THE SPATIAL ECOLOGY AND HABITAT SELECTION OF MALAYAN KRAITS (*Bungarus candidus*) IN SUBURBAN NAKHON RATCHASIMA, THAILAND

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Thesis Submitted in Partial Fulfillment of the Requirements for the

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นิเวศวิทยาเชิงพื้นที่ และการเลือกถิ่นที่อยู่อาศัยของงูทับสมิงคลา (*Bungarus candidus*) ในเขตชานเมือง จังหวัดนครราชสีมา

นายคาเมรอน เวสลีย์ ฮอดเจส

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

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อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน โทมัส สไตร์น. 202 หน้า

งูทับสมิงคลา/ ความขัดแย้งระหว่างมนุษย์ - สัตว์ป่า/ แบบจำลอง dBBMM/ การคัดเลือกตัวแปรแบบขั้นตอน/ ฤดูกาล/ นิเวศวิทยาในเมือง

การถูกงูกัดจัดเป็นหนึ่งในโรคของเขตร้อนในทางการแพทย์ที่มีจำนวนผู้ป่วยทั่วโลกมากถึง 1.8-2.7 ล้านคนต่อปี แต่กระนั้นก็ไม่ได้รับความสนใจในการศึกษาด้านการเคลื่อนที่และนิเวศวิทยาของงูสายพันธุ์ต่างๆ ที่ดำรงอยู่ร่วมกับมนุษย์อันมีความสำคัญทางการแพทย์ในการช่วยลดการเกิดขึ้นของอุบัติการณ์ โดยงูทับสมิงคลา หรือ *Bungarus candidus* (Linnaeus, 1758) จัดเป็นหนึ่งในสายพันธุ์งูพิษที่มีถิ่นที่อยู่อาศัยและมีความสำคัญทางการแพทย์ที่สุดในภูมิภาคเอเชียตะวันออกเฉียงใต้ มีรูปแบบการหากินในช่วงเวลากลางคืนและมักมีรายงานการพบเจอในพื้นที่อยู่อาศัยของมนุษย์

การศึกษานี้มีเป้าหมายในการสำรวจรูปแบบการเคลื่อนที่และเลือกถิ่นที่อยู่อาศัยของ *B. candidus* ที่อาศัยอยู่ร่วมกับมนุษย์จำนวนมากในเมทริกซ์ภูมิทัศน์แบบผสม โดยเทคนิคการติดตามสัตว์ป่าด้วยสัญญาณวิทยุในกลุ่มเป้าหมายจำนวน 14 ตัว (เพศผู้ 13 ตัว เพศเมีย 1 ตัว) วันละ 1 ครั้ง ตั้งแต่วันที่ 30 พฤษภาคม 2561 ถึงวันที่ 24 มีนาคม 2563 และใช้แบบจำลอง dynamic Brownian Bridge Movement (dBBMM) เพื่อประมาณการใช้พื้นที่และคำนวณความแปรปรวนของการเคลื่อนที่ พบว่า *B. candidus* มีการใช้พื้นที่ค่อนข้างเล็ก (ค่าเฉลี่ย = 22.85 ± 9.19 ha) และพบว่าขนาดของร่างกายและระยะเวลาที่ใช้ภายในพื้นที่มีอิทธิพลเพียงเล็กน้อยต่อพื้นที่การใช้งานในรายบุคคล *B. candidus* เพศผู้แสดงแนวโน้มการเคลื่อนที่ตามฤดูกาลการที่ลดลงในฤดูร้อนและเพิ่มขึ้นในฤดูฝน และแสดงความแปรปรวนของการเคลื่อนที่อันดูเหมือนการบ่งบอกถึงการเริ่มต้นของฤดูผสมพันธุ์ในช่วงต้นฤดูหนาว (ระหว่างเดือนตุลาคมถึงพฤศจิกายน) การเปรียบเทียบความแปรปรวนของการเคลื่อนที่ด้วยแบบจำลองการถดถอยแบบเบย์ (Bayesian Regression Models) พบว่า *B. candidus* ตอบสนองต่อการเปลี่ยนแปลงในระดับกิจกรรมของมนุษย์โดยการปรับเปลี่ยนการเคลื่อนที่ของพวกเขา และแสดงถึงความสนใจของ *B. candidus* ต่อการเลือกใช้พื้นที่อาศัยในพื้นที่ธรรมชาติหรืออาคารที่มีการรบกวนน้อยโดยพื้นที่อาคารและคูระบายน้ำคอนกรีตถูกเลือกเป็นที่พักพิงบ่อยกว่าพื้นที่อื่น ๆ

แม้ในการศึกษาเบื้องต้นยังได้รับข้อมูลเชิงลึกที่เป็นประโยชน์เกี่ยวกับพฤติกรรมการหาอาหาร รูปแบบอาหาร พฤติกรรมและรูปแบบการกิน และการตายของ *B. candidus* ที่ดำรงชีวิตอยู่ร่วมกับมนุษย์ ในขณะที่การปรับเปลี่ยนสภาพที่ดินโดยมนุษย์และการถูกงูกัดของมนุษย์ยังคงกลายเป็นข้อกังวลสำหรับการอนุรักษ์และจัดการ จึงแนะนำให้การศึกษาในอนาคตควรตรวจสอบทรัพยากรและข้อกำหนดเชิงพื้นที่ของงูพิษที่มีนัยสำคัญทางการแพทย์และปัจจัยที่นำไปสู่การถูกงูกัด

สาขาวิชาชีววิทยา ลายมือชื่อนักศึกษา________________________

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CAMERON WESLEY HODGES : THE SPATIAL ECOLOGY AND
HABITAT SELECTION OF MALAYAN KRAITS (*Bungarus candidus*) IN
SUBURBAN NAKHON RATCHASIMA, THAILAND.
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BUNGARUS / HUMAN-WILDLIFE CONFLICT / dBBMM / STEP-SELECTION / SEASONALITY / URBAN ECOLOGY

Snakebite is a neglected tropical disease which afflicts at least 1.8-2.7 million people worldwide annually. Studies on the movements and ecology of medically significant species, especially those living among humans, may be imperative in helping reduce snakebite incidents. The Malayan krait, *Bungarus candidus* (Linnaeus, 1758), is a nocturnal active foraging and highly venomous snake from Southeast Asia. Malayan kraits are known to occur among human residencies, and are among the most medically significant snake species in Southeast Asia. This study investigates the space use, habitat selection, and temporal movement patterns of *B. candidus* in a highly heterogeneous patchy landscape matrix with a large human population. Using radio-telemetry, this study tracked the movements of 14 Malayan kraits (M = 13, F = 1), obtaining locations once per day, between 30 May 2018 and 24 March 2020. Using dynamic Brownian Bridge Movement Models to estimate space use and calculate motion variance, I found that Malayan kraits generally used relatively small areas of space (mean = 22.85 ± 9.19 ha), though the area of use appears to be weakly influenced by both the individual's body size and the amount of time spent within settlement habitat. Male Malayan kraits exhibited seasonal trends in movements, reducing activity in the hot season, increasing movement frequency in the wet season, and exhibiting peaks in motion variance which appear to indicate the onset of breeding season in the early cold season (between October and November). Comparing motion variance from during and between the university's terms with Bayesian Regression Models appears to suggest that *B. candidus* react to changes in human activity levels by altering their movements. Additionally, Integrated Step Selection Functions revealed that snakes in my study appear to show some level of attraction to both less-disturbed natural areas and buildings, and snakes used anthropogenic structures, such as buildings and concrete drainage ditches, as shelters more frequently than other shelter types. Though preliminary, this study also gained useful insight into the foraging habits, diet, behavior, diel activity, and mortality of Malayan kraits inhabiting an anthropogenic landscape. As human modification of land and snakebite continue to become concerns for conservation and management, future studies should investigate resource and spatial requirements of medically significant venomous snakes and factors leading to snakebites.

School of Biology
Academic Year 2020

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LIST OF ABBREVIATIONS

AIC = Alkaike’s Information Criterion

BCrI = Bayesian Credible Interval

BRM = Bayesian Regression Model

dBBMM = Dynamic Brownian Bridge Movement Model

df = Degrees of freedom

GLM = Generalized Linear Model

GPS = Global Positioning System

ISSF = Integrated Step Selection Function

KDE = Kernel Density Estimate

MCP = Minimum Convex Polygon

MDD = Mean Daily Displacement

MMD = Mean Movement Distance

mrg = Margin size (dBBMM)

SBR = Sakaerat Biosphere Reserve

SD = Standard Deviation

SUT = Suranaree Univerity of Technology

SVL = Snout-to-vent Length

TL = Tail Length

w_i = Model weight

ws = Window size (dBBMM)

σ^2m = Mean motion variance

CHAPTER I

INTRODUCTION

1.1 Background and Problems

Human activities are rapidly changing natural landscapes, often creating complex mosaic landscapes containing remnants of natural habitats and areas of human development (Rojas-Morales, 2012). Species are often forced to live in agricultural and urban areas, creating new problems (Knoot and Best, 2011). Many snake species use human-modified habitats, thus resulting in a heightened potential for snake-human conflict (Breininger et al., 2012; Marshall et al., 2018; Pandey et al., 2016). As a result, many people intentionally kill snakes out of fear or persecution (Dodd, 1987; Miranda et al., 2016). Snakes also sometimes harm people with lethal envenomings (Kasturiratne et al., 2008). The World Health Organization reclassified snakebite as a neglected tropical disease in 2017 (Chippaux, 2017), and it is estimated that more than 1.8-2.7 million people are afflicted by snakebite worldwide each year (Chippaux, 2017; Kasturiratne et al., 2008; Suraweera et al., 2020). In order to learn how to prevent snakebite while also conserving snake species in ever-growing altered and human-dominated landscapes, we need to understand the requirements and behaviors of highly venomous species in areas where both snakes and humans live together in regions actually afflicted by snakebite.

