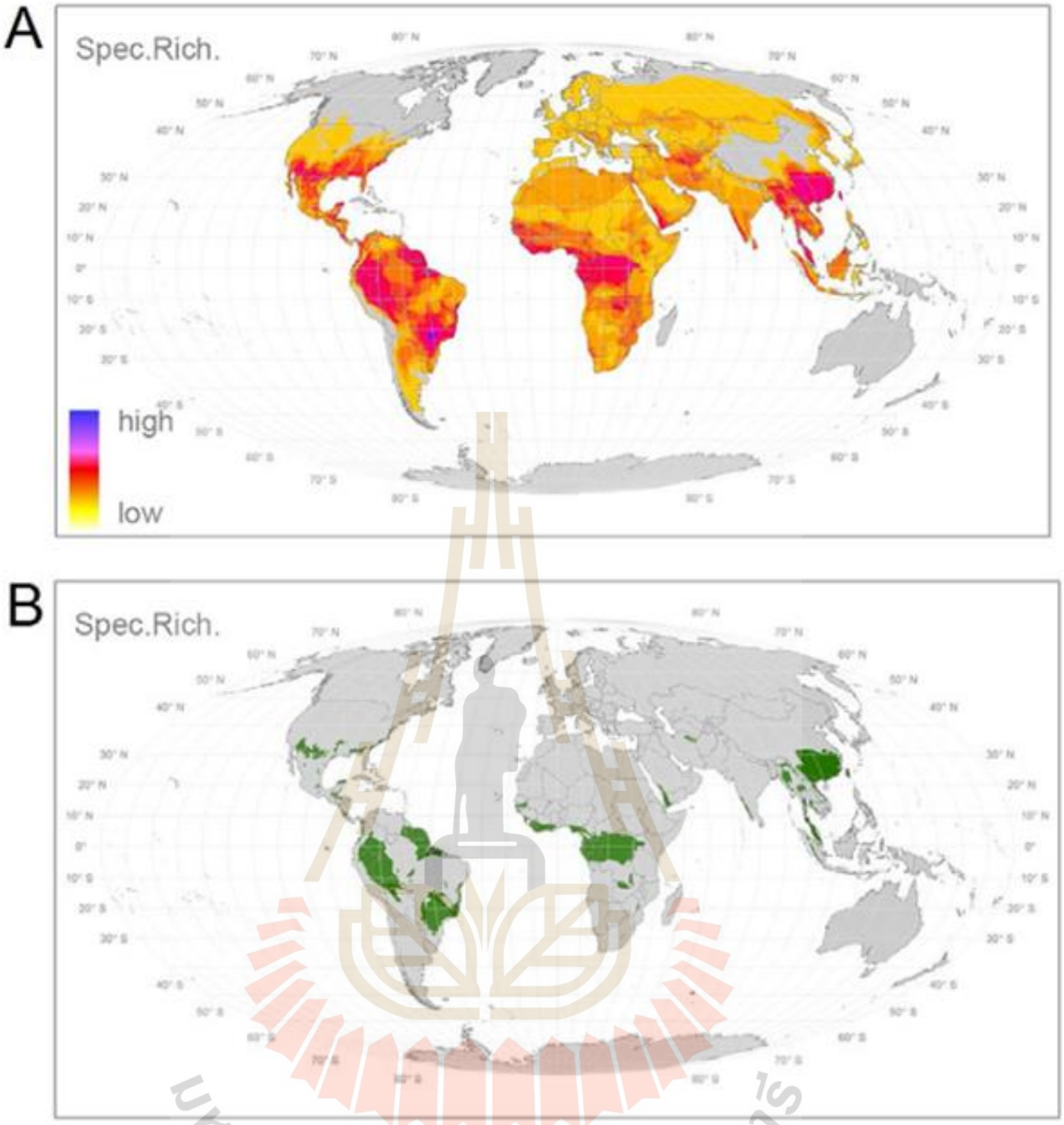

Figure 2.4 Species richness (A) and top 10% species-rich grid cells for vipers (family Viperidae) globally (B). Figure reproduced from Maritz et al. (2016).

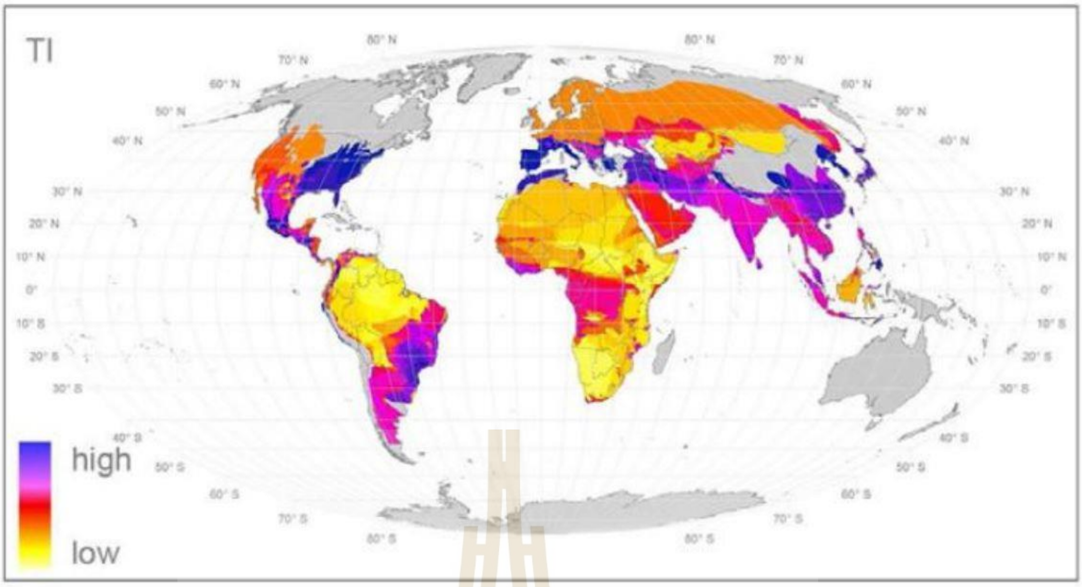

Figure 2.5 Viper species richness weighted by Threat Index (TI). TI was calculated through the size of the geographic distribution (area of the geographic distribution polygon) of each species, the degree of human impact (Global Human Influence Index (WCS and CIESIN, 2005)) within that distribution, percentage of each distribution formally protected (PA; (IUCN and UNEPWCMC, 2015)), and expert opinions. Figure reproduced from Maritz et al. (2016).

Early pit vipers are thought to have diverged from their closest viperid relatives between 16.44 and 30.18 million years ago (between the early Miocene to mid Oligocene; Wuster et al., 2002), which is supported by the earliest known fossil evidence from Asia (Greene, 1992). Beginning in the Eocene to Miocene, desert regions retracted to northwest China and forests expanded in Southeast Asia and it has been hypothesized that forest expansion along with the origin of loreal pits, defensive sound production and parental care prompted rapid speciation during the early radiation of pit vipers (Greene, 1992; Alencar et al., 2016). The Miocene is thought to have been a crucial period (due to forest expansion and complex geological history) for the diversification of Asian pit vipers, and the two major clades (i.e., the clade now consisting of *Trimeresurus*, *Cryptelytrops*, *Parias*, *Popeia*, and *Himalayophis*, and its sister clade consisting of *Protobothrops*, *Ermia*, *Triceratolepidophis*, *Gloydius*, *Ovophis*, and all new World pit viper genera) are estimated to have diverged during the early to mid- Miocene (13.12- 23.85 million years ago, Malhotra and Thorpe, 2004; Tu et al., 2000).

2.4 Green pit vipers

Divergence between the major clades within the "*Trimeresurus*" radiation likely took place only a few million years after the initial viper diversification event- *Parias/Popeia/Himalayophis* clade split from *Viridovipera* and *Cryptelytrops* clade between 10.34 and 19.17 million years ago and the divergence between the Indomalayan *Parias* and *Popeia/Himalayophis* took place almost simultaneously (geologically) at between 9.56 and 18.07 million years ago (summarized from Malhotra and Thorpe, 2004). Species- specific biogeographical information for Asian pitvipers is limited, but several species found within my proposed study sites with extensive distributions have been published. Divergence and ancestral date of the white- lipped viper (*T. Albolabris*) is estimated to have been about 7.15 million years ago in northern Thailand and eastern Myanmar, with mutli- directional dispersal- first north to south, and then east to west (Zhu et al., 2016). The bamboo pit viper (*T. Stejnegeri*) has been proposed to originate about 5.7million years ago in southwest China, and to have then dispersed from west to east (Guo et al., 2016). Jerdon's pit viper (*Protobothrops jerdonii*) is also thought to have originated in southwest China, about 6.6 million years ago, with west to east dispersal followed by vicariance (Guo et al., 2011).

2.4.1 Description and distribution

Green pit vipers are all members of the Viperidae family, sub-family Crotalinae, nested within the infraorder Alethinophidia. All crotalines possess heat sensing pits which function in defense and prey capture. Taxonomy, phylogeny, and nomenclature of green pit vipers is still unclear (David et al., 2011), but approximately 40 species are nested within the group. The *Trimeresurus sensu lato* taxon ranges from southern and central China (including Taiwan and Hainan), India, Sri Lanka, Nepal, Bhutan, Bangladesh, Laos, Vietnam, Cambodia, Thailand, Malaysia, Indonesia (except New Guinea), and the Philippine Archipelago (Orlov et al., 2002).

2.4.2 Natural history and ecology

Natural history and basic biology knowledge of an organism provides critical information for developing models and testing questions of importance to evolution (Mayr, 1963) and critical conservation issues, but there has been substantial decrease in the number of publications relating to the basic ecology of reptiles and amphibians since 1990 (McCallum and McCallum, 2006). There is a significant misconception that such critical baseline data is chiefly anecdotal and requires little to no forethought, perspective, or special training (Greene, 1986).

Green pit vipers inhabit a wide array of habitats, exhibit a diverse range of arboreality, and select a variety of prey species. Previous study has already suggested uniqueness and complexity to green pit viper behavior- ranging from survival from fire (Barnes et al., 2018), caudal defensive display (Barnes and Tipprapatkul, 2019), persistence in highly disturbed habitats (Barnes and Knierim, 2019), and sociality (Barnes et al., 2020). These interesting natural history features, combined with limited movement (Barnes et al., 2017; Strine et al., 2018; Barnes et al. 2019) suggest green pit vipers may serve well as model organisms for ambush foraging predators using fixed camera technology.

2.4.3 Snakebite management and conservation

Snakebite was recently labeled as a neglected tropical disease by the World Health Organization (Chippaux, 2017). Between 1.8- 2.7 million people each year are maimed and killed due to bites by venomous snakes (Chippaux, 1998; Kasturiratne et al., 2008; Suraweera et al., 2020). While direct and analytical evidence is largely lacking, in theory snakebite is a preventable infliction. Clearing understory vegetation, keeping food properly contained and moving brush piles, grain stores and other clutter away from houses have been suggested to deter snakes and their prey (Parkhurst, 2009; WHO, 2016). Wearing boots and using a flashlight and walking- stick during the night can prevent snakebite to people working outside (WHO, 2016). Movement, foraging behavior, and habitat use and general natural history of a focal individual of a medically significant and rarely studied species (Malayan krait, *Bungarus candidus*) living at close proximity to humans as well as mitigation measures when this individual came into direct conflict with humans was recorded in a case study at Suranaree University of Technology, one of the study sites for this dissertation, by Hodges et al. (2021).

2.5 Study sites

2.5.1 Location and history

Two study areas in Nakhon Ratchasima province, Thailand were concurrently utilized for behavior and activity pattern research with a third site in Kanchanaburi province which served as preliminary and primarily descriptive study (Figure 2.6). Study will be conducted concurrently at Sakaerat Biosphere Reserve and Suranaree University of Technology (Nakhon Ratchasima province) as well as Khao Laem National Park (Kanchanaburi province) in the central part of the country. A brief outline of Thai protected areas is summarized in Panusittikorn and Prato (2001), Sharp and Nakagoshi (1997), and Singh et al. (2021), and Suranaree University of Technology in Naithani et al. (2018). Distances (obtained through “st_distance” function in R, using “sf” function, Pebesma, 2018) between study sites are presented in Table 2.1.

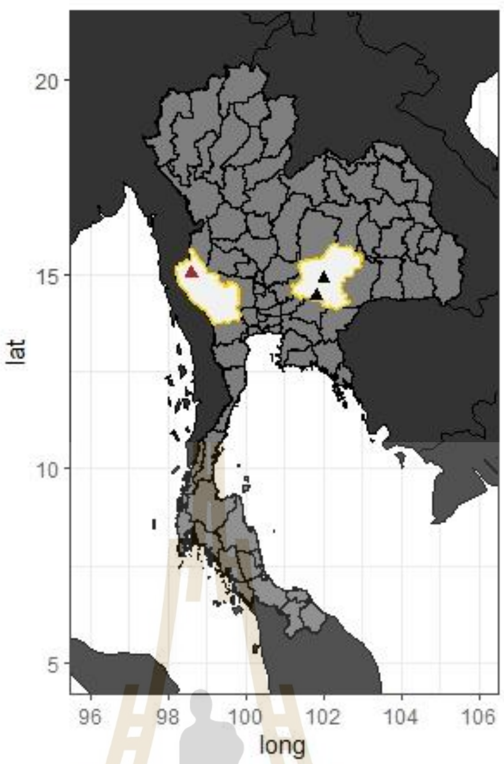

Figure 2.6 Green pit viper study site locations- Khao Laem National Park in Kanchanaburi province (indicated by a brown triangle), and Suranaree University of Technology and Sakaerat Biosphere Reserve in Nakhon Rachasima province (top and bottom black triangles, respectively), Thailand.

Table 2.1 Distances *(km)* between Khao Laem National Park (KLNP), Suranaree University of Technology (SUT), and Sakaerat Biosphere Reserve (SBR) study sites.

	KLNP	SUT	SBR
KLNP	0.00	378.94	366.32
SUT	378.94	0.00	49.91
SBR	366.32	49.91	0.00

2.5.2 Vegetation associations and climate

The Suranaree University of Technology (SUT) campus is 11.2 km2 in size (located at 14.87 29 17°N and 102.02 37°E, third largest university in terms of land area in Thailand, and 10000 students) and comprised primarily of degraded forest but also has a botanical garden, small parks, some natural patches of forest, plantation, and institutional and departmental buildings (Jomnonkwao et al., 2016; Naithani et al., 2018). The university is located approximately 20 kilometers from the city of Nakhon Ratchasima (also known as "Korat" or "Khorat", 9th largest city in Thailand with approximately 126,391 residents; Registration Office Department of the Interior, Ministry of the Interior, 2019), although the immediate area surrounding SUT is primarily agricultural which is characteristic of the province (Nakhon Ratchasima).

Sakaerat Biosphere Reserve (SBR), is located in Nakhon Ratchasima Province, Thailand (14.44-14.55° N, 101.88-101.95° E, approximately 50 km from SUT). The reserve is split into three management areas: approximately 80 km^2 of SBR is designated as a core area and set aside to preserve and maintain species diversity, genetic variation, and landscapes and ecosystems and is characterized by primary and secondary forest types; buffer and transition areas surround the core area and consist primarily of agricultural areas and settlements (together comprising approximately 360 km^2). The Dong Phayayen-Khao Yai Forest Complex is directly adjacent to SBR, which is notable due to its size (230 km in length) and collaboration effort (four national parks and one wildlife sanctuary, ranging in size from 313 to 2,168 km^2 in area). Approximately 15% of Nakhon Ratchasima province (where SUT and SBR are located) is comprised of protected forest area (DNP, 2018).

Established in 1991, Khao Laem National Park (KLNP) is located in central- west Thailand (14.8° N, 98.5° E) and is approximately 1,500 km2 in area. A total of 42, 573 people visited the park in 2018 (DNP, 2018). The central Thailand climate is typified by a rainy season in June- October, a winter period from November through January, and summer between February to May (which KLNP, SUT, and SBR are all included). Habitat of KLNP comprises mainly of mixed deciduous forest and tropical rain forest, with karst interspersed. Approximately 62% of the Kanchanaburi region is comprised of protected forest area (DNP, 2018). The national park is part of the Western Forest Complex, which is comprised of 18 national parks and sanctuaries in Thailand and a nature reserve in Myanmar.

2.5.3 Wildlife

Few wildlife studies have been conducted at the three study sites. Previous study of birds at Suranaree University of Technology was conducted by Naithani et al. (2018). Through opportunistic calls (staff, locals, and emergency rescue personnel) and visual encounter surveys, Cameron Hodges (MSc. student at SUT) has recorded 24 species of snakes on campus (personal communication). At least 105 amphibian and reptile species have been observed at Sakaerat Biosphere Reserve (Inger and Colwell, 1977; Crane et al., 2018). Previous study of other vertebrates which may interact with vipers at this site include Peterson et al. (2018) and Pinmongkholgul (2008) (mammals) and Trisurat and Duemgkae (2011) and Khamcha et al. (2018) (birds). Herpetofaunal diversity for Kanchanaburi Province has not been comprehensively reviewed in the published literature; however, diversity surveys have been conducted at individual sites within the province (but not for KLNP). Nineteen species of amphibians and forty- two species of reptiles were observed during surveys at the Mae Klong Watershed Research Station (Kuntintara and Kamsuk, 1997). No previous study of other vertebrates which may interact with vipers at this site has been conducted.

2.5.4 Viper species present

No formal herpetofaunal inventory has been published at Suranaree University of Technology, but the white- lipped viper (*T. Albolabris*) is the most frequently encountered viper encountered at this site (personal observation). Three green pit viper species and one other pit viper group are confirmed for Sakaerat Biosphere Reserve (*T. albolabris*, *T. macrops*, *T. vogeli*, and *Calloselasma rhodostoma*; Strine, 2015; Hill et al., 2006). Three green pit viper species and one other genera of pit viper (Kuntintara and Kamsuk, 1997; although one of the species they indicate, *Trimeresurus hageni*, is confirmed only from the very south of Thailand by Cox et al. (2012) so this is a likely misidentification and/or incorrect nomenclature). Another source suggests the genera *Ovophis* to be present in Kanchanburi province, also (Cox et al., 2012). Khao Laem National Park is of unique conservation interest due to recent (unpublished) observation of the IUCN Endangered Kanchanaburi (Kanburi) pit viper (*Trimeresurus* (*Cryptelytrops*) *kanburiensis*, see Chan-Ard et al., 2012 for summary of species).

2.6 References

Alencar, L.R.V., Quental, T.B., and Grazziotin, F.G. (2016). Diversification in vipers: phylogenetic relationships, time of divergence and shifts in speciation rates. *Molecular Phylogenetics and Evolution 105*: 50-62.

Arzoumanian, Z., Holmberg, J., and Norman, B. (2005). An astronomical pattern-matching algorithm for computer-aided identification of whale sharks Rhincodon typus. *Journal of Applied Ecology 42*: 999-1011.

Barbour, M.A., and Clark, R.W. (2012). Diel cycles in chemosensory behaviors of free-ranging rattlesnakes lying in wait for prey. *Ethology 118*: 480-488.

Barlow, G.W. (1989). Has sociobiology killed ethology or revitalized it? In P.P.G. Bateson and P.H. Klopfer (Eds). Perspectives in ethology. Volume 8. Whither ethology? (pp. 1-45). New York: Plenum Press.

Barnes, C. (2017). The spatial ecology, habitat selection, and behavior of big- eye green pit vipers (*Trimeresurus macrops*) in human dominated and protected areas in the Sakaerat Biosphere Reserve. Master's Thesis, Suranaree University of Technology, Thailand.

Barnes, C.H., and Knierim, T.K. (2019). Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus* (*Cryptelytrops*) *albolabris* (Reptilia: Squamata: Viperidae) vipers in Bangkok, Thailand. *Journal of Threatened Taxa 11*(12): 14503-14510.

Barnes, C.H., Farren, W., Strine, C.T., Hill III, J., Waengsothorn, S., and Suwanwaree P. (2019). Are the habitat niches of female green pit vipers *Cryptelytrops macrops* and *Viridovipera vogeli* partitioned by vertical stratification? *Herpetological Bulletin 147*: 18-23.

Barnes, C.H., Strine, C.T., Suwanwaree, P., and Hill III, Jacques. (2017). Movement and home range of green pit vipers (*Trimeresurus* spp.) in a rural landscape in Northeast Thailand. *Herpetological Bulletin 142*: 19-28.

Barnes, C.H., Strine, C.T., Suwanwaree, P., and Major, T. (2018). *Cryptelytrops albolabris*: behavior. *Herpetological Review 49*(1): 129-130.

Barnes, C.H., Farren, W., Strine, C.T., and Suwanwaree, P. (2020). Social Behavior Displayed by the Green Pit Viper *Trimeresurus* (*Cryptelytrops*) *macrops*. *Tropical Natural History 20*(1): 95-103.

Beaupre, S.J. (1993). An ecological study of oxygen consumption in the mottled rock rattlesnake, *Crotalus lepidus lepidus*, and the black-tailed rattlesnake, *Crotalus molossus molossus*. *Physiological Zoology 66*: 437-454.

Beaupre, S.J., and Duvall, D. (1998). Variation in oxygen consumption of the western diamondback rattlesnake, *Crotalus atrox*: implications for sexual size dimorphism. *Journal of Comparative Physiology, Part B 168*: 497-506.

Bekoff, M. (1977). Quantitative studies of three areas of classical ethology: social dominance, behavioral taxonomy, and behavioral variability. Pp. 1-46 in Hazlett, B.A. (ed.), Quantitative Methods in the Study of Animal Behavior. New York: Academic Press.

Branson, S., Van Horn, G., Belongie, S., and Perona, P. (2014). Bird Species Categorization Using Pose Normalized Deep Convolutional Nets. British Machine Vision Conference (BMVC).

Brodie III, E.D., and Brodie Jr., E.D. (1999). Costs of exploiting poisonous prey: evolutionary trade-offs in a predator-prey arms race. *Evolution 53*: 626-631.

Brown, W.S. (1991). Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. *Herpetologica 47*: 101- 115.

Burghart, G.M. (1985). Foundations of Comparative Ethology. Van Nostrand Reinhold, New York.

Burghart, G.M. (1993). The comparative imperative: genetics and ontogeny of chemoreceptive prey responses in natricine snakes. *Brain, Behavior, and Evolution 41*: 138-146.

Burghart, G.M., and Gittleman, J.J. (1990). Comparative behavior and phylogenetic analyses: new wine, old bottles. In: Interpretation and explanation in the study of animal behavior. Eds. Beckoff, M., and Jamieson, D. pp. 192- 225. Boulder, Colorado. Westview Press.

Chan-Ard, T., Grismer, L., and Stuart, B. (2012). *Cryptelytrops kanburiensis*. The IUCN Red List of Threatened Species 2012.

Chippaux, J.P. (1998). Snake-bites: Appraisal of the global situation. *Bulletin of the World Health Organization* 76(5): 515-524.

Clark, R.W. (2006). Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* 2: 181-187.

Clark, R.W., Dorr, S.W., Whitford, M.D., Freymiller, G.A., and Putman, B.J. (2016). Activity cycles and foraging behaviors of free- ranging sidewinder rattlesnakes (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. *Zoology 2016*: 1-11.

Cox, M.J., Hoover, M., Chanhome, L., and Thirakhupt, K. (2012). The Snakes of Thailand. Chulalongkorn University Museum of Natural History, Bangkok, Thailand.

Crane, M.S., Strine, C.T., Knierim, T.K., Artchawakom, T., and Suwanwaree, P. (2018). Herpetofaunal species abundance, richness, and diversity in a dry tropical forest and agricultural matrix at the Sakaerat Biosphere Reserve, Thailand. *Herpetological Conservation and Biology* 13(3): 586-597.

Cundall, D., and Greene, H.W. (2000). Feeding in snakes. Pp. 293-333 in Feeding: Form, Function, and Evolution in Tetrapod Vertebrates (Schwenk, K., ed.). Academic Press, USA.

Cutler, Tricia L., and Swann, D.E. (1999). Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27: 571-581.

David, P., Vogel, G., and Dubois, A. (2011). On the need to follow rigorously the Rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: The case of the nominal genus *Trimeresurus* Lacipede, 1804 (Reptilia: Squamata: Viperidae). *Zootaxa* 2992: 1-51.

DeSantis, D.L., Mata-Silva, V., Johnson, J.D., and Wagler, A.E. (2020). Integrative Framework for Long-Term Activity Monitoring of Small and Secretive Animals: Validation with a Cryptic Pitviper. *Frontiers in Ecology and Evolution* 8:169.

Department of National Parks, Wildlife and Plant Conservation, Thailand. (2018). Statistical Data National Parks, Wildlife and Plant 2018. Information and Communication Technology Center.

Dorcas, E.M., and Willson, J.D. (2009). Innovative methods for studies of snake ecology and conservation. Pages 5-37 in Mullin, J.S., and Siegel, A.R., editors. Snakes ecology and conservation. Cornell University Press, New York.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6: 680-687.

Durso, A.M., Moorthy, G.K., Mohanty, S.P., Bolon, I., Salathé, M., and Ruiz de Castañeda, R. (2021). Supervised Learning Computer Vision Benchmark for Snake Species Identification From Photographs: Implications for Herpetology and Global Health. *Frontiers in Artificial Intelligence* 4: 582110.

Duvall, D., Arnold, S.J., and Schuett, G.W. (1993). Pit- viper mating systems: ecological potential, sexual selection, and microevolution. In Campbell, J.A., and Brodie, E.D. (eds.), Biology of the Pitvipers, pp. 321- 326. Selva Press. Tyler, Texas.

Glaudas, X., Kearney, T.C., and Alexander, G.J. (2017). Museum specimens bias measures of snake diet: a case study using the ambush- foraging puff adder (*Bitis arietans*). *Herpetologica 73*: 0-9.

Greene, H.W. (1992). The ecological and behavioural context for pitviper evolution. In: Campbell, J.A., Brodie Jr., E.D. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas, pp. 107-117.

Greene, H.W. (1997). Snakes: the evolution of mystery in nature. Berkeley: University of California Press.

Guo, P., Liu, Q., Li, C., Chen, X., Jiang, K., Wang, Y.Z., and Malhotra, A. (2011). Molecular phylogeography of Jerdon's pitviper (*Protobothrops jerdonii*): importance of the uplift of the Tibetan plateau. *Journal of Biogeography 38*: 2326-2336.

Guo, P., Liu, Q., Zhu, F., Zhong, G.H., Chen, X., Myers, E.A., Che, J., Zhang, L., Ziegler, T., Nguyen, T.Q., and Burbrink, F.T. (2016). Complex longitudinal diversification across South China and Vietnam in Stejneger's pit viper, *Viridovipera stejnegeri* (Schmidt, 1925) (Reptilia: Serpentes: Viperidae). *Molecular Ecolology 25*: 2920-2936.

Hamilton, I.M. (2010). Foraging theory. In: Westneat, D.F., and Fox, C.W. (eds.), Evolutionary Behavioral Ecology. Oxford University Press, UK, pp. 177-206.

Hill, J.G., Chanhome, L., Artchawakom, T., Thirakhupt, K., and Voris, H.K. (2006). Nest attendance by a female Malayan pit viper (*Calloselasma rhodostoma*) in northeast Thailand. *Natural History Journal of Chulalongkorn University 6*(2): 57-66.

IUCN and UNEP-WCMC. (2015). The World Database on Protected Areas (WDPA). Accessed September 2015. UNEP- WCMC, Cambridge, UK (Available at: www.protectedplanet.net).

Jomnonkwao, S., Sangphong, O., Khampirat, B., Siridhara, S., and Ratanavaraha, V. (2016). Public transport promotion policy on campus: evidence from Suranaree University in Thailand. *Public Transportation 8*(2): 185-203.

Kasturiratne, A., Wickremasinghe, A.R., de Silva, N., Gunawardena, N.K., Pathmeswaran, A., Premaratna, R., Savioli, L., Lalloo, D.G., and de Silva, H.J. (2008). The global burden of snakebite: A literature analysis and modelling based on regional estimates of envenoming and deaths. *PLoS Medicine 5*(11): 1591-1604.

Khamcha, D., Corlett, R.T., Powell, L.A., Savini, T., Lynam, A.J., and Gale, G.A. (2018). Road induced edge effects on a forest bird community in tropical Asia. *Avian Research 9*(1).

Kuntintara, K., and Kamsuk, M. (1997). Wildlife diversity at Mae Klong Watershed Research Station, Kanchanaburi Province. *Thai Journal of Forestry 16*: 57-81.

LaRue, M.A., Stapleton, S., and Anderson, M. (2016). Feasibility of using high-resolution satellite imagery to assess vertebrate wildlife populations. *Conservation Biology 31*: 213-220.

Malhotra, A., and Thorpe, R.S. (2004). A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pit vipers *Trimeresurus* and *Ovophis*. *Molecular Phylogenetics and Evolution 32*: 83-100.

Maritz, B., Penner, J., Martins, M., Crnobrnja-Isailović, J., Spear, S., Alencar, L.R.V., Sigala-Rodriguez, J., Messenger, K., Clark, R.W., Soorae, P., Luiselli, L., Jenkins, C., and Greene, H.W. (2016). Identifying global priorities for the conservation of vipers. *Biological Conservation 204*: 94-102.

Mayr, E. (1963). Animal Species and Evolution. Harvard University Press. Cambridge, Massachusetts, USA.

McCallum, M.L., and McCallum, J.L. (2006). Publication trends of natural history and field studies in herpetology*. Herpetological Conservation and Biology 1*(1): 63-68.

Naithani, A., Suwanwaree, P., and Nadolski, B. (2018). Bird community structure of Suranaree University of Technology Campus, Nakhon Ratchasima Province, Thailand. *Pakistan Journal of Zoology 50*(4): 1257-1265.

Orlov, N., Ananjeva, N., and Khalikov, R. (2002). Natural history of pitvipers in Eastern and Southeastern Asia. In: Schuett, G., Hoggren, W.M., Douglas, M.E., and Green, H.W. 83 (eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah. pp. 345-361.

Panusittikorn, P., and Prato, T. (2001). Conservation of protected areas in Thailand: the case of Khao Yai National Park**.** *Protected Areas East Asia 18*(2): 67-76.

Parkhurst, J.A. (2009). Managing wildlife damage: Snakes. *Virginia Cooperative Extension*: 420-021.

Pebesma, E. (2018). sf: Simple Features for R. URL https://CRAN.R-project.org/package=sf. R package version 0.6-1.

Petersen, W.J., Savini, T., Steinmetz, R., and Ngoprasert, D. (2018). Periodic resource scarcity and potential for interspecific competition influences distribution of small carnivores in a seasonally dry tropical forest fragment. *Mammalian Biology 95*: 112- 122.

Pinmongkholgul, S. (2008). Population dynamics and health status of small mammals at Sakaerat Environmental Research Station, Nakhon Ratchasima. Doctoral Dissertation, Suranaree University of Technology, Thailand.

Putman, B.J., Barbour, M.A., and Clark, R.W. (2016). The foraging behavior of free-ranging rattlesnakes (*Crotalus oreganus*) in California ground squirrel (*Otospermophilus beecheyi*) colonies. *Herpetologica 72*: 55-63.

Registration Office Department of the Interior, Ministry of the Interior. (2019). "รายงานสถิติจำนวนประชากรและบ้านประจำปี พ.ศ.2562. "Statistics, population and house statistics for the year 2019. Retrieved 10 March 2020.

Reinert, H.K. (1984). Habitat variation within sympatric snake populations. *Ecology 65*: 1673-1682.

Reinert, H.K., MacGregor, G.A. Esch, M., Bushar, L.M., and Zappalorti, R.T. (2011). Foraging ecology of Timber Rattlesnakes, *Crotalus horridus*. *Copeia 2011*: 430-442.

Sharp, A., and Nakagoshi, N. (1997). National parks and protected area in Thailand. *Journal of International Development Cooperation 3*: 53-67.

Singh, M., Griaud, C.C., and Collins, M. (2021). An evaluation of the effectiveness of protected areas in Thailand. *Ecological Indicators 125*(2021): 107536.

Smith, M.A. (1973). The British Reptiles and Amphibians. London (Collins).

Strine, C. (2015). The ecological study of green pit vipers in Sakaerat Environmental Research Station, Nakhon Ratchasima. Doctoral Thesis, Suranaree University of Technology, Thailand.

Strine, C., Silva, I., Barnes, C.H., Marshall, B.M., Artchawakom, T., Hill III, J., and Suwanwaree, P. (2018). Spatial ecology of a small arboreal ambush predator, *Trimeresurus macrops* Kramer, 1977, in Northeast Thailand. *Amphibia-Reptilia 39*(2018): 335-345.

Suraweera, W., Warrell, D., Whitaker, R., Menon, G.R., Rodrigues, R., Fu, S.H., Begum, R., Sati, P., Piyasena, K., Bhatia, M., Brown, P., and Jha, P. (2020). Trends in snakebite mortality in India from 2000 to 2019 in a nationally representative mortality study. *eLife 9*: 1-37.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie 20*: 410-433.

Trisurat, Y., and Duemgkae, P. (2011). Consequences of land use change on bird distribution at Sakaerat Environmental Research Station. *Journal of Ecology and Field Biology 34*: 203-214.

Tu, M.C., Wang, H.Y., and Tsai, M.P. (2000). Phylogeny, taxonomy, and biogeography of the oriental pitvipers of the genus *Trimeresurus* (Reptilia: Viperidae: Crotalinae): a molecular perspective. *Zoological Science 17*: 1147-1157.

WCS - Wildlife Conservation Society, and CIESIN - Center for International Earth Science Information Network - Columbia University. (2005). Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). NASA 88 Socioeconomic Data and Applications Center (SEDAC), Palisades, NY (http://dx.doi.org/10.7927/H4BP00QC. Accessed: July 2015).

Weinstein, B.G. (2017). A computer vision for animal ecology. *Journal of Animal Ecology 87*: 533-545.

World Health Organization. (2016). Guidelines for the management of snakebites. New Delhi, India: Regional Office for South-East Asia, WHO.

Wuster, W., Salomao, M.G., Quijada-Mascarenas, J.A., Thorpe, R.S., and BBBSP. (2002). Origin and evolution of the South American pitviper fauna: evidence from mitochondrial DNA sequence analysis. In: Schuett, G.M., Hoggren, M., Douglas M.D., Greene, H.W. (Eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Utah, pp. 111- 128.

Zhu, F., Liu, Q., Che, J., Zhang, L., Chen, X., Murphy, R.W., Yan, F., Guo, C., and Guo, P. (2016). Molecular phylogeography of white-lipped tree viper (*Trimeresurus*; Viperidae). *Zoologica Scripta 45*: 252-262.

CHAPTER III

GREEN PIT VIPER BEHAVIOR AND ACTIVITY PATTERNS

3.1 Abstract

Comprehensive organismal behavioral study has the potential to address conservation issues. Between August 2020 and July 2021 continuous feed cameras were set to monitor green pit viper behavior states and events at Sakaerat Biosphere Reserve and Suranaree University of Technology, while also investigating and estimating general (species, age, and sex), microhabitat (canopy cover, perch height, leaf quality and damage, and leaf area), macrohabitat (elevation, canopy height, NDVI, leaf area index, and distance to water and anthropogenic features), and abiotic (temperature, specific humidity, surface pressure, precipitation, cloud cover, wind speed, natural noise, and human noise). All field methods were non- invasive- no handling or capture of vipers was done nor was there direct disturbance to them and their habitats. Variable effects to viper behavior states and events was evaluated using Bayesian GLMM's, and activity pattern of vipers was determined using temporal circular statistics. Vipers were observed to be primarily nocturnal with respect to expression of behavior states (active- ambush and move) and events (all); expression of behavior states was similar between sexes and age classes, but behavior event expression differed by sex and age. Species, leaf quality and damage, distance to buildings, leaf area index, and noise (both anthropogenic and natural) were the best predictors for behavior states and species, sex, leaf quality and damage, distance to roads, leaf area index, and anthropogenic noise were the best predictors for behavior events. Nocturnal behavior supported similar findings by previous studies of green pit viper ecology. Anthropogenic disturbance variables being the best predictors in models poses concern for conservation and snakebite management. This was the first study to comprehensivelyevaluate green pit viper activity patterns and behavior, conservation and snakebite management for the group would benefit from further similar study.

3.2 Introduction

While natural history study dates back to as early as the 18th century, comprehensive study of animal behavior is much more recent with the field of ethology, the biological study of behavior. Validation of the field and recognition of the importance of findings was finally recognized in 1973 with the Nobel Prize for Medicine and Physiology awarded Konrad Lorenz, Niko Tinbergen and Karl von Frisch. Study of organisms in the wild can provide valuable insight into their daily behavior and activity patterns, and can begin to address central themes in behavioral research like constraints (Schoener, 1971) and adaptive significance (Thornhill, 1991) of behaviors. Behavior study of squamates, particularly snakes, is lacking however (Ford, 1995; Doody et al., 2011; Schuett et al., 2017; Burghart, 2020).

Intensive and comprehensive behavior and ethology study has the potential to address conservation issues (Caro, 2007; Caro and Sherman, 2013). Snakes play an important ecological role in many ecosystems, both as predators and prey for many other species (Luiselli, 2006), yet basic behavior and activity pattern knowledge for most species is lacking. Venomous snakebite is a critical global conservation topic (Warrell, 2010). Tropical regions where snake diversity is high and access to appropriate medical care are particularly hard- hit by this issue, and the World Health Organization recently declared snakebite to be a neglected tropical disease. Despite the importance of this issue, with millions of people estimated to be maimed and killed every year worldwide, research on the causes and potential mitigation measures (and their effectiveness) remains limited (Hodges et al., 2021).

Green pit vipers (snakes of the genus *Trimeresurus*) inflict the highest numbers of snakebite of any group of venomous snakes where they occur (Warrell, 2010), yet remain some of the least studied organisms in the wild. eloping countries, particularly in the tropics (Warrell, 2010). White- lipped (*T. albolabris*) and big-eyed (*T. macrops*) green pit vipers have been suggested to account for 40% of total venomous snake bites throughout Thailand (Viravan et al., 1992) and 95 % for the large metropolitan city, Bangkok (Meemano et al., 1987; Mahasandana and Jintakune, 1990). Study of the group within Thailand has previously primarily focused on the specific topics of taxonomy and nomenclature (i.e.- Malhotra et al., 2004; David et al., 2011), venomics (i.e.- Kumkate et al., 2020), and spatial ecology (i.e.- Strine et al., 2018). No comprehensive population studies have been conducted, although at least one Thai species, the Kanchanaburi pit viper (*Trimeresurus kanburiensis*) has been listed by the IUCN as Endangered (Chan-Ard et al., 2021). Observation of extremely small home ranges (< 0.5 km^2 typically) and very limited movement (< 15 moves > 5m within 3 months) by prior green pit viper spatial ecology studies presented novel avenues of investigation for behavioral study. Although not the primary focus, interesting observations of interactions (prey, predators, humans, and conspecifics) and foraging and resting activity patterns and were made during those studies. With high diversity (> 40 species, Uetz and Hallerman, 2015), significant medical concern to humans, and limited prior knowledge about the conservation status of species there is substantial justification for study of green pit vipers in the wild.

This chapter attempted to directly address six of the broader dissertation study objectives- 1) determine and compare behavior states (behavior displayed in relatively long durations) and events (spontaneous behavior) and corresponding activity patterns (when are vipers most active or inactive) of multiple green pit viper species, 2) assess behavior and activity pattern differences between different ages and sexes of vipers, 3) assess how habitat and abiotic traits influence behavior and activity of green pit vipers and co- occurring species, 4) assess threats to vipers from humans, and from vipers to humans, 5) compare sympatric green pit viper and other viper species behavior and activity periods, and objective 6) compare behavioral differences between isolated populations (subpopulations) within species, and objective mentioned in Chapter I.

3.3 Methods

3.3.1 Study sites

Two study areas in Nakhon Ratchasima province, Thailand were concurrently utilized for behavior and activity pattern research (Figure 3.1). Information about Thai protected areas is provided in Panusittikorn and Prato (2001), Sharp and Nakagoshi (1997), and Singh et al. (2021), and Suranaree University of Technology in Naithani et al. (2018). Straight- line distance (obtained through “st_distance” function in R, “sf” package, Pebesma, 2018) between study sites is approximately 50 km.

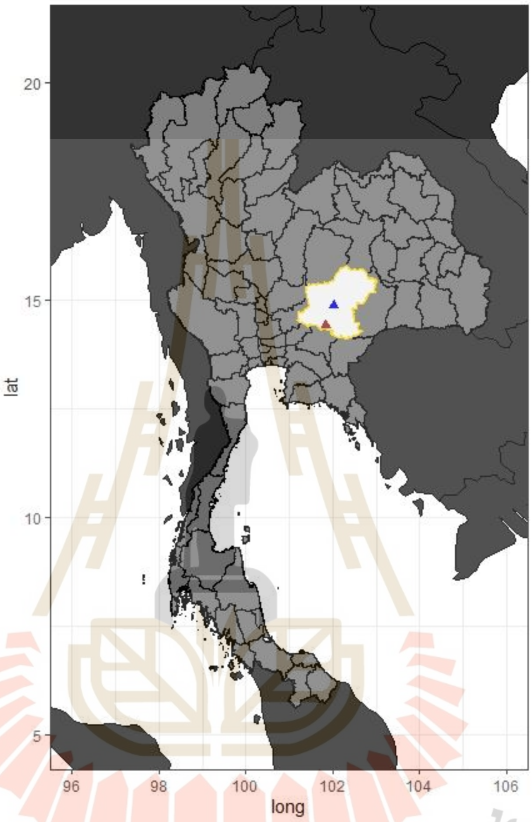

Figure 3.1 Green pit viper behavior and activity pattern study areas Sakaerat Biosphere Reserve (indicated by a red triangle) and Suranaree University of Technology (blue triangle) within Thailand which is shaded in light gray. Within Thailand, provinces are partitioned in black, with Nakhon Ratchasima outlined in yellow.

The Suranaree University of Technology (SUT) campus is 11.2 km^2 in size (about 10000 students) and comprised primarily of degraded forest but also has a botanical garden, small parks, some natural patches of forest, plantation, and institutional and departmental buildings (Jomnonkwao et al., 2016; Naithani et al., 2018). The university is located approximately 20 kilometers from the city of Nakhon Ratchasima (approximately 126,391 residents; Registration Office Department of the

Interior, Ministry of the Interior, 2019), although the immediate area surrounding SUT is primarily agricultural which is characteristic of the province.

Sakaerat Biosphere Reserve (SBR) is split into three management areas: approximately 80 km^2 of SBR is designated as a core area and set aside to preserve and maintain species diversity, genetic variation, and landscapes and ecosystems is characterized by primary and secondary forest types; buffer and transition areas surround the core area and consist primarily of agricultural areas and settlements (altogether comprising approximately 360 km^2).

The global pandemic “severe acute respiratory syndrome coronavirus 2” (shortened to SARS-CoV-2 and COVID- 19) was a significant public safety concern throughout the duration of this dissertation and impacted daily life of all humans. Measures in Thailand specifically to combat this threat were drastic (i.e.- stay- at home-orders and proof of testing for the virus before traveling to populated areas or outside of provinces), as vaccines were not widely available even by the end of this dissertation. Thus, results from this study must be considered both from logistical and direct human impact on wildlife behavior perspectives.

The graduate student leading this project (C. H. Barnes) did reside in the same province as the study sites, which meant that travel was not impacted by province- level quarantines. Full lockdowns and stay- at- home orders did prevent travel. Grant and university budgets did provide funds for virus testing which was required for visiting the study sites at several periods, which also affected data collection. How the sudden drastic shift of human behavior in response to the pandemic has impacted wildlife has been speculated, but not comprehensively, studied. No green pit viper behavioral studies were conducted at SUT before the pandemic, and the technology and methods (which directly impacts inferences) from prior study at SBR were different to this dissertation. Effort was made to identify the bias and impacts the pandemic may have had on the activity patterns in this dissertation through investigation of the number of people present before and during the pandemic and inclusion of anthropogenic variables in statistical models.

3.3.2 Survey methods

Vipers were found for behavioral study via visual encounter and opportunistic encounters. Visual encounter surveys were defined as looking for vipers while walking with no area, distance, or time constraint. Notification of vipers by people not directly associated with the study was defined as opportunistic encounters. Opportunistic encounters did not form a significant source of behavioral observations, as this method is not directly able to quantify population size and estimating sampling effort by future studies.

Research and ethics permissions (SUT #A-8/2562, NRCT #2019/065, and DNP #16177; with Thai IACUC Institute of Animals for Scientific Purpose Development (IAD) licensure initially under Dr. Colin Strine until C. H. Barnes was approved in October 2020) for this study did not allow for direct and intentional disturbance to vipers or their habitats. Non-invasive (no capture or handling) methods using photography to individually identify individuals (upper labial scale lepidosis, I3S program) and estimate overall body length of vipers (ImageJ) appeared successful for those objectives, but ultimately were too stressful for vipers at SUT and to a lesser extent, SBR. Stress from these methods was indicated by movement, infrequently displayed by ambushing and resting vipers.

All data collection in the field (including surveys and encounters) was conducted during 4-night sampling periods each month at each site, separately. Viper species, sex (male or female), and age (neonate/juvenile or adult) was visually determined (no capture or handling) in the field using prior knowledge from Cox et al. (2012) when individuals were first encountered. These variables (sex, species, and age) formed the “general” statistical models of this dissertation section.

3.3.3 Camera methods

Fixed cameras were set approximately 0.5- 3 meters from vipers, depending on vegetation and perch height following Barnes (2017) methodology (Figure 9). However, security cameras (based from Pierce and Pobprasert, 2007) rather than Brinno and Bushnell cameras were utilized for more in- depth behavioral and intraspecific and interspecific study (Figures 3.2 and 3.3). While significant novel observations of green pit vipers were previously made at the Sakaerat Biosphere Reserve in Thailand using Brinno and Bushnell cameras (Barnes, 2017), behavior events (see Camera review methodology section for definition) of short duration could very easily have been missed as cameras were standardized to record pictures only once per minute. Security cameras (Hikvision model DS-2CE16C0T-IRF) in this new study recorded at 29 frames per second of color video and had infrared night recording capability. One viper was the primary subject of each camera focus (although more than one could arrive during the recording duration), thus, this chapter primarily followed a focal animal sampling scheme (Lehner, 1987; Martin and Bateson, 2007).

Figure 3.2 The Ph.D. student associated with the study (C.H. Barnes) using continuous feed security camera equipment for the green pit viper behavior and activity pattern dissertation at Suranaree University of Technology in Thailand.

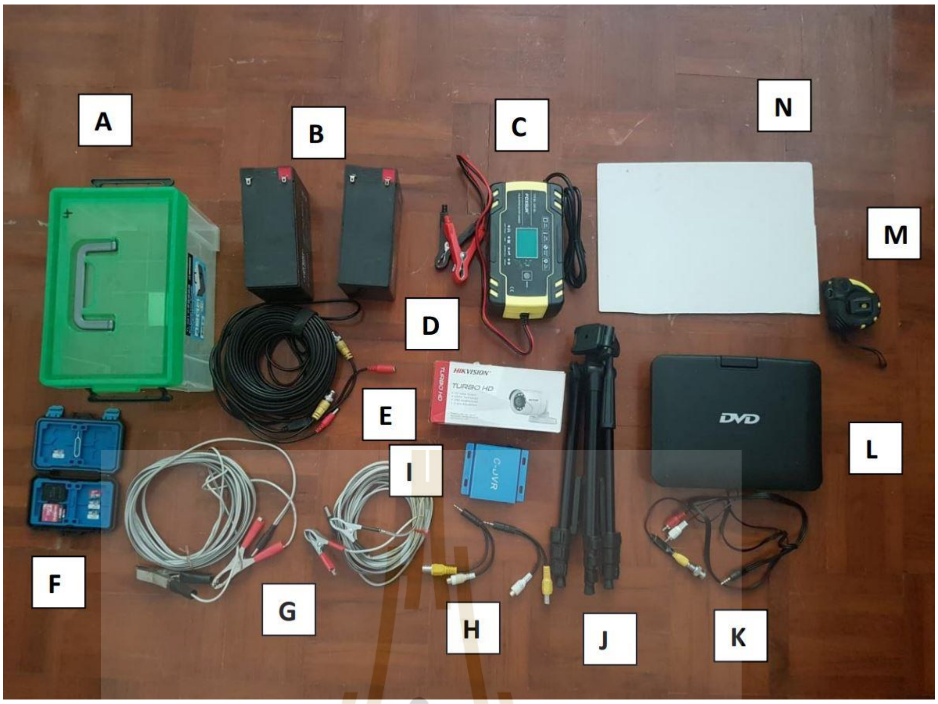

Figure 3.3 Green pit viper activity pattern and behavior field kit including protective plastic box (A), 12v 7.5 ah (motorcycle) batteries for camera and mini DVR (B), portable charger for 12v batteries (C), security camera (Hikvision, 30 frames per second) (D), 10m power and video cable to run from camera and tripod to battery and field setup components within protective box (E), mini SD cards and protective case (F), battery hookup cables for camera and DVR (G), input and output cables for mini DVR (H), mini DVR (I), camera tripod (J), DVD input cables (K), DVD player for viewing footage in the field and setting cameras (L). Microhabitat field gear included was a tape measure for recording viper perch height (M) and a blank white board of known size for leaf quality and damage (using the phone app BioLeaf) and leaf area (using program R) (N).

While it is generally agreed that cameras set to monitor wildlife present significantly less direct disturbance than other methods (such as direct observation by researchers and capture of organisms), the cameras themselves are likely not completely without influence to wildlife through mechanical disturbance (light and sound, which may or may not be perceived and to different degrees), human scent of researchers setting those cameras, and the novel presence of the camera itself in the environment (summarized in Caravaggi et al., 2020). This topic has not been addressed with snake behavior studies utilizing cameras in wild habitats (likely due to limited sample sizes) and would require an experimental approach with direct disturbance to snakes to adequately cover which would not be allowed under research permissions for this current dissertation. However, to address those concerns cameras were set as far away from the vipers themselves as possible (while still allowing for usable recordings; 1- 3 meters), people setting cameras did not use aerosols (deodorant or perfume or insect repellant) for a minimum of half an hour before setting cameras, and time spent setting cameras near vipers was minimized to less than 15 minutes total for each occasion. Cameras were not reported to make noise or vibrate in factory guidelines and the cameras utilized infrared for illumination in low lighting conditions which has not been reported to be perceived by snakes.

From previous study (Barnes, 2017), arboreal (> 3 m in height) and shelter sites were anticipated to be difficult for camera study, which was supported with preliminary study using the security cameras. Camera attachment to tripods and trees for arboreal study can be challenging, as can making sure study individuals are in focus and frame of the camera properly for later review, so arboreal vipers were not included in the study. Sheltering vipers were also not studied, as previous work (Barnes, 2017) revealed they may both forage and rest in these often obscure and difficult to video-record sites. Both arboreal and shelter sites present increased risk of disturbance to viper behavior and their habitats which is not allowed for research and ethics permissions of this dissertation and would directly influence findings.

Understanding where shelter and inactive period sites are located can be important for understanding activity patterns (emergence and retreat times, changes from ambush to resting behavior states), however, and a short period of time (so as not to disturb vipers or their habitat) of about 10 minutes was spent doing a visual search (no habitat disturbance) during mornings following placing cameras at ambush sites (at night) in an attempt to locate these sites. In addition to sheltering and arboreal behaviors, there was also potentially bias against small viper species, males, and juveniles for behavioral events due to their size, which subsequently required placing cameras closer (for clarity) which was often not feasible in dense habitats and sometimes presented ethical concerns. Dense habitats require careful camera placement- vegetation can block views of vipers and cause illumination issues with cameras due to reflection of light.

3.3.4 Ethogram and video review method

This section attempted to follow the guidelines of Lehner (1987) and Martin and Bateson (2007) for behavioral study design. Behavior states and events were analyzed after camera recordings are downloaded from the field. States are behavior patterns of relatively long duration, while events are comparatively discrete behaviors which occur during a short time span (Lehner, 1987; Martin and Bateson, 2007). These behavior states and events formed the ethogram of this section, which is simply a set of terms and descriptions of the behaviors of an animal (Lehner, 1987). Data from cameras were downloaded immediately after returning to the field, from SD cards (in DVR's) to two external hard drives (2 TB each) and backed up online (Microsoft OneDrive). Videos recorded on DVR's were stored in 333 MB files for recording times of five minutes, at a rate of approximately 10 GB per 5 hours of recording time, so it was not feasible to store all recordings indefinitely.

Video recordings were manually reviewed by in the Behavioral Observation Research Interactive Software (BORIS) program (Friard and Gamba, 2016). This is a free, open-source and multiplatform standalone program that allows a user-specific coding environment to be set for a computer-based review of previously recorded videos or live observations, which allows a project-based ethogram to be defined that can then be shared with collaborators, or can be imported or modified. Only videos which were of sufficient length and quality were used for analyses. Whether or not behavior in a video would likely be able to identified using computer vision and could be clearly and consistently classified as the same behavior by a naïve observer were the criteria for quality. One hour was the minimum for a recording to be included in the study to adequately investigate activity pattern analysis and which would not suggest negative influence of the camera or the process of setting it to obtain the recording.

Behavior states (visualized in Figure 3.4) documented in this dissertation were similar to Barnes (2017). Ambush was defined as foraging behavior characterized by the neck and head of the focal animal extended outwards from the body towards a habitat feature. Move defined movement between sites. Move and ambush states were previously observed to be exhibited primarily during the night and crepuscular hours (Barnes, 2017; Barnes and Knierim, 2019). Resting was defined as the state when the head of the focal animal is settled on the body and was previously usually observed during the day (Barnes, 2017; Barnes and Knierim, 2019).

Figure 3.4 Green pit viper behavior states investigated during this study: ambush (A; male *Trimeresurus vogeli*), move (B; female *Trimeresurus albolabris*), and resting (C; female *T. vogeli*). All photographs were taken during prior fieldwork by C.H. Barnes.

Events previously recorded on camera at the Sakaerat Biosphere Reserve (Barnes, 2017) which are studied further in this study include gape and probe. A gape was defined as when the mouth was opened greater than 45 degrees. Probe was defined as a chemosensory event of longer duration than a strike, and was focused towards a habitat feature. Headbob behavior was observed during preliminary study of this chapter (but not by Barnes, 2017 due to use of timelapse cameras) and investigated further due to potential chemsensory or communicative function- this behavior was defined as rapid vertical movement of the head while foraging or resting.

Sample videos of behavior states and events for this dissertation chapter are publicly available via Youtube (https://www.youtube.com/channel/UCdRlzXz9YbUR2eWyEAEGU4g), specified further in Tables 3.1 and 3.2. All short natural history observations and comprehensive works published will cite these media for transparency and clarity.

Table 3.1 Reference website locations for examples of behavior states.

Behavior state	Youtube location
Ambush	https://www.youtube.com/watch?v=U91Ug5XlERs&list=PLe5w_iOLJRVRm24Znv7UUV-64kIySkkhG&index=3
Move	https://www.youtube.com/watch?v=4EtIXouKLjU&list=PLe5w_iOLJRVRm24Znv7UUV-64kIySkkhG&index=4
Resting	https://youtu.be/Z7xG28lSO8I

Table 3.2 Reference website locations for examples of behavior events.

Behavior event	Youtube location
Gape	https://youtu.be/kDayvCYxxok
Headbob	https://youtu.be/aIvezWcL7fk
Probe	https://www.youtube.com/watch?v=PIJ1tLyloaQ&list=PLe5w_iOLJRVRm24Znv7UUV-64kIySkkhG&index=3

3.3.5 Habitat and abiotic variables for behavior analysis

Habitat was collected both in the field, and later in the lab. Data collected in the field (non- invasively, using several smartphone applications) was at micro to meso habitat levels, while data compiled later in the lab was at the meso to macro habitat level.

3.3.5.1 Microhabitat

Microhabitat data was primarily obtained in the field using non-invasive (no removal or disturbance of habitat) smartphone applications. The smartphone application CanopyApp (see Landert, 2016 for summary of method and comparison to others; Figure 3.5) was utilized to quickly and non- invasively estimate canopy cover directly over ambush and resting sites. Herbivory and leaf quality (damage) was estimated using the smartphone application BioLeaf (Machado et al., 2016). This method does not require leaf removal from plants, only that a white background (to reduce "noise") be placed underneath (Figure 3.6). Leaves were photographed (one at each height level; using a cell phone for pictures) for BioLeaf at viper level (leaf quality and damage variable; LQD1), ground level directly below viper (LQD2), and 0.5m directly above viper (LQD3) at each individual viper foraging/resting site with a 18 x 26 mm ("A-11" paper size) white posterboard as a background and size reference. These photographs were also used to calculate leaf area (LA1, LA2, LA3 at the same height levels as LQD), using the R package LeafArea (Katabuchi, 2015, example code can be found at ttps://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fhve7y%2Fdownload). Perch height, using a tape measure, was recorded in the field immediately before collecting CanopyApp data. Field habitat data was collected during the day (morning, when camera SD cards were changed) when vipers were sheltering and/or inactive. All these estimations and measurements (canopy cover, perch height, leaf quality and damage, and leaf area) formed "microhabitat" statistical models.

coverage:
43.317%

name: Test

Figure 3. 5 Sample output produced from open- source program (smartphone application) CanopyApp. Output has the option to calculate canopy cover (“ coverage,” from photo taken directly overhead, estimated from points with vegetation in background manually selected) as well as concurrently store site name (“name”), location (GPS coordinates), time and date, and description of site and conditions.

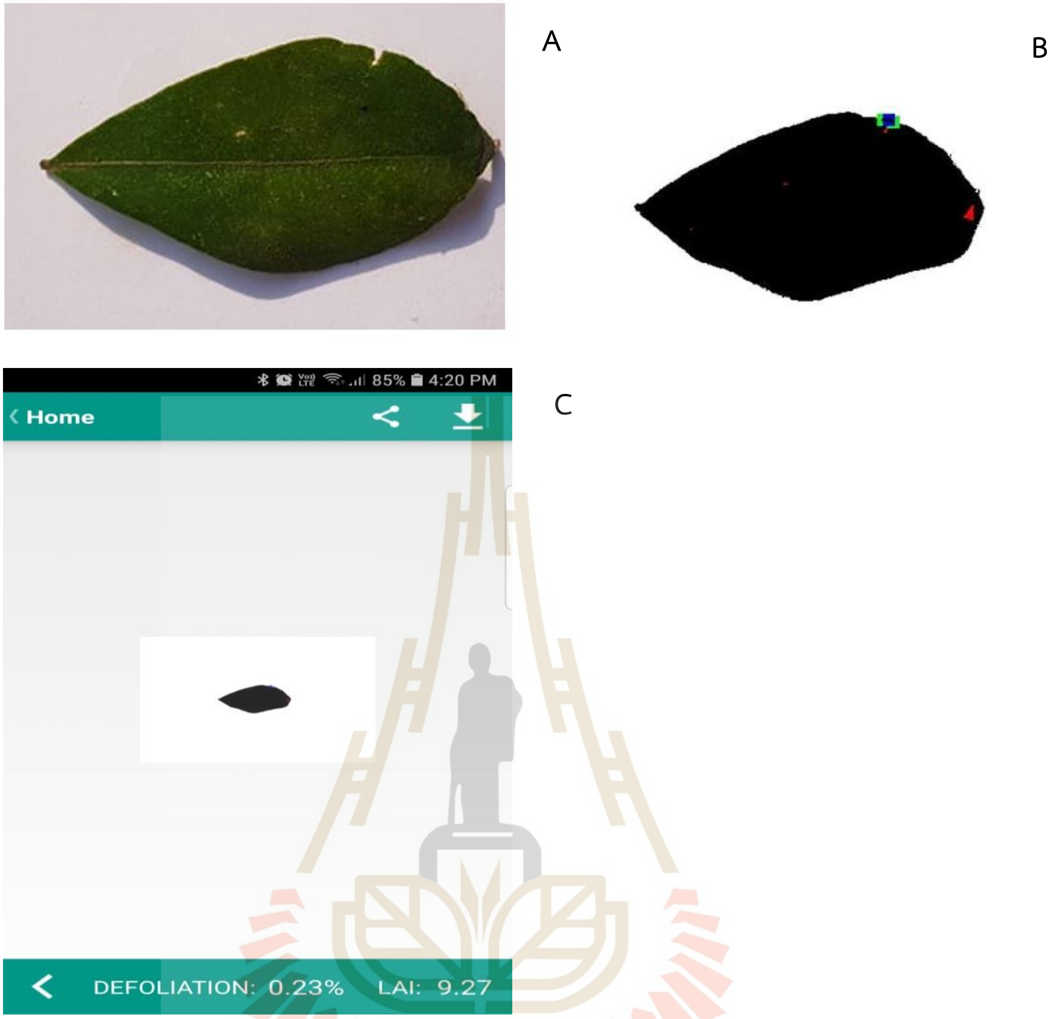

Figure 3.6 Initial sample (A), delineated leaf damage (B), and output (C) produced from open-source program (smartphone application) BioLeaf, suggesting 0.23% damage to leaf.

3.3.5.2 Macrohabitat

Macrohabitat data including normalized difference vegetation index (NDVI; MODIS NDVI V6, eMODIS, 250 m resolution), leaf area index (LAI; MCD15A3H, 500 m resolution), and elevation (SRTM, 30 m resolution) data were retrieved directly from MODIS satellite images, and canopy height models were obtained from Simard et al. (2011; CH; 1 km. resolution). Satellite imagery (obtained from "osm" R package; Padgham et al., 2017) and Euclidean distance (using the "st_distance" function in the "sf" package of R; Pebesma et al., 2018) were used to quantify distance to water bodies and human disturbance (buildings and roads). All these estimations and measurements (elevation, canopy height, NDVI, leaf area index, and distance to water and anthropogenic features) formed "macrohabitat" statistical models for this study.

3.3.5.3 Abiotic

Abiotic data compiled later in the lab was primarily obtained from methods outlined in Kearney et al. (2020) and Maclean et al. (2019). Temperature (degrees Celsius; 2 m above ground level), specific humidity (kg/kg; 2 m above ground level), surface pressure (Pa), precipitation (mm/day), cloud cover (%), and wind speed data (2 m above ground level; m/s) were estimated from satellite imagery obtained from the R packages (primarily "Microclima" and "NicheMapR") outlined in Kearney et al. (2019) and Maclean (2019). The only abiotic data collected in the field was human disturbance and natural noise (decibels), which served as a proxy for interactions and stressors, which may or may not have been observed on cameras. Noise disturbance was recorded non- invasively while microhabitat data was being collected (same time as leaf area, canopy cover, leaf damage/quality, etc., morning) using the smartphone application "Smart Meter." All these estimations and measurements (temperature, specific humidity, surface pressure, precipitation, cloud cover, wind speed, natural noise, and human noise) formed "abiotic" statistical models for this study.

3.3.6 Statistical analyses

Methodology developed by Ridout and Linkie (2009) was used to determine activity patterns of vipers and quantify temporal overlap of with the 'overlap' package (Meredith and Ridout, 2016; example code provided at https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fhy45f%2Fdownload) in program R. A non-parametric circular kernel-density function was employed to comprehensively assess daily activity patterns and then a coefficient of overlap (Δ)

used to measure the extent of overlap between two kernel-density estimates, taking the minimum of the density functions from two sets of samples being compared at each point in time. Overlap was the area under both the density curves, and subsequently the coefficient of overlap ranged from 0 (no overlap) to 1 (complete overlap) (Ridout and Linkie 2009; Linkie and Ridout, 2011). The 95% confidence intervals of each overlap index using smoothed bootstrap with 999 resamples was also calculated (Meredith and Ridout, 2016).

Temporal activity patterns and overlap were evaluated for viper sex and age for active behavior states (ambush and move) collectively and all behavior events (gape, headbob, and probe) separately. Those active behavior states were also evaluated together with inactive (resting and not visible) behavior states to determine how green pit vipers are spending most of their time, comprehensively. These analyses were conducted for all green pit vipers for which there was adequate sample sizes (*T. albolabris* and *T. macrops*) together, as well as separately.

Bayesian generalized linear mixed models (GLMM) were implemented using program R ("brms" package; Bürkner, 2017) to account for repeated observations of individual snakes. Bayesian methodology allows for inclusion of previous knowledge and belief (through "priors"), while providing direct inferential conclusions (probabilities of observing phenomena) which are ecologically meaningful and easy to interpret (crucial for lay- people and managers with limited statistical background; Dixon and Ellison, 1996; Dorazio and Johnson, 2003; Ellison, 1996; Ellison, 2004; Wade, 2000; Wintle et al., 2003). This is a stark contrast to the "frequentist" framework, which may strictly be interpreted only in relation to a sequence of similar inferences that might be made in repeated practice (Gelman et al., 2020). The Bayesian approach is also more robust to small sample sizes, assumptions for the normality of residuals are more relaxed, and estimates are more conservative compared to frequentist methods (Zitzmann et al., 2020) Dependence on the p- value has become widely criticized (frequently leading to statistical fallacies including harking and p- hacking, Fraser et al., 2018; Reckhow, 1990), which simply does not exist within the traditional context of Bayesian frameworks.

Separate Bayesian GLMM's (example code provided at https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fg69hs%2Fdownload) were run with time in ambush (min), time resting (min), time spent moving (min), rate of gapes (per minute), rate of headbobs (per minute), and rate of probes (per minute) as response variables. The "bestNormalize" R package (Peterson and Cavanaugh, 2020) was used to fit these behavior values to a Gaussian distribution. The "brms" package default priors were utilized as no reliable prior information was available for green pit viper behavior. A minimum of 5 chains with 5000 iterations with 1000 iterations of warmup were run for each Bayesian model and model convergence was determined with trace plots and when rhat neared one (Gelman and Rubin, 1992). Additionally, posterior predictive checks were conducted to determine how well the simulated data replicated observed data using the "bayesplot" R package (Gabry and Tristan, 2021).

General (viper sex, age, and species), micro to meso habitat (canopy cover, perch height, leaf quality and damage, and leaf area), and meso to macro habitat (elevation, canopy height, NDVI, leaf area index, and distance to water and anthropogenic features), and abiotic (temperature, specific humidity, surface pressure, precipitation, cloud cover, wind speed, natural noise, and human noise) variables were run as separate models for each behavior state and event, with individual viper ID as a random factor. Teasing apart autocorrelation and interaction of all variables within model types would have been complex and beyond the scope of the exploratory nature of this thesis. Effects of the variables on behaviors were visualized using the "brms" package.

The "loo" R package (Vehtari et al., 2019) was used to produce widely applicable information criterion (WAIC; Gelman et al., 2014; McElreath, 2016) and leave-one- out cross- validation (LOO; Vehtari, Gelman, and Gabry, 2016a, 2016b) within model variable comparisons, which were fully Bayesian, for model assessment. The proportion of variation explained by predictor variables was assessed using the r- square regression metric in the "performance" R package (Lüdecke et al., 2020).

The snake ID random effect factor was used to determine the role individuality and personality plays in viper behavior, how much do individuals vary in their expression of behaviors (see Waters et al., 2017). Within- individual variation of viper behavior expression was not investigated due to the short sampling duration (< 4 days each, likely only one sample session) of each viper, although this should be considered when interpreting results and would be worth studying further in the future.

3.4 Results

The global pandemic COVID-19 directly impacted efforts of this study to determine viper activity patterns and behavior, with multiple periods lockdowns implemented at study sites. Research and ethics permissions required a minimum of at least 2 weeks of notice to local authorities for site visits, which was challenging due to constantly changing pandemic protocols and requirements. Quarantine and testing were required throughout the study duration, which was difficult and costly. Holidays exacerbated these measures, particularly the months of December in 2020 and January, April, and May of 2021. Vaccinations were not readily available in Thailand during the study period, and less than 6% of the population was fully vaccinated by the conclusion of the study (WHO Thailand Situation Update No. 194). Safety of researchers and local communities was prioritized, and subsequent sample sizes were lower than anticipated. No researcher or local contracted COVID- 19 as a result of this study. Following protocols and research permits, no vipers or their habitats were intentionally disturbed during study which also impacted sample size of vipers.

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researchers and local communities was prioritized, and subsequent sample sizes were lower than anticipated. No researcher or local contracted COVID-19 as a result of this study. Following protocols and research permits, no vipers or their habitats were intentionally disturbed during study which also impacted sample size of vipers.

Data was not readily and publicly available for the number of students, staff, and visitors at SUT; classes were primarily hybrid or fully online which made raw student numbers unreliable. Sakaerat Biosphere Reserve staff determined that 18,944 students visited SBR in 2019 (before the pandemic), 10,713 students and 369 visitors came there in 2020, and 7,087 students and 278 visitors went to SBR in 2021 (until July).

Sakaerat Biosphere Reserve and Suranaree University of Technology had a total of 164 surveys conducted at sites within these areas between August 2020 and July 2021-88 surveys at SBR and 76 surveys at SUT (Figure 3.7), for a total of 188.14 hours (371.44 surveyor-hours). A total of 98 green pit vipers (different individuals within-sampling sessions) were encountered during those surveys; 53 vipers at SBR and 45 vipers at SUT (Figure 3.8). Two *T. vogeli* were found on a single survey in September 2020 at SBR, an adult male (moving, so a camera was not able to be set) and an adult female (camera set) but were included later in this dissertation so model comparisons between *T. macrops* (SBR) and *T. albolabris* (SUT) could be made directly and clearly in this current section. No other genera of viper were found during surveys.

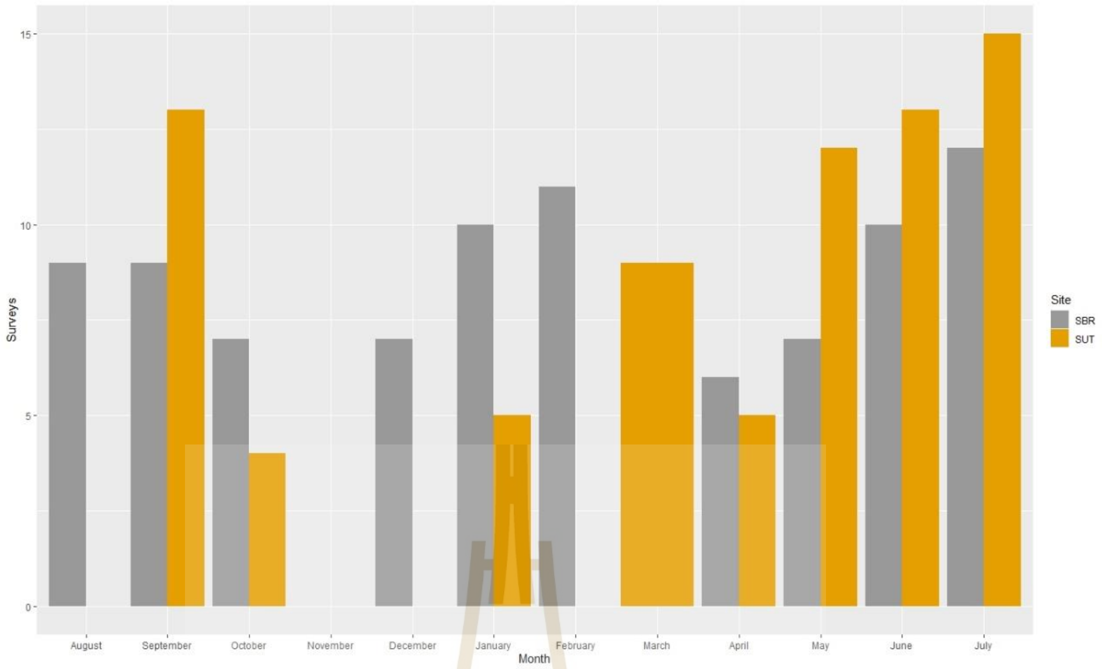

Figure 3.7 Surveys conducted at Sakaerat Biosphere Reserve (grey) and Suranaree University of Technology (orange) by month between August 2020- July 2021.

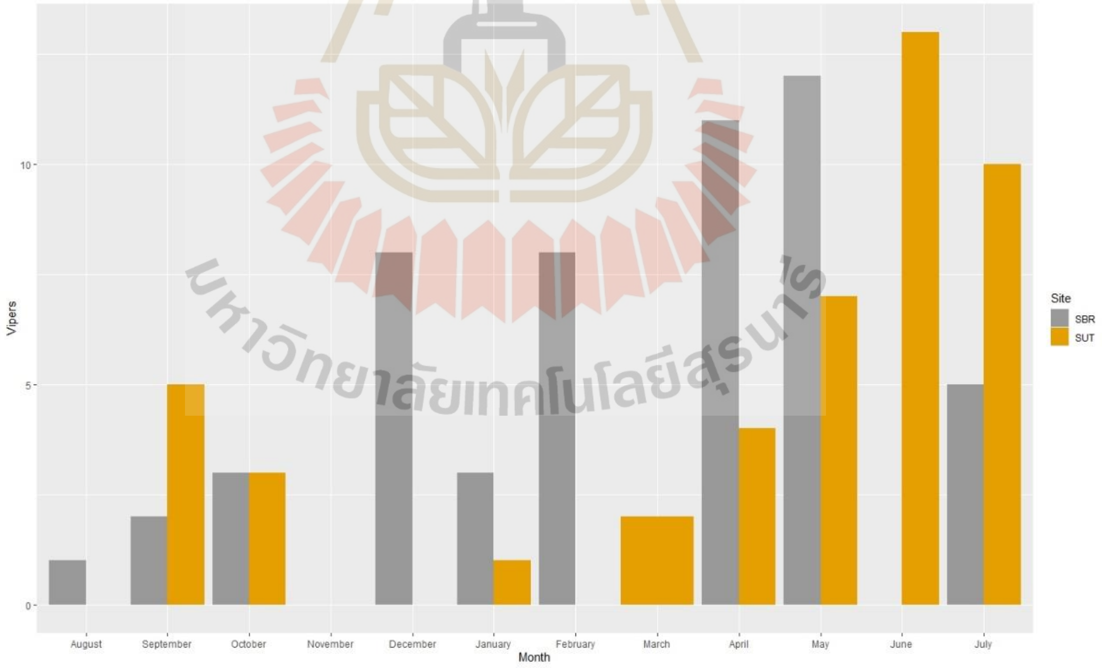

Figure 3.8 Number of vipers found during surveys at Sakaerat Biosphere Reserve (grey) and Suranaree University of Technology (orange) by month between August 2020- July 2021.

Cameras were set to monitor behavior of 72 vipers- 37 at Sakaerat Biosphere Reserve (4 and 26 adult males and females, respectively; 7 non- adult females) and 35 at Suranaree University of Technology (6 and 17 adult males and females, respectively, and 4 adults which were not readily able to be sexed; 3 and 3 non- adult males and females, respectively, and 2 non- adults which were not readily able to be sexed). Of these, 28 vipers, 19 at Sakaerat Biosphere Reserve (2 and 15 adult males and females, respectively; 2 non- adult females) and 9 at Suranaree University of Technology (2 and 4 adult males and females, respectively and 2 adults which were not readily able to be sexed; 1 non- adult female) for a total of 18,610 minutes of recordings (13,963 minutes at SBR; 4,647 minutes at SUT) which were usable for this study within the activity pattern and behavior analyses.

Collectively, green pit vipers were primarily active at night (from between 18:00-06:00) and resting or not visible during the day (from 06:00- 18:00, Figure 3.9A). Females and males both displayed similar foraging activity patterns (Figure 3.9B). Activity pattern overlap was similarly high between foraging adults and non- adults (Figure 3.9C).

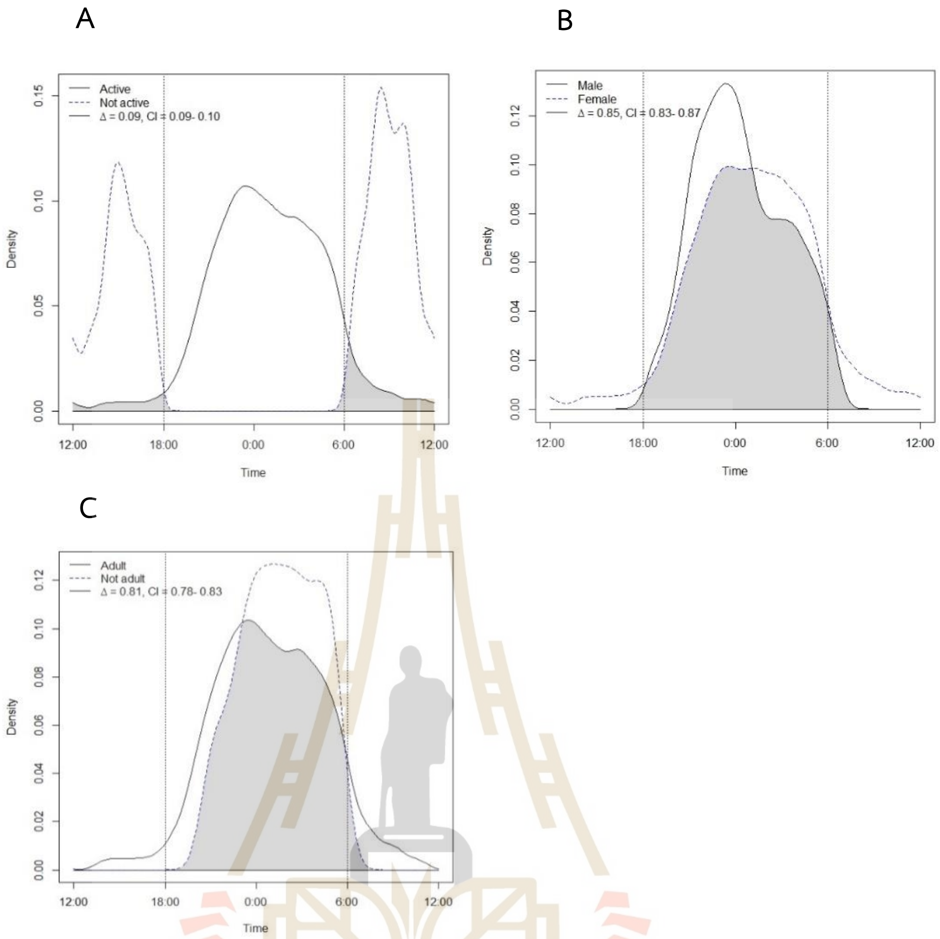

Figure 3.9 Behavior state temporal patterns of *Trimeresurus macrops* at Sakaerat Biosphere Reserve and *T. albolabris* at Suranaree University of Technology by behavior type (A), and foraging viper sex (B), and age (C).

Collectively, green pit vipers were primarily active at night (from between 18:00-06:00) and resting or not visible during the day (from 06:00- 18:00, Figure 3.10A). Females and males both displayed similar foraging activity patterns (Figure 3.10B). Foraging activity pattern overlap was similarly high between adult and non- adults (Figure 3.10C).

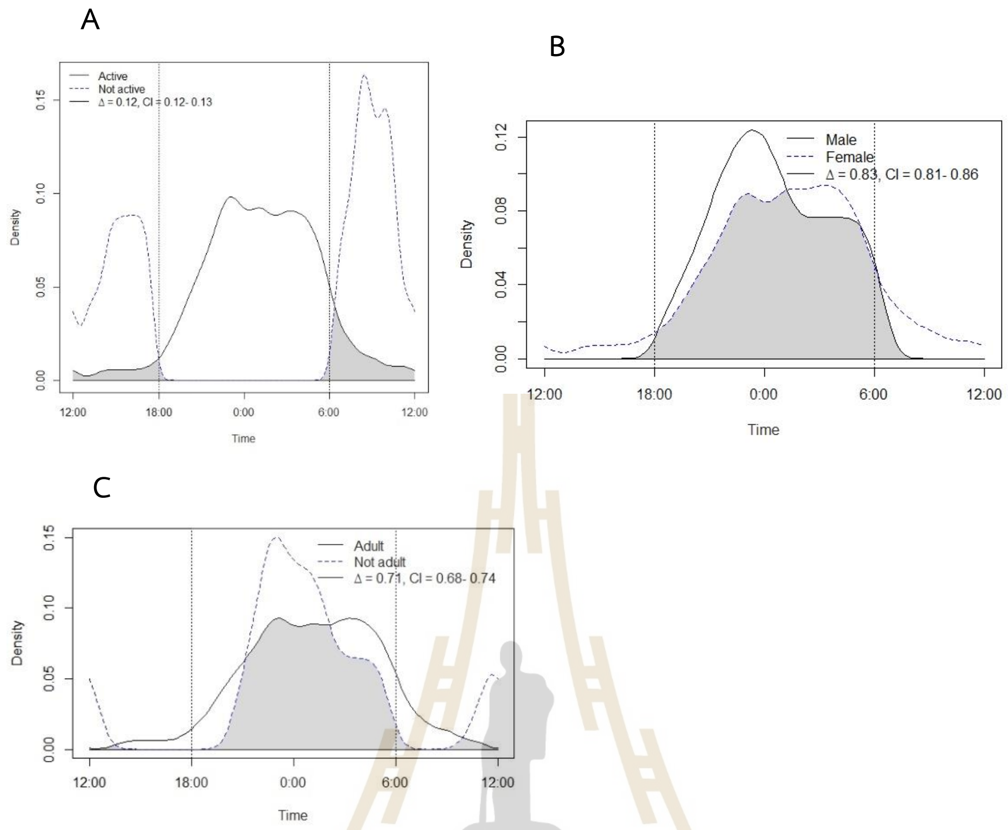

Figure 3.10 Behavior state temporal patterns of *Trimeresurus macrops* at Sakaerat Biosphere Reserve by behavior type (A), and foraging viper sex (B), and age (C).

At SUT, *T. albolabris* were also primarily observed to be clearly visibly active at night and resting or not visible during the day (Figure 3.11A). Active behavior was observed during the night (from between 18:00- 06:00) while resting or not visible was displayed primarily during the day (from 06:00- 18:00) with relatively limited overlap between activity types. Active behavior was displayed very similarly temporally between males and females (Figure 3.11B); adults and juveniles/subadults were somewhat lower (Figure 3.11C).

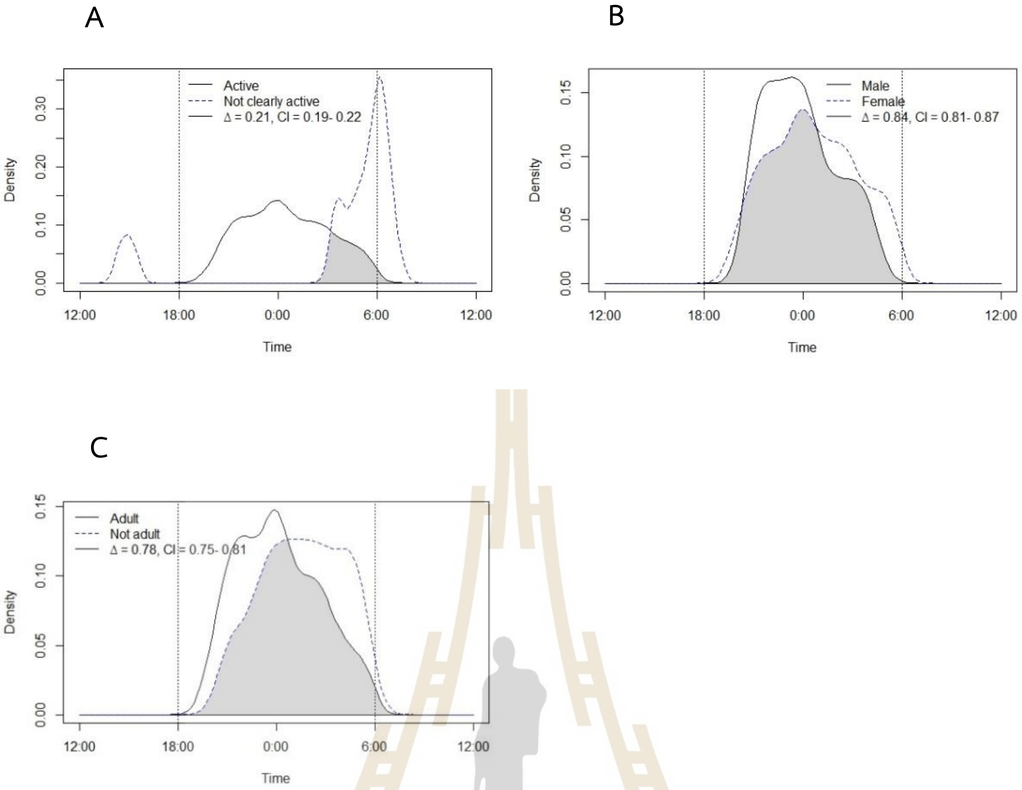

Figure 3.11 Behavior state temporal patterns of *Trimeresurus albolabris* at Suranaree University of Technology by behavior type (A), and foraging viper sex (B), and age (C).

Peak gape activity of male vipers at SBR and SUT was between 18:00- 00:00; there was 3 peaks observed for females with the highest being between 00:00- 06:00 (Figure 3.12A). Adult gaping behavior was fairly well spread out throughout the night, but here were only 2 gape observations for non- adult vipers which were both around midnight (Figure 3.12B). Headbobbing behavior was most frequently observed around 23:00 for males, but later, around 03:00, for females (Figure 3.13A). Adult vipers were observed headbobbing relatively consistently throughout the night-time (with a peak around 03:00), but non- adults were clearly headbobbing almost exclusively around 23:00 (Figure 3.13B). Male and female probing behavior were expressed similarly temporally, almost exclusively observed at night (Figure 3.14A). Overlap of adult and non- adult probing behavior was also relatively high, although non- adults were more limited temporally in expression of this behavior (Figure 3.13B).

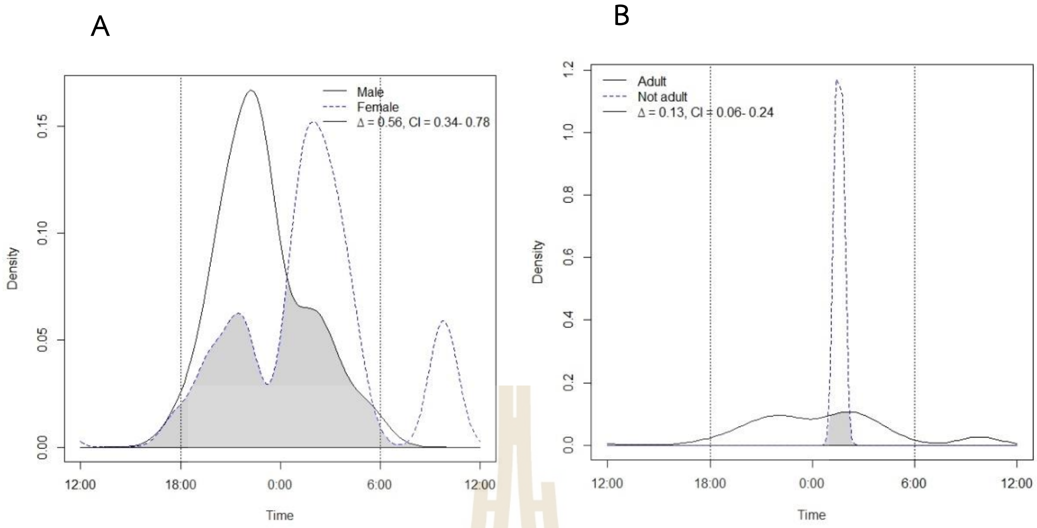

Figure 3.12 Gape behavior temporal patterns of vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology by sex (A) and age (B).

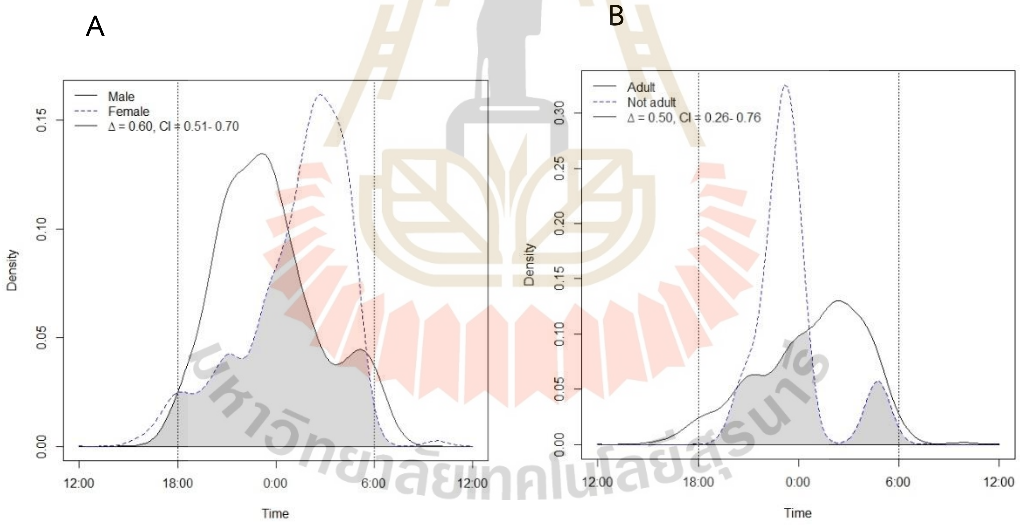

Figure 3.13 Headbob behavior temporal patterns of vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology by sex (A) and age (B).

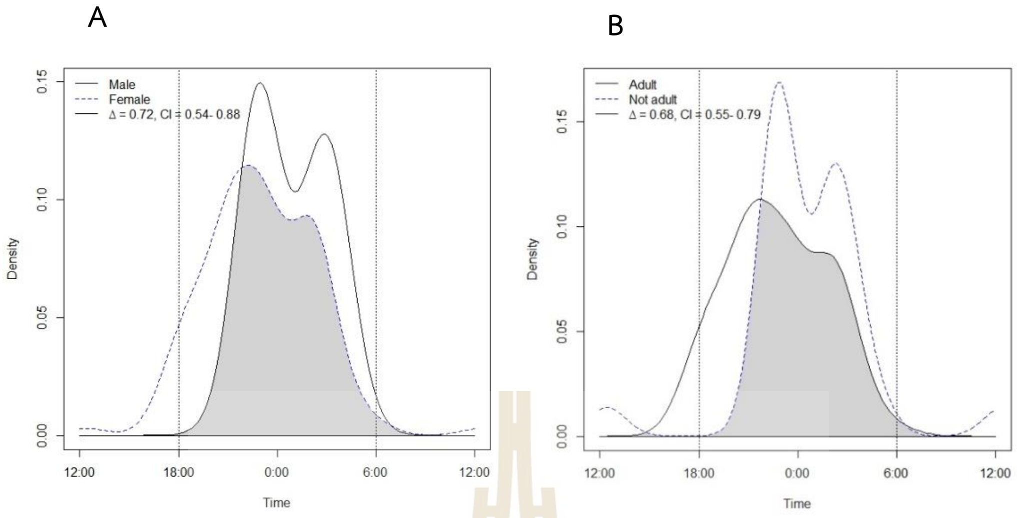

Figure 3.14 Probe behavior temporal patterns of vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology by sex (A) and age (B).