Studies on animal movement and behavior can often provide important and useful information which can be directly implemented into wildlife conservation and management programs (Fraser et al., 2018), and can also help reduce and mitigate human-wildlife conflicts (Gunther and Smith, 2004; Takahata et al., 2014; Braunstein et al., 2020). Despite being directly responsible for snakebite envenomation, ecological studies on snakes are relatively few when compared to those with a focus on endothermic vertebrates (Ford, 1995; Bonnet et al., 2002; Pawar, 2003). Even worse, studies on snake movements rarely address the direct application of findings to snakebite management and prevention strategies, with the vast majority of such studies occurring in regions where snakebite is not a major concern (Kasturiratne et al., 2008; Crane et al., 2020). It is particularly important to understand the ecology of snake species which contribute to medically significant envenomations, as this information will allow us to better construct preventative measures to reduce snake-human conflicts and snakebite (Pandey et al., 2016; Ramesh and Nehru, 2019; Pandey et al., 2020). Information on the habits of snakes can also be disseminated to people who are among communities most at risk of snakebite in an attempt to reduce snake-human conflicts, and thus snakebite (Gutiérrez et al., 2017; Warrell, 2010; WHO, 2016). There is particularly a need for research on venomous snakes in tropical countries where snakebite poses a significant public health problem, such as Thailand (Buranasin, 1993; Warrell, 2010), where it is estimated that 8,500 people are bitten annually in present day (Kasturiratne et al., 2008).

The Malayan krait, *Bungarus candidus* (Linnaeus, 1758), is a terrestrial nocturnal species of snake of the Elapidae family (Slowinski, 1994a). Like most Elapids, *Bungarus* spp. possess potent neurotoxic venom which they use to immobilize their prey (Kerkkamp et al., 2017). *B. candidus* occurs across Southeast Asia (Das, 2010), where the species inhabits agricultural lands (Knierim et al., 2018), forested areas (Mohammadi et al., 2014), and even human settlements (Chanhome et al., 2011). Most human krait bite victims are bitten while sleeping on the ground in rural settlements (Prasarnpun et al., 2005; Warrell, 2010; Tongpoo et al., 2018). In Thailand, *B. candidus* is only responsible for about 1.1% of all venomous snakebite incidents (Viravan et al., 1992), yet the species is responsible for 28.3% of all snakebite related deaths (Looareesuwan et al., 1988). Within Thailand, the majority of recorded bite incidents and bite related deaths from *B. candidus* occur in the northeastern region, where about 70.5% of 78 of the country's krait bite incidents occurred (Looareesuwan et al., 1988; Tongpoo et al., 2018).

Many studies have examined *B. candidus's* venom, its medicinal potential and the production of anti-venom for treating krait envenomations (Warrell et al., 1983; Tan and Ponnudurai, 1990; Laothong and Sitprija, 2001; Ratanabanangkoon et al., 2016; Gomes et al., 2017; Charoenpitakchai et al., 2018). However, despite their medical significance and often shared space use with humans, very few studies have explored the ecological habits of *B. candidus* in the field. This study provides important insight into the space use, habitat selection, and temporal movement patterns of *B. candidus* – and provides useful preliminary information on the natural history, abundance, diet, and mortality of *B. candidus* – on Suranaree University of Technology (SUT) campus and adjacent land in Nakhon Ratchasima, Thailand. This study is the first to examine the movement patterns of more than one telemetered *B. candidus* individual, and is the first study to utilize newer and more robust methods for examining space use, habitat selection, and activity patterns. Findings from this study can be implemented into community awareness programs in order to reduce envenomations from one of Thailand’s most deadly venomous snakes.

1.2 Research Objectives

1.2.1 Estimate space use of male *B. candidus* in a human-dominated landscape of Nakhon Ratchasima, Thailand, using dynamic Brownian bridge movement models.

1.2.2 Identify the best predictors of occurrence distribution size (dBBMM 95%) for *B. candidus* (i.e. number of days tracked, body size, or proportion of fixes within highly disturbed habitats).

1.2.3 Determine whether *B. candidus* site fidelity differs between natural and disturbed habitats using recursive analysis.

1.2.4 Identify if temporal patterns in movement variance exist for *B. candidus*.

1.2.5 Determine if land-use features influence movements of *B. candidus* using Integrated Step Selection Functions.

1.3 Research Hypotheses

1.3.1 Male *B. candidus* at SUT will have a mean 95% dBBMM occurrence distribution greater than the occurrence distribution made from movement data of the adult male telemetered within the SBR by Mohammadi et al. (2014).

1.3.2 The individual’s body size will best predict the occurrence distribution area estimate (dBBMM 95%) in male *B. candidus*.

1.3.3 Male *B. candidus* will revisit sites more frequently among settlement habitat than when in more natural habitats.

1.3.4 Male *B. candidus* movement variance peaks will coincide with their supposed breeding season, which was said to occur between the months of December and January (Chanhome et al., 2011).

1.3.5 Male *B. candidus* movements will be influenced by habitat characteristics, showing association with less-disturbed habitats.

1.4 Scope and Limitations of the Study

Field research for this study was conducted between 30 May 2018 and 24 March 2020 among the human-dominated landscape of Suranaree University of Technology (SUT) campus and the adjacent villages and agricultural lands in Nakhon Ratchasima, Thailand. All data was collected on or within three kilometers of the university campus. In an attempt to limit variables which may affect habitat selection and movement, and because males were far more commonly encountered than are females, the study focused on tracking a single sex (M = 13, F = 1). In order to maximize the number of encountered *B. candidus* which could be added to my study, I tracked males of varying body sizes (total length $\geq$ 64 cm). This variation in body size may also improve our understanding of how body size relates to movements and space use, though it does potentially further divide my sample size, as movement patterns of adults are likely different from juveniles.

Each individual was located daily via radio-telemetry, and the location was determined with a Garmin 64S GPS, which had an average accuracy of about 5 m. The study focused locating animals during the daylight, when kraits are typically not active, in order to identify shelter locations. However, some individuals were located haphazardly (non-randomly) during the night in order to obtain locations when the snakes are active (i.e. moving), though these occasions were few. Thus little is known about their foraging behaviors and nocturnal movements. While I hoped to track multiple male *B. candidus* simultaneously for long durations, that span through the different seasons, in order to help us find trends in their movements in relation to environmental factors, the transmitters I used had relatively short battery lives. I additionally experienced a relatively high degree of premature transmitter failures. As a result individuals were only tracked for total of 106 days on average, which greatly hinders my ability to examine temporal movement patterns and draw comparisons between seasons.

Space use was estimated with dynamic Brownian Bridge Movement Models, while recursive analysis was used to identify core areas of space use and to examine site fidelity of the telemetered individuals. I also used Integrated Step Selection Functions to examine whether habitat features impacted the movements of telemetered *B. candidus*, Generalized Linear Models (GLM) in order to identify which factor(s) best predict home range size, and Bayesian Regression Models to examine seasonal trends in motion variance.

This project provides an opportunity to gather baseline information on the ecology and natural history of a cryptic and medically significant venomous snake species which has been understudied in the field. The study can help us understand how conflicts between *B. candidus* and humans arise, which can help devise management strategies and awareness programs to help reduce such conflicts in Southeast Asia.

CHAPTER II

LITERATURE REVIEW

2.1 Human Habitat Modifications

2.1.1 Habitat Loss and Fragmentation

Anthropogenic induced habitat loss and fragmentation may pose the greatest threat to biodiversity (Wilson, 1992; Czech et al., 2000; Tilman et al., 2001). Increasing human populations and activities have placed biodiversity at risk and continue to degrade the world's biomes as natural habitats are converted for human use (Hoekstra et al., 2005). As of the twentieth century, at least 43% of Earth's land area has been modified for human activities (Barnosky et al., 2012; Ellis, 2011). The destruction and fragmentation of habitats often creates diverse landscapes which include remnants of original habitats among areas of human development (Rojas-Morales, 2012). This creates challenges for species, as they have to survive in complex landscape mosaics that contain their own natural habitats as well as new environments such as agricultural and urban areas (Knoot and Best, 2011; Rojas-Morales, 2012). Boesing et al. (2018) found that biodiversity extinction thresholds are stronger in more complicated matrices, specifically matrices that have more vegetated and forested areas remaining.

Southeast Asia and other tropical ecoregions are considered biodiversity hotspots, as they hold much of the world's species diversity (Sodhi et al., 2004).

Unfortunately these tropical ecosystems are at serious risk due to rapid deforestation (Achard et al., 2002). Despite the high biodiversity and endemism, Southeast Asia has some of the highest deforestation rates globally (Achard et al., 2002; Hughes, 2017a). Southeast Asian forests are being cleared primarily for agriculture and urban development (Hughes, 2017a, 2018). In Thailand the majority of the original natural landscape has been modified to be used by humans, with only 27.4% of forest land cover by the year of 1990, however, this has increased to 32.1% by the year 2015 (FAO, 2015). Despite this increase, many species are limited to protected natural areas, which can result in vulnerable isolated populations (Wilcox and Murphy, 1985; Hanski, 1991). Thailand's urban areas and human population are growing rapidly. In 1960 there were more than 27 million people living in Thailand, however, by the year of 2018 this had increased to nearly 70 million people (The World Bank, 2019). More than 43% of Thailand's original forest land area has been cleared for agriculture (FAO, 2016). It is also important to note that we are underestimating the amount of habitat loss and fragmentation, as many roads and infrastructures which are not mapped are typically not taken into account (Hughes, 2017b, 2018).

2.1.2 Biodiversity Among Human-Modified Lands

Urbanization and agricultural activities result in the homogenization of biota, as humans replace native flora with large monoculture plots and transform lands into concrete-dominated landscapes (McKinney, 2006). While much of the native biota is extirpated as humans convert natural areas to be used for agricultural and urban development, some species persist within less disturbed habitats in or around human-dominated landscapes (Anguiano and Diffendorfer, 2015). However, wildlife populations that live in human-modified landscapes face new threats including direct human killings (Miranda et al., 2016; Marshall et al., 2018), road mortality (Gonçalves et al., 2018), pollution (Strine et al., 2014), domestic and invasive species (Meek, 2012), and accidental killings from construction and agricultural activities (Knierim et al., 2017). Agricultural field margins, dikes, irrigation canals, remnant forest fragments and urban "green spaces" can play a vital role in facilitating biodiversity among human-dominated lands by providing suitable habitat to a variety of biota (Choosai et al., 2009; Knoot and Best, 2011; Hawkeswood and Sommung, 2016; Hughes, 2017a; Marshall et al., 2019, 2020). Often, less-disturbed vegetated habitats within human-dominated areas provide faunal refugia from surrounding high risk areas (Choosai et al., 2009; Hughes, 2017a). Less disturbed vegetated areas provide faunal refugia, often acting as movement corridors for wildlife through cultivated areas (Knierim et al., 2018; Marshall et al., 2020; Whitaker and Shine, 2000).

2.2 Snake-human Interactions

2.2.1 Snake-Human Conflict

As humans encroach onto natural areas, potential for human-wildlife conflict to arise is heightened (Conover, 2001; Woodroffe et al., 2005). Human-wildlife conflict occurs when people and animals come into contact with one another as they compete for space or resources. Human-wildlife conflict commonly arises as native fauna consume or destroy crops or attack domestic livestock or even humans, and in return the humans often kill the wildlife (Woodroffe et al., 2005). Specific examples of resource competition between humans and wildlife include elephants (Sitati et al., 2005), rats (Taylor, 1968), birds (Gebhardt et al., 2011), and insects (Dhaliwal et al., 2010) which consume farmed crops; lions (Bauer and Iongh, 2005), tigers (Nyhus and Tilson, 2004), wolves (Treves et al., 2004), coyotes (Soto-Shoender and Giuliano, 2011), and snakes (Miranda et al., 2016) which attack and feed on livestock or pets; and even raccoons, opossums, skunks, and rats which shelter among human settlements and commonly consume food remains among human garbage (Clark, 1994), which can result in damage to property and even the spread of disease from wildlife to humans (Fitzwater, 1989). Wherever humans and wildlife co-occur, there is always potential for conflict to arise.

Snakes frequently encounter humans in many areas of the world, leading to life-threatening (and often dramatic) conflict (Marshall et al., 2018; Warrell, 2010). Most conflicts arise among rural settlements in tropical countries where there is generally a higher abundance of snakes (Fry, 2018; Kasturiratne et al., 2008). Numerous snake species show considerable resilience to human disturbances (Adams et al., 1994; Shine et al., 1999), and some species can commonly be found living within close proximity to humans (Fearn et al., 2001; Hawkeswood and Sommung, 2016; Wolfe et al., 2018). Some habitat generalist snake species take advantage of the new human-modified habitats and often abundant prey which congregate around human settlements and agricultural land, such as rodents, house geckos, and toads (Fearn et al., 2001; French et al., 2018; Fry, 2018; Graham, 1991; Shankar et al., 2013). In some cases, snake densities are even thought to be higher among agricultural areas due to the high abundance of prey available (Vaiyapuri et al., 2013). Rural areas are the dominant locations for conflict between snakes and humans, however, conflicts also arise in more developed settings, from suburban housing in the United States and Australia (Fearn et al., 2001; Minton, 1987) to dense urban settings such as Singapore, Bangkok, and Hong Kong (Chippaux, 1998; Low, 2018; Yue et al., 2019).

2.2.2 Persecution of Snakes and Other Pressures

Snakes are among the most feared, misunderstood, and mistreated animals worldwide (Pandey et al., 2016). As a result, snakes are highly persecuted, and interactions between snakes and humans frequently result in intentional snake mortalities (Dodd, 1987; Meek, 2012; Pandey et al., 2016). Snakes that live among human dominated habitats are likely to experience population declines due to direct human killings (Bonnet et al., 1999; Dodd, 1987; Godley and Moler, 2013; Marshall et al., 2018; Whitaker and Shine, 2000). Large or venomous snakes are often targeted for persecution, such as king cobras (*Ophiophagus hannah*) in Thailand, which were repeatedly killed directly by humans despite being a protected species and years of local education and awareness programs centered around their conservation (Marshall et al., 2018; Figure 2.1). Miranda et al. (2016) found that larger anacondas were more likely to be killed, especially in areas where human development index and thus education programs were limited. Whereas (Souchet and Aubret, 2016) Souchet and Aubret (2016), found fear to be related to aposematic signaling (conspicuous coloration or patterning in an animal in attempt to warn off predators) which is often related to being venomous. Even nonvenomous juvenile snakes are at great risk of being killed directly by humans (Meek, 2012). Attempting to capture or kill snakes actually increases snakebite risk (Minton, 1987).

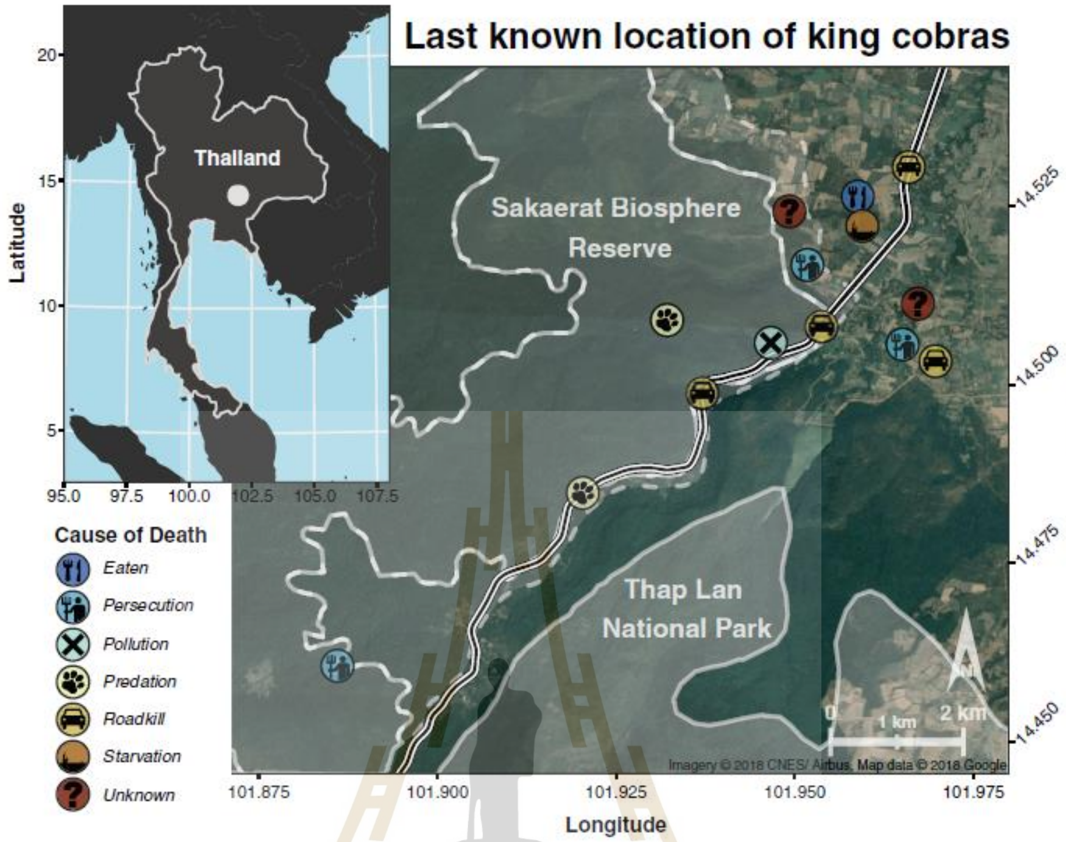

Figure 2.1 Map of the locations and the cause of death of king cobras within the SBR, Thailand (Marshall et al., 2018).

2.2.3 Other Pressures on Snakes Among Humans

Living among human-dominated landscapes comes with many new risks other than intentional human killings to wildlife. One of the greatest of these threats is the increased risk of dying due to motor vehicular collision. Snakes are among the most frequently killed taxa on roads in much of the tropics (Gonçalves et al., 2018; Maschio et al., 2016; Pallares and Joya, 2018; Silva et al., 2020) as well as in temperate regions (Choquette and Valliant, 2016; Shepard et al., 2008). As natural landscapes become more fragmented and continually bisected by roads, there is a reduction in connectivity between natural areas, thus the animals are more prone to attempt to cross roads, consequently increasing their chances of falling victim to road mortality. Moreover, snakes are also at risk of being killed during to agricultural and construction activities (Knierim et al., 2017; Knierim, 2018).

In addition to snakes being killed by human activities, snakes are often killed by domestic animals which are closely associated with human habitations. Both feral and outdoor kept dogs and cats are known to kill numerous small vertebrates, including snakes even large venomous snakes (Whitaker and Shine, 2000; Woinarski et al., 2018). In Thailand there are countless dogs and cats which freely roam suburban areas as well as rural areas near human habitations, and as a result many snakes are killed by free-roaming pets and feral domestic animals alike (Hodges pers. obs.).