Male *T. macrops* displayed peak gape activity at SBR at approximately 0:300 and 10:00, while female gaping activity was almost exclusively nocturnal with peaks at approximately 20:00 and 02:00 (Figure 3.15). Non- adults were not observed gaping at SBR. Males were primarily observed headbobbing between 19:00- 00:00 (Figure 3.16A), while females were primarily observed between 00:00- 06:00. Adults were primarily observed headbobbing generally throughout the night, but non- adult headbobbing behavior was only observed between approximately 18:00- 00:00 (Figure 3.16B). Female probing behavior was primarily observed at night (64 out of 70 observations were between 18:00- 06:00) and the only male probing observation was at 01:18. Adult probe observations were highest at night, the 2 non- adult probe observations (1 individual viper) were at 12:27 and 22:46 (Figure 3.17).

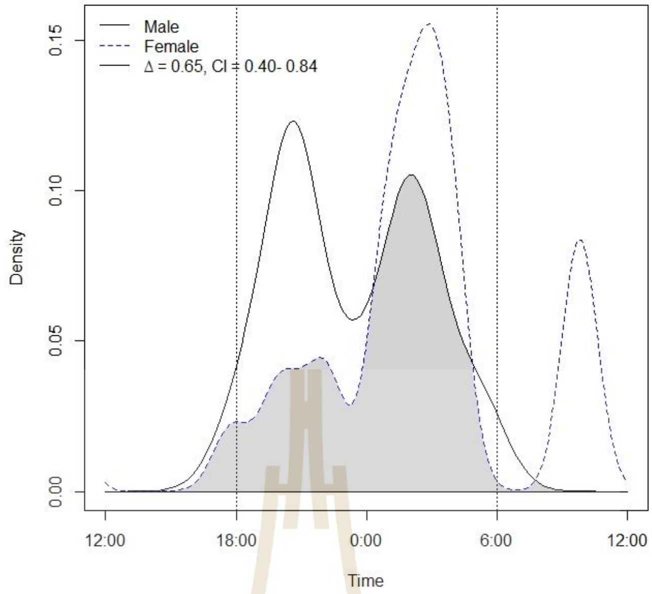

Figure 3. 15 Gape behavior temporal patterns of *Trimeresurus macrops* at Sakaerat Biosphere Reserve by sex.

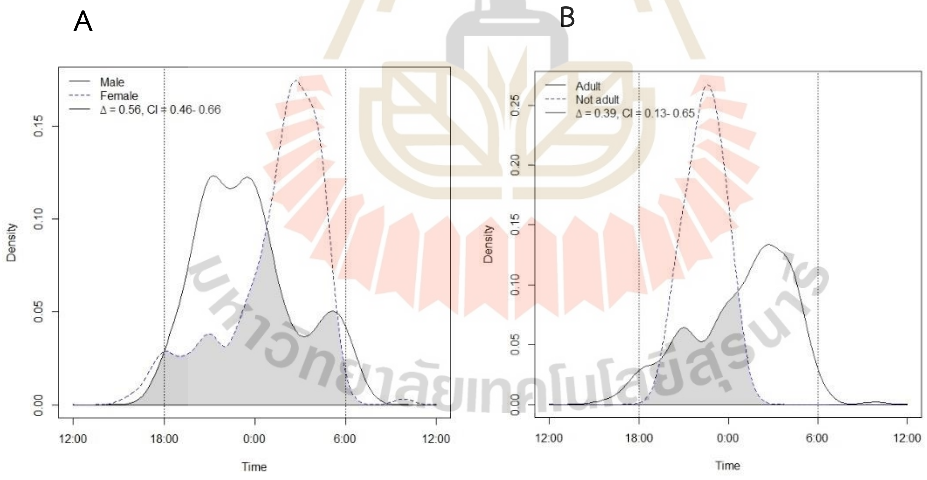

Figure 3.16 Headbob behavior temporal patterns of *Trimeresurus macrops* at Sakaerat Biosphere Reserve by sex (A) and age (b).

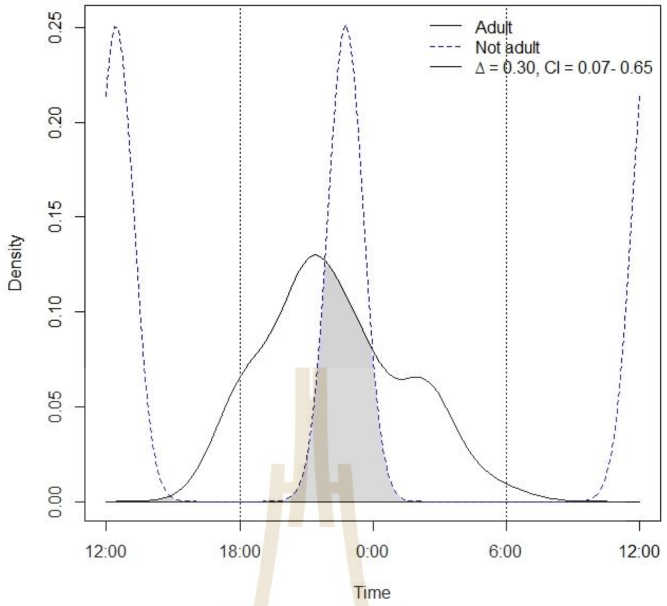

Figure 3.17 Probe behavior temporal patterns of *Trimeresurus macrops* at Sakaerat Biosphere Reserve by age.

All SUT *T. albolabris* gape behavior male and female observations were at night (18:00- 06:00), but females were spread broadly temporally during this period while males were focused between approximately 18:00- 00:00 (Figure 3.18A). Adult *T. albolabris* gape observations at SUT were observed between 19:29- 04:53, the single non- adult focal viper was observed probing at 01:22 and 01:47 (Figure 3.18B). Male and female headbobbing behavior was temporally displayed similarly, primarily nocturnal (Figure 3.19A). Adult *T. albolabris* were observed headbobbing throughout the night, with a peak around 00:00, while non- adults were observed headbobbing around 23:00 and 05:00 (Figure 3.19B). The single male displayed similar probing activity patterns to females, which were observed primarily at night (Figure 3.20A). Adult and non- adult probe behavior was displayed similarly temporally, primarily between 18:00- 06:00 (Figure 3.20B).

A

B

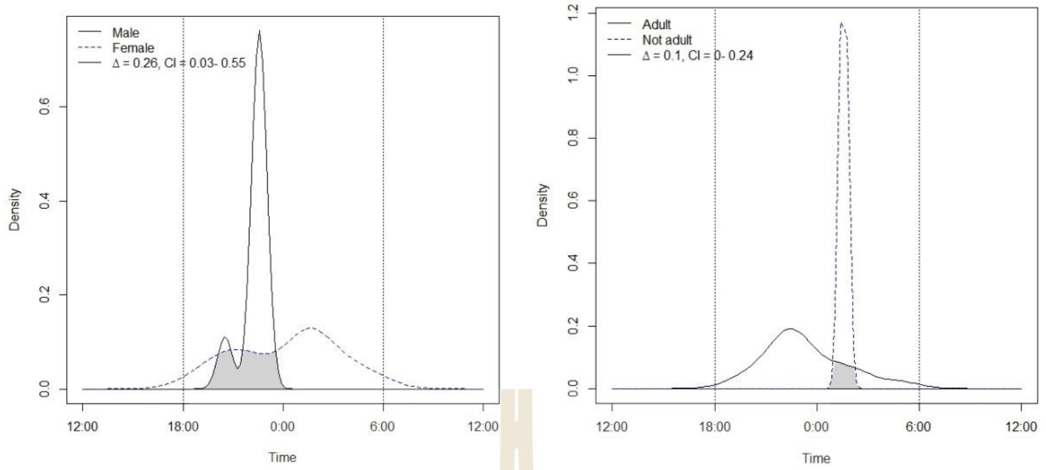

Figure 3.18 Gape behavior temporal patterns of *Trimeresurus albolabris* at Suranaree University of Technology by sex (A) and age (B).

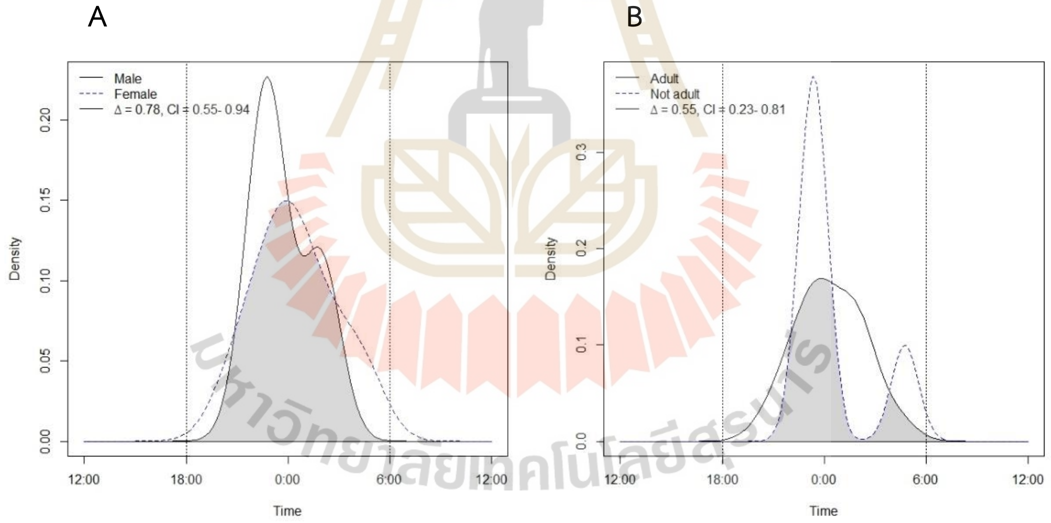

Figure 3. 19 Headbob behavior temporal patterns of *Trimeresurus albolabris* at Suranaree University of Technology by sex (A) and age (B).

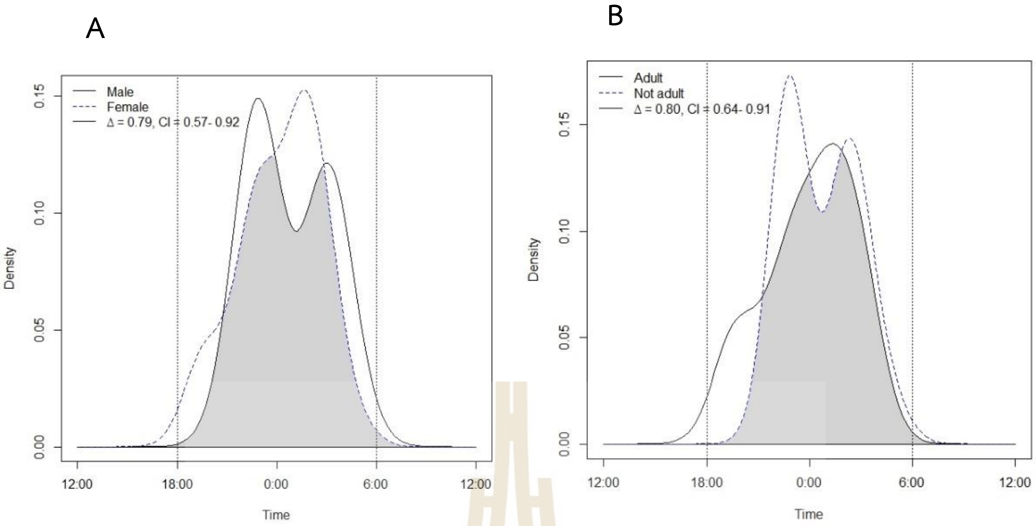

Figure 3.20 Probe behavior temporal patterns of *Trimeresurus albolabris* at Suranaree University of Technology by sex (A) and age (B).

Within the general Bayesian regression model type, species was predicted to be the best fit for ambush and moving behaviors although deviation of fit between models was low (Tables 3.3 and 3.4). Coefficients of ambush behavior for *T. macrops*, males, and non- adult vipers were positive (Figure 3.21), suggesting more time was spent by these groups ambushing while coefficients of females and vipers of which sex was unclear were negative suggesting less ambush behavior (Figure 3.22). Coefficients of *T. albolabris*, males, vipers of unclear sex, and adult vipers were positive which suggest more movement, while coefficients were negative for *T. macrops*, female vipers, and non- adult vipers suggesting less movement for these groups of vipers. All coefficients had values were very close to or overlapped with 0, however, which imply that these variables are poor indicators by themselves.

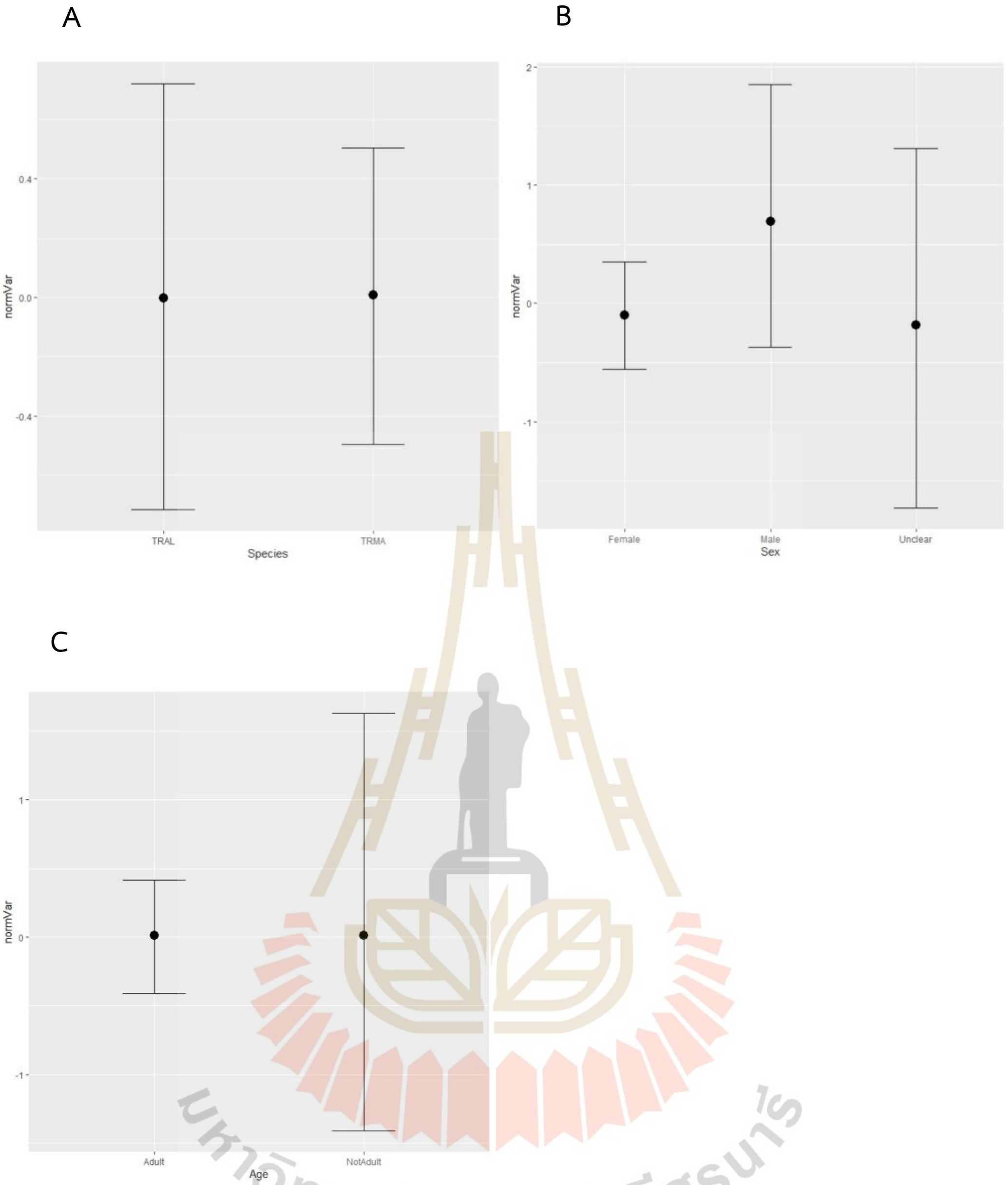

Figure 3.21 General type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL; A), sex (B), and age (C) models.

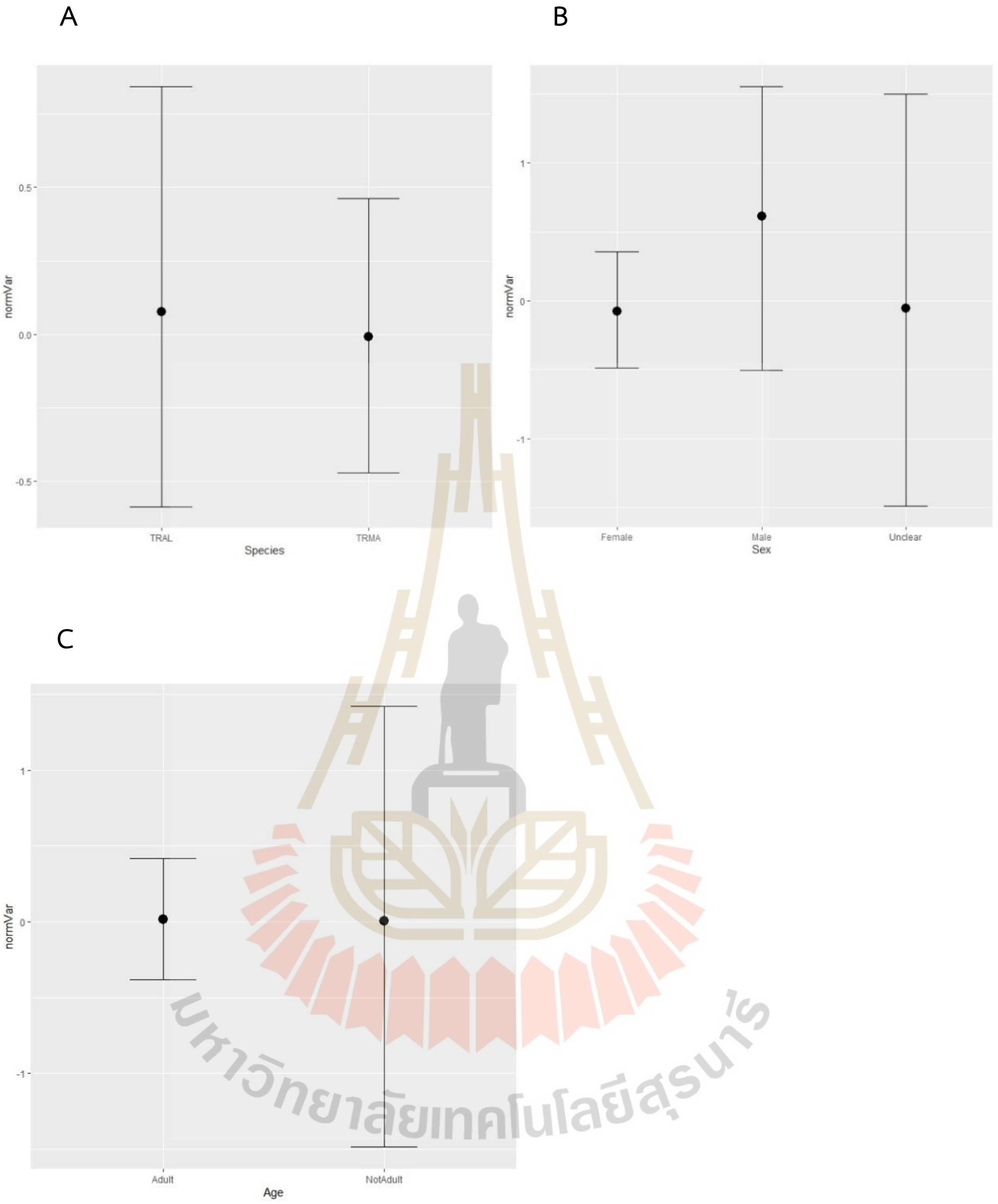

Figure 3.22 General type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL; A), sex (B), and age (C) models.

Table 3.3 General type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL), sex, and age models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Factor	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Species	TRAL	0	0.37	-0.55	0.37	1.01	707	0.398	70	71.6
	TRMA	0.01	0.45	-0.9	0.92	1	2172	0.398	70	71.6
Sex	Male	0.81	0.63	-0.32	2.2	1.02	300	0.483	74.4	77.2
	Female	-0.1	0.23	-0.55	0.37	1.01	707	0.483	74.4	77.2
	Unclear	-0.11	0.79	-1.66	1.46	1.01	771	0.483	74.4	77.2
Age	Adult	0	0.21	-0.43	0.4	1.01	2492	0.453	75.5	79.4
	Not adult	0.02	0.82	-1.45	1.65	1.02	282	0.453	75.5	79.4

Table 3.4 General type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL), sex, and age models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Factor	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Species	TRAL	0.08	0.35	-0.59	0.84	1.01	793	0.471	70.7	73
	TRMA	-0.09	0.43	-1.01	0.73	1.01	786	0.471	70.7	73
Sex	Male	0.67	0.57	-0.5	1.79	1.02	344	0.492	72	74.8
	Female	-0.08	0.22	-0.49	0.36	1.01	966	0.492	72	74.8
	Unclear	0.05	0.77	-1.51	1.62	1.01	949	0.492	72	74.8
Age	Adult	0.02	0.2	-0.38	0.42	1	3830	0.391	73.9	76.9
	Not adult	-0.02	0.75	-1.56	1.46	1	3681	0.391	73.9	76.9

All behavior state general model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the Bayesian models was small for demographics which reflected overall small sample sizes for the study. Ambush and movement data used may not have fit the general models well (r^2= 0.39-0.49, Tables 3.3 and 3.4), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

For behavioral event analysis using Bayesian modelling for general variables, sex was predicted to be the best fit for gape, and species for headbob and probe (Tables 3.5- 3.7). Coefficients of gape behavior for *T. albolabris*, males and unclear sexes, and adult vipers were positive, while coefficients of *T. macrops*, females, and non- adult vipers were negative (Figure 3.23). Coefficients of *T. macrops*, males, and adults were positive; *T. albolabris*, unclear sex, and non- adult were negative; and females was 0 for headbob behavior (Figure 3.24). Probe behavior coefficients were positive for *T. albolabris*, females, unclear sex, adults, and non- adults; negative coefficients were produced for *T. macrops* and males (Figure 3.25). All coefficients had values were very close to or overlapped with 0, however, which imply that these variables are poor indicators by themselves.

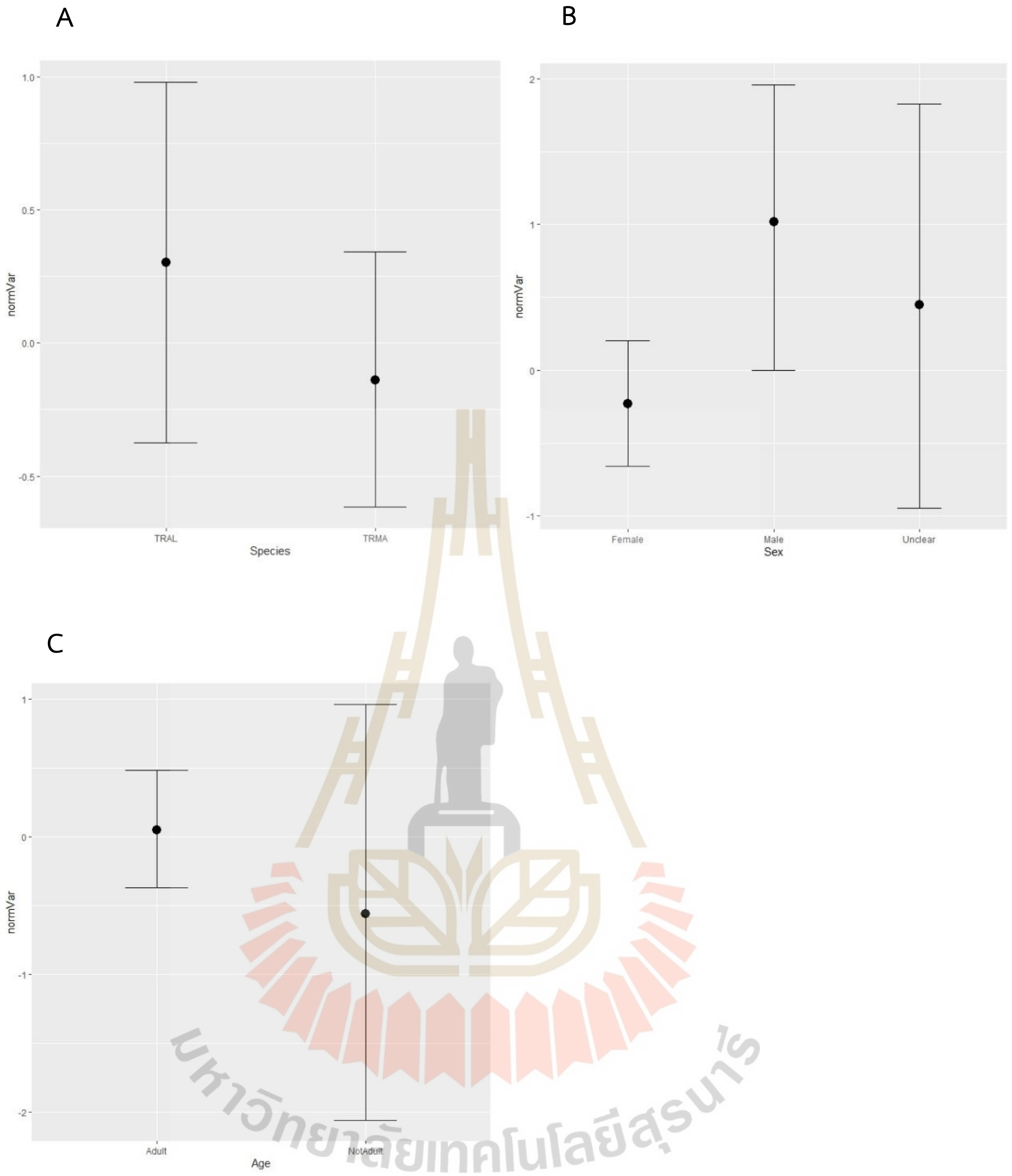

Figure 3.23 General type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL; A), sex (B), and age models (C).

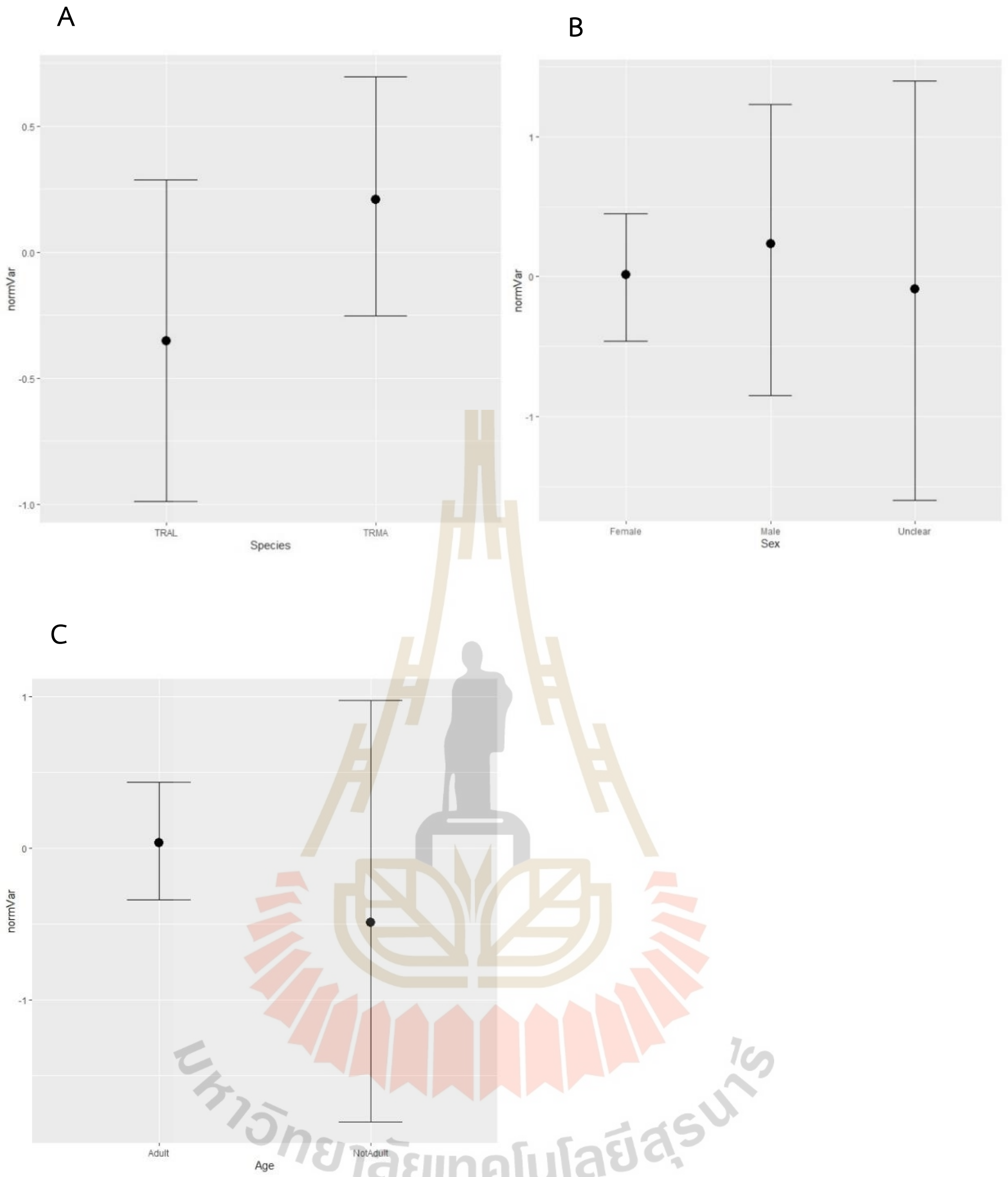

Figure 3.24 General type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL; A), sex (B), and age (C) models.

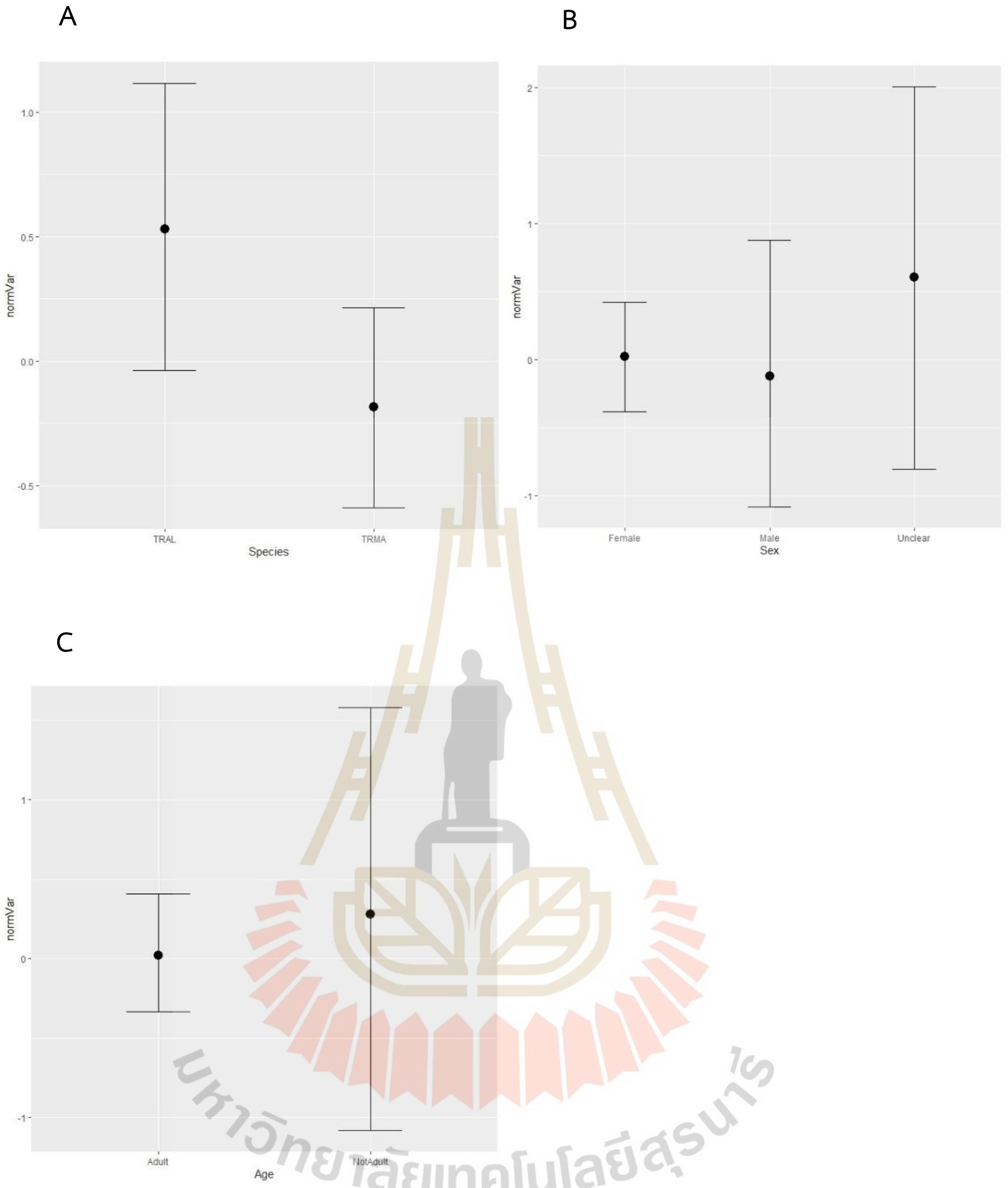

Figure 3.25 General type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL; A), sex (B), and age (C) models.

Table 3.5 General type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL), sex, and age models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Factor	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Species	TRAL	0.3	0.35	-0.37	0.98	1	2640	0.449	73.2	75.8
	TRMA	-0.44	0.43	-1.27	0.42	1	1935	0.449	73.2	75.8
Sex	Male	1.24	0.54	0.18	2.31	1	1873	0.519	70.5	73.1
	Female	-0.23	0.22	-0.66	0.2	1.01	974	0.519	70.5	73.1
	Unclear	0.67	0.74	-0.79	2.11	1	2936	0.519	70.5	73.1
Age	Adult	0.05	0.21	-0.37	0.48	1	1296	0.519	73.1	76.2
	Not adult	-0.61	0.78	-2.16	0.96	1	4454	0.519	73.1	76.2

Table 3.6 General type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL), sex, and age models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Factor	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Species	TRAL	-0.35	0.32	-0.99	0.29	1	2302	0.461	68.7	71.4
	TRMA	0.56	0.41	-0.24	1.39	1	1250	0.461	68.7	71.4
Sex	Male	0.2	0.57	-0.94	1.36	1.02	1787	0.448	71.6	74.5
	Female	0	0.22	-0.46	0.45	1.01	1116	0.448	71.6	74.5
	Unclear	-0.11	0.76	-1.62	1.42	1.01	3142	0.448	71.6	74.5
Age	Adult	0.03	0.21	-0.34	0.44	1.02	182	0.47	68.8	71.4
	Not adult	-0.47	0.72	-1.9	0.95	1.03	1848	0.47	68.8	71.4

Table 3.7 General type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate species (*Trimeresurus albolabris*, TRAL and *T. macrops*, TRAL), sex, and age models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Factor	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Species	TRAL	0.53	0.29	-0.04	1.12	1	2664	0.487	64.4	66.2
	TRMA	-0.72	0.35	-1.42	-0.01	1.01	4625	0.487	64.4	66.2
Sex	Male	-0.14	0.53	-1.17	0.9	1	4145	0.423	68.8	72.3
	Female	0.02	0.21	-0.38	0.42	1	3106	0.423	68.8	72.3
	Unclear	0.58	0.72	-0.88	2.02	1	2934	0.423	68.8	72.3
Age	Adult	0.02	0.19	-0.33	0.41	1.02	190	0.472	65.8	68.5
	Not adult	0.26	0.72	-1.16	1.6	1.01	247	0.472	65.8	68.5

All behavior event general model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the Bayesian models was small for demographics which reflected overall small sample sizes for the study. Behavior event data may not have fit the general models well (r^2= 0.42-0.52, Tables 3.5-3.7), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Of the microhabitat variables, LQD2 was predicted to be the best fit model for ambush behavior and LQD2 and LQD3 were predicted to be best fit for movement behavior (Tables 3.8 and 3.9). Of the ambush variables, LQD1 and LQD2 were positive and LQD3 was negative, which suggests vipers ambush more at microhabitat sites with leaves which are more damaged at the level they are at and below while ambushing less at sites with leaves that are damaged more above them (Figure 3.26). Movement was also positively influenced by LQD1 and LQD2 and to a very limited extent CC, and also negatively influenced by LQD3 (Figure 3.27). All microhabitat coefficients overlapped 0, and several were centered around it, suggesting microhabitat variables to be poor standalone indicators.

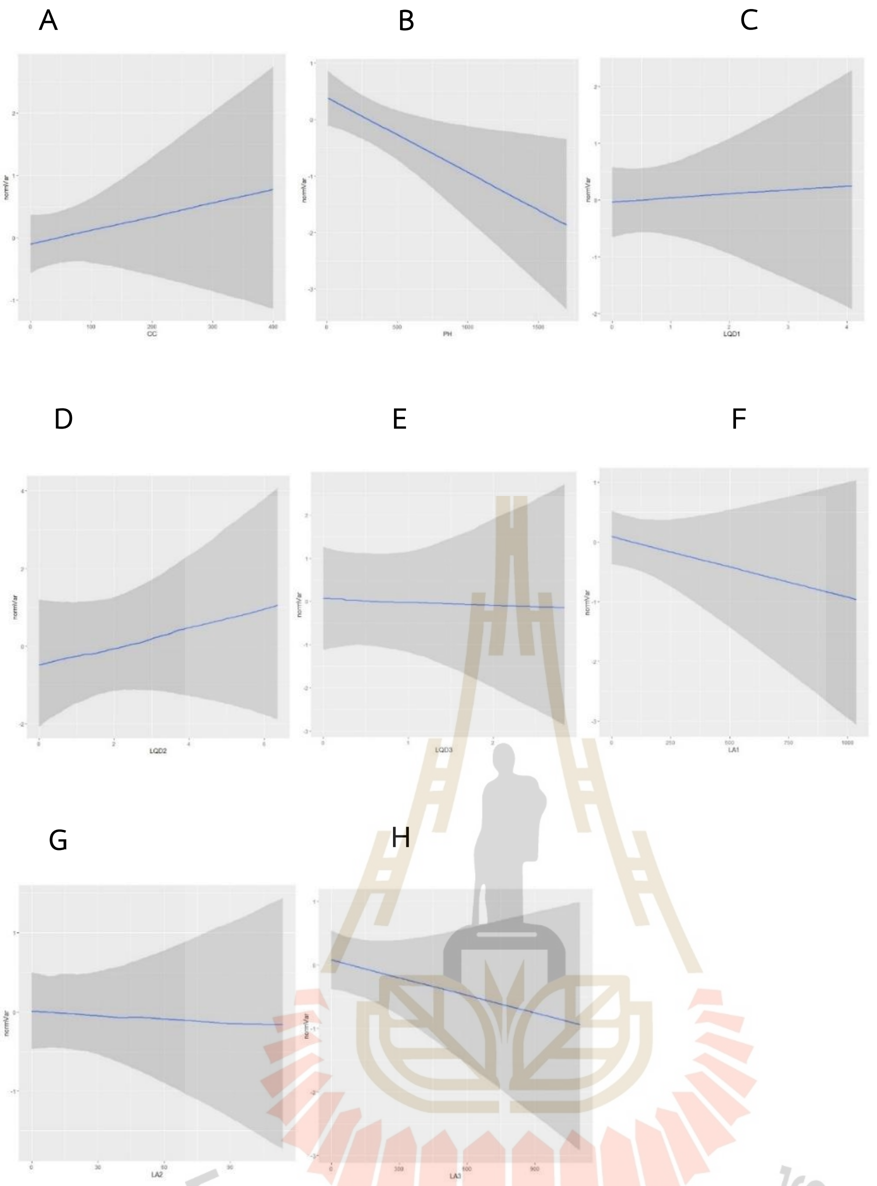

Figure 3.26 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate canopy cover (CC; A), perch height (PH; B), leaf quality and damage at viper level (LQD1, C) and ground level directly below viper (LQD2; D) and 0.5m directly above viper (LQD3; E), leaf area at viper level (LA1; F) and on ground directly below viper (LA2; G) and 0.5m directly above viper (LA3; H) models.

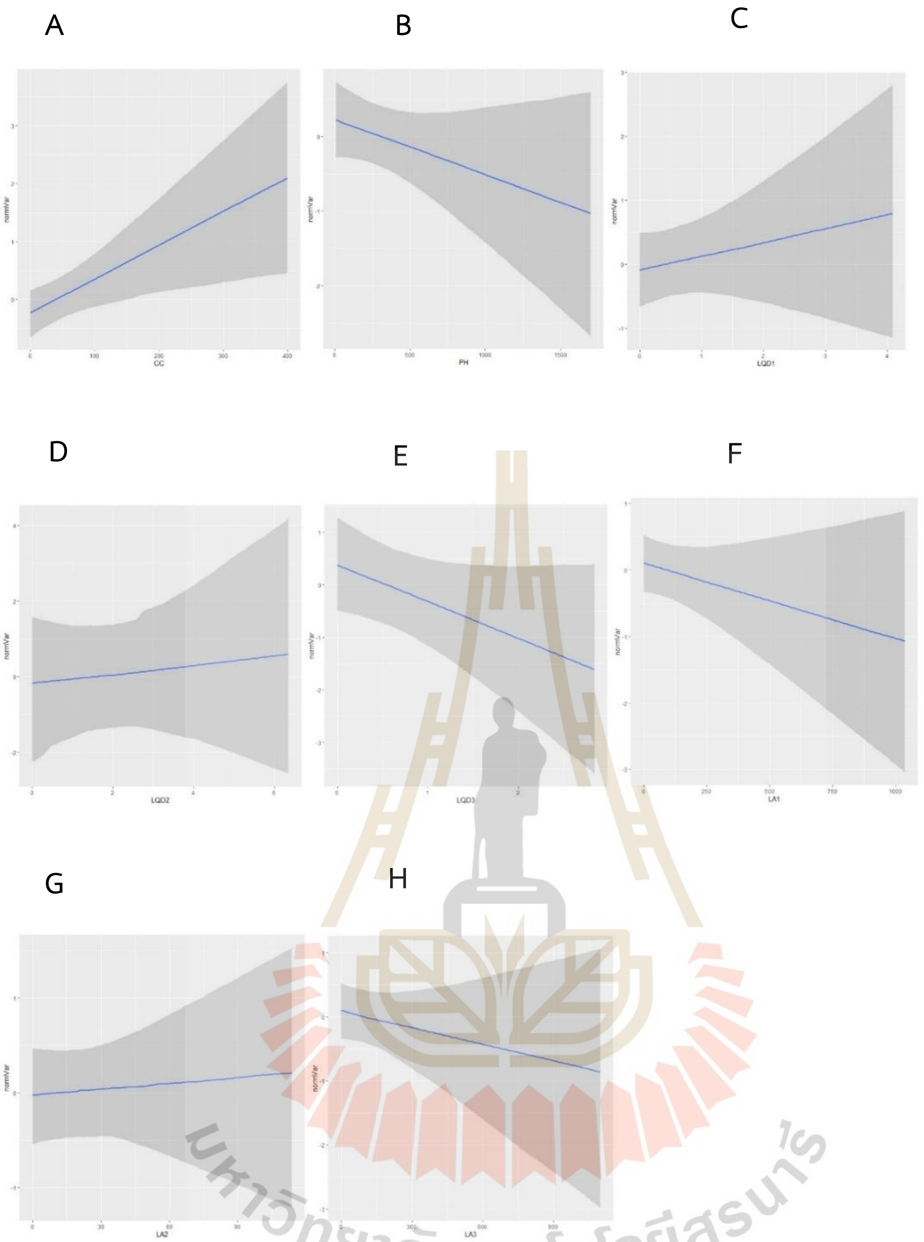

Figure 3.27 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate canopy cover (CC; A), perch height (PH; B), leaf quality and damage at viper level (LQD1; C) and ground level directly below viper (LQD2; D) and 0.5m directly above viper (LQD3; E), leaf area at viper level (LA1; F) and on ground directly below viper (LA2; G) and 0.5m directly above viper (LA3; H) models.