2.2.4 Snakebite

Snakebite envenomation is a significant public health problem in tropical and subtropical countries (Kasturiratne et al., 2008), and it was reclassified as a neglected tropical disease by the World Health Organization in 2017 (Chippaux, 2017). Quantifiable data on the exact number of people afflicted by snakebite is lacking, as most bites occur in rural areas of developing countries, where many incidents may not be reported (Warrell, 2010). Studies estimate between 1.8-2.7 million people are victims of snakebite envenomations globally each year, with deaths of 81,410-137,880 (Chippaux, 1998; Gutiérrez et al., 2017; Kasturiratne et al., 2008). Most snakebites are associated with agricultural work in tropical developing countries (Chippaux, 1998; Warrell, 2010). However, in developed countries, such as the

United States, the majority of snakebite envenomations occur within suburbs and city edges bordering natural areas (Minton, 1987).

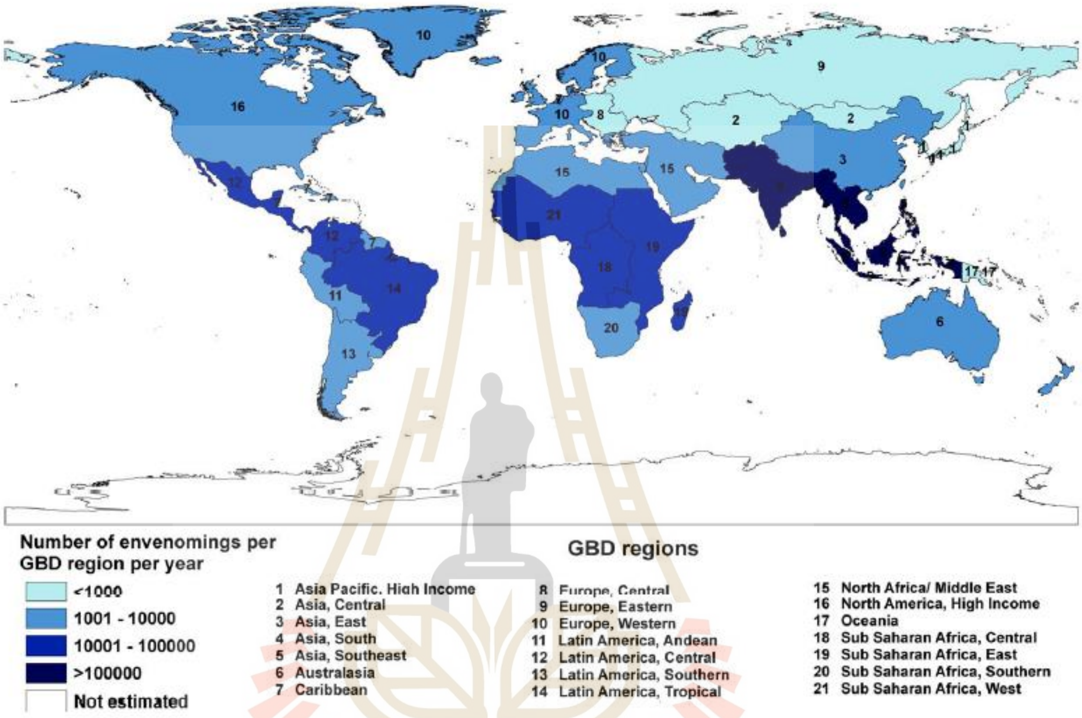

Figure 2.2 Regional conservative estimates of snakebite envenomation incidents throughout the globe (Kasturiratne et al., 2008).

South and Southeast Asia have the most snakebite incidents and deaths compared to the rest of the world (Chippaux, 1998; Swaroop and Grab, 1954); Figure 2.2), with an upper mortality estimate of 19,000 snakebite related deaths within Southeast Asia every year (Kasturiratne et al., 2008). Most snakebites occur on the victims property or in homes (Minton, 1987). People living in poverty in tropical rural areas are disproportionately affected by snakebite – these areas often contain grain stores, which attract rodents; the main prey items for many snake species (Harrison et al., 2009; Vaiyapuri et al., 2013). Prasarnpun et al. (2005) suggested that rural households in tropical developing countries often have structural gaps, allowing snakes entry into the home, which then increases snakebite risk. Understanding how snakes and humans interact and how to mitigate conflicts is especially important among developing tropical countries, where snakebite is a real threat to many of the people.

Snakebite envenomation is a significant public health problem in Thailand (Buranasin, 1993), with an average of 2,316 snakebites and 179 deaths reported each year in the early 1950s (Purananda, 1957). In the late 1960s there were approximately 3,058 bites and 80 deaths recorded each year (Trishnananda, 1979). However, reported numbers greatly underrepresent the actual number of incidents, as some people in rural Thailand still seek traditional treatments or simply do not go to the hospital (Looareesuwan et al., 1988). The majority of people bitten in Thailand are agricultural workers (Looareesuwan et al., 1988), and most snakebites from at least some venomous snake species coincide with heavy rains, when farmers work more in the fields and snakes are thought to become more active (Tongpoo et al., 2018; Vaiyapuri et al., 2013). Snakebite in Thailand may not be as prevalent as in some South Asian countries, but it still causes damage to livelihoods of thousands of people each year.

2.2.5 Conflict Mitigation

Education programs coupled with conflict mitigation are important for snake conservation and snakebite prevention. Balakrishnan (2010) showed that community based education programs and conflict mitigation efforts are capable of decreasing intentional killings of snakes. Though the literature is lacking, snake-human conflicts can theoretically be reduced by simply keeping properties around households well-manicured and moving brush piles, grain stores, and other clutter away from the house, as well as sealing gaps in the structure where snakes may be able to enter the household (Mengak, 2002; Parkhurst, 2009). One conflict mitigation technique is the translocation of “nuisance” animals, where snakes are removed from human settlements and released unharmed into less disturbed habitats (Devan-Song et al., 2016; Low, 2018; Shankar et al., 2013). Fearn et al. (2001) removed 220 *Morelia spilota* during a six year period from suburban homes in south-eastern Queensland after the residents called requesting the snake be removed. Similarly, Shankar et al. (2013) removed 106 *Ophiophagus hannah* from human settlements around Agumbe, India within a four year period. Without these translocation efforts, many of these snakes would likely be killed by the humans (Low, 2018; Roshnath, 2017; Vyas, 2013). Often snakes are translocated great distances after being removed from human homes, however, research has shown that this can result in mortality to the “rescued” snake (Nowak et al., 2002). Devan-Song et al. (2016) used radio telemetry to compare the movements and general ecology of translocated and resident (non-translocated) *Trimeresurus albolabris* in southern China, and found that translocated female *T. albolabris* had increased movement distances and movement frequencies, and that it appeared to have a negative impact on reproduction in both male and female *T. albolabris*. Long distance translocations may additionally spread diseases to conspecifics (Massei et al., 2010). Instead, snakes should be released as near to the initial capture location as possible in order to keep the snake within its home range, and thus causing less harm to the individual, and reducing chances of spreading disease (Barve et al., 2013; Bauder et al., 2014). Conflict has several mitigation methods, by incorporating information from both natural history and the social sciences we can identify and target the most effective methods to minimize interactions between humans and snakes

2.3 Radio Telemetry and Spatial Ecology

Wildlife radio telemetry is a field technique to manually determine a free-ranging animal’s location through very high frequency (VHF) radio waves transmission via a battery-powered radio-transmitter attached to a free-ranging individual, to a VHF radio receiver (Andrusiak et al., 1998). Researchers have used radio telemetry globally since the 1960’s to assess wildlife movement and resource use (Moorcroft et al., 2006). There are other methods of tracking an animal’s movements, including using spools of string (Lemckert and Brassil, 2000), fluorescent powders (Rittenhouse et al., 2006), and harmonic radar diode tags (Gourret et al., 2011; O’Neal et al., 2004), however, these techniques are greatly limited to animals which do not move far or often. Automated global positioning system (GPS) transmitter telemetry systems have become very useful for studying the movements of some animals, however they are only ideal for large species which have large movements, as the accuracy is greatly reduced and GPS transmitters are quite large in size, especially in order to have long enough battery life to gain much data (Rodgers, 2001; Tomkiewicz et al., 2010). Presently, VHF radio telemetry remains one of the most popular due to the potential for highly accurate location data points, and the radio transmitters have a relatively long battery life, a small size, and are available at significantly lower prices than GPS transmitter telemetry systems (Cooke et al., 2004; Hebblewhite and Haydon, 2010).

Since its development, wildlife biology studies have employed telemetry on a variety of taxa, including large terrestrial mammals (Karanth and Sunquist, 2000), marine mammals (Watkins et al., 2002), birds (Meretsky and Snyder, 1992), amphibians (Lemckert and Brassil, 2000), reptiles (Bauder et al., 2016), fish (Cooke et al., 2004), bats (Shiel et al., 1999), and even arthropods (Liégeois et al., 2016). The technique is particularly useful in gaining important information on animal species which are otherwise difficult to study in the wild (Marzluff et al., 2001; Újvári, B., and Korsós, 2000). Radio telemetry is an important tool for studying wildlife behavior, movements, space use, resource and habitat selection, physiology, survival rates, and activity patterns (Amelon et al., 2009; Marzluff et al., 2001). Findings from such studies can often provide important and useful information which can be implemented into management and conservation programs, and can also help reduce and mitigate human-wildlife conflicts (Braunstein et al., 2020; Gunther and Smith, 2004; Takahata et al., 2014).