Table 3.8 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate canopy cover (CC), perch height (PH), leaf quality and damage at viper level (LQD1) and ground level directly below viper (LQD2) and 0.5m directly above viper (LQD3), leaf area at viper level (LA1) and on ground directly below viper (LA2) and 0.5m directly above viper (LA3) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
CC	0	0	0	0.01	1.01	1303	0.457	67.5	75.9
PH	0	0	0	0	1	1926	0.555	59.5	61.4
LQD1	0.06	0.28	-0.5	0.61	1	3309	0.43	44.5	46.4
LQD2	0.23	0.29	-0.36	0.81	1.02	294	0.641	18	19.4
LQD3	-0.07	0.55	-1.14	1.05	1.01	475	0.468	25.3	27
LA1	0	0	0	0	1.01	3236	0.445	66.1	69.4
LA2	0	0.01	-0.02	0.01	1.03	1871	0.386	59.7	61.8
LA3	0	0	0	0	1	4896	0.422	63.4	66.1

Table 3.9 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate canopy cover (CC), perch height (PH), leaf quality and damage at viper level (LQD1) and ground level directly below viper (LQD2) and 0.5m directly above viper (LQD3), leaf area at viper level (LA1) and on ground directly below viper (LA2) and 0.5m directly above viper (LA3) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r-square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
CC	0.01	0	0	0.01	1	3268	0.53	59.9	62.8
PH	0	0	0	0	1	3636	0.438	62.4	65.1
LQD1	0.22	0.27	-0.3	0.75	1	1253	0.437	44.4	46.7
LQD2	0.13	0.35	-0.55	0.88	1.01	433	0.525	19.9	21
LQD3	-0.7	0.4	-1.5	0.1	1	5213	0.707	19.9	21
LA1	0	0	0	0	1	3906	0.422	62.3	64.8
LA2	0	0.01	-0.01	0.01	1.01	469	0.573	55.6	58
LA3	0	0	0	0	1.03	94	0.469	59.1	61.6

All behavior state microhabitat model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the microhabitat Bayesian models was relatively small. Ambush and movement data used for green pit viper microhabitat may not have fit the models well (r^2= 0.39- 0.71; Tables 3.8 and 3.9), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Of the microhabitat behavior event variables, LQD2 (leaf quality and damage below viper level) was the most fit for gape, headbob, and probe (Tables 3.10- 3.12). The LQD2 and LQD3 variables were positive (Figures 3.28- 3.30). All coefficients had values that were very close to or overlapped with 0, however, which imply that these variables are poor indicators by themselves.

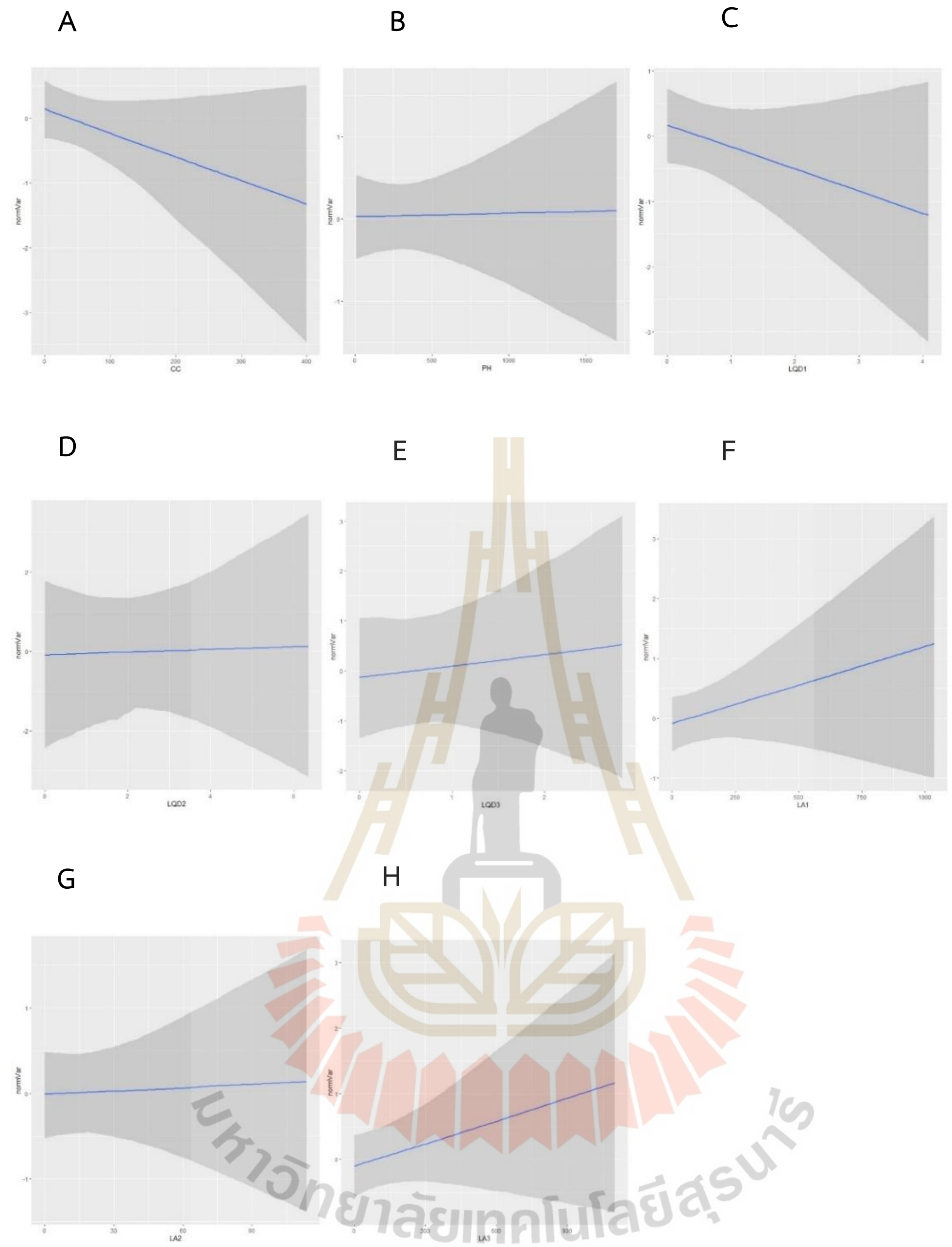

Figure 3.28 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate canopy cover (CC; A), perch height (PH; B), leaf quality and damage at viper level (LQD1; C) and ground level directly below viper (LQD2; D) and 0.5m directly above viper (LQD3; E), leaf are at viper level (LA1; F) and on ground directly below viper (LA2; G) and 0.5m directly above viper (LA3; H) models.

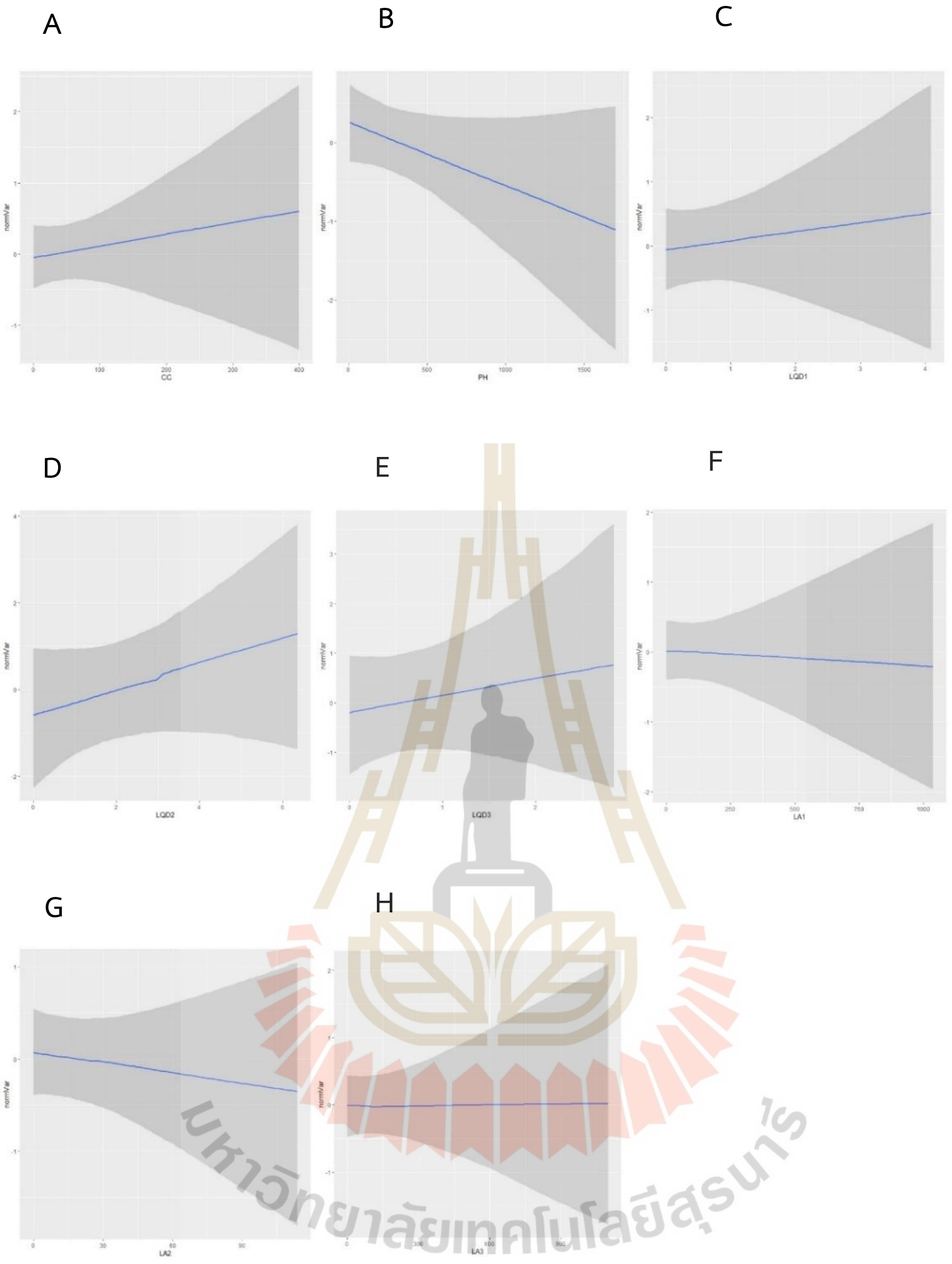

Figure 3.29 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate canopy cover (CC; A), perch height (PH; B), leaf quality and damage at viper level (LQD1; C) and ground level directly below viper (LQD2; D) and 0.5m directly above viper (LQD3; E), leaf are at viper level (LA1; F) and on ground directly below viper (LA2; G) and 0.5m directly above viper (LA3; H) models.

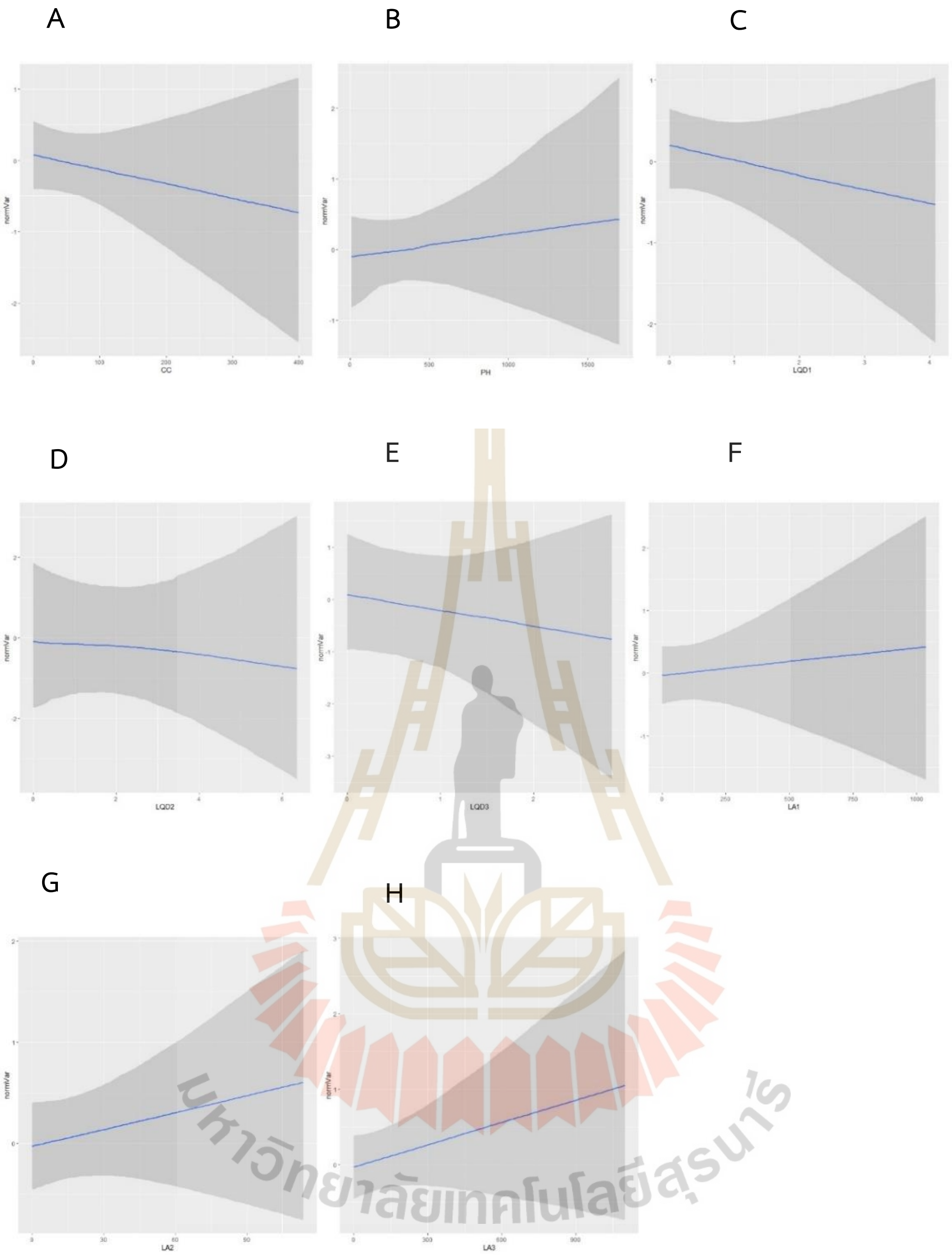

Figure 3.30 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate canopy cover (CC; A), perch height (PH; B), leaf quality and damage at viper level (LQD1; C) and ground level directly below viper (LQD2; D) and 0.5m directly above viper (LQD3; E), leaf are at viper level (LA1; F) and on ground directly below viper (LA2; G) and 0.5m directly above viper (LA3; H) models.

Table 3.10 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate canopy cover (CC), perch height (PH), leaf quality and damage at viper level (LQD1) and ground level directly below viper (LQD2) and 0.5m directly above viper (LQD3), leaf area at viper level (LA1) and on ground directly below viper (LA2) and 0.5m directly above viper (LA3) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r-square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
CC	0	0	-0.01	0	1.02	263	0.515	66.9	69.3
PH	0	0	0	0	1.01	6636	0.402	63.2	66.4
LQD1	-0.33	0.27	-0.85	0.22	1	3955	0.493	44.5	46.8
LQD2	0.05	0.35	-0.63	0.88	1.01	1033	0.475	20.1	21.3
LQD3	0.23	0.57	-0.88	1.32	1	6355	0.473	24.8	26.9
LA1	0	0	0	0	1	890	0.452	65.4	68.5
LA2	0	0.01	-0.01	0.02	1	2373	0.421	61.5	63.7
LA3	0	0	0	0	1	6351	0.459	63.2	65.6

Table 3.11 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate canopy cover (CC), perch height (PH), leaf quality and damage at viper level (LQD1) and ground level directly below viper (LQD2) and 0.5m directly above viper (LQD3), leaf area at viper level (LA1) and on ground directly below viper (LA2) and 0.5m directly above viper (LA3) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
CC	0	0	0	0.01	1.01	838	0.396	69.8	72.3
PH	0	0	0	0	1.01	1553	0.469	62.1	64.4
LQD1	0.14	0.28	-0.43	0.69	1	2806	0.423	46.3	48.6
LQD2	0.32	0.3	-0.26	0.84	1.1	33	0.696	16.4	17.1
LQD3	0.36	0.54	-0.65	1.54	1	1371	0.527	23.7	25.2
LA1	0	0	0	0	1	2250	0.549	59.1	61.2
LA2	0	0.01	-0.02	0.01	1.02	296	0.426	58.8	61.4
LA3	0	0	0	0	1.07	42	0.532	62.9	65.9

Table 3.12 Microhabitat model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate canopy cover (CC), perch height (PH), leaf quality and damage at viper level (LQD1) and ground level directly below viper (LQD2) and 0.5m directly above viper (LQD3), leaf area at viper level (LA1) and on ground directly below viper (LA2) and 0.5m directly above viper (LA3) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r-square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
CC	0	0	-0.01	0	1.01	2948	0.419	70.9	73.9
PH	0	0	0	0	1.07	52	0.434	66.6	69.5
LQD1	-0.19	0.23	-0.65	0.28	1	5004	0.632	39.7	41.4
LQD2	-0.08	0.32	-0.71	0.62	1.38	2676	0.574	19.9	20.9
LQD3	-0.33	0.49	-1.33	0.65	1.04	2271	0.552	22.4	23
LA1	0	0	0	0	1	5578	0.41	66.9	70.2
LA2	0.01	0.01	-0.01	0.02	1	3951	0.407	55.7	58.2
LA3	0	0	0	0	1	6848	0.414	58.2	61.8

All behavior event microhabitat model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the Bayesian models was small for demographics which reflected overall small sample sizes for the study. Behavior event data used for the general green pit viper may not have fit the models well (r^2= 0.40-0.70, Tables 3.10- 3.12), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Distance to buildings was predicted to be the best fit model for ambush behavior, while LAI was predicted to be the best fit model for move behavior for macrohabitat models although deviation of fit between models was low (Tables 3.13 and 3.14). Vipers were suggested to ambush more at sites with higher NDVI values and marginally more with increased distance to roads but ambush less with increased LAI and marginally less with increased canopy height (Figure 3.31). Vipers also moved more at sites with macrohabitat with increased NDVI, and less with increased LAI and canopy height (Table 3.32). All macrohabitat coefficients overlapped 0, and several were centered around it, suggesting macrohabitat variables to be poor indicators by themselves.

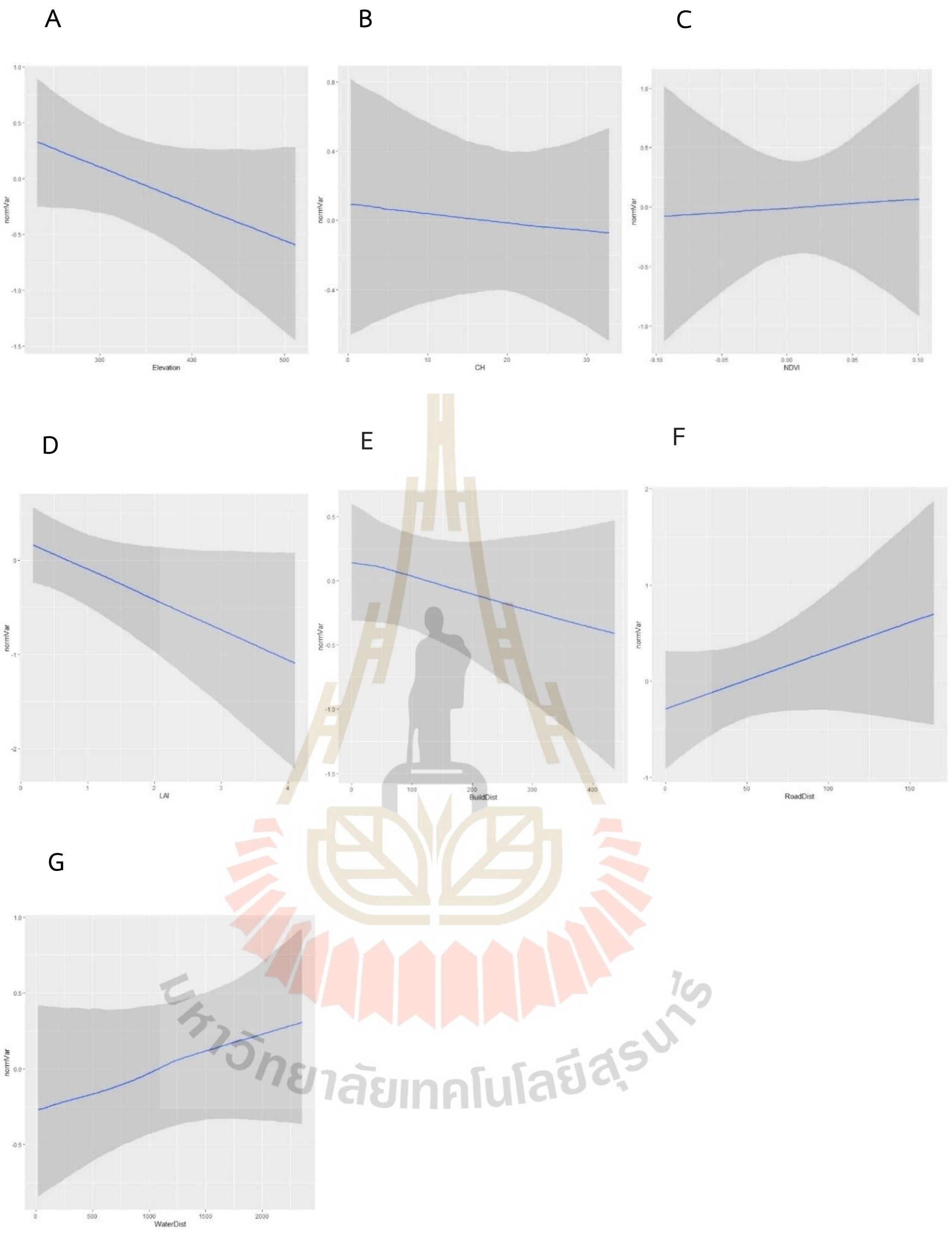

Figure 3.31 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate elevation (A), canopy height (CH; B), normalized difference vegetation index (NDVI; C), leaf area index (LAI; D), Euclidean distance to nearest building (BuildDist; E), Euclidean distance to nearest road (RoadDist; F), and Euclidean distance to nearest water body (WaterDist; G) models.

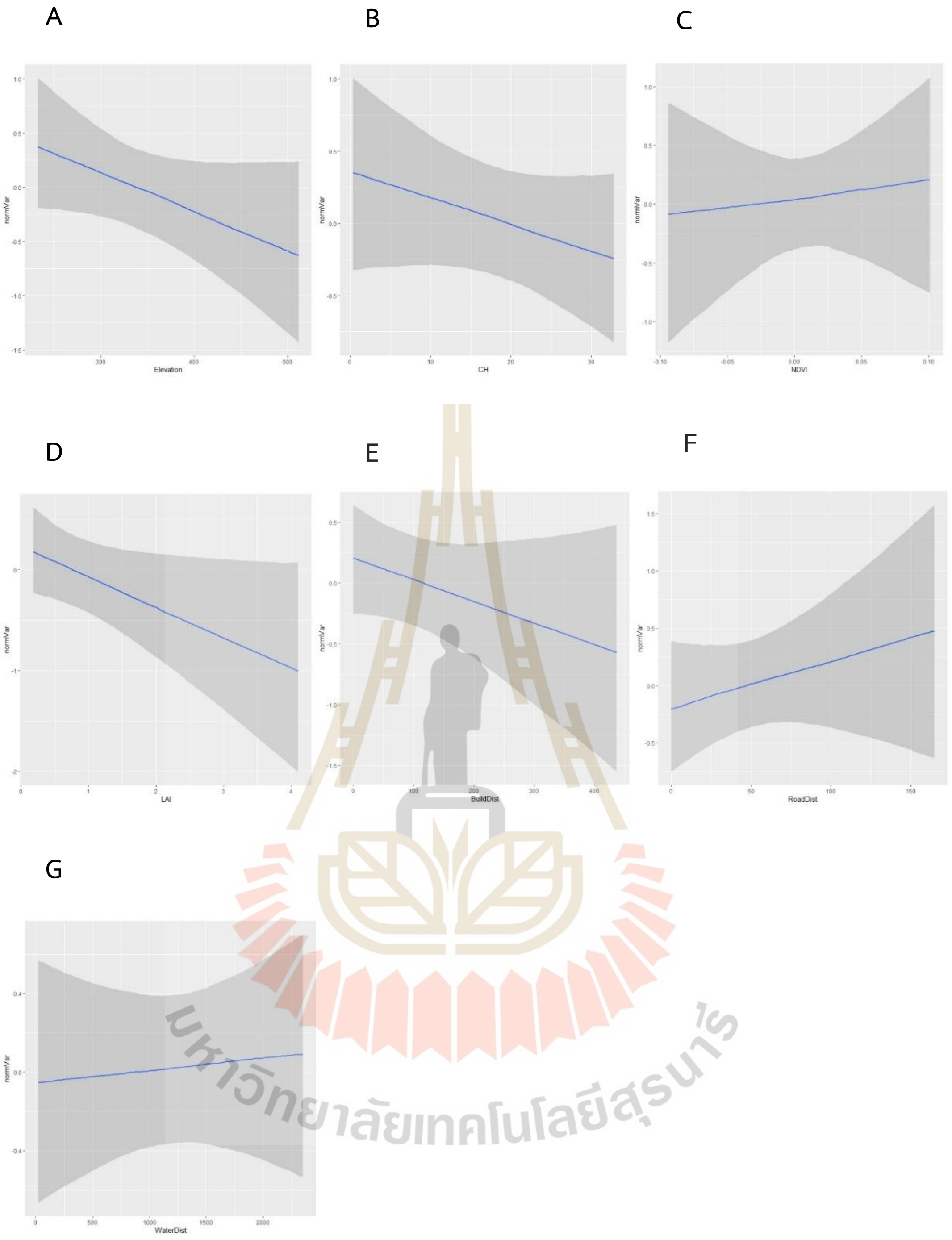

Figure 3.32 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate elevation (A), canopy height (CH; B), normalized difference vegetation index (NDVI; C), leaf area index (LAI; D), Euclidean distance to nearest building (BuildDist; E), Euclidean distance to nearest road (RoadDist; F), and Euclidean distance to nearest water body (WaterDist; G) models.

Table 3.13 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate elevation, canopy height (CH), normalized difference vegetation index (NDVI), leaf area index (LAI), Euclidean distance to nearest building (BuildDist), Euclidean distance to nearest road (RoadDist), and Euclidean distance to nearest water body (WaterDist) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Elevation	0	0	-0.01	0	1	5447	0.495	71.4	74
CH	-0.01	0.02	-0.04	0.03	1.01	1002	0.385	76.4	78.7
NDVI	0.65	5.02	-9.48	10.31	1	1208	0.389	76.5	79.1
LAI	-0.32	0.16	-0.62	0	1	2579	0.485	71.6	74.6
BuildDist	0	0	0	0	1.04	86	0.628	65.5	77
RoadDist	0.01	0	0	0.02	1	2332	0.434	74.1	77
WaterDist	0	0	0	0	1.21	16	0.526	70	71.6

Table 3.14 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate elevation, canopy height (CH), normalized difference vegetation index (NDVI), leaf area index (LAI), Euclidean distance to nearest building (BuildDist), Euclidean distance to nearest road (RoadDist), and Euclidean distance to nearest water body (WaterDist) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Elevation	0	0	-0.01	0	1.06	57	0.505	67	70.6
CH	-0.02	0.02	-0.05	0.01	1.03	189	0.434	70.5	73.1
NDVI	1.56	4.56	-7.48	10.59	1.02	885	0.467	70.4	73.2
LAI	-0.29	0.15	-0.59	0.02	1.01	4259	0.529	66.9	69.2
BuildDist	0	0	0	0	1.03	130	0.486	68.9	71.7
RoadDist	0	0	0	0.01	1.01	1050	0.499	68	70.1
WaterDist	0	0	0	0	1	6054	0.386	73.4	76.1

All behavior state macrohabitat model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the macrohabitat Bayesian models was relatively small, but the distance to water variable in the ambush model was especially low. Ambush and movement data used for green pit viper macrohabitat may not have fit the models well (r^2= 0.38- 0.62, Tables 3.13 and 3.14), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

The best fit model for gape behavior was LAI, road distance for headbob, and LAI for probe (Tables 3.15- 3.17). Coefficients of NDVI, LAI, and road distance were positive; CH was negative; and elevation, building distance, and water distance were 0 for gape behavior (Figure 3.33). The coefficients CH and NDVI were positive; LAI was negative; and elevation, building distance, road distance, and water distance were 0 for headbobbing behavior (Figure 3.34). Coeffiecients of NDVI and water distance were positive, CH and LAI were negative, and elevation, building distance, and road distance were 0 for probe behavior (Figure 3.35). All macrohabitat coefficients overlapped 0, and several were centered around it, suggesting macrohabitat variables to be poor indicators by themselves.

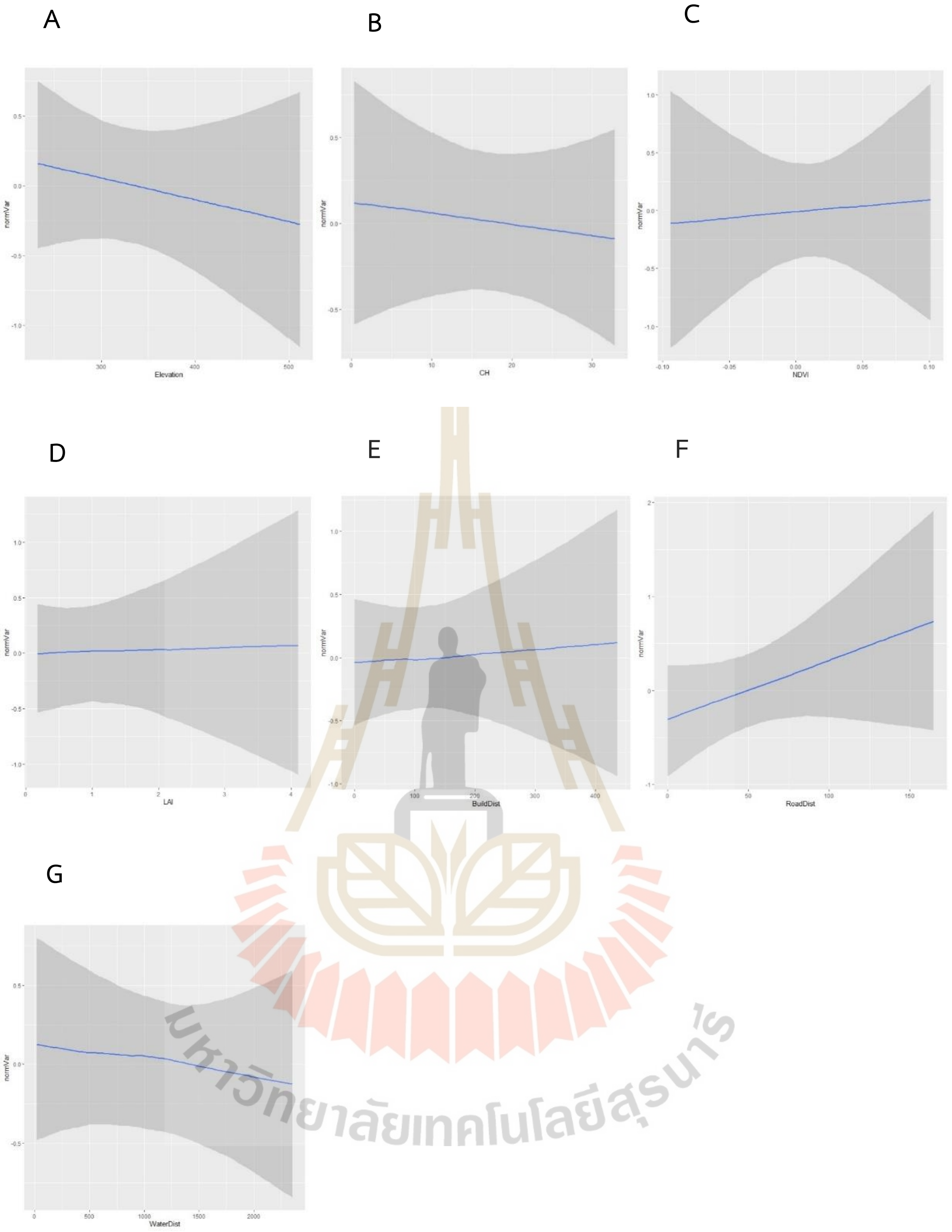

Figure 3.33 Macrohabitat Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate elevation (A), canopy height (CH; B), normalized difference vegetation index (NDVI; C), leaf area index (LAI; D), Euclidean distance to nearest building (BuildDist; E), Euclidean distance to nearest road (RoadDist; F), and Euclidean distance to nearest water body (WaterDist; G) models.

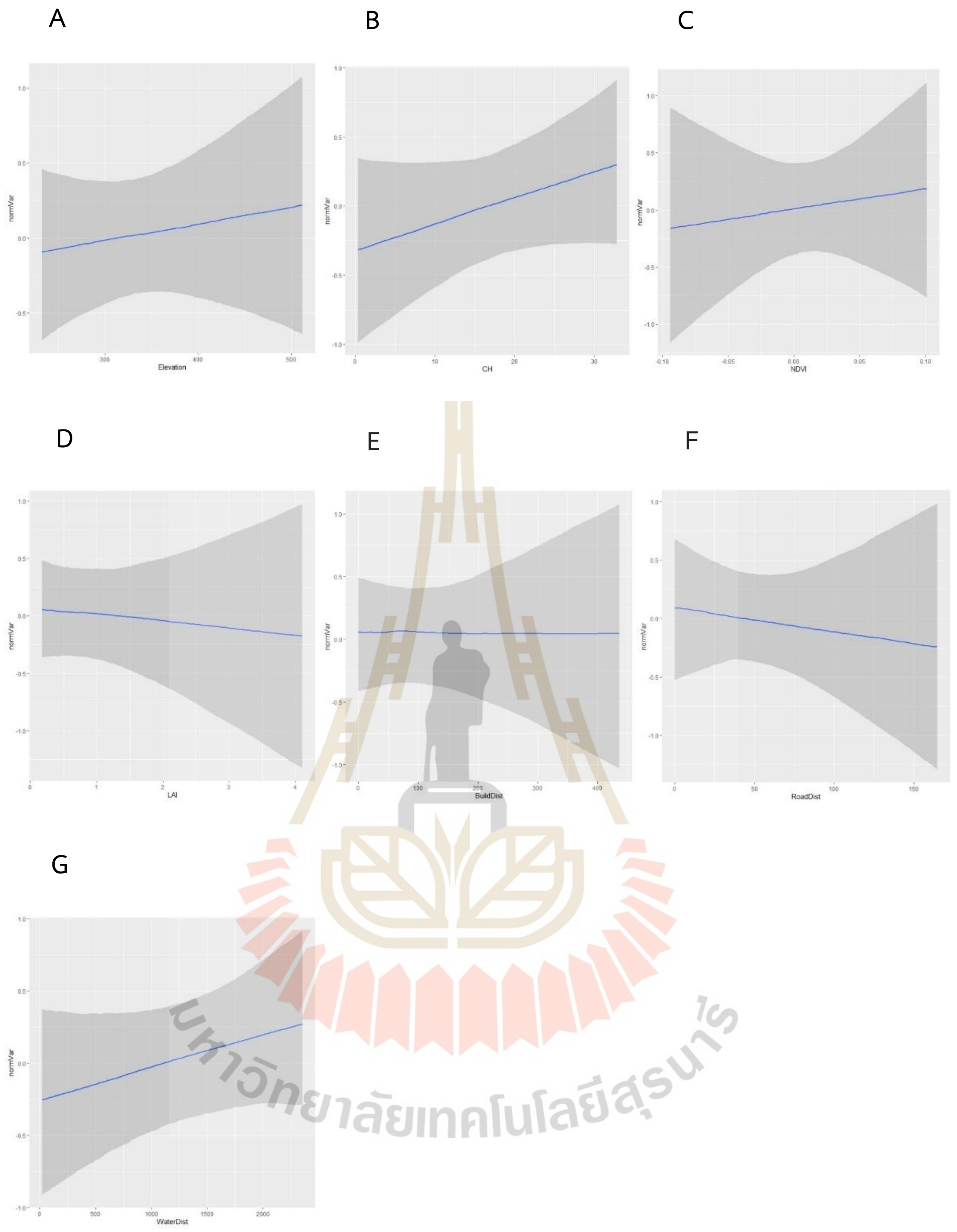

Figure 3.34 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate elevation (A), canopy height (CH; B), normalized difference vegetation index (NDVI; C), leaf area index (LAI; D), Euclidean distance to nearest building (BuildDist; E), Euclidean distance to nearest road (RoadDist; F), and Euclidean distance to nearest water body (WaterDist; G) models.

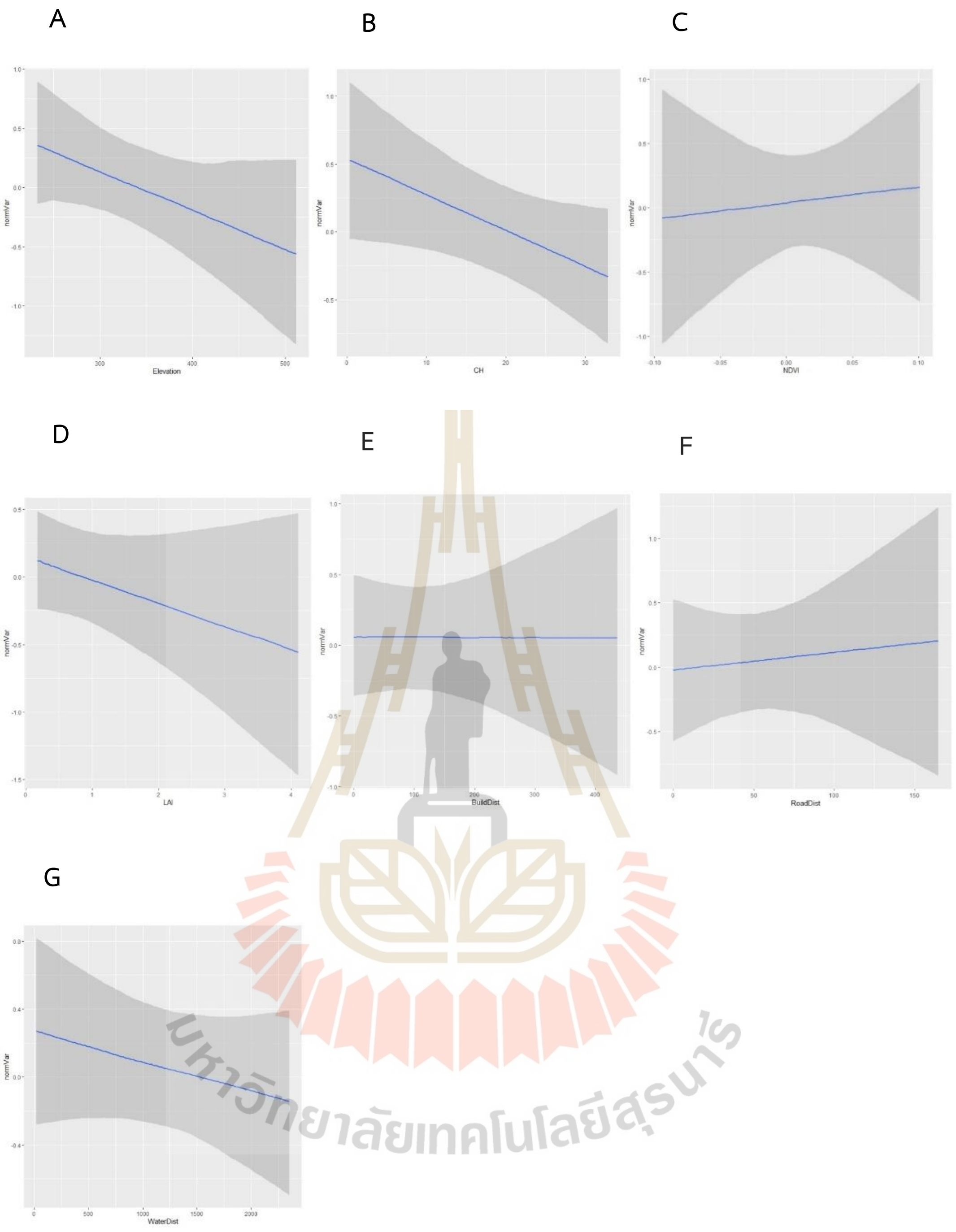

Figure 3.35 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate elevation (A), canopy height (CH; B), normalized difference vegetation index (NDVI; C), leaf area index (LAI; D), Euclidean distance to nearest building (BuildDist; E), Euclidean distance to nearest road (RoadDist; F), and Euclidean distance to nearest water body (WaterDist; G) models.

Table 3.15 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate elevation, canopy height (CH), normalized difference vegetation index (NDVI), leaf area index (LAI), Euclidean distance to nearest building (BuildDist), Euclidean distance to nearest road (RoadDist), and Euclidean distance to nearest water body (WaterDist) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Elevation	0	0	-0.01	0	1	4078	0.43	74.3	77.4
CH	-0.01	0.02	-0.04	0.03	1	3791	0.375	75.5	78.4
NDVI	0.97	5.04	-9.39	11.02	1.01	1537	0.418	74.1	72.2
LAI	0.02	0.18	-0.33	0.36	1.01	638	0.466	68.8	75.7
BuildDist	0	0	0	0	1.02	310	0.423	73.7	76.4
RoadDist	0.01	0	0	0.02	1	1948	0.443	72.2	75.3
WaterDist	0	0	0	0	1.12	27	0.451	72.4	74.9

Table 3.16 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate elevation, canopy height (CH), normalized difference vegetation index (NDVI), leaf area index (LAI), Euclidean distance to nearest building (BuildDist), Euclidean distance to nearest road (RoadDist), and Euclidean distance to nearest water body (WaterDist) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Elevation	0	0	0	0.01	1	3310	0.408	72	75.1
CH	0.02	0.02	-0.01	0.05	1.01	1099	0.467	68.7	71.1
NDVI	1.69	4.73	-7.69	10.88	1	3741	0.366	73.7	77
LAI	-0.06	0.17	-0.38	0.26	1.01	518	0.445	69.4	73.4
BuildDist	0	0	0	0	1.02	225	0.484	68.8	71
RoadDist	0	0	-0.01	10.01	1.03	187	0.524	67	69.1
WaterDist	0	0	0	0	1	1672	0.402	72.1	75

Table 3.17 Macrohabitat model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate elevation, canopy height (CH), normalized difference vegetation index (NDVI), leaf area index (LAI), Euclidean distance to nearest building (BuildDist), Euclidean distance to nearest road (RoadDist), and Euclidean distance to nearest water body (WaterDist) models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95% CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Elevation	0	0	0	-0.01	0	1.02	0.54	60.9	62.6
CH	-0.03	0.01	-0.05	0	1.02	2773	0.53	62.3	64.4
NDVI	1.18	4.42	-7.82	9.61	1.01	533	0.435	65.5	68.1
LAI	-0.16	0.14	-0.43	0.11	1.15	430	0.584	59.7	61.3
BuildDist	0	0	0	0	1	2293	0.407	66.1	71.4
RoadDist	0	0	-0.01	0.01	1	6349	0.405	67.9	71.4
WaterDist	0.56	0.29	0.03	1.04	1.04	99	0.457	66.5	68.6

All behavior event macrohabitat model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the macrohabitat Bayesian models was relatively small. Behavior event data used for green pit viper macrohabitat may not have fit the models well (r^2= 0.37- 0.58, Tables 3.15- 3.17), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Natural noise was predicted to be the best fit for ambush and human noise was the best fit for move abiotic models (Tables 3.18 and 3.19). Ambush behavior was predicted to be positively influenced by natural noise, temperature, and wind speed, but negatively influenced by humidity and precipitation (Figure 3.36). Humidity, precipitation, and natural noise were predicted to positively influence move behavior, and temperature, wind speed, and human noise were predicted to negatively influence it (Figure 3.37). All abiotic coefficients overlapped 0, and several were centered around it, suggesting macrohabitat variables to be poor indicators by themselves.

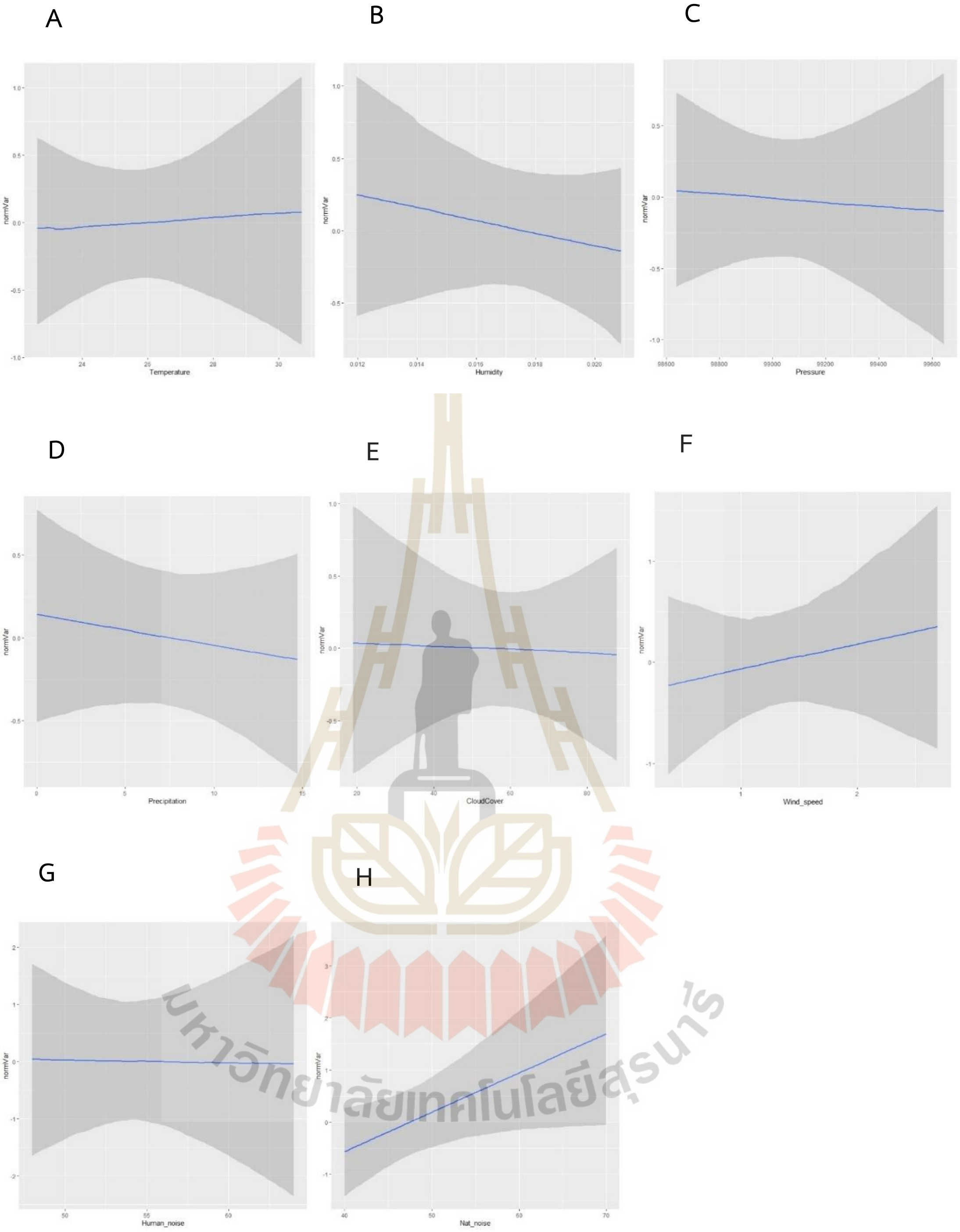

Figure 3.36 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate temperature (A), humidity (B), pressure (C), precipitation (D), cloud cover (E), wind speed (F), human noise (G), and natural noise (H) models.

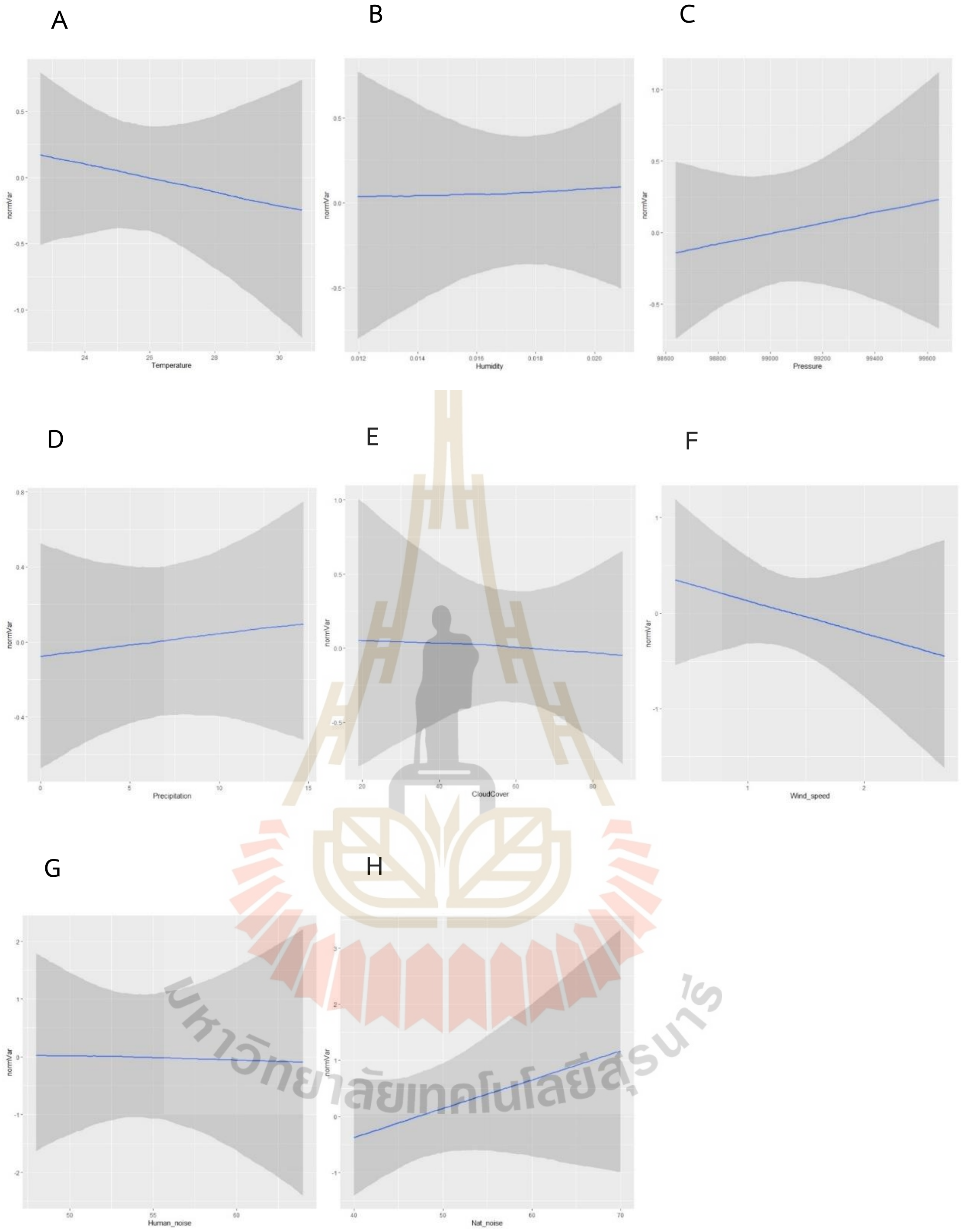

Figure 3.37 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate temperature (A), humidity, pressure (B), precipitation (C), cloud cover (D), wind speed (E), human noise (F), and natural noise (H) models.

Table 3.18 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper ambush behavior state with separate temperature, humidity, pressure, precipitation, cloud cover, wind speed, human noise, and natural noise models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Temperature	0.02	0.09	-0.17	0.2	1.01	1248	0.42	74.6	77.7
Humidity	-43.84	66.47	-178.24	86.25	1.01	410	0.404	74.3	76.7
Pressure	0	0	0	0	1	4490	0.378	75.1	77.6
Precipitation	-0.02	0.03	-0.09	0.05	1	2847	0.422	74.4	76.8
Cloud cover	0	0.01	-0.02	0.02	1	1598	0.421	74.3	76.6
Wind speed	0.25	0.42	-0.59	1.09	1	1200	0.425	73.9	76.2
Human noise	0	0.1	-0.21	0.2	1	4334	0.448	24.9	26.2
Natural noise	0.08	0.04	0	0.15	1	5864	0.673	23.5	25.1

Table 3.19 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper move behavior state with separate temperature, humidity, pressure, precipitation, cloud cover, wind speed, human noise, and natural noise models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Temperature	-0.05	0.09	-0.22	0.13	1.01	1244	0.401	73.2	75.9
Humidity	6.93	59.81	-116.4	126.27	1.11	2472	0.444	68.6	70.4
Pressure	0	0	0	0	1.01	1791	0.412	71.7	74.8
Precipitation	0.01	0.03	-0.05	0.08	1	2491	0.398	72.8	75.2
Cloud cover	0	0.01	-0.02	0.02	1.1	560	0.502	68.5	70.5
Wind speed	-0.34	0.42	-1.15	0.51	1	1843	0.403	72.4	75.8
Human noise	-0.01	0.1	-0.22	0.2	1	6360	0.441	24.9	26.4
Natural noise	0.05	0.05	-0.04	0.14	1	4905	0.569	27.5	29.3

All behavior state abiotic model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the abiotic Bayesian models was relatively high (> 400). Abiotic ambush and movement data may not have fit the models well (r^2= 0.37- 0.67, Tables 3.18 and 3.19), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Human noise was suggested to be the best fit abiotic model for gape, headbob, and probe behavior events (Tables 3.20-3.22). Coefficients of temperature, precipitation, cloud cover, wind speed, and human noise were positive; humidity and natural noise were negative; and pressure was 0 for gape behavior (Figure 3.38). Temperature, human noise, and natural noise coefficients were positive; humidity, precipitation, cloud cover, and wind speed were negative; and pressure was negative for headbob behavior (Figure 3.39). Coefficients of windspeed and natural noise were positive; temperature, humidity, precipitation, cloud cover, and human noise were negative; and pressure was 0 for probe (Figure 3.40). All coefficients had values were very close to or overlapped with 0, however, which imply that these variables are poor indicators by themselves.

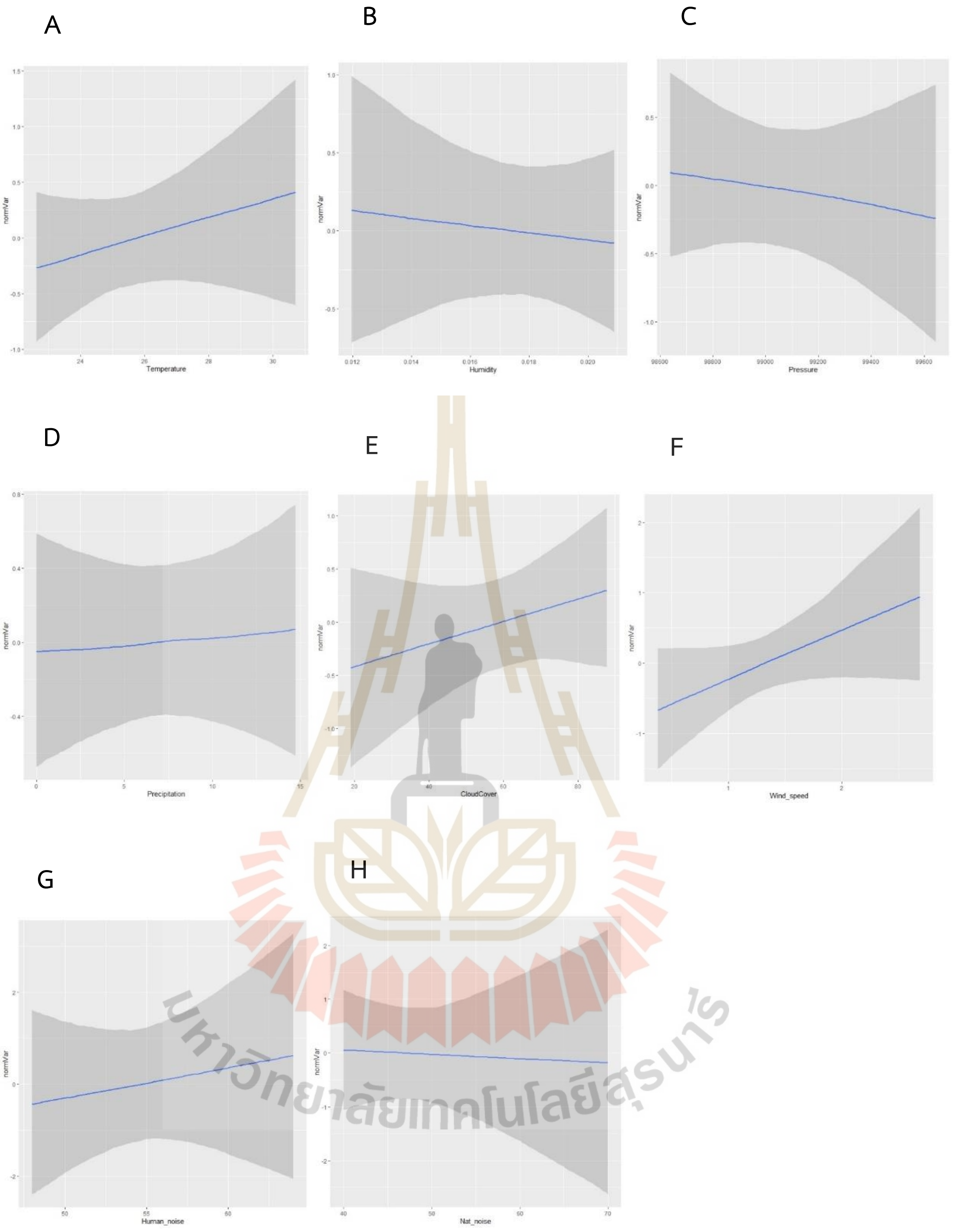

Figure 3.38 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate temperature (A), humidity (B), pressure (C), precipitation (D), cloud cover (E), wind speed (F), human noise (G), and natural noise (H) models.

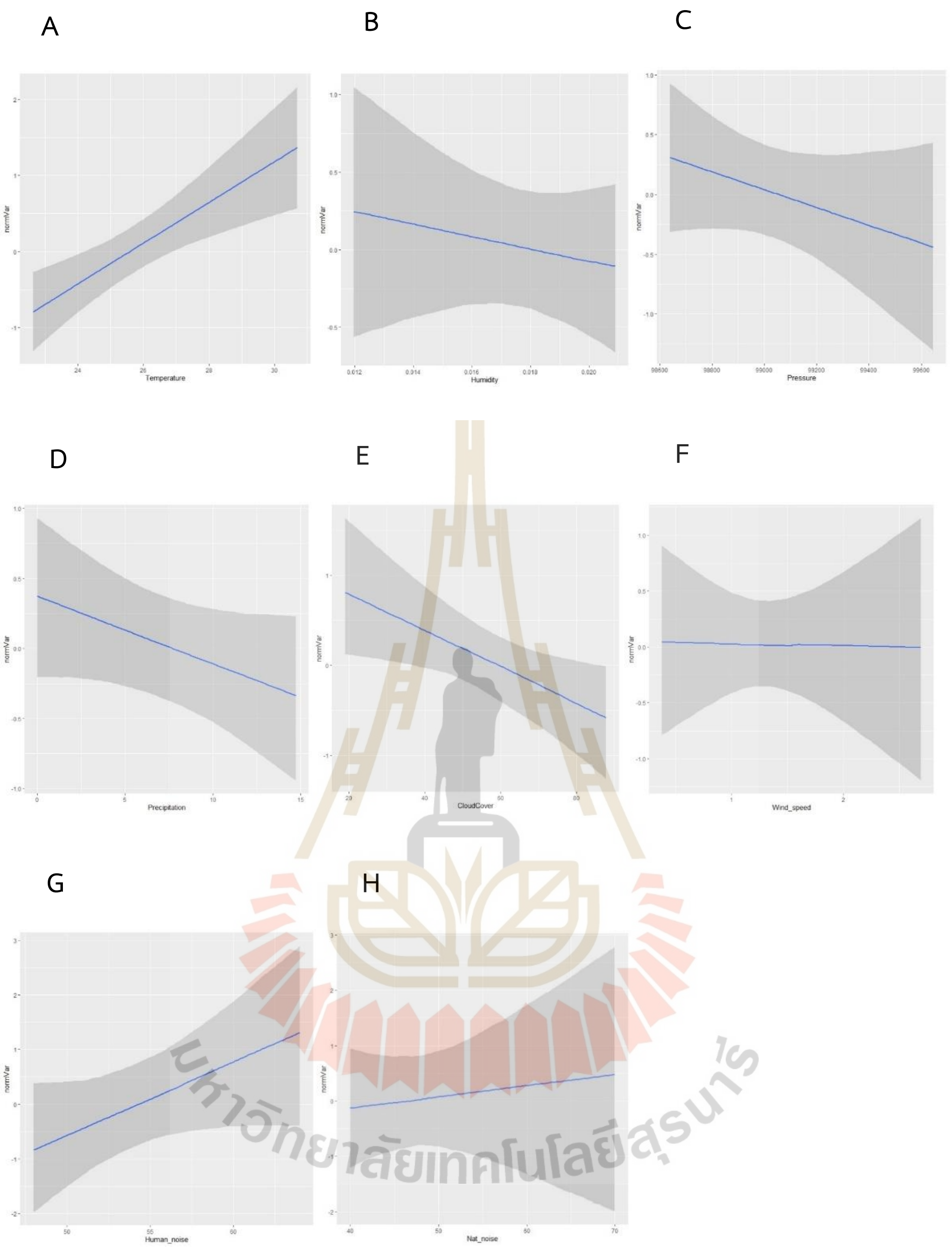

Figure 3.39 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate temperature (A), humidity (B), pressure (C), precipitation (D), cloud cover (E), wind speed (F), human noise (G), and natural noise (H) models.

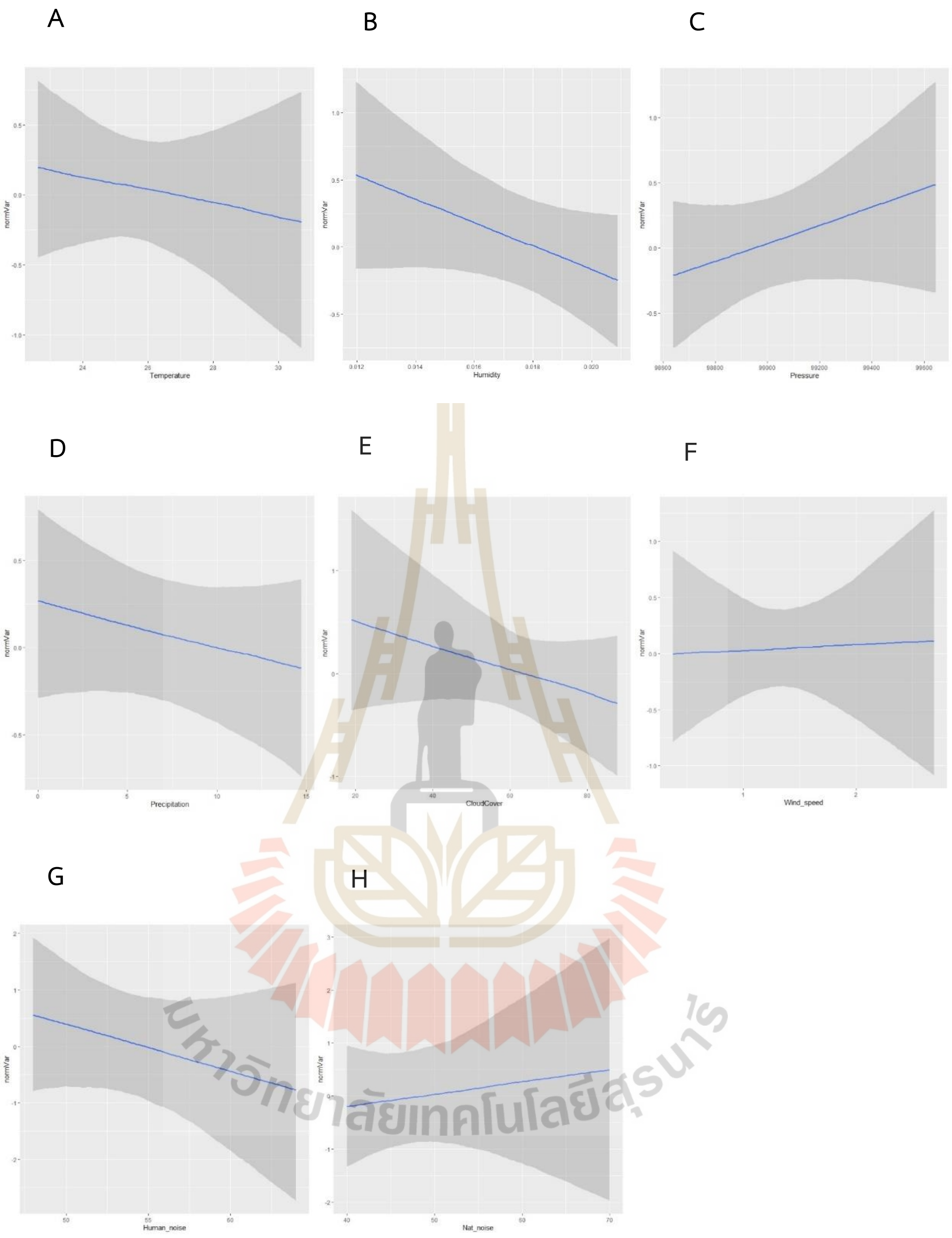

Figure 3.40 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior event with separate temperature (A), humidity (B), pressure (C), precipitation (D), cloud cover (E), wind speed (F), human noise (G), and natural noise (H) models.

Table 3.20 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper gape behavior event with separate temperature, humidity, pressure, precipitation, cloud cover, wind speed, human noise, and natural noise models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Temperature	0.08	0.09	-0.1	0.27	1.01	1475	0.441	72.8	76.1
Humidity	-22.8	66.1	-155.21	108.4	1	2890	0.378	75.9	78.3
Pressure	0	0	0	0	1.01	2269	0.473	72.2	74.8
Precipitation	0.01	0.04	-0.06	0.08	1.02	309	0.427	72.8	76.1
Cloud cover	0.01	0.01	-0.01	0.03	1	3757	0.438	74	76.4
Wind speed	0.7	0.43	-0.14	1.58	1.01	388	0.487	69.2	71.6
Human noise	0.07	0.12	-0.18	0.31	1	4718	0.493	27.4	28.5
Natural noise	-0.01	0.05	-0.11	0.09	1	6509	0.454	29.1	30.8

Table 3.21 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper headbob behavior event with separate temperature, humidity, pressure, precipitation, cloud cover, wind speed, human noise, and natural noise models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Temperature	0.27	0.07	0.12	0.41	1.01	864	0.623	59	61.4
Humidity	-39.78	63.04	-166.12	82.64	1	2446	0.396	71.9	75.1
Pressure	0	0	0	0	1	3638	0.428	69.1	72.1
Precipitation	-0.05	0.03	-0.11	0.01	1	2852	0.447	69.2	71.5
Cloud cover	-0.02	0.01	-0.04	0	1.02	172	0.587	62.7	64.3
Wind speed	-0.02	0.41	-0.84	0.77	1	1433	0.407	72.3	75.7
Human noise	0.13	0.07	-0.02	0.28	1	3265	0.717	17.9	18.8
Natural noise	0.02	0.05	-0.08	0.12	1	1822	0.481	27.4	29.4

Table 3.22 Abiotic model type Bayesian generalized linear mixed effects model results for green pit viper probe behavior with separate temperature, humidity, pressure, precipitation, cloud cover, wind speed, human noise, and natural noise models. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), effective sample size (ESS), r- square, widely applicable criterion (WAIC), and leave-one- out (LOO).

Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS	Rsquare	WAIC	LOO
Temperature	-0.05	0.08	-0.21	0.12	1.01	828	0.421	67.7	70.1
Humidity	-88.49	56.64	-196.87	18.89	1.01	728	0.476	64.7	67.2
Pressure	0	0	0	0	1	2313	0.435	66.9	69.2
Precipitation	-0.03	0.03	-0.09	0.03	1.03	676	0.533	61.7	63.3
Cloud cover	-0.01	0.01	-0.03	0.01	1.04	107	0.472	64.3	66.8
Wind speed	0.04	0.4	-0.81	0.86	1.02	217	0.438	66.9	69.6
Human noise	-0.08	0.09	-0.25	0.09	1	3900	0.576	21.2	22.3
Natural noise	0.02	0.05	-0.08	0.13	1	3826	0.493	30.1	33

All behavior event abiotic model rhat values were close to 1 which indicated chain convergence and traceplots suggested adequate mixing. Effective sample size used in the Bayesian models was small for demographics which reflected overall small sample sizes for the study. Behavior event data used for the general green pit viper may not have fit the models well (r^2= 0.38-0.72, Tables 3.20-3.22), and subsequently the simulated data in the Bayesian models appeared not to perfectly replicate actual data (as observed in predictive check plots), further supporting relatively low model fit.

Variation of vipers, included in each of the Bayesian models as the random effect of individual ID, was relatively low for behavior states (Tables 3.23-3.26). While all model variation coefficients were less than 1.10 and positive, none of the 95% credible intervals overlapped 0. Individual variation coefficients were highest for age within the general models for ambush and species for movement, LQD2 for ambush and move microhabitat models, distance to buildings for ambush and distance to roads for move macrohabitat models, and human noise for ambush and move abiotic models.

Table 3.23 Green pit viper ambush behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for general and microhabitat model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
General	Species	0.63	0.34	0.04	1.25	1	1221
	Sex	0.64	0.34	0.04	1.23	1.01	576
	Age	0.66	0.34	0.04	1.22	1.03	236
Microhabitat	CC	0.65	0.35	0.04	1.26	1.01	883
	PH	0.56	0.3	0.03	1.09	1.01	911
	LQD1	0.7	0.39	0.04	1.46	1.01	1362
	LQD2	0.97	0.68	0.06	2.54	1.02	292
	LQD3	0.91	0.59	0.04	2.29	1	1312
	LA1	0.65	0.34	0.04	1.24	1.01	386
	LA2	0.65	0.34	0.03	1.25	1.01	620
	LA3	0.63	0.34	0.03	1.22	1.01	774

Table 3.24 Green pit viper ambush behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for macrohabitat and abiotic model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
Macrohabitat	Elevation	0.6	0.32	0.03	1.17	1.01	1130
	CH	0.62	0.33	0.04	1.22	1.01	378
	NDVI	0.62	0.33	0.03	1.2	1.02	532
	LAI	0.58	0.31	0.04	1.12	1	1218
	BuildDist	0.68	0.31	0.05	1.17	1.08	66
	RoadDist	0.62	0.34	0.04	1.25	1.01	559
	WaterDist	0.67	0.33	0.05	1.18	1.08	46
Abiotic	Temperature	0.65	0.35	0.04	1.28	1.02	175
	Humidity	0.62	0.33	0.04	1.2	1.02	360
	Pressure	0.63	0.34	0.04	1.26	1	889
	Precipitation	0.64	0.34	0.04	1.22	1.01	695
	Cloud cover	0.64	0.34	0.04	1.22	1.01	399
	Wind speed	0.64	0.34	0.04	1.22	1	508
	Human noise	0.87	0.58	0.05	2.25	1	2823
	Natural noise	0.58	0.38	0.03	1.47	1	3915

Table 3.25 Green pit viper move behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for general and microhabitat model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
General	Species	0.65	0.34	0.04	1.26	1.01	351
	Sex	0.64	0.32	0.04	1.18	1.01	571
	Age	0.6	0.33	0.03	1.17	1.01	570
Microhabitat	CC	0.54	0.29	0.03	1.08	1.01	799
	PH	0.58	0.32	0.03	1.16	1.01	1487
	LQD1	0.63	0.36	0.03	1.34	1	1196
	LQD2	1.08	0.8	0.06	3.01	1.01	685
	LQD3	0.61	0.42	0.03	1.58	1	4001
	LA1	0.59	0.32	0.03	1.17	1	1296
	LA2	0.71	0.36	0.05	1.41	1.09	39
	LA3	0.64	0.35	0.04	1.28	1.03	122

Table 3.26 Green pit viper move behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for macrohabitat and abiotic model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
Macrohabitat	Elevation	0.61	0.32	0.03	1.15	1.07	51
	CH	0.59	0.32	0.03	1.16	1.01	544
	NDVI	0.62	0.32	0.03	1.14	1.04	100
	LAI	0.57	0.3	0.03	1.1	1.01	827
	BuildDist	0.61	0.31	0.04	1.11	1.04	116
	RoadDist	0.63	0.31	0.04	1.13	1.01	325
	WaterDist	0.59	0.32	0.03	1.15	1	1128
Abiotic	Temperature	0.6	0.33	0.03	1.25	1.01	337
	Humidity	0.63	0.34	0.34	1.16	1.11	29
	Pressure	0.62	0.34	0.03	1.26	1.04	79
	Precipitation	0.6	0.33	0.03	1.2	1.01	661
	Cloud cover	0.66	0.32	0.04	1.13	1.1	33
	Wind speed	0.59	0.32	0.03	1.16	1.01	899
	Human noise	0.87	0.58	0.05	2.17	1	4428
	Natural noise	0.71	0.44	0.04	1.68	1	3509

Viper individual variation was also relatively low for behavior events (Tables 3.27-3.29). While all model variation coefficients were less than 1.10 and positive, none of the 95% credible intervals overlapped 0. Individual variation coefficients were highest for age within the general models, LQD2 for microhabitat models, distance to water for macrohabitat models, and human noise for abiotic gape models. Individual viper variation was highest for age and sex within the general models, LQD2 for microhabitat models, distance to roads for macrohabitat models, and natural noise for abiotic headbob models. The highest variation observed for probe behavior was for age within the general models, LQD2 for microhabitat models, LAI for macrohabitat models, and natural noise for abiotic models.

Table 3.27 Green pit viper gape behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for general and microhabitat model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
General	Species	0.63	0.33	0.03	1.19	1.01	732
	Sex	0.58	0.32	0.03	1.16	1	719
	Age	0.63	0.34	0.03	1.21	1.01	1158
Microhabitat	CC	0.65	0.33	0.04	1.2	1.03	172
	PH	0.58	0.32	0.03	1.14	1.02	443
	LQD1	0.64	0.36	0.04	1.35	1	2269
	LQD2	1.08	0.8	0.06	3.24	1.01	1192
	LQD3	0.87	0.58	0.05	2.26	1	4673
	LA1	0.61	0.33	0.03	1.2	1	1322
	LA2	0.67	0.36	0.04	1.3	1.01	656
	LA3	0.63	0.34	0.03	1.23	1	1139

Table 3.28 Green pit viper headbob behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for general and microhabitat model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
Macrohabitat	Elevation	0.63	0.34	0.04	1.24	1	1483
	CH	0.61	0.34	0.03	1.21	1.02	739
	NDVI	0.64	0.34	0.03	1.24	1.01	536
	LAI	0.67	0.35	0.04	1.26	1.01	447
	BuildDist	0.64	0.034	0.04	1.19	1.03	124
	RoadDist	0.6	0.32	0.04	1.18	1.01	1032
	WaterDist	0.69	0.39	0.04	1.4	1.24	15
Abiotic	Temperature	0.64	0.34	0.03	1.28	1.02	290
	Humidity	0.62	0.34	0.04	1.23	1.01	631
	Pressure	0.68	0.35	0.04	1.3	1.03	207
	Precipitation	0.66	0.36	0.04	1.32	1.02	186
	Cloud cover	0.63	0.33	0.04	1.22	1.01	955
	Wind speed	0.63	0.34	0.04	1.25	1.01	343
	Human noise	1.03	0.68	0.05	2.57	1	3879
	Natural noise	0.8	0.49	0.04	1.86	1	4221

Table 3.29 Green pit viper probe behavior Bayesian generalized linear mixed effects model individual variation (random effect) results for general and microhabitat model types. Output includes estimate, estimate error (EE), 95% low and high credible intervals (95%CI_L and 95%CI_H), Gelman- Ruben statistic (Rhat), and effective sample size (ESS).

Model type	Model	Estimate	EE	95%CI_L	95%CI_H	Rhat	ESS
General	Species	0.59	0.32	0.03	1.13	1.01	558
	Sex	0.63	0.33	0.04	1.17	1.01	566
	Age	0.63	0.33	0.04	1.16	1.04	93
Microhabitat	CC	0.59	0.31	0.04	1.13	1.01	454
	PH	0.58	0.31	0.04	1.13	1.01	593
	LQD1	0.67	0.38	0.04	1.4	1	1483
	LQD2	0.94	0.67	0.04	2.29	1.08	41
	LQD3	0.83	0.57	0.04	2.12	1	1787
	LA1	0.61	0.33	0.03	1.19	1.01	597
	LA2	0.61	0.33	0.04	1.19	1.01	369
	LA3	0.74	0.39	0.05	1.36	1.13	26

3.5 Discussion

All aspects of field study between 2020 to 2021 must be evaluated uniquely to prior years due to the global pandemic COVID- 19. Although estimation of deaths (in the millions) linked to the virus has been controversial (Ioannidis, 2021), the significant impact to humans has been undeniable. This unique worldwide public health emergency (Cruz et al., 2021) significantly influenced human contact with one another, especially through trade, travel, and recreation. Impact to wildlife is a topic of great interest with this reduced activity by humans (Rabdou, 2020; Zelmer et al., 2020), which is still ongoing as of submission of this written dissertation (2021).

The pandemic clearly influenced logistics for this section. Travel even within provinces was severely limited at times, particularly during or close to holidays, and study sites were completely closed or required strict protocols such including testing and vaccination. Unfortunately, testing was not covered by funding sources and vaccinations were not widely available during throughout the study period (< 7% of Thailand was vaccinated by the conclusion of this dissertation). Effects of the pandemic on study results should be viewed in two ways, the first, this dissertation activity and behavior pattern study represents an anomaly and should not be directly compared to "normal" conditions pre- and post- pandemic years; and second, these results are a unique opportunity to see how wildlife may behave and survive when human activities are drastically minimized.

The **STRANGE** framework (Webster and Rutz, 2020) to address ability to generalize results from animal sampling was discussed and addressed to the best of our ability in the early planning stages (refer to dissertation preprints reposited online, discussed in the introduction of this dissertation) and is worth explicitly discussing post-hoc due to small sample sizes, unequal and irregular sampling regimes, and possible sources of sampling biases. **S**ocial background: social behavior of tropical snakes is scarce, but observations of green pit vipers interacting with conspecifics has been observed prior (Barnes et al., 2020) and in this dissertation, suggesting that conspecifics can alter the behavior (cause them to abandon foraging sites, cease ambushing, increasing movement behavior). **T**rappability and self-selection likely had the largest influence on this study which was likely biased towards vipers which were visible and perhaps highly exposed to predators (not in shelter sites), against small individuals (males and juveniles, particularly), against species not clearly visible due to color (*T. kanburiensis*), against arboreal individuals which can be more difficult to locate and not logistically feasible to set cameras near, and towards individuals near anthropogenic features due to accessibility- all of which were compounded by inability to reliably re- identify individuals. **R**earing history was not a direct factor to this study as only wild individuals were sampled, but should certainly be considered if results are extended to a laboratory setting. **A**cclimation and habituation: whether vipers (and predators, prey, and conspecifics) were influenced by the act of humans getting fairly close and leaving an object which may have human scent/recognition for a period of time requires consideration which was addressed directly by recording and/or excluding vipers which showed clear negative response to initial camera setup and indirectly with randomly set cameras, future studies would benefit from an experimental study design which was not possible due to ethics and research permissions for this dissertation. **N**atural changes in responsiveness was addressed through attempting to sample through all seasons, but logistics (local conditions and global pandemic) made this challenging. **G**enetic make-up: not well- understood for green pit vipers with respect to behavior, but male, female, and species morphometrics and spatial ecology (i.e.- Strine et al., 2015) have suggested genetic differences exist and care should be taken with behavior extrapolations at these and population levels. **E**xperience: very similar to A, individual re- identification should be considered as repeated sampling was potentially possible although recording viper size, sex, and location likely helped address this.

While extremely logistically challenging with the pandemic, intensive study of activity and behavior of green pit vipers from this study provide invaluable contributions to a scarcely studied group of organisms in the wild. Much of this chapter supplements prior study, such as observations that green pit viper species are primarily nocturnally foraging predators which can spend long periods of time ambushing (Strine et al. 2018). Active behavior was observed to be displayed at night and inactive to be observed during the day similarly to Strine et al. (2018), as were behavior events which were also observed similarly primarily at night in this dissertation and in Bangkok with *T. albolabris* by Barnes and Knierim (2019). Probe and gape behaviors also being primarily observed at night by similarly nocturnal sidewinder rattlesnakes was explained by Barbour & Clark (2012) as being due to decreased viper vision capabilities at night and exhibiting these behaviors during the day could increase detection of visually vigilant prey.

From radiotelemetry fieldwork ambush and resting behaviors were observed to be positively correlated with temperature and humidity for *T. macrops* at Sakaerat by Strine et al. (2018), which is supported to a limited extent by data obtained through remote sensing from this current dissertation which also observed green pit viper (*T. macrops* at SBR and *T. albolabris* at SUT) ambushing marginally more during conditions with higher temperatures, but differed from that prior study in that they ambushed less frequently with higher humidity. Resting was not observed frequently enough by this current dissertation to assess this behavior, and Strine et al. (2018) did not observed tracked vipers moving often for comparisons. The many other abiotic variables assessed in this dissertation have not been investigated by any behavioral study with green pit vipers, unfortunately interactions between them were not assessed due to the preliminary nature of this work. Which abiotic variables may be most important indicators and vital to viper basic biology were independently identified; further investigation of these and interactions between them require additional study. Benefits of such research could prove invaluable for optimizing survey and field efforts as well as further illuminating behavior and activity patterns.

Of direct interest to snakebite management and conservation are interpretations of viper behavior to natural and anthropogenic factors which can be gleaned from this dissertation. Unfortunately surveys and subsequent cameras monitoring behavior were biased towards roads and buildings due to logistics, access and size of camera equipment especially, but behaviors did not all show clear bias towards positive or negative effects which is interesting to discuss. Buildings appeared to negatively influence ambush and move behavior states as well as the headbob behavior event, a positive influence on gape event, but had little to no influence for probe event. Sheltering under man- made structures was rarely observed (8% of total observations) by Strine et al. (2018), which could explain the negative effect of buildings on ambush behavior which appears to be closely associated from observations with movement ecology studies (Barnes et al., 2017; Strine et al., 2018).

Ambush and move behaviors were observed in this dissertation to be more frequently observed near roads; previous study has not investigated this variable directly prior with green pit vipers but vipers in rural areas of SBR were observed to have smaller home ranges and move less there (Barnes et al., 2017) than in forests (Strine et al., 2018) which is an interesting comparison to the dissertation results. The observation of more movement during this current study could be explained by the pandemic, with fewer people appearing to drive on roads at SBR and SUT perhaps there is less fear by vipers or their prey of this anthropogenic habitat feature. Indirect measures of human presence, human and natural noise, were investigated by this dissertation but not prior work and present interesting conclusions when viewed with the pandemic; human noise which was almost certainly diminished during the pandemic (less people present and active) appeared to have almost no influence on ambush or move behavior but for more spontaneous behavior events effects were mixed (probe was negative but gape and headbob positive), however, all behavior and events except for gape (little to no influence) were positively affected by natural noise.

Observer and human influence to green pit viper behavior and behavior study as at SUT with *T. albolabris* (displaying stress behavior when approached at night, thus resulting in low sample sizes) was not observed in previous behavior study of *T. macrops* in rural areas of SBR (this dissertation and Barnes et al., 2017) or *T. albolabris* in suburban Bangkok (Barnes and Knierim, 2019) and also requires further study, specifically. Humans influenced vipers, but vipers also factored into daily life of humans at SUT and SBR. Humans were observed on cameras at both SBR and SUT (further elaborated in Chapter 5), and during the course of this dissertation two students were bitten by green pit vipers at SUT. Students at SUT frequently wear improper footwear, do not use lights, or display situational awareness at night (Hodges et al., 2021) and this dissertation highlights the danger of these failings with activity (foraging and movement) of the most frequently encountered group of venomous snakes on campus displayed primarily at that time.

Behavior states, particularly ambush and move, have been moderately well studied with green pit vipers particularly within the context of movement ecology (i.e.- Devan- Song et al., 2016, Barnes et al., 2017, and Strine et al., 2018) but published behavior events occurring within the ambush behavior are lacking. This dissertation was exploratory with regards to behavior events, focusing primarily on the presence of these behaviors and what variables might possibly affect the display of them. Ultimate factors such as the role they play in greater ecology of the vipers, such as for chemosensory purposes and stress responses, as well as how they might interact with each other.

Although prior radiotelemetry studies with green pit vipers, Barnes et al. (2017) in rural areas of Sakaerat and Strine et al. (2018) in forested parts, had similar or larger sample sizes than this dissertation neither clearly discussed individual viper behavior difference. Although variation was relatively low for behavior states and events in this dissertation, none of the credible intervals overlapped zero which would suggest nearly complete lack of individuality. Some of this variation can be inferred through the general model variables (species, age, and sex), but further work is required as are more in- depth topics like personality and boldness which are severely lacking within snake behavioral studies.

This current dissertation and previous movement ecology work with green pit vipers have only just begun to address proximate expression of some behaviors for this group. The surface has barely been scratched for broader behavioral and ethological questions for green pit vipers- what is the development, causation, survival value, and evolution (Tinbergen, 1963) of the foraging behavior observed by those previous studies? What role do instinct (postulated by Charles Darwin to vary between individuals with potential to be heritable; Darwin, 1873) and learning play with behaviors? While green pit vipers may serve as poor models for traditional space use behavior studies due to their limited movement, this dissertation suggests that same limitation may make them good candidates for traditional behavior study compared to other vertebrates- it is clearly possible to effectively monitor foraging green pit vipers for long periods of time and observe interesting behavior events and natural history observations from which the aforementioned complex behavior and ethological questions can be formed.

3.6 Conclusion

Although field study was significantly impacted by the global COVID- 19 pandemic, comprehensive study of green pit viper activity pattern and behavior at two sites in Nakhon Ratchasima was carried out. Limited travel for researchers presented a unique opportunity in that lockdowns at Suranaree University of Technology and closure of

Sakaerat Biosphere Reserve to general public resulted in an extended period of reduced human activity. As such, this study likely presented results of vipers displaying more natural behavior in areas where they likely would have experienced more anthropogenic influence which requires consideration for evaluation and comparison to other studies.

Collectively summarized, green pit vipers displayed activity patterns similar to prior radiotelemetry studies- active foraging and moving behaviors primarily observed at night, and inactive resting behavior almost exclusively during the day. Active behavior was consistently still primarily displayed at night when viper sex and age were further examined. Temporal expression of behavior events differed, however, within sex and age which could be attributed to much fewer observations compared to behavior states and potentially behavior states experiencing more constraints and serving different functions. Further activity pattern and behavioral study is required for green pit vipers, both continuing with species investigated in this dissertation but especially the many (> 35 species) others which have received very little study in the wild, within general natural history (theoretical) and snakebite management (applied) contexts.

Interestingly, anthropogenic variables were suggested to be important for all models they were included in. Ambush behavior was negatively associated with increased building distance but at sites with higher levels of natural noise. Gape and headbob behavior events were positively associated with anthropogenic noise, but probe behavior was negatively associated. Further study is required to adequately assess the impact of anthropogenic disturbance, both direct and indirect, to green pit vipers.

Despite the global pandemic significantly altering daily lifestyles of humans, resulting in drastic prevention and mitigation measures including travel restrictions and closure of recreation and protected areas which directly affected data collection measures for this dissertation and current chapter especially, four of the study objectives were still able to be moderately well addressed. The following objectives 1) behavior and activity patterns were determined for the big- eyed pit viper and white-lipped viper, 2) how much and when different sexes (small sample size of age created overlapping intervals which rendered estimates largely not useful) express different behaviors, 3) what potential influences abiotic and habitat features might have on green pit vipers (no co- occurring species were found at Suranaree, and sample size of 1 for a second co- occurring species at Sakaerat), and 4) what threats vipers and humans may face from each other were adequately analytically investigated in this chapter. Caution should be derived when interpreting these results and comparing them to prior and future study as direct human activity influence to viper and other wildlife behavior was unique and likely highly limited during the study period due to the global pandemic. Unfortunately, especially small sample sizes primarily induced by decreased sampling effort availability during the pandemic prevented inferences from being made to objectives 5) investigation of sympatric and co- occurring viper species behavior and activity patterns and 6) comparison of behavior and activity patterns between isolated populations (subpopulations) of vipers.

3.7 References

Barbour, M.A., and R.W., Clark. (2012). Diel cycles in chemosensory behaviors of free-ranging rattlesnakes lying in wait for prey. *Ethology 118*: 480-488.

Barnes, C. (2017). The spatial ecology, habitat selection, and behavior of big- eye green pit vipers (*Trimeresurus macrops*) in human dominated and protected areas in the Sakaerat Biosphere Reserve. Master's Thesis, Suranaree University of Technology, Thailand.

Barnes, C.H., and Knierim, T.K. (2019). Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus* (*Cryptelytrops*) *albolabris* (Reptilia: Squamata: Viperidae) vipers in Bangkok, Thailand. *Journal of Threatened Taxa 11*(12): 14503-14510.

Barnes, C.H., Strine, C.T., Suwanwaree, P., and Hill III, Jacques. (2017). Movement and home range of green pit vipers (*Trimeresurus* spp.) in a rural landscape in Northeast Thailand. *Herpetological Bulletin 142*: 19-28.

Burghart, G.M. (2020). The learning repertoire of reptiles. In: Zoo Animal Learning and Training, First Edition. Edited by Melfi, V.A., Dorey, N.R., and Ward. S.M. pp. 227-230. John Wiley & Sons Ltd.

Bürkner, P.C. (2017). brms: An R package for bayesian multilevel models using stan. Journal of Statistical Software.

Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., Hobaiter, S., Hofmeester, T. R., Kalan, A. K., Rabaiotti, D., and Rivet, D. (2020). A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice 8*: e239.

Caro, T. (2007). Behavior and conservation: a bridge too far? *Trends in Ecology and Evolution 22*: 394-400.

Caro, T., and Sherman, P.W. (2013). Eighteen reasons animal behaviourists avoid involvement in conservation. *Animal Behavior 85*: 305-312.

Chan-Ard, T., Grismer, L., and Stuart, B. (2012). *Cryptelytrops kanburiensis*. The IUCN Red List of Threatened Species 2012.