Snakes can be difficult to study, as they are highly cryptic, and often occur at low densities, thus resulting in low detection rates during active surveys and passive trapping (Dorcas and Willson, 2009). However, radio telemetry has revolutionized the way snakes are studied, greatly improving the ability to study snake movements, habitat selection, activity patterns, diet, behavior, and mortality (Clark, 2006; Fizzotti, 2018; Miller et al., 2012; Walters et al., 2016; Whitaker et al., 2010). Radio telemetry has been used on snakes since the 1970s (Fitch and Shirer, 1971). Early on transmitters were force-fed to snakes, thus the telemetered individuals could only be tracked briefly until the transmitter was passed through the digestive system and excreted (Reinert and Cundall, 1982). This method may only provide information on the snakes' movements during digestion, as the transmitter is often sizeable enough that the snake's body will respond to its presence by attempting to digest it. Additionally, this method can potentially result in blocking the snake's digestive tract, as the transmitter, which is hard and relatively large, may not be able to pass through the small intestines. If this occurs the transmitter must be surgically removed, or the snake may die. Other studies implanted transmitters subcutaneously (Weatherhead and Anderka, 1984) or attached transmitters to the snake's dorsal surface (Maritz and Alexander, 2012). However, most current radio telemetry studies on snakes surgically implant small radio transmitters within the coelomic cavity, as described by Reinert and Cundall in 1982. Implanted snakes may show some detrimental effects, as Weatherhead and Blouin-Demers (2004) found that *Pantherophis obsoleta* which were implanted with radio transmitters showed lower annual growth in mass when compared to individuals without transmitters. This of course could impact their survival, however typically the effects are very minimal and the authors believe that this method is still necessary.

Though understanding the habits and ecology of medically significant snakes which live among humans can help us create more effective snakebite and conflict preventative measures (Pandey et al., 2020; Pandey et al., 2016; Ramesh and Nehru, 2019), the knowledge gained from studies on the movements of venomous snakes is scarcely linked to snakebite prevention management strategies. Despite this, few snake behavioral and ecological studies are held in comparison to the number of studies focusing on the ecology of endothermic taxa (Bonnet et al., 2002; Ford, 1995; Pawar, 2003), with the vast majority of studies on the movements of snakes are held in more developed countries, which tend to be areas where snakebite is not a major issue, such as the United States, Australia, Canada, and South Africa (Crane et al., 2020). Most snakebite envenomations occur within South and Southeast Asia, Tropical Central and South America, and Eastern, Western, and Central Sub Saharan Africa, and mortalities are greatest within the same regions (though they are particularly higher in South Asia, followed by Eastern and Western Sub Saharan Africa; Chippaux, 1998; Kasturiratne et al., 2008; Suraweera et al., 2020).

2.4 Application of Radio Telemetry to Space Use

There are a number of methods used to estimate space use of telemetered animals, ranging from simple but widely used methods such as minimum convex polygons (MCPs) and kernel density estimates (KDEs), ranging to newer and more accurate methods such as Dynamic Brownian Bridge Movement Models (dBBMMs). There are multiple issues with methods such as MCP and KDE, KDEs incorrectly assume that an animal’s movement locations are independent (doesn’t account for movement trajectories), MCPs however do not account for the amount of time spent in a given area, both tend to greatly overestimate space use, both are greatly inaccurate, and neither methods account for uncertainty (Silva et al., 2020). Despite the clear inaccuracy and issues with using MCPs and KDEs as animal space use estimates, numerous studies, particularly those on herpetofauna, commonly still use these methods to this day (Crane et al., 2020; Knierim et al., 2018; Marshall et al., 2019; Silva et al., 2020). One of the common arguments made for continuation of these older methods is so that results may be compared with findings from other studies, which presents a number of problems, as comparisons rarely control for difference in sampling regimes or tracking durations, thus very little can be extrapolated from such comparisons.

One of the best currently available methods for estimating space use by individual animals with lower tracking resolutions are dBBMMs, as they generally produce a more conservative and accurate estimate of space utilization. Dynamic Brownian bridge movement models account for an animal’s movement trajectories, time intervals between known locations, and location uncertainty (GPS accuracy; Kranstauber et al., 2012). Using dBBMMs not only more accurately estimates total space use by an individual animal, but the model also produces motion variance as an output, which can be used to examine changes in the animal’s behavior and activity through changes in their movement (Marshall et al., 2020; Ward et al., 2020). Furthermore, dBBMMs can be particularly useful in identifying important movement corridors (Kranstauber et al., 2012; Silva et al., 2020). Lastly, activity centers can be identified within the animal’s occurrence distribution by simply reducing the value of the contour to reveal areas the animal utilized the most (i.e. where it was most likely to be occur at any given time), which can be useful in identifying areas and features of particular importance (Horne et al., 2007).

2.5 Habitat Selection

Habitat is the place or type of environment in which an organism or population of organisms occupies, and organisms often select for habitats which provide the resources and conditions suitable for survival and reproduction (Hall et al., 1997). Habitat selection can be defined as the disproportionate use of a resource or habitat type by an organism (Mayor et al., 2009). Habitat selection studies provide information on what environmental resources and conditions are required by animals, thus improving our knowledge on how best to develop conservation policies (Calenge, 2007). Understanding a species' habitat selection can also help us understand how human-wildlife conflict occurs, and thus, how to reduce or mitigate the conflicts (Takahata et al., 2014).

Studying habitat selection of an animal species requires habitat-use data. For many animal species, this can be difficult to record through surveys and/or trapping, rather habitat use data can be obtained through the use of radio telemetry (Reinert and Cundall, 1982; Rettie and McLoughlin, 1999). Radio telemetry studies allow us to analyze an individual's habitat selection at different spatial scales by determining the usage and availability of quantified habitat types, vegetation, shelter sites, and food items (Johnson, 1980). Furthermore, habitat use for a species can be different across its geographic distribution, even between different populations just 20 km away, as the climate, prey availability, habitat types available, and predators present may differ across the species' range (Shine, 1987). Changes in habitat use can also occur on more than one spatial or temporal levels (Harvey and Weatherhead, 2006), and can be influenced by the individual’s age, sex, or reproductive class (Reinert, 1984; Weatherhead and Madsen, 2009).

Many different methods have been used to examine the habitat selection of snakes. However, most of the analyses being used for spatial habitat selection and spatial ecology studies on snakes are older and dated methods which may misidentify important habitat feature, or possibly miss valuable features entirely due to the nature of the analyses. One newer method which is commonly applied to telemetry data from mammals is a resource selection model called Integrated Step Selection Function (ISSF). This method models the likelihood that an animal will move to an available location given its resource value (Avgar et al., 2016). This is done by comparing environmental attributes of recorded movements with alternative randomly generated movements from the same starting location (Prokopenko et al., 2017; Thurfjell et al., 2014). Integrated Step Selection Functions can help us study habitat selection of an animal, as well as human-wildlife interactions, movement corridors, and movement processes, and it is also possible to examine resource selection at multiple spatial and temporal scales (Thurfjell et al., 2014). This method also allows for the use of categorical variables (i.e. habitat or vegetation type) continuous variables (i.e. canopy cover or terrain ruggedness), or distance measures (i.e. distance to roads or streams). Through the use of ISSF, Prokopenko et al. found that elk (*Cervus elaphus*) responded to roads as they would a natural predation risk, by generally selecting for areas farther from roads and seeking vegetated cover more when nearer to roads (2017). There is a need for more studies on what factors influence snake movement through better methods such as resource selection functions such as Integrated Step Selection Functions.

Another method which can help us identify valuable areas and habitat features for wildlife with telemetry data, is examining the animal's site fidelity, so that we may identify specific sites which are reused the most frequently. Some relatively recent studies have begun using recursive analysis, which looks at number of revisits to a given spatial unit, as well as incorporating the total time spent within the location and the number of times the animal was known to pass through the location given the known movement trajectories (Bracis et al., 2018). Recursive analysis can be particularly useful in determining valuable foraging sites, movement corridors, nesting sites, and shelter sites (Bracis et al., 2018). Smith et al. (2020) used this method with telemetry data from Burmese pythons, and found that the pythons generally did exhibit shelter site fidelity among modified areas, which may be due to a reduction in available suitable refuges.

Very few habitat selection studies have been done on elapid snakes, and even fewer on nocturnal elapids. One previous study on *B. candidus* showed preference to sheltering among field margins, which were less disturbed than the surrounding agricultural land and were riddled with rodent burrows which the snake could shelter within, however, this study used non-standardized tracking regimes and only tracked a single individual, thus the findings from this are very weak (Knierim et al., 2018). Knierim et al. (2019) found that it appears that *Bungarus fasciatus*, a close relative to *B. candidus*, selected for permanent water features and field margins based on proportions of use compared to proportions of availability within occurrence distributions, though this method tends to be less accurate and inferior to newer resource selection models. Another nocturnal elapid snake, *Hoplocephalus bungaroides*, selected for microhabitats based on their thermal ecology, selecting for rock shelters with less canopy cover overhead during the cooler months, while tree shelters were used more frequently during the hot summer months (Pringle et al., 2003). The species also selects for different shelter types seasonally, sheltering under rocks and in sandstone crevices during the colder months, and then migrating from the outcrops to shelter within tree hollows during the summer months (Webb and Shine, 1997). Few studies have examined habitat and shelter selection and if seasonal shifts in this selection occur in nocturnal elapid species.

2.6 Study Species

2.6.1 Biology and Ecology of Malayan Kraits

Malayan kraits, *Bungarus candidus* (Linnaeus, 1758), belong to the second largest family of snakes, Elapidae (Uetz et al., 2018). This clade represents 371 of the 3,977 extant snake species recognized today, with 55 genera (Uetz et al., 2018). Elapids are proteroglyphous; injecting venom via two relatively short hollow fangs fixed anteriorly to the maxillary bone (Kerkkamp et al., 2017). *Bungarus* species, like most elapids, produce potent neurotoxic venoms which they use to immobilize their prey (Kerkkamp et al., 2017). Many species within this clade produce venoms which are medically significant to humans and can result in human mortalities (Fry, 2015).

Kraits (*Bungarus* species) are moderate to large sized (1-2.25 meters) terrestrial snakes (Das, 2010), which are set apart from other elapids by their large hexagonal shaped mid-dorsal scales and unique vertebrae with laterally enlarged processes and abnormally high neural processes (Slowinski, 1994a). As a result of the high neural processes, kraits have a raised mid-dorsal ridge, which gives most species a relatively triangular shape in cross-section (Slowinski, 1994a). There are currently 15 recognized krait species (Uetz et al., 2018) distributed throughout southern, southeastern, and middle eastern Asia (Abtin et al., 2014; Ahsan and Rahman, 2017). Kraits are secretive nocturnal ophiophagous active predators (Kuch et al., 2005), which commonly enter human households in search of prey (Hodges et al., 2020; Prasarnpun et al., 2005). As a result of their close proximity to humans and potent neurotoxic venom, *Bungarus* species are among the most medically significant venomous snakes throughout their range (Prasarnpun et al., 2005; WHO, 2016).

Figure 2.3 Photo of the study a Malayan krait, *Bungarus candidus*.

Bungarus candidus can grow to a length of 1.6 meters in total length (Das, 2010), although most individuals are closer to 1.3 meters in total length (Chan-ard et al., 2015; Chanhome et al., 2011). The dorsum of this species is patterned with broad and relatively equal crossbands of alternating black or greyish blue and white, while the venter is an un-patterned cream or white color (Chanhome et al., 2011). *Bungarus candidus* is known to occur in Peninsular Malaysia, Singapore, Thailand, Cambodia, Indonesia, Vietnam (Uetz et al., 2018), Laos (Kuch and Stuart, in press), and China (Xie et al., 2018), where they inhabit a variety of habitats, including tropical wet and dry forests, agricultural lands, and human settlements between 200 and 1500 m above sea level (Chan-ard et al., 2015; Chanhome et al., 2011; Knierim et al., 2018; Mohammadi et al., 2014). *Bungarus candidus* has been documented to feed on snakes, lizards, amphibians, and rodents (Das, 2010; Kuch, 2001; Kuch, 2004). In Thailand, *B. candidus* is known to breed between December and January, with clutches of 4 to 10 eggs being laid between February and March (Chanhome et al., 2011). Neonates hatch from the eggs after approximately 50 days of incubation (Chanhome, 2007). Comparative LD50 venom toxicity studies have identified *B. candidus* venom as the most potent of all *Bungarus* species which have been examined (Tan et al., 2010; Tan and Ponnudurai, 1990), making it one of the most toxic species of terrestrial venomous snakes in the world (Steinhoff, 2019).

2.6.2 Malayan Krait Bites to Humans

Though *B. candidus* produces potent neurotoxic venom, the species is generally shy and unaggressive; attempting to escape from a potential threat when possible, and when unable usually relies on a head-hiding defensive behavior (Tan and Ponnudurai, 1990). *Bungarus candidus* commonly occur among human-modified landscapes, where they are known to enter human households in search of prey (Prasarnpun et al., 2005). As a result, many human victims are bitten by *Bungarus* species at night while sleeping on the ground in rural settlements near forests and agricultural land (Kularatne, 2002; Warrell, 2010). Reported bite incidents from *Bungarus* species to humans are relatively few (Abtin et al., 2014; Viravan et al., 1992; D. A. Warrell et al., 1983), however, mortality rates among bite victims are high, as the potent neurotoxic venom causes paralysis and respiratory failure (Looareesuwan et al., 1988; Pe et al., 1997; Warrell et al., 1983). In Thailand, *B. candidus* is responsible for the majority of human deaths by snakebite (Looareesuwan et al., 1988), which can be attributed to most victims being bitten during their sleep and the potent, yet nearly painless, neurotoxic venom that *B. candidus* produces (Warrell et al., 1983). While lethal, bites from *B. candidus* are generally painless and do not result in localized symptoms. As a result, victims may not seek immediate professional medical help, as the victims may believe the bite to not be dangerous (Warrell et al., 1983).

Table 2.1 Summary of the published data on bite occurrences by *B. candidus*, with mortality percentages and regional hotspots of documented bite incidents in Thailand (TH), with a couple of instances from Peninsular Malaysia (MY).

Reference	**Study Area**	**Total No. bites**	**No. krait bites**	**No. fatal bites by *B. candidus***	**Regional Hotspots**
Warrell et al., 1983	Chanthaburi, TH & Kedah, MY	5	5 (*B. candidus*)	1 (20% all, 33% of envenomed)	3 of 5 in E TH
Looareesuwan et al., 1988	TH	46 (fatal only)	14 (13 *B. candidus*, 1 *B. fasciatus*)	13 of 46 fatal bites (28.26% of fatal bites)	10 of 13 in NE TH (76.9%)
Viravan et al., 1992	TH	1145	15 (13 *B. candidus*, 2 *B. fasciatus*)	Unknown	6 of 13 in NE TH (46.2%)
Buranasin, 1993	Nakhon Ratchasima, TH	199	4 (either *B. candidus* or *B. fasciatus*)	1-2 of 7 fatal bites (14.29%-28.57% of fatal bites)	NA
Tongpoo et al., 2018	TH	78	78 (68 *B. candidus*, 9 *B. fasciatus*, 1 *B. flaviceps*)	5 out of 68 bites (7.35% of B. candidus bites)	55 of 78 krait bites in NE TH (70.5%)

In Thailand, *Bungarus candidus* was only responsible for about 1.1% of all reported venomous snakebite incidents (Viravan et al., 1992). Yet, Looareesuwan et al. (1988) found that *B. candidus* was responsible for 28.3% of 46 fatal snakebites, making it one of Thailand's deadliest snake species (Looareesuwan et al., 1988). Most of the bite victims in Thailand are agricultural workers ((Looareesuwan et al., 1988), and most *B. candidus* bites occur within the rainy season (Tongpoo et al., 2018). Within Thailand, the majority of recorded bite incidents and bite related deaths from *B. candidus* occur in the northeastern region (Tongpoo et al., 2018; Looareesuwan et al., 1988), with about 70.5% of *Bungarus* species bites occurring in the Northeast (Tongpoo et al., 2018). Records at the Nakhon Ratchasima Regional Hospital in reveal that kraits only contribute to about 2% of snakebites, however, they are responsible for 28.6% of snakebite related deaths (Buranasin, 1993).

Aposematic coloration is a conspicuous coloration or patterning of an animal which signals to predators that the animal is dangerous or toxic. The characteristic aposematic color patterning of black and white cross-bands across the dorsum of *B. candidus* is shared by several sympatric genera of non-venomous snake species in Thailand. This leads to frequent mis-identifications, and in some cases improper administration of antivenin to victims which were bitten by harmless colubrid species (Viravan et al., 1992). *Bungarus candidus* is commonly confused with Batesian mimic (mimicry in which a non-toxic animal species resembles a toxic or noxious species which is avoided by predators) *Dryocalamus* spp. and *Lycodon* spp. (Viravan et al., 1992), and some *Dryocalamus* species may even mimic *Bungarus candidus* behaviors (Karraker et al., 2015). This highlights a need for education, as this confusion can lead to preventable snakebites and complications in hospital treatment.

2.6.3 Spatial Ecology of Malayan Kraits

At this time three past radio telemetry studies have investigated the spatial ecology of free-ranging *B. candidus*. However, each study only radio-tracked a single individual for relatively short durations of time (Table 3), thus providing limited insight into their movements and space use. Radio-tracked commonly *B. candidus* sheltered under mixed high vegetation (>50 cm) and underground within animal burrows and termite mounds (Crane et al., 2016; Knierim et al., 2018; Mohammadi et al., 2014). Within a human-dominated landscape a single individual showed preference for available less-disturbed habitats, such as field margins and eucalyptus plantations (Knierim et al., 2018). Crane et al. (2016) demonstrated that *B. candidus* may use man-made irrigation canals as corridors through a human-dominated landscape. Telemetered individuals also occasionally sheltered quite near human settlements (Crane et al., 2016; Knierim et al., 2018). The individual tracked within the core area of the Sakaerat Biosphere Reserve remained within the deciduous and dry evergreen forests, using a variety of shelters including termite mounds, holes under rocks, and even a hole in a tree (Mohammadi et al., 2014). Mohammadi et al. hypothesized that *B. candidus* may even be hunting for prey such as blind snakes (*Argyrophis muelleri* and *Indotyphlops braminus*) or other fossorial or sheltering snakes while within the termite mounds. Of the two studies which have published space use estimates for the telemetered *B. candidus*, both used older methods, minimum convex polygons (MCP; Mohammadi et al., 2014; Knierim et al., 2018), which are known to be wildly inaccurate (Silva et al., 2020). Therefore, due to the limitations of previous studies (i.e. sample sizes of 1 individual, use of outdated methods, non-standardized and irregular sampling regimes, short tracking durations and few relocations) there remains many knowledge gaps in our knowledge of the spatial ecology of *B. candidus*, especially regarding the species' movements among human-dominated areas and their interactions with humans.

Table 2.2 Review of the previous studies on *Bungarus candidus* movement.

No. of individuals	No. of days tracked	No. of fixes	No. of moves	MCP (ha)	Reference
1	22	19	11	12.3	Mohammadi et al., 2014
1	14	14	5	NA	Crane et al., 2016
1	68	34	19	3.23	Knierim et al., 2018

2.7 Study Site (Suranaree University of Technology)

The study area covers the campus of Suranaree University of Technology (SUT) and its surrounding landscape. The university campus is located about 20 km from central Nakhon Ratchasima city (also commonly known as Korat city) in Nakhon Ratchasima province, Northeast Thailand (14.879°N, 102.018°E). The study site is located within the Korat Plateau region, and has an altitude range of 205-285 m above sea level. Much of the agriculture within the Korat Plateau region depends heavily on irrigation channels to carry water and nutrients to their crops. The region is part of the Mekong River's lower basin (Gupta, 2009), and holds particularly high concentrations of small irrigation channels which divert directly off the main river channel (Hoanh et al., 2009).