Cox, M.J., Hoover, M., Chanhome, L., and Thirakhupt, K. (2012). The Snakes of Thailand. Chulalongkorn University Museum of Natural History, Bangkok, Thailand.

David, P., Vogel, Gb, and Dubois, A. (2011). On the need to follow rigorously the Rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: The case of the nominal genus *Trimeresurus* Lacipede, 1804 (Reptilia: Squamata: Viperidae). *Zootaxa 2992*: 1-51.

Devan- Song, A., Martelli, P., and Karraker, N.E. (2017). Reproductive biology and natural history of the white lipped pit viper (*Trimeresurus albolabris* Gray, 1842) in Hong Kong. *Herpetological Conservation and Biology 12*: 41-55.

Dixon, P., and Ellison, A.M. (1996). Introduction: Ecological applications of Bayesian inference. *Ecological Applications 6*: 1034-1035.

Doody, J.S., Burghardt, G.M., and Dinets, V. (2013). Breaking the social-non-social dichotomy: a role for reptiles in vertebrate social behavior research? *Ethology 199*: 1-9.

Dorazio, R., and Johnson, F. (2003). Bayesian inference and decision theory- a framework for decision making in natural resource management. *Ecological Applications 13*: 556- 563.

Ellison, A.M. (1996). An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecological Applications 6*: 1036-1046.

Ellison, A.M. (2004). Bayesian inference in ecology. *Ecology Letters 7*: 509-520.

Ford, N. (1995). Experimental design in studies of snake behavior. *Herpetological Monographs 9*: 130-139.

Fraser, H., Parker, T., Nakagawa, S., Barnett, A., and Fidler F. (2018). Questionable research practices in ecology and evolution. *PLoS ONE 13*(7): e0200303.

Friard, O., and Gamba. M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution 7*(2016): 1325- 1330.

Gabry, J., and Mahr, T. (2021). bayesplot: Plotting for Bayesian Models. R package version 1.8.1.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. (2020). Bayesian data analysis third edition. Electronic edition by authors.

Gelman, A., Hwang, J., and Vehtari, A. (2014). Understanding predictive information criteria for Bayesian models. *Statistics and Computing 24*: 997-1016.

Jomnonkwao, S., Sangphong, O., Khampirat, B., Siridhara, S., and Ratanavaraha, V. (2016). Public transport promotion policy on campus: evidence from Suranaree University in Thailand. *Public Transportation 8*(2): 185-203.

Katabuchi, M. (2015). LeafArea: an R package for rapid digital image analysis of leaf area. *Ecological Research 30*: 1073-1077.

Kearney, M.R., Gillingham, P.K., Bramer, I., Duffy, J.P., and Maclean, I.M.D. (2020) A method for computing hourly, historical, terrain- corrected microclimate anywhere on Earth. *Methods in Ecology and Evolution 11*(1): 38-43.

Landert, K.A. (2017). Comparing photographic and GIS-based applications for estimating canopy cover in Southern Appalachian bogs. Proceedings of The National Conference On Undergraduate Research (NCUR): 66-73.

Lehner, P.N. (1987). Design and Execution of Animal Behavior Research: An Overview. *Journal of Animal Science 65*(5): 1213-1219.

Machado, B.B., Orue, J.P., Arruda, M.S., Santos, C.V., Sarath, D.S., Goncalves, W.N., Silva, G.G., Pistori, H., Roel, A.R., and Rodrigues-Jr., J.F. (2016). BioLeaf: A professional mobile application to measure foliar damage caused by insect herbivory. *Computers and Electronics in Agriculture 129*: 44-55.

Maclean, I.M.D., Mosedale, J.R., and Bennie, J.J. (2019). Microclima: An R package for modelling meso- and microclimate. *Methods in Ecology and Evolution 10*(2): 280-290.

Mahasandana, S., and Jintakune, P. (1990). The species of green pit viper in Bangkok. *The Southeast Asian Journal of Tropical Medicine and Public Health 21*: 225-230.

Malhotra, A., and Thorpe, R.S. (2004A). A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pit vipers *Trimeresurus* and *Ovophis*. *Molecular Phylogenetics and Evolution 32*: 83-100.

Martin, P., and Bateson, P. (2007). Measuring behavior: an introductory guide. King's College, England.

Meemano, K., Pochanugool, C., and Lim Thongkul, S. (1987). Incidence of snakebites at Chulalongkorn hospital. In: Gopalakrishnakone, P., & Tan, C.K. (Eds), Progress in Venom and Toxin Research. National University of Singapore, Singapore, pp. 36-40.

Meredith, M., and Ridout, M. (2016). Overlap: estimates of coefficient of overlapping for animal activity patterns. R package version 0.3.2: http://CRAN.R-project.org/package=overlap

Naithani, A., Suwanwaree, P., and Nadolski, B. (2018). Bird community structure of Suranaree University of Technology Campus, Nakhon Ratchasima Province, Thailand. *Pakistan Journal of Zoology 50*(4): 1257-1265.

Padgham, M., Rudis, B., Lovelace, R., and Salmon, M. (2017). osmdata. Version 0.1.8.

Panusittikorn, P., and Prato, T. (2001). Conservation of protected areas in Thailand: the case of Khao Yai National Park. *Protected Areas East Asia 18*(2): 67-76.

Pebesma, E. (2018). sf: Simple Features for R. URL https://CRAN.R-project.org/package= sf. R package version 0.6-1.

Peterson, R.A., and Cavanaugh, J.E. (2019). Ordered quantile normalization: a semiparametric transformation built for the cross-validation era. *Journal of Applied Statistics 47*: 1-16.

Pierce, A.J. and Pobprasert, K. (2007). A portable system for continuous monitoring of bird nests using digital video recorders. *Journal of Field Ornithology 78*: 322-328.

Registration Office Department of the Interior, Ministry of the Interior. (2019). "รายงานสถิติจำนวนประชากรและบ้านประจำปี พ.ศ.2562" Statistics, population and house statistics for the year 2019. Retrieved 10 March 2020.

Ridout, M.S., and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics 14*: 322-337.

Schuett, G.W., Clark, R.W., Repp, R.A., Amarello, M., Smith, C.F., and Greene, H.W. (2017). Social behavior of rattlesnakes: a shifting paradigm. In: Schuett, G.W., Feldner, M.J., Smith, C.F., and Reiserer, R.S. (eds.). Rattlesnakes of Arizona, vol. 2. Eco Publishing, Rodeo, NM, USA. p. 161-244.

Sharp, A., and Nakagoshi, N. (1997). National parks and protected area in Thailand. *Journal of International Development Cooperation 3*: 53-67.

Singh, M., Griaud, C.C., and Collins, M. (2021). An evaluation of the effectiveness of protected areas in Thailand. *Ecological Indicators 125*(2021): 107536.

Strine, C., Silva, I., Nadolski, B, Crane, M., Barnes, C., Artchawakom, T., Hill, J., and Suwanwaree, P. (2015). Sexual dimorphism of tropical green pit viper *Trimeresurus* (*Cryptelytrops*) *macrops* in Northeast Thailand. *Amphibia-Reptilia 36*: 1-12.

Strine, C., Silva, I., Barnes, C.H., Marshall, B.M., Artchawakom, T., Hill III, J, and Suwanwaree, P. (2018). Spatial ecology of a small arboreal ambush predator, *Trimeresurus macrops* Kramer, 1977, in Northeast Thailand. *Amphibia- Reptilia 39*(2018): 335-345.

Thornhill, R. (1991). The study of adaptation. In: Interpretation and explanation in the study of behavior. Eds. Beckoff, M., & Jamieson, D. Boulder, CO: Westview Press.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie 20*: 410-433.

Uetz, P.and Hallermann, J. (2015). Reptile database. http://reptile-database.reptarium .cz. Accessed on March 01, 2015.

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., and Gelman, A. (2019). loo: Efficient leave one-out cross-validation and WAIC for Bayesian models. R package version 2.2.0: https://mc-stan.org/loo

Viravan, C., Looareesuwan, S., Kosakarn, W., Wuthiekanun, V., McCarthy, C. J., Stimson, A.F., Bunnag, D., Harinasuta, T., and Warrell, D.A. (1992). A national hospital-based survey of snakes responsible for bites in Thailand. *Transactions of the Royal Society of Tropical Medicine and Hygiene 86*: 100-106.

Warrell, D.A. (2010). Guidelines for the clinical management of snake-bites in the south-east Asia region. World Health Organization, Regional Office for South East Asia, New Delhi, pp. 1-67.

Waters, R.M., Bowers, B.B., and Burghardt, G.M. (2017). Personality and individuality in reptile behavior. In: Personality in Non- human Animals (eds. Vonk, J., Weiss, A., and Kuczaj, S.), pp. 153-184. New York, NY: Springer.

Webster, M., and Rutz, C. (2020). How STRANGE are your study animals? *Nature 582*: 337-340.

Wintle, B.A., McCarthy, M.A., Volinsky, C.T., and Kavanagh, R.P. (2003). The use of Bayesian model averaging to better represent uncertainty in ecological models. *Conservation Biology 17*: 1579-1590.

CHAPTER IV

COMPUTER VISION FOR AMBUSH FORAGING PREDATOR BEHAVIOR ANALYSIS

4.1 Abstract

Computer vision is a form of image based artificial intelligence which mimics human ability to distinguish or classify things by generating rules for the form, grouping, and changing of image pixels. The MotionMeerkat program and Keras deep learning in program R were used in this study to understand the efficacy and efficiency of computer vision for addressing a key conservation and snakebite management concern, behavior of green pit vipers. A total of 24202 scans/minutes of recordings from 8 *Trimeresurus macrops* reviewed by MotionMeerkat and manually by a human reviewer to detect behavior events (gape, headbob, and probe), and 3 models (field only, field with supplementation of online images for training and validation, and online images only for training and validation) were evaluated for *T. macrops* and *Crotalus viridis* convolutional neural network deep learning models to categorize ambush/rest and move behavior states as well as images with no vipers ("background"). More time was required for MotionMeekat to review (210.7 seconds) compared to manual review (129.2 seconds), and the program greatly overestimated (2162 flagged potential observations) behavior events compared to manual review (159 observations). Deep learning model run time was long (0.5- >6 hours) and accuracy proposed by the models varied (0.3-98%). The MotionMeerkat program was straightforward and easy to use and able to be run as a background task, but manual review should still be undertaken of flagged observations due to overestimation. Deep learning had potential for high accuracy, but required significant computational power and time, as well as high conceptual prior knowledge. There is great potential for

computer vision to address conservation issues, but serious consideration is required for conceptual prior knowledge, computational power, and ability of these methods to adequately address topics.

4.2 Introduction

Large and comprehensive ecology datasets are now possible to store and accessible to broad audiences with the advent of cloud- based storages systems. Nearly all forms of computer vision, from machine learning to deep learning, are now possible for ecologists due to the advent of advanced computer algorithms made accessible in open programs (such as MotionMeerkat) and frequently used programs like R (through packages like Platypus and Keras). Furthermore, computing power has surged since the 1990's, making it feasible to train large neural networks in a reasonable amount of time and powerful graphics processing unit (GPU) cards have recently become available due to the progression of the gaming industry (Islam, 2020). Publicly online available central processing units (CPU) and GPU's (i.e.- Kaggle) are further facilitating acceptance and utilization of computer vision.

Machine learning, most simply, refers to algorithms which can automatically generate predictive models by detecting patterns in data (Christin et al. 2019). Learning can occur with or without supervision and input by human users. Without supervision, computers automatically discover patterns and similarities in unlabeled and unclassified data, subsequently this method is frequently used in exploratory analyses to detect features in data, reduce its dimensions, or condense similar data into groups (Valletta et al., 2017). Alternatively, learning can occur with supervised training- a labelled dataset with target objects is provided first to computers to train associations with those labels, with the ultimate goal of being able to recognize and identify those associations in other datasets (LeCun et al., 2015). Machine learning, within the overarching field of computer vision and artificial intelligence, provides system to learn and improve automatically from experience through an explicit program with minimal human interaction (unsupervised learning, Islam, 2020). Within machine learning, deep learning is a richer structure of neural networks in which image features are not a priori designed, but rather learned from existing labelled images (supervised learning, Islam, 2020). Computer vision has been successfully applied within the field of ecology to classification tasks (Cutler et al., 2007), ecological modelling (Recknagel, 2001), and studying animal behaviour (Valletta et al., 2017).

To understand how far computer vision has progressed and potential application of two subfields, machine learning and deep learning, the programs MotionMeerkat (machine learning, pixel detection change specifically) and Keras R package (deep learning) were applied for a significant ecology and conservation topic- venomous snake behavior image analysis (Objective 7 in Chapter I - "Assess effectiveness and feasibility of computer vision (such as deep learning) to behavioral study with wild green pit vipers"). Worth noting is that artificial intelligence and the subfields within are complex, indeed entire theses have been written on these topics and their application to wildlife and behavior (i.e., Islam, 2020). The chapter of this current thesis, "Computer vision for ambush foraging predator analysis" condenses much of the theory and concepts to address an audience with limited understanding of AI and might be considering applying these methods to their own projects.

Traditionally and theoretically, large datasets are desired and even necessary for machine learning application depending on the complexity of the research question but the reality is many wildlife projects (particularly behavioral studies) may be limited by a variety of factors (machine learning and deep learning application discussion specifically is provided in Christin et al., 2021) including species detection/population size, logistics (number of cameras and subsequently number of hours available to use, camera recording quality, ability to store/reposit recordings, personnel safety in the field for camera maintenance, to name a few), and ethics (potential influence of setting and leaving cameras to monitor wild animals). Adequate conceptual (theoretical) and practical (computing skills and coding) of models requires consideration. Computing power is a significant limitation for AI application, also. Both comparatively small dataset size and computing power were issues that were presented within this thesis, which should serve as a baseline for behavioral wildlife studies considering implementing AI technology.

4.3 Methods

4.3.1 Datasets

For solving image classification questions, the dataset refers to a collection of images where each image is a data point (Rosebrock, 2017). Machine learning algorithms are heavily dependent on the size, quality, and representation (application potential for future test data) of training datasets (Islam, 2020). Image data was drawn from two different sources, timelapse pictures and videos and continuous feed videos.

Data used for green pit viper pixel change detection methodology was sourced from this dissertation and a prior MSc. thesis (Barnes, 2017). All vipers were *Trimeresurus macrops* and recorded at Sakaerat Biosphere Reserve, 3 vipers were from the prior thesis which utilized a combination of timelapse cameras and 5 were from this current dissertation which utilized continuous feed cameras.

Continuous feed videos used for training deep learning models were drawn from green pit viper data collected during the course of this thesis at Sakaerat Biosphere Reserve. An additional dataset was made available for this study by Dr. Rulon Clark's lab, prior timelapse video recordings of prairie (*Crotalus viridis*). Online images using CalPhotos and iNaturalist repositories using keywords "green pit viper" and "prairie rattlesnake" were used to supplement continuous feed image data in separate models to determine influence of this type of data supplementation.

4.3.2 Manual review method

The graduate student leading the research for this dissertation (C. H. Barnes) reviewed all recordings utilized for the study. A single field assistant opportunistically reviewed recordings for timelapse cameras set between 2016- 2017 to corroborate findings. Behavior state and event descriptions were derived from field observations of vipers during previous study (Strine, 2015; Strine et al., 2018) and this dissertation, and applied to subsequent videography. Briefly, timelapse pictures (Bushnell cameras) were reviewed frame-by-frame, and timelapse videos (Brinno) and continuous feed videos were watched at 1-8 × speed. In this protocol, C. H. Barnes and field assistant recorded in Excel datasheets behavior events observed in the videos, noting the video time stamp when an animal behavior event or state (behaviors of short and long duration, respectively; see Chapter III for full definitions) in specified categories occurred. Behavior states were of interest to deep learning models, including move and for simplicity of the model ambush and rest were combined into a single classification. The pixel detection method program, MotionMeerkat, was primarily designed and intended to be used to identify observations and behaviors of short duration (Weinstein, 2015) so behavior events (gape, headbob, and probe) and were investigated. Full definitions for specific behavior events and states, and links to example recordings, are provided in Chapter III. A random subset of 2 recordings per viper were selected using the "runif" function in R for efficiency comparisons, duration required for manual (C. H. Barnes) and MotionMeerkat methods.

4.3.3 Pixel change detection method

Efficacy and efficiency of computer vision for application to viper behavior events was evaluated using the program MotionMeerkat (Weinstein, 2015). MotionMeerkat has the ability to determine when shifts to different behaviors occur, when discrete behavior events take place, as well as indicate disturbance to vipers from other organisms. This program falls under the subfield of machine learning within computer vision, as it is unsupervised (no training data or prior input by a user is required).

MotionMeerkat was run for recordings haphazardly with three laptop computers. Settings used within MotionMeerkat included 5 for background movement and 0 for organism movement speed with "draw motion objects" (boxes). A total of 24,202 scans (timelapse cameras set to record at 1 minute intervals; 18,871) or minutes (continuous feed cameras; 5,331) for eight female green pit vipers (Table 4.1) were included in MotionMeerkat analyses.

Table 4.1 Summary of big- eyed pit vipers (*Trimeresurus macrops*) observed on timelapse (Bushnell or Brinno) or continuous feed (video) cameras at Sakaerat Biosphere Reserved, Thailand.

Viper ID	Season	Forest or disturbed	Timelapse or video	Scans or minutes reviewed
TRMA271	Cold	Forest	Timelapse (Bushnell)	7930
TRMA273	Cold	Disturbed	Timelapse (Bushnell)	4092
TRMA274	Cold	Forest	Timelapse (Brinno, Bushnell)	6849
MA002	Rain	Disturbed	Video	275
TRMA003	Rain	Disturbed	Video	655
TRMA006	Rain	Disturbed	Video	577
TRMA007	Rain	Disturbed	Video	1769
TRMA012	Rain	Disturbed	Video	699
			Total	24202
			Bushnell total	14925
			Brinno total	3946
			Timelapse total	18871
			Video total	5331

4.3.4 Deep learning method

Convolutional neural networks (CNN) are a specialized type of neural network (a supervised, requiring data to train models, form of computer vision) designed for “convolution” operation of dimensional data (one and two) and three-dimensional image data (Islam, 2020). These networks are composed of three types of layers- convolution, pooling, and fully connected (Figure 4.1). Three types of models were run for two different types of image recordings (video compiled timelapse images for rattlesnake, continuous feed video images for green pit vipers)- Model 1) training and validating a single species of viper (big- eyed green pit viper, *Trimeresurus macrops*;

and prairie rattlesnake, *Crotalus viridis*) being tested on the same trained and validated viper species only using images collected in the field by the two projects, Model 2) the same methodology as Model 1 but using online images supplemented for training images. A third model (Model 3) was run with only rattlesnake online training and validation images, except for background category, to assess potential for training and validation data and model structure to be created before field data is collected and then only use field data for running the model. It was not feasible to comprehensively evaluate all potential influences of inputs to models, but batch size and epoch were briefly evaluated for the prairie rattlesnake model 2 as these images were the most clear and homogenous with respect to habitat compared to green pit viper models.

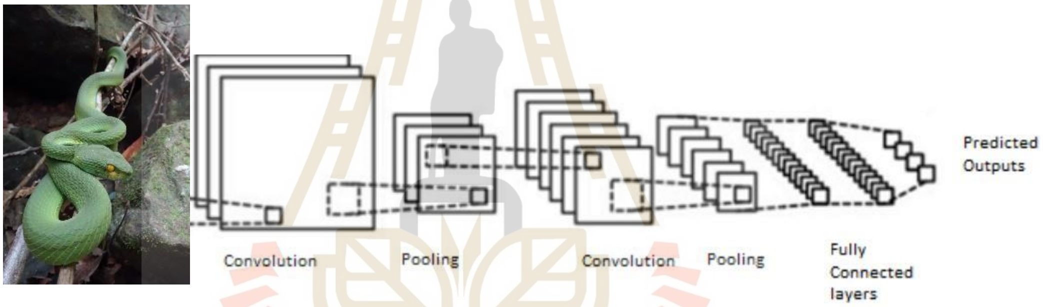

Figure 4.1 Condensed summary of deep learning layer types with online image of a green pit viper used as an example.

A total of 83714 images were used for green pit viper and 28640 images were used for prairie rattlesnake models of Model 1 type. For the green pit viper models this consisted of 31304 (15719 ambush/rest, 559 background, 15026 move) training, 23451 (7731 ambush/rest, 7513 background, 8207 move) validation, and 28959 (7513 ambush/rest, 7513 background, 13933 move) test images. For the rattlesnake models this consisted of 12382 (8677 ambush/rest, 3291 background, 864 move) training, 6638 (2467 ambush/rest, 3922 background, 249 move) validation, and 9170 (2732 ambush/rest, 4097 background, and 2341 move) test images.

For Model 2 type, 72 (50 ambush/rest, 22 move) images were used to supplement training green pit viper datasets and 98 (56 ambush/rest, 42 move) images for prairie rattlesnake datasets from repositories online. For Model 3, images of rattlesnakes of many species were used for training (150 ambush/rest, 150 move) and validating (50 ambush/rest, 50 move). Sources for these images included CalPhotos (https://calphotos.berkeley.edu/) and iNaturalist (https://www.inaturalist.org/; "Research Grade"). Green pit viper online images used were not species specific to the training dataset (*T. macrops*) due to difficulties confirming to species level, clear species mis- identifications even at "Research Grade" level, and sparse number of photographs at the species level (95 total for *T. macrops*, not accounting for mis-identifications).

To standardize and simplify the flow of script, all CNN models were conducted on picture images. This was accomplished through conversion of timelapse and continuous feed videos in .AVI format to still photographs in .JPG format using the "av" R package (Ooms, J. 2021; example code provided at https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fsp48m%2Fdownload), which took about 5 minutes per video. These photographs represented frame rate of the original photographs. Resulting photographs were of large (which could slow down the model computing) and differing sizes, which was remedied through standardization of all images to 120 x 120 pixels within models themselves in the "Keras" R package (Chollet et al., 2021, example code provided at https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Facxpr%2Fdownload). Data augmentation was applied to training photographs using the "image_data_generator" function of the "Keras" package with rotation, shear, zoom, horizontal flip, and height and width shift ranges applied to bolster this dataset.

Model architecture was consistent for all three main models. Models were all consistently optimized during compilation through tuning of batch size, epochs, learning rate, and dropout. Model batch size selects a set of samples from the training dataset to work through before the internal parameters of a model are updated, which were set to 10. Epoch denotes the number of times the entire training is set to pass through the neural network (Islam, 2020), which was set to 35 for models. Learning rate controls how much the optimization algorithm's weight will be updated (Islam, 2020) and was set to 0.0001 for my models. Dropout seeks to address overfitting and regularization issues, for my models this value was set at 0.25 for the max pooling layer, and 0.5 was used for the flattened max filtered output into feature vector and fed into the dense layer.

All models were first compiled in program R, using R studio on a personal laptop. Code was initially run on this computer using small batches (< 200 training and validation images) to troubleshoot potential problems with the code. Once the code was deemed acceptable, analyses shifted to the website Kaggle. Kaggle, a subsidiary of Google, is well known for hosting computer vision competitions (since 2010) but is much more inclusive. Kaggle is a public data platform, a cloud-based workplace for data science, and a source for AI education. Furthermore, it has its own incorporation of R and free offering of GPU. The R studio laptop computer tested code was applied to the Kaggle platform and ran all models using their version of R, while accelerating model run time using their GPU. To test model and computational optimization (accuracy and run time, respectively), several different batch sizes and epochs were utilized with the rattlesnake model 2.

4.4 Results

4.4.1 Pixel change detection method

MotionMeerkat flagged many more observations as behavior events than the manual observation method recorded (Table 4.2). A random sample of 2 recordings per viper suggested mean run time to be 210.7 seconds for MotionMeerkat, which was much longer than the mean 129.2 seconds for manual review.

Table 4.2 Number of behavior event observations recorded for green pit vipers via manual review and MotionMeerkat (MM) program, with number of boxes on flagged observation files for MotionMeerkat.

Viper ID	Manual event observations	MM event observations	MM event boxes
TRMA271	103	742	1375
TRMA273	0	253	500
TRMA274	17	385	547
TRMA002	27	56	72
TRMA003	10	130	174
TRMA006	2	117	292
TRMA007	85	335	1247
TRMA012	9	144	7812
Total	159	2162	12019

4.4.2 Deep learning method

Several deep learning models were able able to achieve satisfactory accuracy for test data (up to 98% for green pit viper models and 70% for rattlesnake models), but run time was nearly always long. The most fit models (35 epochs and 10 batch size) are summarized in Table 4.3. Training data accuracy was very high and validation data accuracy low for all models, potentially suggesting overfitting. Fitting models required the most computing power and longest run- time duration, requiring between 30 minutes for the rattlesnake Model 3 to nearly 6 hours for the green pit viper Model 2. Models were able to be run in the background of the laptop while not logged in and also preemptively scheduled to run overnight while not logged in and saved, however. Once Model Type 2 was run for both viper types, testing images for Model Type 3 required less than 10 minutes to run using those models saved.

Table 4.3 Results from green pit viper and rattlesnake models with field data only (Model 1) and image augmentation (Model 2) including duration required to fit those models in hours and model test dataset accuracy (%). A model was run using only online images for the rattlesnake training and validation dataset (Model 3).

Viper group	Model	Fit run time	Accuracy
Green pit viper	1	4.76	0.3
Green pit viper	2	5.9	98
Rattlesnake	1	2.5	70
Rattlesnake	2	4.63	11
Rattlesnake	3	0.5	25

Model 1 of the prairie rattlesnake CNN models, four runs were conducted with differing batch sizes and epochs- 120 batch size and 30 epochs, 120 batch size and 40 epochs, 10 batch size and 35 epochs, and 10 batch size and 45 epochs. Of these Model 1 runs, the least optimized was the 120 batch size and 30 epochs with low test dataset accuracy (% 20) and computing time of two hours although the run with 120 batch size and 40 epochs exceeded the nine hour daily limit of computing time by Kaggle and was unable to produce a result. Decreasing batch size appeared to increase optimization, with the 10 batch size and 35 epoch run taking two hours and thirty- eight minutes while achieving a moderately higher level of accuracy on the test dataset (% 70). The 10 batch size and 45 epoch run required 2hrs 40 minutes and only achieved 20% test accuracy.

4.5 Discussion

Technology has advanced significantly within the last decade with regards to wildlife study. Field methods to relatively noninvasively and remotely monitor organisms, thus theoretically decreasing investigator bias, cost of direct monitoring using field assistants, and addressing ethics and conservation issues associated have supported innovation with cameras and methods to review large datasets they accumulate. Free and open source methods have significantly advanced, however, wildlife studies present unique challenges which can limit their effectiveness. User comprehension of concepts and required input reduces application of technology to review camera images.

The main point of this dissertation section was to investigate application of computer vision, pixel change detection and deep learning specifically, by potential users with high familiarity of study organisms but low initial knowledge or use of technology to review and classify topics of interest. Entire theses and papers with significant contribution by and collaboration with computer scientists (i.e.- Islam, 2020) have been written on camera review technology, but little investigation has been done on widespread application and use by wildlife researchers lacking specialized knowledge of computer theory. Similarly, specialized computer programs and models have been created to assist wildlife researchers however, these have primarily been for charismatic and threatened species.

While pixel change detection and deep learning are becoming highly appealing to many wildlife researchers, results from this dissertation do provide the caveat that significant time is required for application of these technologies- both for comprehension as well as utilization. Manual review of image data, particularly for studies with small sample sizes (thus unable to adequately account for variation), still appears to be the most viable review method both for time required to go through images and also achieve satisfactory accuracy. Time required to become familiar with image data was not accounted for with manual review for this dissertation due to the pandemic (COVID- 19), but image classes should be clear and consistent so as to facilitate accountability and sharing of data by a variety of audiences, suggesting training time to be low as a prerequisite (i.e.- less than 1 hour to familiarize research assistants or even the general public).

4.5.1 Pixel change detection method

The program MotionMeerkat did present many benefits. It was very easy and straightforward to use, all settings were able to be selected within an application with directions to selections uncomplicated. Time required to run the program was slower than manual reviewing images, but faster than the deep learning method and was able to be run in the background of the computer while other tasks were being performed. The similarity of time required to run MotionMeerkat during this study was also observed by Sheehan et al. (2020) which investigated presence of marine fauna, although this topic is not frequently employed for studies which utilize this program. Worth mentioning is many previous studies utilizing MotionMeerkat simply mention use without discussing, investigating, or addressing benefits or limitations of the program (i.e.- Emerson et al., 2018; Hardt et al., 2018; Lagomarsino and Muchhala, 2019). The primary disadvantage of MotionMeerkat identified in this current dissertation was the vast overestimation of behavior events, which was similar to findings (up to 60% observations tagged by the program than by manual review) by Marcot et al. (2019) which investigated application of MotionMeerkat to detect woodpeckers visiting nests.

While it was not possible to conclusively determine which pixels were suggested by the pixel change detection method were indicated by the MotionMeerkat program, abiotic and habitat features clearly appeared to be improperly classified as behavior events. Leaves shifting in the wind, reflection of light on water bodies as well as on vegetation due to rain, and change in camera lighting conditions appeared to be the most prevalent misclassifications. This dissertation did seek to address the complexity of habitat and weather experienced during the study duration within the program itself by selecting the highest setting anticipated for background variation expected from recordings.

Future studies would benefit from inclusion of comprehensive investigation and evaluation of pixel change detection methodology within study designs. An interesting influence to MotionMeerkat accuracy was identified after this dissertation began by Sheehan et al. (2020), which suggested distance to influence whether an organism was detected or not. Background “noise”, the abiotic and habitat factors identified previously, have been broadly suggested to influence motion detection with MotionMeerkat (Weinstein, 2017) but which features exactly, how much, and what steps investigators can take to mitigate this problem beyond the settings feature in the program itself requires further research.

4.5.2 Deep learning method

Deep learning is rapidly becoming popular with ecologists and wildlife biologists. Models like Snapshot Serengeti, Camera CATalogue, Elephant Expedition, and Snapshot Wisconsin which present high accuracy for test images (up to between 80- 98%) are highly appealing and frequently entice researchers working with wild organisms to the field of computer vision (Willi et al., 2019). However, the complexity of deep learning, both conceptually and computationally, requires a dearth of knowledge and experience. This section illustrates the many considerations of both for entry by the average student of behavior and ecology.

Some deep learning models used in this study performed poorly. The clearest culprit is overfitting, which is very apparent from the high training data accuracy (close to 100% at the end of all model runs). Concisely, there are two ways to address overfitting which mirror some of the problems encountered in statistics- 1) improve the model, and the more drastic but greater influence 2) improve the data.

There are many methods to address the overfitting problem within the model structure, some of which were addressed in the viper models like dropout and simplifying the model while other improvements like early stopping, feature selection, f- score selection, and recursive feature elimination were beyond the exploratory nature of this dissertation section. Model train duration can also address overfitting in some cases, but for this study validation was still increasing at the end of running and models with fewer epochs performed even more poorly, indicating shorter train duration to not be advised.

Addressing data itself is usually far more influential to model performance than model structure for deep learning (Christin et al., 2019). While the number of images utilized in the viper training models (minimum 12382 field images for Model 1 and 2, 300 for the online only image Model 3) could appear large to many ecologists unfamiliar to deep learning methods, successful (> 80% accuracy on test data) and relatively widely applicable models utilize far more training images (the previously mentioned Snapshot Serengeti, Camera CATalogue, Elephant Expedition, and Snapshot Wisconsin datasets each had between 0.4 to 7.3 million photographs for empty/species models). As important to number of images is the ability to account for variation within those images. The background habitat was very complex for the green pit viper models, and further hindered by similarity of the vipers to them as well as overall quality of the videos.

The clarity of rattlesnake timelapse recordings was higher and background habitat comparatively simpler, but the smaller number of individuals available and to a lesser extent, number of images per individual were problematic for these vipers. Variation of background ("noise") could be eliminated for images via image subtraction, however, accomplishing this manually (ImageJ or OpenCV or the like) would be challenging with the large number of images and the alternative of actually training another model to recognize what is background (indirectly addressed in this current dissertation with the category "Background") would almost certainly be as complex computationally and conceptually (model structuring) as the model to identify the organism itself.

Augmenting deep learning training datasets within model structure and similar images can help increase model accuracy. Model structure image augmentation was applied for all models by rotating, shifting width and height, shearing, zooming, and flipping horizontally images (creating additional training images with further variation) within the code for the image data generator. Reviewed and research grade still photographs were sought to additionally supplement the datasets, but this was challenging. While > 3000 images were available of varying quality of *C. viridis* on iNaturalist, < 90 were available for *T. macrops* in the same location and many of these were clearly incorrectly identified at the species level even when verified. Being primarily citizen science focused, there was a clear bias towards anthropogenic habitats (near roads and buildings) in images which was not the primary habitat of the rest of the datasets used for deep learning models in this dissertation. Unfortunately, many of the *C. viridis* images on iNaturalist also featured dead animals (more than several decapitated or run over) as well as humans holding these rattlesnakes behind the head or with hooks or tongs rendered these photographs unusable for this current dissertation. Review of image repositories, including the two used in this chapter (iNaturalist and CalPhotos), which many reptile enthusiasts and reptile researchers utilize, was conducted by Marshall et al. (2021) and would prove useful for future deep learning application for reptiles.

Very few humans were observed in either the rattlesnake or the green pit viper model datasets, but classification of people has become a very controversial topic within the field of deep learning (Castelvecchi, 2020). Thus, it is imperative that wildlife studies utilizing photographs and videos (not just for image classification) account for the possibility of encountering images of people in datasets. It is possible to blur faces in photographs or even exclude images or videos with people entirely, depending on the study question.

Worth discussing and perhaps investigating by future studies is the ease and familiarity of programs for running deep learning models. Program Python with the aid of massive computing power is the most popular method, but Python is only infrequently utilized for other tasks by ecologists and behavior scientists and adequate computing power required for optimizing deep learning models is rarely available to these groups. Program R is the most used open source software by these groups, but the packages within it like Keras, Platypus, and YOLO lack much of the functionality of Python. Running Python or R deep learning models also require dedicated computers unable of adequately running background tasks which can be restrictive. The Kaggle website was extremely valuable for addressing the computational power (via free GPU) and ability to run background tasks on the same computer (even a small personal laptop), but the version of R utilized by Kaggle had even less functionality than program R itself for deep learning and had much less support for troubleshooting errors.

What many consider to be the primary advantage of deep learning models was likely the biggest limitation of the green pit viper and rattlesnake models- ability of models to learn topics, behaviors and when a viper is not present for this current study, without a user to initially outline or indicate them specifically. Not enough different individuals in different backgrounds and habitats in clear enough recordings were possible for the green pit viper and prairie rattlesnake models to consistently accurately predict behavior and presence for test images in relatively to very complex habitats and backgrounds. The deep learning reptile study most similar to this current chapter Islam (2020) utilized 4500 supplementary online images for each topic of interest with a minimum 600 field images of which less than 150 consecutive pictures were from any single individual which did not fall under the viper study design, distance was standardized between camera and the ground which formed the background for the test dataset which was not possible for vipers, test data was much less complex with regards to background (background habitat scarcely discussed but appeared to primarily be limited to grasses and leaves on the ground itself) compared to this current dissertation, and the graduate student had access to a high-performance computing cluster within the same university system which was not for the pit viper models, which highlights the concerns about adequate training field data sample size and variation, supplemental training data inclusion, and computing power.

Future studies considering applying deep learning should anticipate models performing best with large numbers of individuals or individuals in a variety of conditions rather than large numbers of images for few individuals which are very similar to each other. However, this could still not be enough to achieve adequate accuracy without background subtraction methods, either manually which is time consuming or creating a separate model which could present similar computational and model structuring conceptual difficulties to the methodology used in this section. Accuracy models can attain through options available to any aspiring wildlife deep learning student, researcher, or enthusiast without direct access to significantly more computing power than clusters can provide has not been adequately studied but is of significant concern to widespread deep learning application. Outside of the study design for this chapter, but also worth investigating would be inclusion of non- species specific but morphologically similar with similar habitats recorded during the day or with flash at night to species specific deep learning models utilizing primarily infrared lighting sources for recordings like this current dissertation.

4.6 Conclusion

Artificial intelligence has the potential to address a variety of ecological issues, although consideration is required for ease of use and conceptual design, ability of technology to adequately address complex topics, sample size necessary, and time and computing power required. We utilized two forms of computer vision, machine and deep learning, with two different computer programs, which provided unique insight into the applicability of AI to ecology and wildlife behavior study.

One of the broadest forms of artificial intelligence and computer vision, machine learning, was investigated in this dissertation chapter using the program MotionMeerkat (MM). This unsupervised (very little input by user for method and no specific training dataset) approach presented many advantages including ease of use and being comparatively fast to run, including ability to be run as a background task on a personal computer. Because there was very little user input in the way of training, however, MM greatly overestimated behavior events. Habitat features and abiotic factors presented the greatest causes for false positive detections.

Alternatively, one of the most complex forms of artificial intelligence and computer vision, deep learning, was also studied in this dissertation chapter using program R, specifically with the R package Keras, and run through the Kaggle website. Supervision, setting aside data to be used to train models, helped to attain comparatively high accuracy of behavior state classification. However, this accuracy came at a cost, especially time (up to and > 6 hrs) and model complexity in coding and input. Training models with field data also required a significant proportion of data collected to be reviewed manually to confirm behavior states to be used as a benchmark. Utilization of images available online in repositories was attempted so as to reduce user time and bolster small field data sample size, but presented its own set of difficulties in the form of misidentifications of species by repository users, limited number of images reposited for certain species and behaviors, and bias towards anthropogenic features including roads and buildings.

Findings from this study should provide behaviorists, ecologists, managers, and general public interested in artificial intelligence, computer vision specifically, a better idea of some of the benefits, disadvantages, and limitations of this technology. Prior work has primarily focused on successful utilization of these methods, with limited discussion of challenges and failures. This dissertation arguably experienced both with study of green pit viper behavior, and hopefully was able to provide a stimulating open discussion of findings. Potential was observed for machine and deep learning application, however, important considerations are required for success and this current work suggests especially small datasets, researchers with limited access to computing power and internet, and studies with complex topics and backgrounds are likely unsuitable for those methods. No previous artificial intelligence study employed similar methods (vipers in complex forest and anthropogenic habitats and camera technology) which excluded utilization of pretrained deep learning models, despite the success of some of our models and amount of time and effort required for the training and validation steps it is worth following prior study suggestion of caution for employing models from this dissertation to other works- habitat, weather, and even individual camera locations and features can influence ability to effectively apply models to new datasets.

Addressing the seventh objective of this dissertation, "Assess effectiveness and feasibility of computer vision (such as deep learning) to behavioral study with wild green pit vipers"), this chapter should provide those interested in artificial intelligence and computer vision within the contexts of behavior and ecology some of the opportunities and challenges of utilization of those methods. Utilization of technology to address pressing issues to humankind and the environment, particularly little studied topics explored in this dissertation like snake ecology and conservation and snakebite management, should be further investigated and applied.

4.7 References

Christin, S., Hervet, É., and Lecomte, N. (2019). Applications for deep learning in ecology. *Methods in Ecology and Evolution 10*: 1632-1644.

Barnes, C. (2017). The spatial ecology, habitat selection, and behavior of big- eye green pit vipers (Trimeresurus macrops) in human dominated and protected areas in the Sakaerat Biosphere Reserve. Master's Thesis, Suranaree University of Technology, Thailand.

Castelvecchi, D. (2020). Is facial recognition too biased to be let loose? *Nature 587*(7834): 347-350.

Christin, S., Hervet, É., and Lecomte, N. (2019). Applications for deep learning in ecology. *Methods in Ecology and Evolution 10*: 1632-1644.

LeCun, Y., Bengio, Y., and Hinton, G. (2015). Deep learning. *Nature 521*(7553): 436-444.

Rosebrock, A. (2017). Deep Learning for Computer Vision with Python. 1st Edition, PYIMAGESEARCH.

Strine, C. (2015). The ecological study of green pit vipers in Sakaerat Environmental Research Station, Nakhon Ratchasima. Doctoral Thesis, Suranaree University of Technology, Thailand.

Strine, C., Silva, I., Barnes, C.H., Marshall, B.M., Artchawakom, T., Hill III, J., and Suwanwaree, P. (2018). Spatial ecology of a small arboreal ambush predator, *Trimeresurus macrops* Kramer, 1977, in Northeast Thailand. *Amphibia- Reptilia 39*(2018): 335-345.

Weinstein, B. G. (2015) MotionMeerkat: Integrating motion video detection and ecological monitoring. *Methods in Ecology and Evolution 6*: 357-362.

Valletta, J.J., Torney, C., Kings, M., Thornton, A., and Madden, J. (2017). Applications of machine learning in animal behaviour studies. *Animal Behaviour 124*: 203-220.

CHAPTER V

GREEN PIT VIPER AND KANCHANABURI PIT VIPER ECOLOGY AND NATURAL HISTORY

5.1 Abstract

Basic natural history and ecological knowledge of Asian green pit vipers is lacking, despite being of significant medical concern to humans and conservation. To address this knowledge gap, infrequently observed behavior events and interactions (prey, predators, humans, and conspecifics) were investigated for green pit vipers at Suranaree University of Technology (SUT) and Sakaerat Biosphere Reserve (SBR) in Thailand using fixed continuous feed camera technology. Comprehensive behavior (states and events), activity patterns, interactions, and natural history was also recorded for a Vogel's pit viper (*Trimeresurus vogeli*) specifically at SBR using fixed cameras. The first comprehensive investigation of the endangered Kanchanaburi pit viper (*T. kanburiensis*) was undertaken and behavior (state and events), activity patterns, interactions, and natural history were recorded using cameras, habitat use was described, and a brief wildlife trade review (CITES, LEMIS, and Thai DNP) was conducted. Tail undulation was observed on camera for a single juvenile *T. macrops*, 17 strikes were made by vipers (11 by *T. macrops*, 6 by *T. albolabris*) of which 1 was successful (*T. macrops*, *Hemidactylus* gecko) on camera, prey activity largely overlapped viper foraging activity (0.84, CI = 0.82- 0.87 SUT; 0.64, CI = 0.60-0.68 SBR), no predators were observed but invasives (domestic cat, 1 minute, SBR) and humans (SUT= 1 minute, SBR = 29 minutes) were rarely directly observed on camera as were conspecific interactions (SUT = 12 minutes, SBR = 19 minutes). Novel natural history observations were made using the camera technology including a strike by a viper on a toad (*Duttaphrynus melanostictus*, with subsequent release and behavioral display

of potential contact with poison from toad by the focal *T. macrops*) and biting behavior by a female *T. macrops* towards a conspecific outside of the mating season. An adult female *T. vogeli* was observed on camera for about 10 hours and interesting natural history observations were made including predation (of a *Hemidactylus* gecko) and house centipede interaction. More than 60 hours of recordings were made of an adult male *T. kanburiensis*, which displayed primarily nocturnal foraging activity, behavior events displayed infrequently (2 gape, 85 headbob, and 3 probe observations), and prey infrequently visible (*Cyrtodactylus* and *Hemidactylus* geckos = 243 min., squirrel = 5 min., rat = 3 min., and bird = 1 min.) in limestone karst interspersed with bamboo habitat with a paved road < 30m, utilization of an inactive termiate mound, and moderate overhead canopy cover (66%). No *T. kanburiensis* were recorded in CITES, LEMIS, and Thai DNP publicly accessible databases but other green pit vipers were. Basic natural history and ecology have scarcely been studied for green pit vipers, but is necessary for adequately addressing snakebite management and conservation issues for this interesting group of snakes.

5.2 Introduction

Investigation of natural history and ecology is crucial for wildlife conservation and management. Additionally, creating measures to adequately address specific wildlife issues like snakebite requires understanding of basic biology of species. Even baseline and preliminary study to obtain such information for wild organisms can be challenging, however.

Green pit vipers (genus *Trimeresurus*) are a specious (> 40 species, Uetz and Hallerman, 2015) group of primarily arboreal venomous snakes for which basic biology, ecology, and natural history is critically lacking. Collectively, these species also inflict the highest number of venomous snakebites where they are found (Warrell, 2010). Information about wild individual and populations of vipers have primarily been omitted from primary literature aside from initial species descriptions, with broad generalizations and application of general knowledge taking precedence for implementation for species identification and venomics. This knowledge gap presents significant implications for snakebite management and conservation for green pit viper species.

Thai green pit vipers present an interesting case study for the group. Venomics (i.e.- Kumkate et al., 2020) and species taxonomy and nomenclature (i.e.- Malhotra et al., 2004; David et al., 2011) are topics of popular study, as has been the description of new descriptions and splitting of species (i.e.- Chen et al., 2021). Comprehensive basic biology, ecology, and natural history study which could complement and bolster those works has been lacking, however. To identify and address this gap, green pit vipers were studied at three sites in Thailand during the course of this dissertation.

This current study specifically sought to investigate green pit vipers at a site in Kanchanaburi province, in addition to the two sites in Nakhon Ratchasima province comprehensively studied in Chapter 3. The karst and bamboo habitat of this site makes it unique compared to the other two Nakhon Ratchasima province study sites (SUT and SBR) of this dissertation. The Kanchanaburi pit viper (*T. kanburiensis*) is thought to be endemic to the karst and bamboo habitat of this region and perhaps into neighboring Myanmar, although comprehensive study of wild vipers has not been conducted. The species was listed as "Endangered" by the IUCN (Chan-Ard et al., 2012), although it was arguably similar to the other three species studied in this dissertation in that inadequate support (natural history, habitat selection, and population study) was provided by assessors. Restricted distribution (little more than 3,000 km^2), presence in fewer than five locations, and continuing decline in the number of mature individuals due to illegal harvest for pet trade were listed as justifications for the listing.

The goals of this study were to 1) to investigate basic natural history and ecological knowledge gaps of two relatively frequently encountered species in Nakhon Ratchasima province, Thailand, 2) provide further but more intensive behavior and natural history information for which ecological knowledge is lacking for the Vogel's pit viper, 3) describe rarely observed behavior events green pit vipers display in the wild, and 3) to provide the first comprehensive study of the Kanchanaburi pit viper in the wild and factors influencing its persistence as indicated by the 2012 IUCN listing of the species (Chan-Ard et al., 2012). This chapter attempted to explore seven of the broader dissertation study objectives- 1) determine and compare behavior states (behavior displayed in relatively long durations) and events (spontaneous behavior) and corresponding activity patterns (when are vipers most active or inactive) of multiple green pit viper species, 2) assess behavior and activity pattern differences between different ages and sexes of vipers, 3) assess how habitat and abiotic traits influence behavior and activity of green pit vipers and co- occurring species, 4) assess threats to vipers from humans, and from vipers to humans, 5) compare sympatric green pit viper and other viper species behavior and activity periods, 6) compare behavioral differences between isolated populations (subpopulations) within species, and objective 8) investigate interactions (predator-prey, conspecific, etc.) green pit vipers and sympatric viper species experience mentioned in Chapter I.

5.3 Methods

5.3.1 General green pit viper study methods

During the course of regular fieldwork for this dissertation, interesting and novel natural history observations were made at the Sakaerat Biosphere Reserve and Suranaree University of Technology. Vipers were initially located for natural history study during visual encounter surveys and opportunistic encounters (either by C. H. Barnes or notification). Notification of vipers by people not directly associated with the study defined opportunistic encounters. All data collection in the field (including searches, surveys, and encounters) was conducted during 4-night sampling periods each month at each site, separately. Viper species, sex (male or female), and age (neonate/juvenile or adult) was visually determined (no capture or handling) in the field using prior knowledge from Cox et al. (2012) when individuals were first encountered. Effects of the global pandemic COVID-19 on this dissertation, including this chapter are comprehensively outlined previously earlier in this dissertation but succinctly, pandemic protocols (especially lockdowns) directly impacted fieldwork and likely behavior of vipers themselves.

The SUT site is rural yet close (within 25 km) of the 9th largest city in Thailand (approximately 126,391 residents; Registration Office Department of the Interior, Ministry of the Interior, 2019). This site is a habitat matrix of semi-natural, invasive vegetation, and buildings surrounded by agriculture which presents a unique opportunity for green pit viper natural history research. Study, including basic biology and ecology, of green pit vipers at the second site, SBR, is among the most comprehensive for the group. Most of this work has been conducted at the reserve research station and adjacent dry evergreen habitat, however. In-depth site detail is provided for both SBR and SUT earlier in this dissertation.

This study focused on the white-lipped pit viper (*Trimeresurus albolabris*) at the Suranaree University of Technology campus study site. This species is listed by the IUCN as "Least Concern" (Stuart et al., 2012A). Another species, the big-eyed pit viper (*T. macrops*) is thought to be found close to the university (within 5 km) but was not confirmed during this dissertation fieldwork. At Sakaerat Biosphere Reserve the most frequently encountered green pit viper species, the big-eyed pit viper (listed by the IUCN as "Least Concern"; Stuart et al., 2012B), was the primary focus of this current study although significant effort was spent to study the Vogel's pit viper (*T. vogeli*; listed by the IUCN as "Least Concern", Stuart and Nguyen, 2012) which has been less studied due to lower detection due to potential preference for higher elevation habitat (Malhotra et al., 2004) and arboreal behavior (> 3m above ground level; Barnes et al., 2019).

Fixed cameras (Hikvision model DS-2CE16C0T-IRF, set to a rate of 29 frames per second) were set approximately 0.5-3 meters from vipers, depending on vegetation and perch height as outlined in Chapter III. Following protocols and research and ethics permits (SUT #A-8/2562, NRCT #2019/065, and DNP #16177; with Thai IACUC Institute of Animals for Scientific Purpose Development (IAD) licensure initially under

Dr. Colin Strine until C. H. Barnes was approved in October 2020), no vipers or their habitats were intentionally disturbed during study.

Strike and tail undulation behavior events and successful predations were rarely observed but still interesting and part of the general ecology of green pit vipers, during green pit viper activity pattern and behavior study for this dissertation. Strikes were rapid attempts to subdue prey and were categorized as successful or unsuccessful following Clark et al. (2016). A strike was defined as successful if 1) the head of the focal viper appears to contact prey and 2) focal viper holds on to prey or exhibits signs of strike induced chemosensory searching (SICS), a stereo-typed behavior viperids exhibit when relocating envenomated prey (Chiszar et al., 1992); unsuccessful strikes will be defined as strikes which do not meet those criteria. Previous study (Barnes, 2017; Barnes and Knierim, 2019) does suggest green pit vipers to hold on to prey (frogs and geckos), rather than release before ingestion. Tail undulation was described following Barnes and Knierim (2019), which followed the definition proposed by Clark et al. (2016), as continuous, clear movement of the tail.

Natural history study was also focused on interactions of green pit vipers with conspecifics and other organisms. All vertebrates on camera were documented according to time and lowest taxonomic order. A small (due to time constraints and limited number of cameras) sample of “random” set of data was created from cameras set at sites within study areas where vipers were known to occur but were not actually present on camera so as to assess prey and predator presence when vipers were not visible.

Conspecific interactions were defined following Barnes et al. (2020). They were direct if a viper came within half of a body length (or closer) to another viper, and indirect if further but still visible on camera. Outcome of interactions were defined as neutral, distracting, or agonistic. Interactions were classified as neutral when the focal viper did not appear to be aware of or did not acknowledge a conspecific. The interaction was distracting when the focal viper appeared aware of or acknowledged a conspecific, but no subsequent responses were evident. Agonistic outcomes included active responses, requiring subsequent movement, of a focal viper to a conspecific.

Classification of Vogel pit viper behavior states and events followed methodology outlined earlier in this dissertation. General natural history including observations and interactions with conspecifics, predators, and prey were documented when observed.

5.3.2 Kanchanaburi pit viper study methods

Natural history, behavior, and activity patterns were recorded for vipers encountered in Khao Laem National Park in Kanchanaburi province (Figure 3.8). Vipers were initially located during visual encounter surveys at the national park. These surveys were characterized by looking for vipers both during the day and night with no area, distance or time constraint. Visual encounter surveys were defined as looking for vipers while walking with no area, distance, or time constraint. Opportunistic driving road surveys via car and motorcycle, including travel to/from the park and getting to/from visual encounter survey sites were also recorded when possible. Driving speed was not consistent nor documented. These types of surveys were used for documenting natural history and basic ecological observations due to relatively few number of visits and very low encounter rate, so standardization was not attempted nor post analyses such as occupancy calculated.

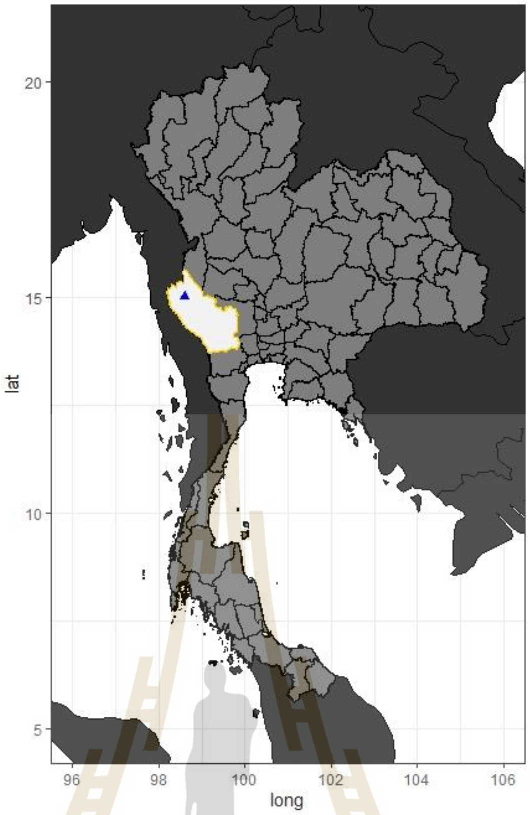

Figure 5.1 Kanchanaburi and other green pit viper species activity pattern, behavior, and natural history at Khao Laem National Park (indicated by a blue triangle) study area within Thailand which is shaded in light gray. Within Thailand, provinces are partitioned in black, with Kanchanaburi outlined in yellow.

All data collection in the field at Khao Laem National Park was conducted during 4-night sampling periods each month. Viper species, sex (male or female), and age (neonate/juvenile or adult) was visually determined (no capture or handling) in the field using prior knowledge from Cox et al., (2012) when individuals were first encountered. Fixed, continuous feed, cameras (Hikvision model DS-2CE16C0T-IRF, set to a rate of 29 frames per second) were set approximately 0.5- 3 meters from vipers, depending on vegetation and perch height. Following protocols and research and ethics permits (SUT #A-8/2562, NRCT #2019/065, and DNP #16177; with Thai IACUC Institute of Animals for Scientific Purpose Development (IAD) licensure initially under

Dr. Colin Strine until C. H. Barnes was approved in October 2020), no vipers or their habitats were intentionally disturbed during study. Fieldwork was not conducted prior to permission approval in July 2020 at Khao Laem National Park so as to foster positive collaboration and trust. Local conditions (routine park maintenance and weather conditions) and COVID- 19 pandemic restrictions and lockdowns did not allow for fieldwork in 2021 at this site.

As mentioned prior in this dissertation, the global pandemic COVID-19 greatly influenced travel and daily life. Fieldwork in Kanchanaburi was significantly constrained both due to travel to the site (province level and complete lockdowns) and the number of people allowed to participate with the pandemic. Local conditions, mudslides, fire, and renovation construction also prevented fieldwork. Interestingly, visitor numbers at Khao Laem National Park continued to increase despite the pandemic (66192 visitors in 2019 and 73598 in 2020, DNP)- this could be the secluded nature of the park compared to much larger adjacent parks and close proximity to historical monuments.

The ethogram, a set of terms and descriptions of the behaviors of an animal (Lehner, 1987), for Kanchanaburi pit viper study comprised of behaviors and events outlined earlier in this dissertation (ambush, rest, and move states; headbob, probe, and gape events) as well as the infrequently observed behaviors strike and tail undulation. Analysis via non-parametric circular kernel-density function was employed to delineate temporal differences and similarities of behaviors to each other and also specifically presence of prey on camera to ambush behavior displayed by *T. kanburiensis*, and then a coefficient of overlap (Δ) used to measure the extent of overlap between two kernel-density estimates in the “overlap” R package (Ridout and Linkie, 2009; Linkie and Ridout, 2011) which is comprehensively detailed earlier in this dissertation. General microhabitat notes were made, and canopy cover was estimated using CanopyApp (see Landert, 2016 for summary of method and comparison to others) and leaf damage was estimated using BioLeaf (Machado et al., 2016) smartphone applications.

Because wildlife trade is suspected to directly influence and negatively impact Kanchanaburi pit viper populations, brief review of literature post- 2001 (when consensus was reached regarding species status) was conducted to investigate this topic. Records from CITES, LEMIS, and Thailand DNP were reviewed. Records publicly available from the Convention on International Trade in Endangered Species (CITES) and Law Enforcement Management Information System (LEMIS) were both reviewed using R packages, “rcites” (Geschke et al., 2021) and “lemis” (Eskew et al., 2020). Data was collected from Thailand DNP through their website.

5.4 Result

5.4.1 General green pit viper ecology and natural history

A variety of fascinating natural history and basic ecology observations were made while conducting study with green pit vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology. Novel confirmation of tail undulation behavior event by a juvenile green pit viper in the wild, unsuccessful strikes, predation by a green pit viper, temporal descriptions of prey within close proximity to green pit viper foraging site, natural history of green pit vipers in close proximity to buildings, and further supplementary ecological information for Vogel’s pit viper were fascinating findings.

A behavior event suspected to have been observed during previous study of green pit vipers, tail undulation was observed on two occasions for a single female neonate *T. macrops* (TRMA039) at Sakaerat Biosphere Reserve during this dissertation. Both observations were at night and within 3 minutes of each other for less than a minute induration (20:35 and 20:38). No prey was observed on the camera either an hour before or after these observations.

Striking behavior was observed on 11 instances by 5 *T. macrops* at SBR- 1 adult male, 3 adult female, and 1 female not classified as an adult; the male and one of the adult females were in the transition zone of SBR, the rest were at the research station. Two strikes by an adult female at SERS were towards a rat which was too large for ingestion, suggesting a defensive and communication rather than predatory function- one strike was very slow and after the rat had already passed by, and the other strike appeared to make contact but resulted in release by the viper without subsequent trailing. A total of 6 strikes were against geckos appearing to be of the genus *Hemidactylus* (either *frenatus* or *platyurus*, not clearly visible on camera), of which 1 was successful (retention and then ingestion).

A strike was made on a frog (unclear genus) at the Sakaerat Environmental Research Station which appeared unsuccessful, but resulted in the viper immediately leaving the ambush site in what appeared to be active foraging (chasing). An interesting observation of a strike where a viper (TRMA007) successfully bit, held on, and immediately released a toad (*Duttaphrynus melanostictus*) was made on 28 October at 23:18- immediately after letting go of the toad the focal viper gaped and rubbed its mouth on its body, suggesting toxin was released by the toad. All but one observation, an unsuccessful strike at SERS against a skink which occurred at 15:47, were at night (between 18:00- 06:00). Worth noting is 2 strikes were preceded (within 1 minute) of other behavior events, one was after a probe event and another by 6 consecutive headbobs.

There were fewer observations of strikes by *T. albolabris* at Suranaree University of Technology, 3 by an adult male, 2 by an adult female, and 1 by a female not classified as an adult. The adult female was observed close to a lab building, the adult male and not- adult female were in forest near the botanical gardens. Of the strikes, 3 were to geckos of the genus *Hemidactylus*, 2 were to frogs (unclear genus), and no other organism was visible for the last strike. The strike with no organisms present was preceded by a headbob event with 4 consecutive headbobs. None of the strikes were successful, interestingly one of the strikes clearly made contact but the viper was unable to hold on (adult male *T. albolabris* to a gecko). All strikes were made between 21:00-05:30.

Only 1 successful strike, predation, was observed at SBR and none were observed at SUT. This predation was by an adult female (TRMA007) on a gecko (*Hemidactylus* genus) within 10 m of a building at SERS, which occurred after unsuccessful 2 strikes on rats, 1 skink, and 2 geckos. The entire predation process, from strike to complete ingestion (viper did not release the prey) was observed between 18:08-18:27 on 28 October. The viper still continued to ambush after the successful predation, and approximately five hours after struck at a toad which was released as previously mentioned. Probe behavior was observed by the focal viper on 40 occasions, gape 4 occasions, and headbob 48 occasions in the 3 nights it was observed on camera.

Potential prey of *T. macrops* observed on camera at SBR while vipers were present regardless of life stage included geckos (approximately 365 minutes with them present), frogs (24 minutes), toads (12 minutes), squirrels (9 minutes), passerine birds (6 minutes), rats (6 minutes), unclear small mammals (3 minutes), and skinks (2 minutes). Toad (447 minutes), geckos (204 minutes), frogs (11 minutes), squirrels (3 minutes), and a single skink (1 minute) and small mammal (1 minute) were potential prey observed at SUT with cameras focused on *T. albolabris*. Viper foraging (ambush) behavior and observation of potential prey temporal overlap was high (Figure 5.2).

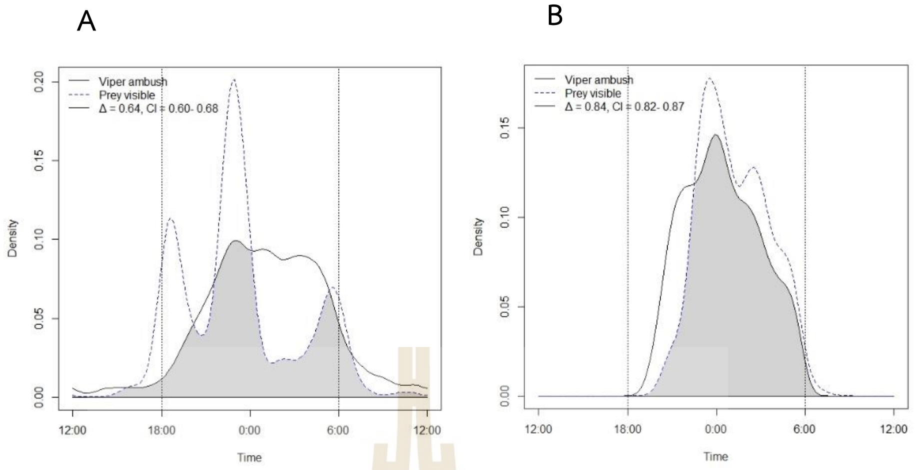

Figure 5.2 Temporal patterns overlap of ambushing focal *Trimeresurus macrops* at Sakaerat Biosphere Reserve (A) and *T. albolabris* at Suranaree University of Technology (B) and potential prey on fixed continuous feed cameras.

Non- prey organisms encountered by *T. macrops* included a bat (1 minute), domestic cat (1 minute), deer (1 minute), and humans (29 minutes). Humans were encountered at SERS (20 minutes, 3 focal vipers) and the transition zone (9 minutes, 2 focal vipers) of SBR. Only a single non- prey organism was observed on camera at SUT at 19:59 on 12 March, clearly a headlight a headlight from a human who wasn't the one setting the camera. Because of the close proximity to a building and students generally not utilizing light sources, this observation was probably of a security guard who may or may not have been aware of the fieldwork. The viper clearly displayed uncharacteristic movement at the ambush site with 3 consecutive headbobs for 9 minutes after the light being flashed at it before it settled back into clearly stationary foraging state (ambush) again. The domestic cat at SERS was the only potential green pit viper predator observed on camera.

Logistical constraints, few camera sets and both time setting/removing cameras and then later reviewing footage, prevented adequate random sampling of sites with cameras for viper conspecifics, predators, and prey. A total of 32.8 hours of video were recorded at SBR (18.3 hours) and SUT (14.5 hours) random sites in which focal vipers were not present. Observations of prey at both study areas, together (Figure 5.3) and separately (Figure 5.4), were dissimilar between recordings with and without vipers present. No humans were observed on random cameras at SUT, and similar to prey, overlap was low for observations of humans when vipers were and were not present on recordings at SBR (Figure 5.5). No predators were observed on either random or focal viper cameras. Conspecifics were not visible on randomly set security cameras. While not novel, but still interesting, a toad was observed chasing and ingesting a centipede on 17 June 2021 at 04:34 at SUT on one of the random placed videos which could help explain observations of toads at the site for recordings with and without vipers present.

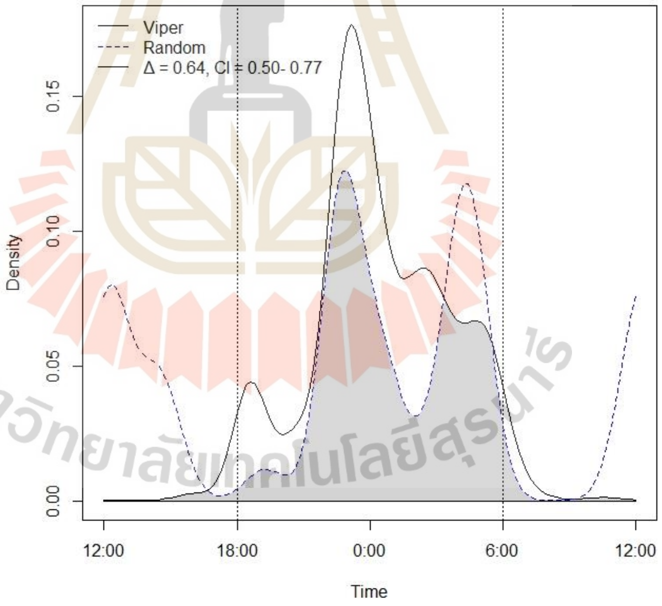

Figure 5.3 Overlap of prey visible on focal green pit viper and randomly set (without vipers present) security cameras at Sakaerat Biosphere Reserve and Suranaree University of Technology.

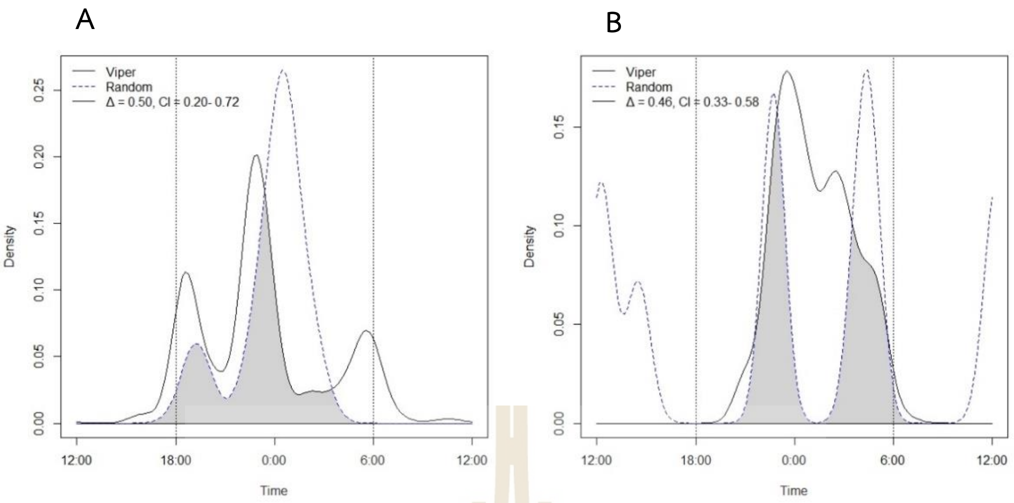

Figure 5.4 Overlap of prey visible on focal green pit viper and randomly set (without vipers present) security cameras at Sakaerat Biosphere Reserve (A) and Suranaree University of Technology (B).

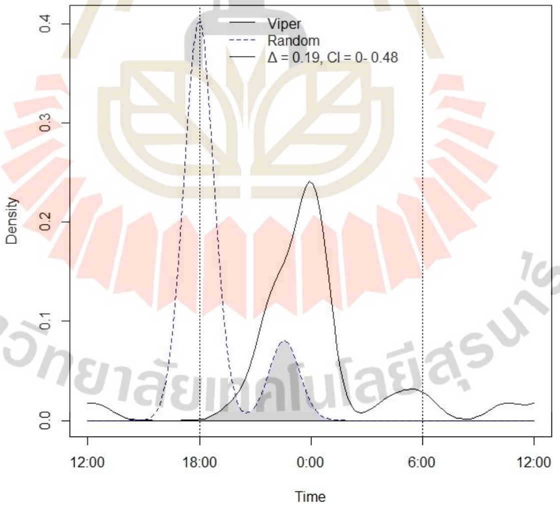

Figure 5.5 Overlap of humans visible on focal green pit viper and randomly set (without vipers present) security cameras at Sakaerat Biosphere Reserve.

Three adult female T. macrops were observed ambushing on and in garbage containers at the Sakaerat Environmental Research Station during the study. Research station staff were aware of all three, and these observations provided observations for education and outreach for both students and other staff members. Two were monitored with cameras (TRMA003, 16 September, 250 minutes; TRMA012, 27 October, 700 minutes), but the last viper observed (TRMA020, 11 December, Figure 5.6) was in a meeting area so a camera was not set due to privacy concerns. Squirrels and geckos were observed in close proximity to the vipers monitored on camera in the trashcans (6 and 11 observations, respectively). These vipers displayed gape behavior on 3 occasions, headbob on 9 occasions, and probe on 7 occasions. All displays of gape behavior were within 1 minute of headbob behavior.

Figure 5.6 An adult female big- eyed pit viper (*Trimeresurus macrops*, TRMA020) ambushing on a garbage container at the Sakaerat Environmental Research Station on 11 December, 2020.

Comprehensive habitat use and selection within the framework of vegetation and anthropogenic features has recently become of interest for natural history study of green pit vipers. These topics are very good introductory frameworks for forming basic ecological questions, which were touched upon in this dissertation. When setting cameras during this latest study at the Sakaerat Environmental Research Station, ants were observed moving in large numbers during recordings of two adult female vipers (climbing up and down a tree, TRMA024; on the ground, TRMA030). Another ambush site was observed directly below an active stingless beehive in the rural transition zone of Sakaerat Biosphere Reserve (Figure 5.7). As well as being a foraging and sheltering location for a *T. macrops* (TRMA034), it was also an ecdysis site for a juvenile red- necked keelback snake (*Rhabdophis subminiatus*) for several nights. Additionally, high desirability of this site, perhaps due to the bees, might further be inferred from an observation of a conspecific interacting with the focal viper on camera.

Figure 5.7 Ambush site of a focal *Trimeresurus macrops* (indicated by an orange circle) observed in rural habitat in Sakaerat Biosphere Reserve directly below a tree with an active stingless beehive (purple circle). A red- necked keelback (*Rhabdophis subminiatus*) was observed undergoing ecdysis for several nights in the immediate vicinity (yellow circle).

Conspecific vipers interacted both with focal *T. macrops* at SBR (19.5 minutes, 2 focal vipers) and *T. albolabris* at SUT (14 minutes, 1 focal viper; summarized in Table 5.1). These interactions were primarily direct (3 observations, 19.8 minutes) with neutral outcomes (3 observations, 20.7 minutes). All interactions occurred at night, all focal individuals were female (2 adults and 1 juvenile), and 2 were within 30 meters of buildings (transition zone of SBR) and 1 was in forest (botanical gardens, SUT). The conspecific interacting with the juvenile *T. macrops* at SBR may have been another juvenile, likely male due to clear presence of a postocular stripe, observed within 2 meters of it on the last night of the sampling session. None of the focal vipers abandoned ambush sites within 1 hour of interacting. The single agonistic interaction included two clear instances of lunging and biting at the conspecific by the focal viper.

Table 5.1 Summary of focal white-lipped (*Trimeresurus albolabris*, TRAL) and big-eyed pit viper (*T. macrops*, TRMA), location (Suranaree University of Technology, SUT; Sakaerat Biosphere Reserve, SBR), biometrics (sex, age), and number and duration (in minutes) of interactions observed.

Viper ID	Study site	Location	Sex	Age	Number	Duration
TRAL032	SUT	Botanical gardens	Female	Adult	3	12
TRMA034	SBR	Transition zone	Female	Adult	1	8
TRMA039	SBR	Transition zone	Female	Juvenile	1	11

Searches specifically for Vogel's pit viper's were concentrated around two sites in the core zone of Sakaerat Biosphere Reserve. One site ("Site 1") was where spatial ecology of the species (see Barnes et al., 2019) was conducted concurrently with big-eyed vipers prior, and a white-lipped viper was tracked also prior to that (Strine, 2015). The other site ("Site 2") was recently (within the last 3 years) found by snake researchers to have the species also. Vogel's pit viper are the least encountered green pit viper species at SBR, due to the relative inaccessibility- a 15 minute drive up the main road from the station and then hiking into an area with a wide variety of trails splitting off (Site 1), and a 15 minute drive up the main highway outside of the station followed by a short drive up a well maintained dirt road with three locked gates to access a relatively poorly maintained trail splitting off of it (Site 2). Both sites are composed of dense dry evergreen forest with heterogenous forest layers, which preliminary study has found to all be used by Vogel's pit viper (Barnes et al., 2019).

A total of 32.4 surveyor hours of surveys were conducted at the first (11.9 surveyor hours) and second (20.5 surveyor hours) Vogel's sites between September 2020 through June 2021. Two female *T. macrops* were observed moving at Site 1 (17 September 2020 at 18:50, 10 December 2020 at 19:00) with cameras placed (although dense foliage and the vipers being arboreal prevented detailed behavior analysis) and a single male *T. macrops* was observed moving at Site 2 (31 March 2021 at 19:35). Several *T. vogeli* were observed by a fellow graduate student working with herpetofauna at the station at a third site further past the second site, but no vipers were observed during 6.5 surveyor hours for this current project at the location. No *T. albolabris* were found at SBR during this entire study. No *T. vogeli* were found during surveys at Site 1, but a female (TRVO001) and male (Figure 5.8, TRVO002) were found in close proximity (< 15 m from each other) at Site 2 at 20:40 within 10 minutes of each other less than an hour after rain on 14 September 2020. The male was moving and did not settle into an ambush site within the survey period, but the female was ambushing when initially discovered and a camera was set to record basic behavior and activity patterns.

Figure 5.8 Male *Trimereusurus vogeli* encountered moving during a survey for green pit vipers at Sakaerat Biosphere Reserve on 14 September 2020 at 20:40 after a rain event and within close proximity of a female *T. vogeli*.

The camera was set near the female *T. vogeli* for approximately 10.7 hours and was able to record detailed basic behavior and natural history details. Despite the small sample size, the monitoring was still able to provide valuable supplementary insight into the scarce basic biological knowledge of the species.

Potential prey items were observed for about 4 minutes during the night of the Vogel's pit viper recording; one minute of a small gecko (likely *Hemidactyllus* sp., about 23:18), two small mammals which were not able to be clearly identified due to dense vegetation for about a minute each (23:22 and 23:31), and a rat for about one minute (02:42), none of which appeared to elicit a reaction from the focal viper. At about 05:20, the *T. vogeli* was observed with a prey item in its mouth. The strike was not visible due to vegetation in front of the viper, but it was clear at the aforementioned time after the viper had lifted its head above the vegetation with what appeared to be a relatively small species gecko (likely a *Hemidactyllus* sp.). Either the prey shook the viper in an attempt to escape, or the viper shook the prey to get a better grasp or for digestion shortly after the head of the viper was lifted above the vegetation. The viper then moved up the small tree it was ambushing on while still ingesting, and immediately abandoned the site (kept moving up the branch) after feeding was concluded at about 05:30.

Interestingly, while invertebrates appear to rarely elicit reaction from ambushing green pit vipers (personal observation, C. H. Barnes) the focal Vogel's recorded in this current study did appear to display a clear defensive reaction to a house centipede- a house centipede could clearly be seen moving from the top left side of the camera screen to directly in contact with the viper, which prompted rapid retraction followed immediately by a fast extension of the head for what may have been a defensive strike although the mouth did not appear to open with immediate retraction of the head again into the body coils. The house centipede immediately ran quickly up a tree following this reaction, with neither the viper nor the centipede appearing harmed. After several minutes the viper appeared to extend its head a small amount, signaling resumed ambushing. A potential mesocarnivore was observed in dense vegetation at 22:16 for about a minute in duration, which did not result in a visible response by the focal viper. Perhaps most interestingly, a second snake was observed moving through the brush just behind the focal female T. vogeli on camera between approximately 22:28- 22:30. The second snake did not approach within a body length and no visible response was observed by the focal viper (making the conspecific interaction classification indirect and neutral), the semi-arboreal nature and movement patterns of this snake suggested it to be another viper but clear confirmation of species was not possible due to distance to camera and clarity of the recording.

5.4.2 Kanchanaburi pit viper ecology and natural history

A total of 22 surveys (14 visual encounter and 8 road) for a total of 96.9 surveyor hours were documented at Khao Laem National Park in 2020 (Figure 5.9). Local national park management were notified a minimum of two weeks in advance of every survey session. Pandemic spikes (COVID- 19; January, April, and May especially), accommodation construction (February), and seasonal closure of accommodations (March and April) prevented fieldwork from being conducted at KLNP in 2021. A KLNP ranger was present during every survey, by park request for DNP inclusion and researcher safety. A total of 6 snakes were encountered (4 during visual encounter, 2 on the road) during quantified searches, and an additional 2 snakes were observed during opportunistically (pictures taken of them as they were encountered) on roads and an additional single snake was found opportunistically while walking.

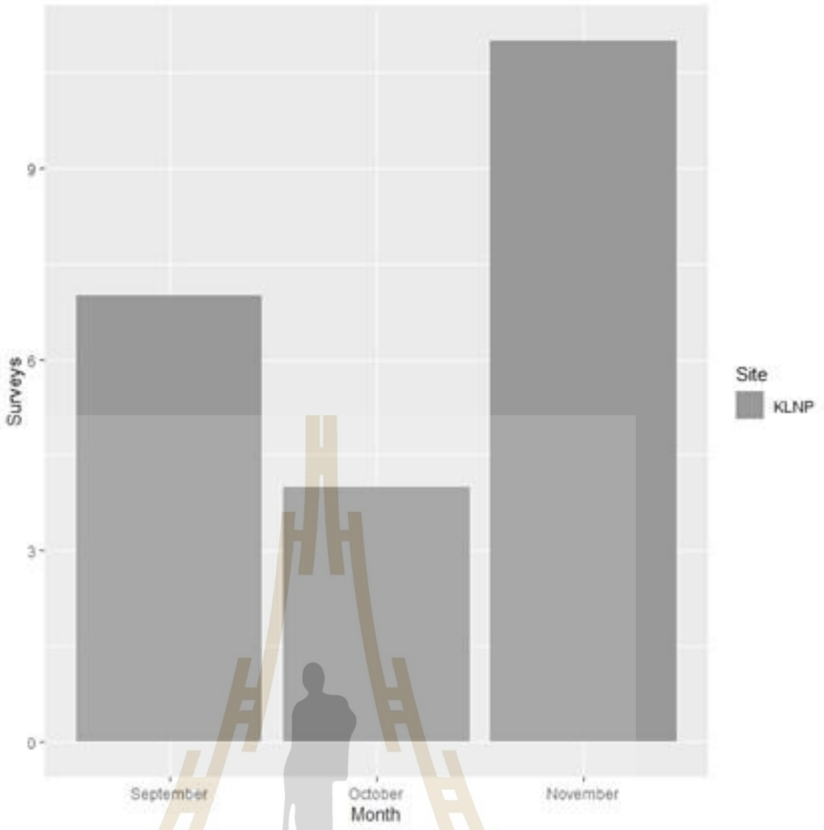

Figure 5.9 Surveys conducted at Khao Laem National park, Kanchanaburi province, Thailand to study unique herpetofauna, particularly the Kanchanburi pit viper (*Trimeresurus kanburiensis*).

Non- viper snakes encountered on visual encounter surveys included an adult mock viper (*Psammodynastes pulverulentus*, on a trail near a temple, at 10:45, 15 October), an adult Oriental vine snake (*Ahaetulla prasina*, near the trail at Dai Chong Thong Waterfall, at 09:45, 3 November), and a mountain slug snake (*Pareas margaritophorus*, near Kroeng Krawia checkpoint, at 19:30, 4 November). On roads a live adult keeled slug snake (*Pareas carinatus*, between Pom Pi Campground and the southern police checkpoint, about 19:07, 1 September), a dead adult green catsnake (*Boiga cyanea*, entrance of Pom Pi campground, between 08:00- 09:00, 4 September). Opportunistically, a dead adult oriental ratsnake (*Ptyas korros*) was observed dead on the road (killed by a vehicle) on 14 October near the park headquarters, and a subadult banded krait (*Bungarus fasciatus*) just outside of a temple at the edge of the park boundary on 16 October. A live adult bridle snake (genus *Dryocalamus*) was observed climbing about 3 meters above the ground less than 15 meters away from the single Kanchanaburi pit viper observed at KLNP on the night 3 November.

Multiple species of lizards were encountered during surveys (Supplementary figures), which may have served as potential prey items for green pit vipers at Khao Laem National Park. Lizards within 15m of the Kanchanaburi viper found during surveys included a juvenile masked horned tree lizard (*Acanthosaura crucigera*) and a species of bent- toed geckos (suggested to be *Cyrtodactylus saiyok*). Species not in close proximity but within the national park boundaries included Oldham's bent- toed gecko (*Cyrtodactylus oldhami*), (*Hemidactylus frenatus*), Tokay geckos (*Gecko gekko*), and skinks. Evidence of monitor lizards in the park was found, but no direct observations were made. One frog species was encountered within 5m of the Kanchanaburi viper. Asian toad (*Duttaphrynus melanostictus*) and multiple species of frogs were encountered within the park, also.

Just two vipers were encountered during visits to Khao Laem National Park. A green pit viper was found dead on the road (killed by traffic) in just recognizable condition on the morning of 16 September between Kroeng Krawia and Pom Pi, an adult female white- lipped viper (*Trimeresurus albolabris*, Figure 5.10). A Kanchanaburi pit viper (*Trimeresurus kanburiensis*) was found on a visual encounter survey, initially moving slowly as if searching for a potential ambush site, on 3 November at 19:40 in the general area of the Kroeng Krawia checkpoint. Body plan, size, and coloration suggested the individual to be an adult male (Figure 5.11).

Figure 5.10 Adult female white- lipped viper (*Trimeresurus albolabris*) observed dead on the road, killed by traffic on the morning of 16 September in Khao Laem National Park, Thailand.

Figure 5.11 An adult male Kanchanaburi pit viper (*Trimeresurus kanburiensis*) observed initially moving in limestone karst habitat interspersed with bamboo in Khao Laem National Park, Kanchanaburi province, Thailand. Consistent with project ethics and research permissions, neither the viper nor its habitat were disturbed and just this one photograph was taken with flash (one was taken without flash immediately after, and then later in the sampling session during the day) which did not appear to evoke stress response. This viper ambushed several meters away from this location for the rest of the duration of the sampling session, which was recorded on a continuous feed camera.

Consistent with project research and ethics permissions the single Kanchanaburi pit viper was not disturbed directly (handling, measuring, etc.) nor indirectly (habitat or non- viper animals). The viper was initially spotted with a headlight, one photograph was taken without flash and one with flash from a distance of > 2 m and neither of which appeared to disturb the slowly moving viper- pace and direction did not appear to change. After these photographs (taking less than several minutes) were taken, we moved away from the viper (> 10 m) and waited with headlights off for 10 minutes. After those 10 minutes, we approached slowly and pointed headlights on lowest setting in the general direction the viper was first observed. We could see the viper was still moving slowly in the same direction we first observed so I waited another 15 minutes at a distance > 10 m with headlights turned off. After this time we repeated the same check procedure and observed that the viper was now ambushing less than 10 meters away from where we had originally spotted it, on a termite mound (about 1 m in height). We quickly turned our headlight off and walked back to vehicles to grab camera equipment, which also allowed the viper to acclimate to the ambush site with relatively low disturbance.

It took between 15- 20 minutes to get camera gear back to the viper, and about 5 minutes to set the camera while pointing a light on the ground or away from the viper (never directly at the viper). After the camera was set, we resumed surveying the general area but were unable to find another viper. No further data was collected within 5 meters of the viper that or any other night, the presumption being presence or a headlight would disturb it and any potential prey, predators, or conspecifics in close proximity. The camera was set from 3 November night to 6 November morning (0945), when the camera was retrieved the last morning the Kanchanaburi viper was observed and left ambushing on the same branch it had been on most of those days.

The SD card failed on the first night (3 November), but a total of 61.5 hours of video recording were accumulated for the single Kanchanaburi pit viper between 3- 5 November . The viper was primarily observed ambushing during the night and was usually not visible during the day, with limited movement between those behaviors (Figure 5.12). On 4 November, the viper was confirmed visually on the camera entering the termite mound for shelter. Likely it was resting (not ambushing or foraging), but there was no way to confirm without disturbing the viper and the habitat.

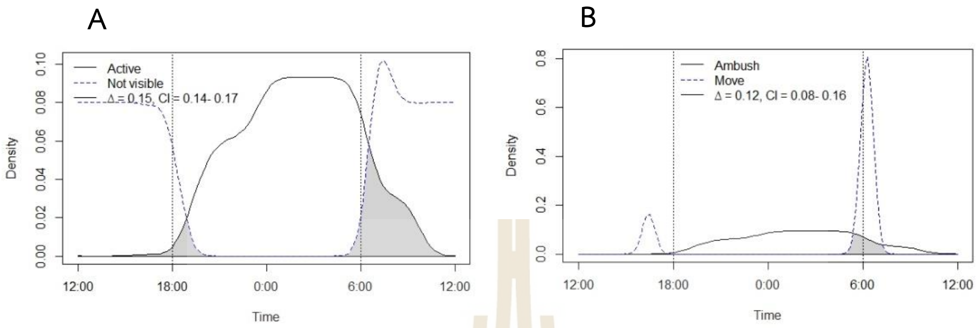

Figure 5.12 Temporal activity patterns observed for an adult male Kanchanaburi pit viper (*Trimeresurus kanburiensis*) at Khao Laem National Park, Thailand. This viper was primarily active during the night (between 18:00- 06:00) and usually not visible during the day (A). Move behavior was primarily observed in the early morning and early evening (B), close to the overlap periods of ambush and when the viper was not visible.

Behavior events were infrequently observed, as were prey. No conspecifics or predators were visible on the camera. The most frequent behavior event displayed by the focal Kanchanaburi viper was headbobbing, which was observed 85 times between 19:03 to 06:28. Only three probes (approximately 20:02, 03:24, 03:25, and 03:26) and two gapes were observed (approximately 21:25 and 01:07). One strike was observed (approximately 20:19), but no prey was visible for more than four hours prior nor any other organism which could have elicited a defensive strike. Potential prey which was seen on camera included geckos (*Cyrtodactylus* and *Hemidactlyus* sp.), a squirrel, a bird (passerine), and rats. Potential prey was primarily observed at night which largely overlapped the focal Kanchanaburi viper foraging period (Figure 5.13), although it is worth noting that the squirrel, bird, and rats were too large for the viper to ingest.

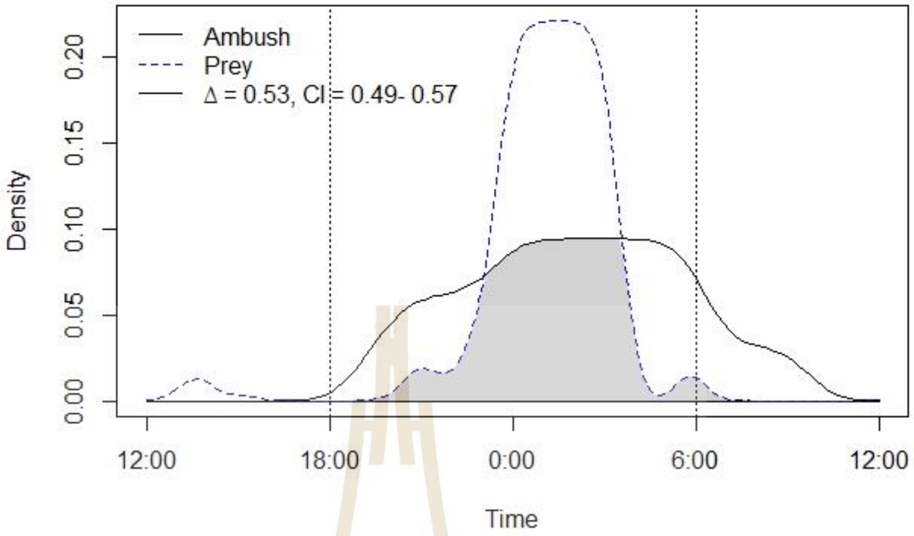

Figure 5.13 Temporal activity patterns observed for an adult male Kanchanaburi pit viper (*Trimeresurus kanburiensis*) and prey observed on a continuous feed camera at Khao Laem National Park, Thailand.

The immediate habitat of the Kanchanaburi viper recorded on camera matched previous descriptions for the species- limestone karst interspersed with bamboo. However, the viper ambush site was within 30 m of a well- traveled paved road. Similar habitat was also present of the opposite side of the road as the viper. The termite mound (Figure 5.14A) that the *T. kanburiensis* was ambushing on and sheltering in appeared be old or abandoned, and no termites were visible, but overall appearance of the mound indicated the termites might be of the genus *Macrotermes*. Two potential species were *cabonarius* and *annadalia*, which can be visually differentiated by soldier head color (black or red, respectively; personal communication, Warin Boonriam). Canopy cover at the microhabitat level (Figure 5.14B; estimated with CanopyApp) was 66.2% and leaf damage on the ground near the viper (1.5 m away) was 0.04%. It was not possible to make estimations at and above viper level due to the viper being present from start to conclusion of monitoring at the same site-attempts would have potentially disturbed the viper which was forbidden under study research and ethics permissions.