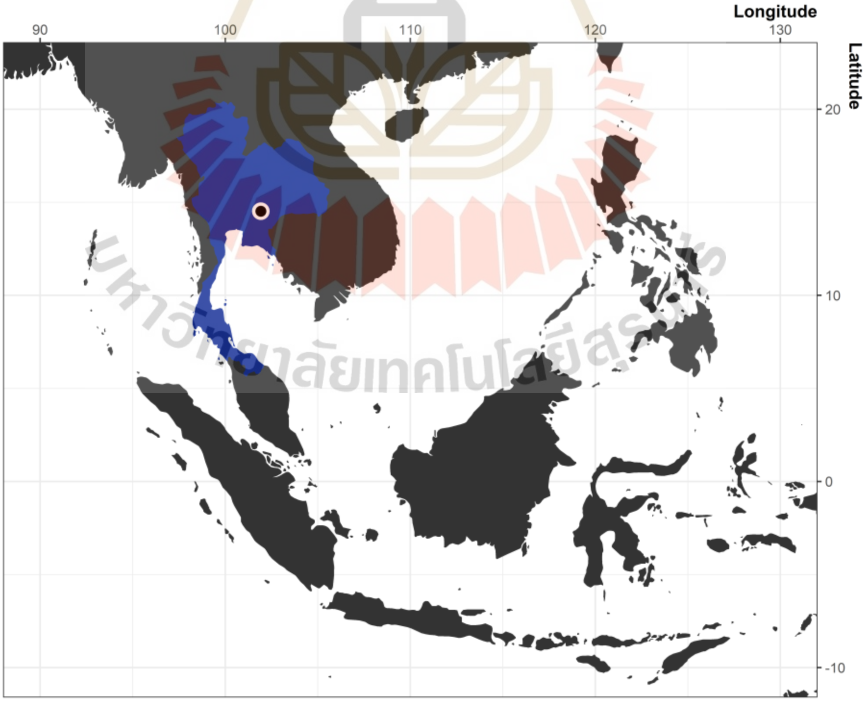

Figure 2.4 Map showing the location of the study site relative to Thailand and Southeast Asia.

Northeast Thailand has a tropical climate, and within the region average temperatures vary from 19.6 to 30.2°C and average annual rainfall ranges from 1270 to 2000 mm (Babel et al., 2011). There are three relatively distinct seasons in Northeast Thailand, cold season, wet season, and hot season, each of which are classified by annual changes in temperature and rainfall. Cold season is typically between mid-October and mid-February, hot season is generally from mid-February to May, while the highly unpredictable rainfall of the wet season is predominately concentrated between the months May to October (Babel et al., 2011; Thai Meteorological Department, 2014).

Suranaree University of Technology was founded in the year 1990, on an 11.2 km^2 area of degraded dipterocarp forest land in the Huay Yang Reservoir area of Muang District, Nakhon Ratchasima (Suranaree University of Technology, 2020). The campus of SUT is one of the largest university campuses in Thailand and is comprised of a matrix of human-modified landscapes interspersed with severely degraded remnant dipterocarp forest fragments (Figure 2.5). The surrounding landscape is primarily composed of suburban housing divisions and monoculture plots of upland crops such as cassava, maize, and Eucalyptus. In 2017 there were more than 15,000 students enrolled at SUT (SUT Division of Planning), and the majority of these students, as well as the numerous SUT staff, live in residential areas on campus. Housing within the campus is often adjacent to forested areas, thus, people regularly encounter snakes inside and among their homes. Though rarely seen, *B. candidus* occurs on SUT campus (Hodges et al., 2020), providing an opportunity to better understand how these cryptic venomous snakes live within human-dominated landscapes.

Figure 2.5 Satellite imagery of Suranaree University of Technology and the surrounding human modified landscape. Imagery from Google Earth (2020).

CHAPTER III

MATERIALS AND METHODS

3.1 Study Site

Suranaree University of Technology campus and the surrounding area provides a perfect study site to examine the movements of a highly venomous snake in a matrix landscape of human-modified habitats. While most studies on wildlife in tend to focus on protected areas, natural forests only represent a small portion of present Thailand, thus it is important to examine the ecology and threats of species living among humans in heavily modified habitats. Due to the representation of agriculture, semi-urban, and suburban areas with patches of more natural areas all within a relatively small area (Figure 3.1), the university campus provides an ideal setting to examine how land-use features and human activity influence the movements of my study species within NE Thailand, where according to past studies on bite occurrences, is the region where most bites by *B. candidus* occur (Tongpoo et al., 2018; Looareesuwan et al., 1988).

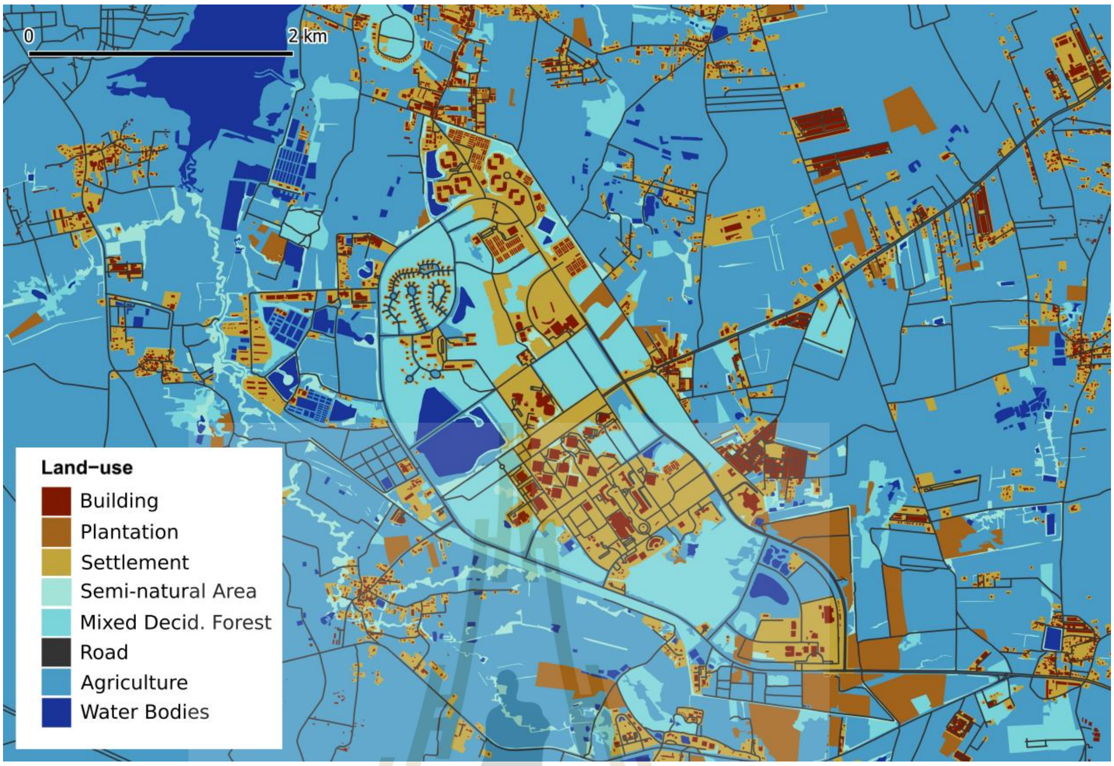

Figure 3.1 Land-use map of the study site in Muaeng Nakhon Ratchasima disctict, Thailand

3.2 Locating and Capturing Kraits

Bungarus candidus are highly cryptic nocturnal snakes, thus detection probabilities during active visual encounter surveys are quite low. As a result, I relied on a variety of techniques to increase my sample size. Non-standardized nocturnal visual encounter surveys were conducted in areas where I expected *B. candidus* to be present. Active visual encounter surveys were conducted both through habitat on foot as well as by motorbike on lands on and adjacent to SUT campus. Survey effort was particularly concentrated to times when I believed conditions to be optimal for *B. candidus* to be active, such as warm humid nights or just after rainfall, however, I searched for *B. candidus* at a variety of times (ranging from just after sunset to 03:30 am) and under a wide variety of environmental conditions. I also briefly used several passive drift fence trapping arrays with funnel traps in forest fragments on the university's campus. Traps were checked every morning, and any non-target captured animals are freed from the trap as discovered. However, drift-fence trapping arrays were not used long-term (only used for a few months), as checking traps daily and maintaining fencing required a large time investment which I could not afford, especially since the traps were not successful in capturing the targeted study species.

The most effective method I used to locate my study species was through notifications from locals which encountered *B. candidus* among homes or university campus. These sighting notifications were a resulting byproduct from my community outreach efforts, where I dispersed flyers and advertised my free nuisance snake removal services and informed the locals of my need to find additional *B. candidus* individuals for study. Social media was also used to help build awareness and encourage people to notify me in the case that they encountered *B. candidus* around SUT, and the Facebook page rapidly gained a lot of attention and following from SUT students. Upon receiving notification of a *B. candidus* sighting, I acted promptly to arrive at the scene in order to capture the snake. All captured snakes were carefully placed individually within clean dark colored cloth bags in order to be transported to the laboratory.