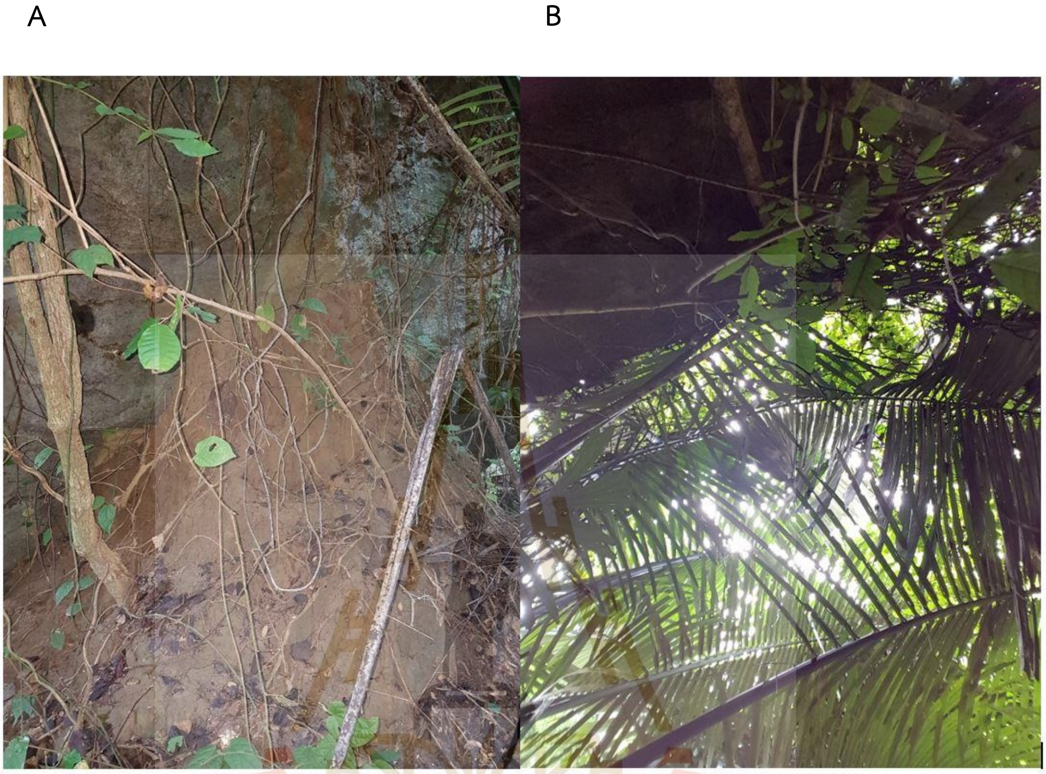

Figure 5.14 Microhabitat where the focal *Trimeresurus kanburiensis* was observed ambushing (on an inactive termite mound, A) and directly above the foraging site (B).

Two of the three justifications presented within the IUCN ENB1ab(v) listing for *T. kanburiensis* are habitat related- restricted distribution of little more than 3,000 km² and presence in fewer than five locations. These have been indirectly addressed through surveys, but the third justification for listing the viper as endangered, trade, has not been investigated. With few exceptions, Thai wildlife trade appears to follow CITES which does not list the Kanburi viper (although there was discussion about it in 2014 and 2015 CITES meetings). The Thai Red List and Thai wildlife protection act (WARPA) do not appear to list *T. kanburiensis* either. The only record of any *Trimeresurus*/green pit viper being reported/seized by Thai authorities (DNP) dating back to 2003 was in 2009 (56 live, 240 dead *Trimeresurus trigonocephalus*; non- native if correct). Interestingly, there were 20 records provided by CITES of *Trimeresurus* between 2013- 2020- 1 of which was listed as "*Trimeresurus* sp." ("specimen") in 2017, the other 19 records being designated specifically as "*Trimeresurus mangshanensis*" which is listed under CITES Appendix II. LEMIS 2000- 2014 records just had "*Trimeresurus* sp." and "*Trimeresurus albolabris*" records listed (158 and 1, respectively), with just one ("*Trimeresurus* sp.") listed from Thailand as a country of origin which was to a natural history museum.

5.5 Discussion

5.5.1 General green pit viper ecology and natural history

In the very first sentence of his abstract in the inaugural issue of the journal Herpetological Conservation and Biology, Bury (2006) states "natural history and field ecology are essential building blocks for successful conservation and management of herpetofauna." Basic natural history, ecology, and behavior of green pit vipers in the wild is limited, which was sought to be addressed in this dissertation chapter.

Tail undulation behavior event was suspected to have been observed prior (Barnes and Knierim, 2019; personal observation, C. H. Barnes) for several green pit viper species on fixed cameras, but could not be confirmed reliably until this dissertation due to low frame rate (one picture recorded every minute). No other organism was visible during the tail undulation event in this dissertation study, but Barnes and Knierim (2019) observed several *T. albolabris* tail undulating in the presence of frogs and toads and Barnes and Barnes and Tipprapatkul (2019) observed a *T. macrops* tail wriggling in a defensive manner which could provide explanations of potential functions for the observed behavior. It is also possible that either prey or threat was observed or detected by the viper but was outside of the frame of the camera.

Strike was a rarely observed behavior event (17 observations) during this dissertation at Sakaerat Biosphere Reserve and Suranaree University of Technology.

This behavior was one of the primary factors for utilizing continuous feed cameras-distinguishing between strike and probe behavior was difficult with timelapse cameras set at one minute intervals and there was concern that either behavior could be easily missed. Predatory strikes, both successful (predations) and unsuccessful were clearly observed in this current study as well as novel likely defensive strikes on rats. Strike success rate was low, of 9 which were clearly against geckos and 3 which were towards frogs, only a single full predation (complete ingestion) was observed. Previous study of green pit vipers and toads is limited, but evidence of selection against (Yang and Mori, 2021) and observation of likely mortality of a *Trimeresurus cf. flavomaculatus* after attempting to ingest an invasive cane toad (*Rhinella marina*, Cruz et al. 2020) may explain the novel behaviors including release and subsequent mouth rubbing of the *T. macrops* in this dissertation after striking a toad.

Just two citations were included in the last listing of *T. vogeli* (2011), the natural history portion being supported by Malhotra et al. (2004) and threat (use for wine) by Somaweera and Somaweera (2010). This is concerning, basic natural history being derived from a single source and no sources for even subpopulation level abundance estimates or threats to optimistically list the species as "Least Concern" (Stuart and Nguyen, 2011) rather than "Unknown" which would likely better reflect the knowledge gap. This dissertation sought to address the missing basic natural history information and prey, another snake, and other organisms in close proximity were all recorded. Observation of the focal *T. vogeli* dragging prey up vertically into the vegetation is new, but may be explained by previous spatial ecology study of the species which suggests adult females at SBR may be highly arboreal and this could extend to predation behavior also (Barnes et al., 2019). Confirmed observation of a male *T. vogeli* in nearby proximity and a potential other individual close enough to be detected on camera may be due to increased sexual activity, as the time they were observed was during the previously suggested mating period (Malhotra et al., 2004).

Earlier in this dissertation, human influence to vipers and vipers to humans was indirectly addressed through estimates of distance to anthropogenic features and how much noise was emitted. Humans were only rarely observed on cameras, which can best be explained through restricted travel and access during the pandemic. A domestic cat was observed on camera pointed at a focal viper at the Sakaerat Environmental Research Station, this was not a pet of staff or visitors (not allowed) but rather from the rural area in the reserve- both domestic dogs and cats are actively trapped regularly at the research station and illustrates many of the conservation and social issues presented by (Lessa et al., 2016) by these animals in protected areas.

5.5.2 Kanchanaburi pit viper ecology and natural history

Unfortunately, logistics due to the global COVID- 19 pandemic and local conditions prevented complete sampling at Khao Laem National Park with just three months sampled during 2020 and none during 2021. Although observation of just a single Kanchanaburi pit viper may appear concerning, detection must be considered. The combined ability of observers to actually spot snakes and the natural history of green pit vipers specifically to remain stationary, frequently in or under cover, were particularly challenging. Detection probabilities (most simply, what organisms are present but not observed) are low for many snake species (3-46% for what are typically thought to be commonly encountered water snakes, Durso et al. 2011), and green pit vipers can be especially difficult to consistently locate due to low detection (22% for commonly encountered *T. macrops* at SBR, Barnes, 2017). For further reference, just two *T. vogeli* were encountered during the entire dissertation study period and although time required to locate them was much lower (32.4 surveyor hours at the specific sites in SBR, compared to 96.9 surveyor hours in KLNP) worth considering is that exact locations where they could be found was known and the vipers themselves are much more conspicuous (adults are much larger, and coloration is highly visible at night). The behavior and natural history of *T. albolabris* at the Khao Laem National Park study area, confirmed by the single road- kill observation, requires further study as there may likely be habitat and behavior partitioning between this species and *T. kanburiensis*.

Although many different types of habitat were searched within Khao Laem National Park, the single *T. kanburiensis* was observed in limestone karst interspersed with bamboo which was previously recorded to be used by the species (summarized in Chan-Ard et al., 2012). Microhabitat, what habitat features vipers are ambushing on and resting in, description has been limited to that limestone and bamboo habitat generalization prior (i.e.- Malhotra and Thorpe, 2004 and Warrell, 1992), so this current observation of both ambushing and sheltering behavior in a termite mound is novel for the species. Observation of the viper in such close proximity to a paved, well- used road suggest population connectivity and mortality to be future avenues of research for the conservation of the species.

While perhaps a result of small sample size and duration, the expression of ambush behavior by the focal *T. kanburiensis* on camera through the early morning is interesting. This dissertation (current chapter and earlier) and several green pit viper behavior studies with *T. macrops* (my study) and *T. albolabris* (Barnes and Knierim, 2019) suggest this group to primarily be active (ambushing and moving) at night, so further study is required to determine whether it was individual variation, seasonal, or typical for *T. kanburiensis* to ambush during daylight hours. Appropriately sized prey was only observed on camera (geckos, *Cyrtodactylus* and *Hemidactlyus* sp.) and in close proximity (within 5m while changing camera batteries and SD cards, frogs) at night; inappropriately sized prey including a squirrel and a bird were observed during the day on camera. Just one strike was observed, although no potential prey was observed within four hours of this behavior.

Although not consisting of data collected during fieldwork during this dissertation, the review of wildlife trade records for *T. kanburiensis* provides valuable insight into the dire Endangered status IUCN listing (Chan-Ard et al., 2012) for the species. New and rare species are sought after in the reptile trade (pet, specifically; Altherr and Lameter, 2020) which may have been considered by IUCN assessors for *T.*

kanburiensis. Although 75% of reptile species are not listed in CITES (Altherr and Lameter, 2020), the Kanchanaburi pit viper is an interesting case in that it has been clearly suggested in multiple CITES meetings that it should be. Thai wildlife trade listing, protections, and monitoring appears to strongly mirror CITES. Green pit viper records from LEMIS and CITES monitoring do indicate there is at least some trade internationally with these species. Non- enforcement monitoring and study via publications does not appear to report trade of *T. kanburiensis*, but international and local works like Altherr et al. (2020) require further investigation and translation. A decade has passed since the 2011 *T. kanburiensis* assessment, but still not comprehensive study or review has been conducted to bring together knowledge available so as to assess whether and what protections are required.

Actions taken to assess wildlife trade of *T. kanburiensis* would directly benefit two other Thai green pit vipers which are morphologically highly similar. The beautiful pit viper (*T. venustus*) is indistinguishable externally so much to *T. kanburiensis* that it was the subject of multiple publications debating whether it was a separate species or not (i.e.- Warrell et al., 1992 and Viravan et al., 1992). Adequate natural history study has not been conducted for this species but it is thought to use limestone karst similarly to *T. kanburiensis* (Malhotra and Thorpe, 2004B). The beautiful pit viper has been reported in multiple works to be in the reptile trade in Europe and South America and other areas (Magalhães and São Pedro, 2012; Visser, 2015; Fuchs et al., 2019), although it does have a much larger distribution than *T. kanburiensis*. In their publication describing a new Thai green pit viper species which is highly similar in coloration to *T. kanburiensis* and *T. venusustus* and likely found in a single massif the year this dissertation was written (2021), Sumontha et al. (2021) wrote a direct call to action "there is a substantial risk that *Trimeresurus kuiburi* sp. nov. becomes hunted for the pet trade, and we strongly recommend the Thai authorities to legally protect it." For effective conservation of any of the three similarly colored and potentially habitat limited green pit viper species, *T. kanburiensis* and *T. venustus* and *T. kuiburi*, study and monitoring effort appears to be necessary for all three.

Although highly centralized and still maintaining the presumed habitat characteristics necessary for the species (karst with bamboo), three confirmed sites (Erawan National Park and Sai Yok military camp, with "hills in the vicinity of Kanchanaburi" as the last) were presented by Malhotra and Thorpe (2004) were likely included in IUCN assessment at which time was limited to just a few observations within each area- since then one unprotected area was confirmed in a publication (Prasopsin and Aksornneam, 2014), and at least two protected areas remain unpublished (Sai Yok National Park, and Khao Laem National Park from this dissertation) as populations of the species. Worth mentioning is research and ethics permissions are difficult to obtain and enforcement of handling animals is comparatively strict for the region, which has driven local herpetological enthusiasts to successfully locate multiple additional sites with *T. kanburiensis* and other endemic herpetofauna outside of the protected areas. Published literature for herpetofauna in adjacent Myanmar is still limited and at least one country wide survey (Wogan et al., 2008) failed to document presence of *T. kanburiensis*. A recent survey specifically in the Tenassarim region (Tanintharyi; Mulcahy et al., 2018) utilizing both field observations and eDNA interestingly found three green pit viper species- mangrove (*Trimeresurus purpureomaculatus*), bamboo (*Trimeresurus stejnegeri*), and a new species (proposed to be in the genus/subgenus *Popeia*).

Spatial and long term (more than just one ambush/resting site per individual) behavioral study would require following individuals, which is currently challenging due to *T. kanburiensis* small body size. Frequently, this is done through radio telemetry, but ethics for snakes typically specify that transmitters do not exceed 5% of body mass which is a challenge for small snakes. Furthermore, being arboreal, *T. kanburiensis* are relatively thin which requires consideration if an internal implant method is to be used and if external transmitters are instead used as an alternative they can frequently get tangled in vegetation (personal observation, C. H. Barnes). Internal transmitters can take time for individuals to recuperate (up to several hours just for anesthesia) and external transmitters should be carefully monitored to ensure individuals do not become entangling, such impacts to findings (particularly behavior) need to be carefully considered in study design planning and discussed explicitly later in findings. Current technology with the body mass constraints limits following individuals to several hours or days and can be expensive (primarily transmitters, telemetry equipment and field staff to track individuals), but such study could provide a more comprehensive picture for individuals which employ multiple sites and illuminate short term movement patterns for the species. At least one study is currently utilizing radio telemetry with *T. kanburiensis*, which should provide additional novel natural history and ecological knowledge with this thesis.

5.6 Conclusion

As elaborated previously, the global COVID- 19 pandemic significantly affected fieldwork at the dissertation study sites Sakaerat Biosphere Reserve and Suranaree University of Technology- because Khao Laem National Park is located outside of the province of the other two sites travel was highly monitored and severely limited. Despite the travel restrictions, valuable basic biology, ecology, and natural history contributions were made to the scarce prior body of literature of green pit vipers in the wild.

Foraging behavior of temperate vipers has been moderately well- studied, particularly rattlesnakes in North America, but remains scarce for tropical regions. Strike success and factors which influence it are topics to be further explored. Observations of geckos and frogs as prey in this dissertation supports prior study, however, selection (for or against certain prey items) requires further study. Additionally, better understanding of potentially toxic prey naturally co- evolving with green pit vipers like Asian toads observed our study could provide additional insight to other similar systems (i.e.- newts and garter snakes in North America) and invasion ecology (i.e.- cane toads in Australia and snake and monitor lizard interactions with them).

Anthropogenic disturbance in the form of visual interactions was limited for this study, but is worth further investigation. The global COVID-19 pandemic limited travel and was the likely cause of limited direct observation of humans in this study, and should be considered when evaluating this work and preparing for future investigations. Indirect disruption of green pit viper behavior by human activity was observed at SUT and SBR. Display of headbob behavior by a *T. albolabris* at SUT when the light from a presumed security guard focused on it suggests visual stimulation (distraction and/or stress) to be possible. Humans were more frequently observed in close proximity vipers on cameras at the Sakaerat Environmental Research Station and within the transition area of the biosphere reserve than at SUT. Utilization of anthropogenic features like rubbish bins as observed in this work in protected areas requires further study. Impacts of domestic animals like the cat observed during this fieldwork also requires further study within the context of green pit viper behavior and natural history.

This chapter was able to comprehensively evaluate behavior and natural history of a focal Vogel's pit viper close to the lowest extreme in elevation it has been found thus far. Potential prey visible in close proximity, and even a successful predation instance was observed during this work. Other animals of interest elicited mixed reactions from the focal Vogel's pit viper, a mesocarnivore passing by did not appear to provoke a response yet a house centipede did. Similarly, a second snake (likely another viper due to movement pattern and semi- arboreal location) moving past did not result in a visible reaction by the focal viper. Further behavioral and natural history study is necessary for Vogel's pit viper, particularly at the lower elevation part of their distribution where they appear to be highly irregularly encountered.

Although field study remains scarce for nearly all green pit viper species, unfortunately it is still lacking even for those of perceived high conservation concern like the Kanchanaburi pit viper. Despite listing by the IUCN Red List in 2011, no major field studies have been published for the species since then nor has comprehensive evaluation of the factors proposed for listing been compiled. Although multiple additional sites of presence have since been identified, formal identification (publication) and follow- up study has been limited. Study of potentially suitable habitat in Myanmar also still remains scarce. Illegal harvest of mature individuals through international pet trade remains paradoxical, with no clear formal protection or monitoring efforts in place to justify or address this factor. Not mentioned in previous literature, but worth discussing is our observation of a Kanchanaburi pit viper foraging in close proximity (< 30m) of a well- used paved road. The role of this habitat feature with regards to basic Kanchanaburi pit viper natural history, disturbance (light, sound to potential prey and predators, and potential increased ability for humans to come into contact with vipers with better access to viper specific habitat), and influence to gene flow require further study.

Green pit viper habitat selection with regards to vegetation and anthropogenic features and disturbance has recently been of interest, however, broader ecological factors are likely also influencing where they choose to forage (and consequently shelter and rest). Vipers might be selecting ambush sites near hymenopterans either due to prey species being drawn to these sites, or maybe as these hymenopterans themselves may serve as a defensive deterrent for potential conspecifics or predators. Further studies of green pit viper predators, prey, and conspecifics are required to better understand how these vipers select foraging sites. Snakebite management and conservation studies were topics explored in this chapter which desperately need further study, both for perceived locally common species like *T. albolabris* and *T. macrops* which inflict the highest number of venomous snakebites where they occur and for *T. kanburiensis* which has received relatively little attention and study despite the dire endangered species listing by the IUCN a decade ago.

5.7 References

Chan-Ard, T., Grismer, L., and Stuart, B. (2012). *Cryptelytrops kanburiensis*. The IUCN Red List of Threatened Species. Accessed on January 5, 2017.

Altherr, S., Freyer, D., and Lameter, K. (2020). Strategien zur Reduktion der Nachfrage nach als Heimtiere Gehaltenen Reptilien, Amphibien und kleinen Säugetieren; BfN Skripten 545; Bundesamt für Naturschutz: Bonn, Germany, p. 465.

Barnes, C. (2017). The spatial ecology, habitat selection, and behavior of big- eye green pit vipers (*Trimeresurus macrops*) in human dominated and protected areas in the Sakaerat Biosphere Reserve. Master's Thesis, Suranaree University of Technology, Thailand.

Barnes, C.H., and Knierim, T.K. (2019). Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus* (*Cryptelytrops*) *albolabris* (Reptilia: Squamata: Viperidae) vipers in Bangkok, Thailand. *Journal of Threatened Taxa 11*(12): 14503-14510.

Barnes, C.H., Farren, W., Strine, C.T., Hill III, J., Waengsothorn, S., and Suwanwaree P. (2019). Are the habitat niches of female green pit vipers *Cryptelytrops macrops* and *Viridovipera vogeli* partitioned by vertical stratification**?** *Herpetological Bulletin 147*: 18-23.

Barnes, C.H., Farren, W., Strine, C.T., and Suwanwaree, P. (2020). Social Behavior Displayed by the Green Pit Viper *Trimeresurus* (*Cryptelytrops*) *macrops*. *Tropical Natural History 20*(1): 95-103.

Chan-Ard, T., Grismer, L., and Stuart, B. (2012). *Cryptelytrops kanburiensis*. The IUCN Red List of Threatened Species. Accessed on January 5, 2017.

Chen, Z., Shi, S., Gao, J., Vogel, G., Song, Z., Ding, L., and Dai, R. (2021). A new species of *Trimeresurus* Lacépède, 1804 (Squamata: Viperidae) from Southwestern China, Vietnam, Thailand and Myanmar. *Asian Herpetological Research 12*(2): 167-177.

Chiszar, D., Lee, R.K.K., Radcliffe, C.W., and Smith, H.M. (1992). Searching behaviors by rattlesnakes following predatory strikes. Pp. 369-382 in *Biology of the Pitvipers* (Campbell, J.A. and Brodie, Jr., E.D., eds.). Selva, USA.

Clark, R.W., Dorr, S.W., Whitford, M.D., Freymiller, G.A., and Putman, B.J. (2016). Activity cycles and foraging behaviors of free- ranging sidewinder rattlesnakes (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. *Zoology 2016*: 1-11.

Cox, M.J., Hoover, M., Chanhome, L., and Thirakhupt, K. (2012). The Snakes of Thailand. Chulalongkorn University Museum of Natural History, Bangkok, Thailand.

Cruz, C.J.P.D., Pauyo, G.N., and Gil, J.R. (2020). Predation of the Philippine Pit Viper *Trimeresurus cf. flavomaculatus* (Gray, 1842) on the Invasive Cane Toad *Rhinella marina* (Linnaeus, 1758) in Albay, Philippines.

Department of National Parks, Wildlife and Plant Conservation, Thailand. (2018). Statistical Data National Parks, Wildlife and Plant 2018. Information and Communication Technology Center.

Durso, A.M., Moorthy, G.K., Mohanty, S.P., Bolon, I., Salathé, M., and Ruiz de Castañeda, R. (2021). SupervisedLearning Computer Vision Benchmark for Snake Species Identification from Photographs: Implications for Herpetology and Global Health. *Frontiers in Artificial Intelligence 4*: 582110.

Geschke, J., Cazelles, K., Bartomeus, I., Goldenberg, J., Leduc, M., Verzelen, Y., Ross, N., and Siple, M. (2021). rcites: An R package to access the CITES Species+ database. R package version 1.2.0

Kumkate, S., Chanhome, L., Thiangtrongjit, T., Noiphrom, J., Laoungboa, P., Khow, O., Vasaruchapong, T., Sitprija, S., Chaiyabutr, N., and Reamtong, O. (2020). Venomics and cellular toxicity of Thai pit vipers (*Trimeresurus macrops* and *T. hageni*). *Toxins 12*(1): 54.

Landert, K.A. (2017). Comparing photographic and GIS-based applications for estimating canopy cover in Southern Appalachian bogs. Proceedings of The National Conference On Undergraduate Research (NCUR): 66-73.

Lehner, P.N. (1987). Design and Execution of Animal Behavior Research: An Overview. *Journal of Animal Science 65*(5): 1213-1219.

Lessa, I., Guimarães, T.C.S., de Godoy Bergallo, H., Cunha, A., and Vieira, E.M. (2016). Domestic dogs in protected areas: a threat to Brazilian mammals? *Natureza & Conservação 14*(2), 46-56.

Machado, B.B., Orue, J.P., Arruda, M.S., Santos, C.V., Sarath, D.S., Goncalves, W.N., Silva, G.G., Pistori, H., Roel, A.R., and Rodrigues-Jr., J.F. (2016). BioLeaf: A professional mobile application to measure foliar damage caused by insect herbivory. *Computers and Electronics in Agriculture 129*: 44-55.

Malhotra, A., Thorpe, R.S., and Stuart, B.L. (2004). A morphometric analysis of *Trimeresurus vogeli* (David, Vidal and Pauwels, 2001), with new data on diagnostic characteristics, distribution and natural history. *Herpetological Journal 14*(2): 65-78.

Prasopsin, S., and Aksornneam, A. (2014). Richness of reptiles at Mahidol University, Kanchanaburi campus, Kanchanaburi province. *Journal of Wildlife in Thailand 21*(1): 15-25.

Registration Office Department of the Interior, Ministry of the Interior. (2019). "รายงานสถิติจำนวนประชากรและบ้านประจำปี พ.ศ.2562." Statistics, population and house statistics for the year 2019. Retrieved 10 March 2020.

Ridout, M.S., and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics 14*: 322-337.

Stuart, B., and Nguyen, T.Q. (2012). *Viridovipera vogeli*. *The IUCN Red List of Threatened Species 2012*: e.T192057A2034223. Downloaded on 03 December 2021.

Stuart, B., Thy, N., Nguyen, T.Q., and Auliya, M. (2012A). *Cryptelytrops albolabris. The IUCN Red List of Threatened Species 2012*: e.T178433A1534017. Downloaded on 03 December 2021.

Uetz, P., and Hallermann, J. (2015). Reptile database. http://reptile-database.reptarium.cz. Accessed on March 01, 2015.

Warrell, D.A. (1999). Guidelines for the clinical management of snake-bites in the south-east Asia region. *Asian Journal of Tropical Medicine and Public Health 30*: 1-20.

Warrell, D.A. (2010). Guidelines for the clinical management of snake-bites in the south-east Asia region. World Health Organization, Regional Office for South East Asia, New Delhi, pp. 1-67.

Yang, C. K., and Mori, A. (2021). The Green Bamboo Pit Viper, *Trimeresurus stejnegeri*, Discriminates Chemical Stimuli Among Anuran Species. *Current Herpetology 40*(2): 159-168.

CHAPTER VI

CONCLUSION AND RECOMMENDATION

6.1 Conclusions

This dissertation sought to analytically investigate activity patterns and behavior of two relatively frequently encountered green pit vipers at two sites in Nakhon Ratchasima province, Thailand- Sakaerat Biosphere Reserve and Suranaree University of Technology. Unfortunately, logistical difficulties associated with the global pandemic COVID-19 throughout the entire duration of the study prevented adequate sampling. Low sample size thus prevented investigation of two of the original study objectives, study of behavior expression of sympatric vipers (more than one species was found at two study sites, but each was only a single individual) and subpopulations (too few individuals at each study site monitored), but supplementary or novel behavioral and ecological information was collected for the other six objectives

Behavior states expressed over long durations of time and spontaneous behavior events were investigated temporally and within the context of general, macrohabitat, microhabitat, and abiotic influences. The ability of modern technological advancement, computer vision, was assessed to aid with these behavior investigations. General natural history, particularly of the scarcely encountered Vogel's pit viper at Sakaerat Biosphere Reserve, rarely observed successful and failed predations, and stimulating social behavior further supplement previous green pit viper study. Novel natural history observations and review of literature thus far for the endangered Kanchanaburi pit viper provide valuable insight towards its conservation. Overall the results observed in this dissertation emphasize the many natural and anthropogenic factors which influence green pit viper behavior and ecology, while further illustrating key knowledge gaps of study with this interesting but still scarcely studied group of snakes.

6.1.1 Green pit viper behavior and activity patterns

Despite the global pandemic significantly altering daily lifestyles of humans, resulting in drastic prevention and mitigation measures including travel restrictions and closure of recreation and protected areas which directly affected data collection measures for this dissertation and current chapter especially, four of the study objectives were still able to be moderately well addressed. The following objectives 1) behavior and activity patterns were determined for the big- eyed pit viper and white- lipped viper, 2) how much and when different sexes (small sample size of age created overlapping intervals which rendered estimates largely not useful) express different behaviors, 3) what potential influences abiotic and habitat features might have on green pit vipers (no co- occurring species were found at Suranaree, and sample size of 1 for a second co- occurring species at Sakaerat), and 4) what threats vipers and humans may face from each other were adequately analytically investigated in this chapter. Caution should be derived when interpreting these results and comparing them to prior and future study as direct human activity influence to viper and other wildlife behavior was unique and likely highly limited during the study period due to the global pandemic. Unfortunately, especially small sample sizes primarily induced by decreased sampling effort availability during the pandemic prevented inferences from being made to objectives 5) investigation of sympatric and co- occurring viper species behavior and activity patterns and 6) comparison of behavior and activity patterns between isolated populations (subpopulations) of vipers.

6.1.2 Computer vision for ambush foraging predator behavior analysis

Computer vision is an incredible technological tool that has recently garnered interest within ecology. Relatively straightforward computer programs and applications have been created for relatively simple ecological questions, such as presence and absence of organisms or behavior events on pictures or recordings through methods like detection of pixel changes. While tools to perform more complex tasks including classification of images and videos have rapidly advanced, review of accessibility and success achieved by average students, researchers, and enthusiasts has lagged. Whether prospective behavioral or ecological research are considering simple tasks such as pixel change detection or more complex classification modeling, this dissertation suggests consideration be made to time required to become adequately familiarized with deep learning model building and basic computing processes, what basic biology conceptual problems may be encountered such as heterogeneity of habitat and abiotic features, how and if those problems can be addressed with sample size and variation within samples, and computer processing power required to run those computational tasks.

Results from this study suggest while run time for pixel detection is comparable to manual review there is high potential to overestimate behavior event observations with complex backgrounds and habitats. Studies anticipating small sample sizes and of short duration are potentially unlikely to be able to capture the variation required to adequately achieve even modest accuracy for deep learning models for image classification and much time is required for training even comparatively small datasets without computing clusters. Background subtraction methods and supplementation of training sets by morphologically and environmentally similar online images to aid with these tasks could be useful for future study.

6.1.3 General green pit viper and Kanchanaburi pit viper ecology and natural history

The global COVID- 19 pandemic significantly affected fieldwork at the dissertation study sites Sakaerat Biosphere Reserve and Suranaree University of Technology- because Khao Laem National Park is located outside of the province of the other two sites travel was highly monitored and severely limited. Despite the travel restrictions, valuable basic biology, ecology, and natural history contributions were made to the scarce prior body of literature of green pit vipers in the wild.

Green pit viper habitat selection with regards to vegetation and anthropogenic features and disturbance has recently been of interest, however, broader ecological factors are likely also influencing where they choose to forage (and consequently shelter and rest). Vipers might be selecting ambush sites near hymenopterans either due to prey species being drawn to these sites, or maybe as these hymenopterans themselves may serve as a defensive deterrent for potential conspecifics or predators. Further studies of green pit viper predators, prey, and conspecifics are required to better understand how these vipers select foraging sites. Snakebite management and conservation studies were topics explored in this chapter which desperately need further study, both for perceived locally common species like *T. albolabris* and *T. macrops* which inflict the highest number of venomous snakebites where they occur and for *T. kanburiensis* which has received relatively little attention and study despite the dire endangered species listing by the IUCN a decade ago.

6.2 Recommendations

While large studies investigating venomics, nomenclature, and taxonomy of green pit vipers has received moderate research interest, ecological foundations for key applied topics including conservation and snakebite management are lacking. Foraging, moving, and sheltering behaviors with implications to habitat and anthropogenic disturbance are topics which have only recently been investigated. How vipers and all wildlife respond to decreased levels of direct anthropogenic disturbance as potentially observed during this dissertation due to the global pandemic COVID-19 would be worth further study.

Deep learning models are not one-size fits all for study organisms and questions. Consideration must be made for the variety of conceptual (background habitat and feature "noise") and computational (high run time, high model layer complexity) factors which have been outlined. Best performing models for organisms and wildlife suggest test datasets with the most similarities to training and validating data will provide the most accurate classifications. Ethologists and wildlife biologists considering exploring deep learning for projects and studies should not only possess or have access to datasets with as much variation as possible but also expect to invest significant amounts of time learning about deep learning theory (model construction) for independent model training to achieve moderate to high levels of classification if datasets expecting to be tested do not match variation accounted for by models already available ("transfer learning"). Large datasets with a variety of individuals in a variety of habitats and the knowledge required for building models suggest multi- year large study sample projects and studies to be the best candidate for this method, with exploratory (similar to this chapter) and smaller sample sized research less suited.

Much previous study with green pit vipers has been dedicated to venomics and taxononomy or nomenclature. While these topics are commendable, little natural history and basic ecology study has been published for most green pit viper species outside of original species descriptions. Consequences of this significant knowledge gap of even the most basic biological information carries significant consequences for green pit viper conservation and snakebite management. Behavior studies, including prey, predators, conspecifics, and humans and interactions of all those organisms with different species of green pit vipers are questions worth pursuing and would pose direct impact to those key issues.

The Kanchanaburi pit viper (*Trimeresurus kanburiensis*) is a beautiful but thought to be highly threatened species of snake which has received little attention and study. This study conducted at Khao Laem National Park, Kanchanaburi province, Thailand, is the first comprehensive natural history study for the species in the wild. Although limited to a single individual, findings include confirmation of previously published limestone karst with bamboo habitat use, addition of a new observation of termite mound foraging and sheltering microhabitat use, novel activity pattern and behavior state and event descriptions, and observations of potential prey temporal activity in the immediate proximity.

As a species, like many, *T. kanburiensis* would greatly benefit from re- assessment or implementation of measures to investigate and address prior justifications for IUCN

Red List status. Further behavioral, ecological, and reptile trade study of the Kanchanaburi pit viper would directly benefit two other Thai green pit vipers which are highly similar to *T. kanburiensis* in coloration, morphology, likely high desirability in the reptile pet trade, and potential preference for specific habitat types.

APPENDIX

APPENDIX

GREEN PIT VIPER BEHAVIOR AND ACTIVITY PATTERN MODEL DATA

Table 1 Summarized total monitoring effort for each viper (minutes, "MinMon"), behavior state (ambush, move, rest) observations in minutes, and event (gape, headbob, probe) observations as a rate per minute for big-eyed (*Trimeresurus macrops*, TRMA) and white-lipped (*T. albolabris*, TRAL) pit vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology.

Viper ID	MinMon	Ambush	Move	Rest	Gape	Headbob	Probe
TRMA002	275	173	7	85	0.004	0	0.022
TRMA003	249	259	2	0	0.008	0	0
TRMA006	103	422	45	0	0.011	0.021	0.02
TRMA007	3132	60	3	0	0	0	0
TRMA012	699	396	5	0	0.002	0.002	0.011
TRMA014	180	211	11	0	0.007	0.042	0.002
TRMA017	265	574	13	0	0.004	0.027	0.008
TRMA018	446	793	6	0	0.001	0.056	0.002
TRMA019	683	931	14	0	0.002	0.007	0.02
TRMA022	676	273	2	0	0.011	0.025	0.004
TRMA023	1492	203	29	0	0	0.012	0.028
TRMA024	540	77	4	0	0	0.01	0
TRMA025	1335	2188	36	365	0.001	0.015	0.013
TRMA026	274	699	0	0	0.004	0.008	0
TRMA030	958	86	0	93	0.028	0.005	0
TRMA031	70	0	0	265	0	0	0
TRMA033	160	418	26	0	0	0.016	0
TRMA034	1128	31	0	638	0	0	0.001
TRMA039	1298	461	8	0	0.001	0.016	0
TRAL001	265	1209	18	0	0.009	0.099	0
TRAL003	261	488	32	0	0	0.1	0
TRAL004	560	1097	29	0	0.004	0.122	0.0007
TRAL010	63	274	0	0	0.007	0.317	0
TRAL023	433	789	28	0	0.005	0.162	0.001
TRAL024	423	46	3	0	0	0.128	0
TRAL031	655	147	2	0	0.006	0.169	0.006
TRAL032	854	877	73	0	0	0.018	0.0009
TRAL033	1133	821	26	0	0	0	0.001

Table 2 Data collected for use in general Bayesian regression models including site (Suranaree University of Technology, SUT; Sakaerat Biosphere Reserve, SBR), species (*Trimeresurus macrops*, TRMA; *T. albolabris*, TRAL), age, and sex. Species, age, and sex data was estimated visually- no animals were handled, captured, or directly disturbed.

Viper ID	Site	Species	Age	Sex
TRMA002	SBR	TRMA	Adult	Female
TRMA003	SBR	TRMA	Adult	Female
TRMA006	SBR	TRMA	NotAdult	Female
TRMA007	SBR	TRMA	Adult	Female
TRMA012	SBR	TRMA	Adult	Female
TRMA014	SBR	TRMA	Adult	Female
TRMA017	SBR	TRMA	Adult	Female
TRMA018	SBR	TRMA	Adult	Female
TRMA019	SBR	TRMA	Adult	Female
TRMA022	SBR	TRMA	Adult	Female
TRMA023	SBR	TRMA	Adult	Male
TRMA024	SBR	TRMA	Adult	Female
TRMA025	SBR	TRMA	Adult	Male
TRMA026	SBR	TRMA	Adult	Female
TRMA030	SBR	TRMA	Adult	Female
TRMA031	SBR	TRMA	Adult	Female
TRMA033	SBR	TRMA	Adult	Female
TRMA034	SBR	TRMA	Adult	Female
TRMA039	SBR	TRMA	Adult	Female
TRAL001	SUT	TRAL	Adult	Female
TRAL003	SUT	TRAL	Adult	Male
TRAL004	SUT	TRAL	Adult	Male
TRAL010	SUT	TRAL	Adult	Female
TRAL023	SUT	TRAL	Adult	Unclear
TRAL024	SUT	TRAL	Adult	Unclear
TRAL031	SUT	TRAL	Adult	Female
TRAL032	SUT	TRAL	Adult	Female
TRAL033	SUT	TRAL	NotAdult	Female

Table 3 Microhabitat data collected for big- eyed (*Trimeresurus macrops*, TRMA) and white- lipped (*T. albolabris*, TRAL) pit vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology including canopy cover (CC), perch height (PH), leaf quality and damage (at viper level, LQD1; ground directly below viper, LQD2; and 0.5m directly above viper, LQD3), and leaf area (at viper level, LA1; ground directly below viper, LA2; and 0.5m directly above viper, LA3).

Viper ID	CC	PH	LQD1	LQD2	LQD3	LA1	LA2	LA3
TRMA002	27.86	60	0		0	1037.49	0	1100.26
TRMA003	16.82	230			0	0	0	221.657
TRMA006	3.148	150	0.09		0.04	33.115	0	65.114
TRMA007	14.777	400				0	0	0
TRMA012	0	200				0	0	0
TRMA014	26.4	370				0	0	0
TRMA017	26.416	1700	0.59			124.293	0	0
TRMA018	31.892	100	0			9.26	0	0
TRMA019	29.731		0.68	2.59	1.5	90.239	46.982	148.159
TRMA022	23.07	50	1.95			1.172	0	0
TRMA023	17.6	70	0			1.862		
TRMA024	190	50.5	4.09		0	2.059		2.615
TRMA025	21.324	90	0.03	6.36		31.698	103.088	0
TRMA026	19.693	160	0		2.84	36.271	0	178.217
TRMA030	22.265	360	0.33			39.069	0	0
TRMA031								
TRMA033	20.583							
TRMA034	400	23.13				0	0	0
TRMA039	35.659	10	0			1.178	0	0
TRAL001	26	1008	0.54	0.03	0	201.055	113.867	332.4
TRAL003	20.1	320	0.16			145.244	0	0
TRAL004	8	400	0	2.54		1.902	9.959	0
TRAL010	11.8	160	0	0	0	28.4	34.9	19.4
TRAL023	0	70				0	0	0
TRAL024	72.2	800	0	0				
TRAL031	10.8	210				0	0	0
TRAL032	25	230				0	0	0
TRAL033	17.1	150				0	0	0

Table 4 Macrohabitat data estimated and utilized for Bayesian regression models for big-eyed (*Trimeresurus macrops*, TRMA) and white-lipped (*T. albolabris*; TRAL) pit vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology, including elevation, canopy height (CH, m), normalized difference vegetation index (NDVI), leaf area index (LAI), distance to buildings (BuildDist), distance to roads (RoadDist), and distance to water (WaterDist).

Viper ID	Elevation	CH	NDVI	LAI	BuildDist	RoadDist	WaterDist
TRMA002	387.0	27.1	0.00	0.2	12.8	6.2	2242.4
TRMA003	386.4	27.1	0.00	0.3	2.7	0.2	2248.7
TRMA006	390.2	27.1	-0.09	0.2	0.0	44.4	2352.1
TRMA007	390.2	27.1	-0.09	0.2	0.0	44.4	2352.1
TRMA012	383.2	27.1	0.00	0.2	0.0	61.6	2203.6
TRMA014	491.9	32.8	0.01	4.1	363.0	0.1	21.9
TRMA017	384.6	27.1	0.00	0.2	10.6	48.5	2270.4
TRMA018	385.2	27.1	0.00	0.2	2.1	6.2	2195.6
TRMA019	511.7	32.8	0.01	4.1	312.3	2.6	86.6
TRMA022	386.3	27.1	0.00	0.2	13.2	39.6	2212.0
TRMA023	270.7	31.0	0.03	1.4	75.6	164.8	1370.5
TRMA024	386.3	27.1	0.00	0.2	13.2	39.6	2212.0
TRMA025	383.8	27.1	0.00	0.2	7.2	57.5	2223.7
TRMA026	386.3	27.1	0.00	0.2	8.6	38.6	2250.1
TRMA030	386.3	27.1	0.00	0.2	7.2	35.1	2213.6
TRMA031	491.9	32.8	0.01	4.1	363.0	0.1	21.9
TRMA033	244.3	15.9	0.10	0.5	44.4	17.9	216.3
TRMA034	243.9	1.0	0.10	0.5	36.9	44.7	179.6
TRMA039	245.1	15.9	0.10	0.5	41.0	51.6	242.8
TRAL001	241.1	0.4	0.01	0.3	56.8	141.9	402.7
TRAL003	238.0	0.4	0.01	0.3	69.2	66.3	430.3
TRAL004	241.3	0.4	0.01	0.3	93.8	84.9	333.7
TRAL010	232.8	0.4	0.01	0.3	137.4	59.6	729.5
TRAL023	232.8	0.4	0.01	0.3	154.6	59.6	729.5
TRAL024	240.3	0.4	0.01	0.2	12.8	147.5	403.2
TRAL031	243.0	11.4	0.01	0.3	436.6	9.1	575.5
TRAL032	238.6	0.4	0.01	0.3	436.6	54.1	402.2
TRAL033	243.6	11.4	0.01	0.2	2.2	51.5	541.3

Table 5 Abiotic data estimated and utilized for Bayesian regression models for big-eyed (*Trimeresurus macrops*, TRMA) and white- lipped (*T. albolabris*; TRAL) pit vipers at Sakaerat Biosphere Reserve and Suranaree University of Technology, including temperature, humidity, pressure, precipitation, cloud cover (CloudCover), wind speed (Wind_speed), anthropogenic noise (Human_noise), and natural noise (Nat_noise).

Viper ID	Temperature	Humidity	Pressure	Precipitation	CloudCover	Wind_speed	Human_noise	Nat_noise
TRMA002	26.59	0.02	98773.84	13.78	73.66	1.37		40.00
TRMA003	26.59	0.02	98773.84	13.78	73.66	1.37		40.00
TRMA006	26.59	0.02	98773.84	13.78	73.66	1.37		
TRMA007	24.10	0.02	99004.75	14.74	78.96	1.17		
TRMA012	24.10	0.02	99004.75	14.74	78.96	1.17		
TRMA014	24.10	0.02	99004.75	14.74	78.96	1.17		
TRMA017	22.66	0.01	99391.35	0.11	39.09	1.52		
TRMA018	22.66	0.01	99391.35	0.11	39.09	1.52		
TRMA019	22.66	0.01	99391.35	0.11	39.09	1.52		
TRMA022	26.14	0.01	99377.14	0.00	68.51	2.16		
TRMA023	26.62	0.01	99200.04	0.00	18.99	0.82	52.00	
TRMA024	26.62	0.01	99200.04	0.00	18.99	0.82		40.00
TRMA025	30.70	0.02	98639.88	0.03	37.43	1.81		70.00
TRMA026	30.70	0.02	98639.88	0.03	37.43	1.81	64.00	
TRMA030	30.70	0.02	98639.88	0.03	37.43	1.81	56.00	
TRMA031	25.52	0.02	98844.67	9.34	58.64	1.18		
TRMA033	25.52	0.02	98844.67	9.34	58.64	1.18		47.00
TRMA034	26.01	0.02	98861.42	6.92	57.16	1.21	48.00	
TRMA039	26.01	0.02	98861.42	6.92	57.16	1.21		
TRAL001	25.65	0.02	98756.19	13.26	79.61	1.01		45.00
TRAL003	26.04	0.02	98874.25	13.78	74.19	0.99		45.00
TRAL004	26.04	0.02	98874.25	13.78	74.19	0.99		46.00
TRAL010	24.09	0.02	99040.32	12.41	87.81	1.22		54.00
TRAL023	22.64	0.01	99644.46	0.00	52.61	2.69	48.00	
TRAL024	24.13	0.02	99398.98	6.03	68.57	1.80	58.00	
TRAL031	25.03	0.02	99429.65	6.00	50.30	0.38	57.00	
TRAL032	25.03	0.02	99429.65	6.00	50.30	0.38	51.00	
TRAL033	25.16	0.02	98697.93	9.64	74.90	1.48		47.00

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Selected publications

Hodges, C.W., **Barnes, C.H.**, Patungtaro, P, and Strine, C.T. (2021). Deadly dormmate: a case study on *Bungarus candidus* living among a student dormitory with implications for human safety. **Ecological Solutions and Evidence**. 2021: 2:e12047.

Barnes, C.H., Farren, W., Strine, C.T., and Suwanwaree, P. (2020). Social Behavior Displayed by the Green Pit Viper *Trimeresurus* (*Cryptelytrops*) *macrops*. **Tropical Natural History.** 20(1): 95-103.

Barnes, C.H., Farren, W., Strine, C.T., Hill III, J., Waengsothorn, S., and Suwanwaree P. (2019). Are the habitat niches of female green pit vipers *Cryptelytrops macrops* and *Viridovipera vogeli* partitioned by vertical stratification? **Herpetological Bulletin**. 147: 18-23

Barnes, C.H., and Knierim, T. (2019). Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus* (*Cryptelytrops*) *albolabris* in Bangkok, Thailand. **Journal of Threatened Taxa**. 11(12): 14503-14510.

Barnes, C.H., and Tipprapatkul, W. (2019). *Cryptelytrops macrops*: defensive tail display. **Herpetological Review**. 50(1): 154.