3.3 Processing and Surgical Transmitter Implantation

Captured animals were immediately brought back to the laboratory for processing and to await transmitter implantation surgery. Isoflurane was used to temporarily anaesthetize the snakes, allowing us to collect precise measurements and perform the implantation surgery while the snake is unconscious. A certified veterinarian from the Korat Zoo supervised use of anesthesia and handled all surgical incisions and procedures (Figure 3.2). During processing, I collected biometric measurements, including: snout to vent length, tail length, mass, head length, and head width (Figure 3.3). I also determined the sex of snakes via cloacal probing and sampled scale clips from two ventral scales for potential use as genetic samples. Additionally, I collected fecal samples whenever possible in order to provide insight into their diet. The veterinarian will perform the surgeries following the methodology described by Hardy and Greene (2000) and Reinert and Cundall (1982). To avoid adverse effects, only snakes large enough to be implanted with a radio transmitter - which weighed well below 5% of that animal's mass - underwent the implantation operation. We did not implant any snakes which had an SVL less than 645 mm and a mass below 55 g. Most individuals were implanted with Holohil BD-2 1.8 g transmitters, however, larger individuals may be implanted with Holohil SB-2 3.6 g transmitters. After surgery, we intubated and monitored the snakes until they made a full recovery from the anesthetic, and then housed them in a clean plastic box awaiting release after nightfall.

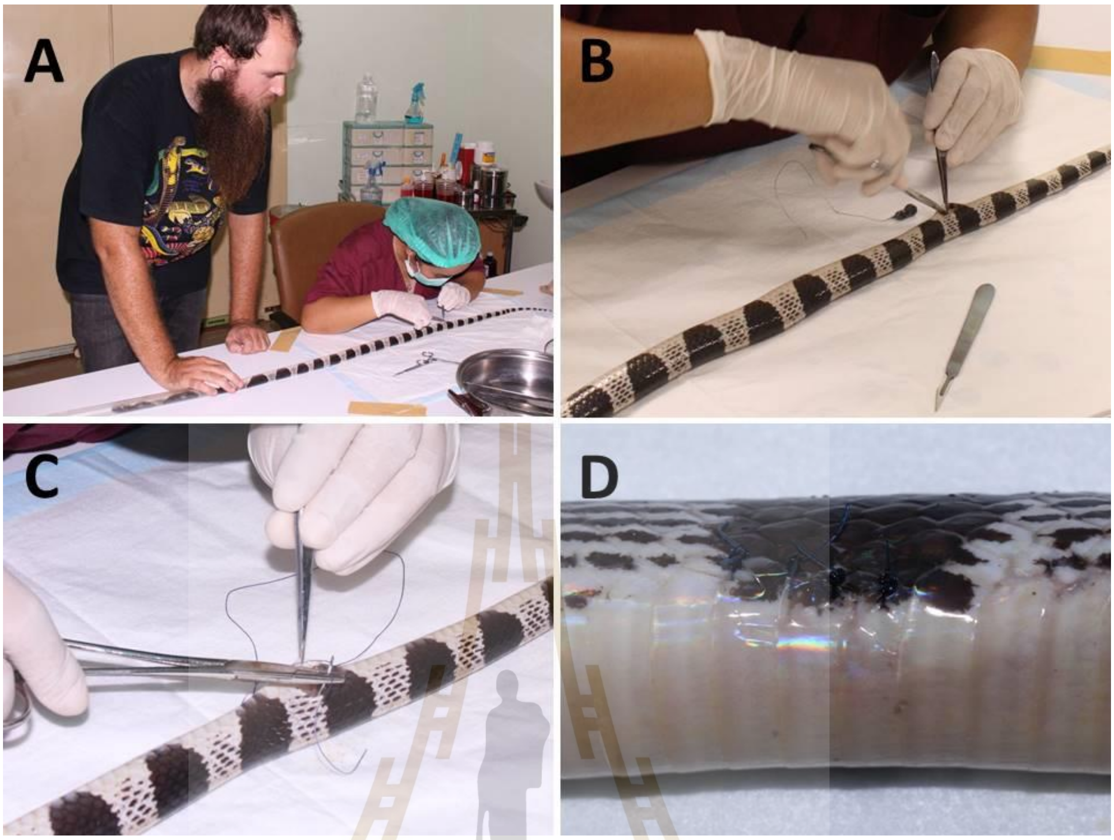

Figure 3.2 Photos of the surgical transmitter implantation process a) The snake is anaesthetized while secured in a tube b) Incisions made by the certified veterinarian c) Implantation of the transmitter into the coelomic cavity d) The wound is carefully closed with both internal (coelom closure) and external sutures (skin closure).

I did not monitor snakes in captivity for additional days after the surgery, as the snakes would better be able to thermoregulate in the wild than when housed within a small plastic box in captivity, thus facilitating proper healing of the wound and limiting chances of infections or other complications. However, there was one occasion where the ambient temperature following an implantation was particularly low, therefore the individual was retained in the laboratory until the next night when conditions were more conducive for its release. In an attempt to minimize the animals' stress, snakes were released softly approximately three hours after dusk, where I carried the snake in a cloth bag to a location as near to their capture locations as safely possible (ideally into a vegetated area), gently slid the snake out of the bag, and remained motionless until the snake had moved out of my line of sight into nearby vegetation. I then saved the release location on a Garmin 64S GPS device and returned the following day to determine where the snake had sheltered.

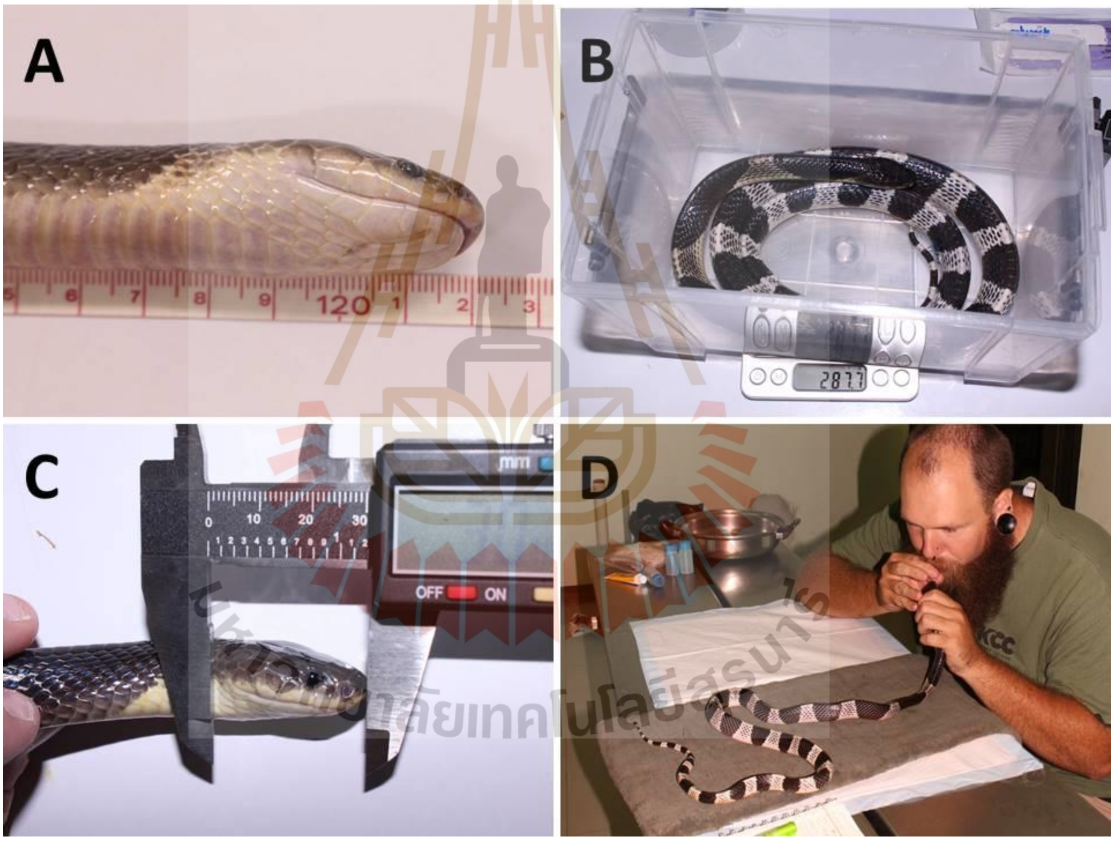

Figure 3.3 Photos of the process for gathering biometric a) while the snake is still anaesthetized I record the snake's body length b) weigh the snake with a digital scale to obtain its mass c) head measurements taken with calipers d) intubate the snake to help it recover from anesthetic.

3.4 Field Methodology

I used very high frequency (VHF) radio telemetry to manually locate the telemetered free-ranging study animals, aiming to locate telemetered individuals once roughly every 24 hours during the daylight hours (between 06:00-18:00 h) in order to identify shelter locations and determine how often individuals changed shelter locations. However, I occasionally was unable to locate snakes for several consecutive days due to a snake having moved far away and the limited radio signal range, or simply due to extended durations of heavy rainfall. In addition to daily diurnal location checks, snakes were also occasionally tracked during the nighttime (18:00-06:00 h) both ad hoc and in an attempt to gain information on their behavior and activity when snakes were perceived as being likely to be active. As the goal was to track individuals for as long as possible, I attempted to recapture individuals in order to replace transmitters as the end of a battery's average lifespan drew near. In the case that any individuals were still being tracked at the end of the study period I attempted to recapture the implanted snake for transmitter removal and release.

Figure 3.4 Using radio-telemetry equipment to locate an implanted free-ranging *B. candidus* in a forest fragment at SUT.

Snakes were located by manually honing in on signal via a VHF radio receiver (as described by Amelon et al., 2009; Figure 3.4), and locations were saved as UTMs by holding a Garmin 64S GPS device directly above the sheltered snake. However, in some cases I resorted to determining an individual's location via triangulation, where multiple lines cast from different vantage points towards the snake intersect on the snake's location on the GPS, allowing for determination of the animal's coordinate location from approximately 10-25 m away. This helped ensure that locations were recorded with greater accuracy, as it allowed us to move away from large buildings that hindered the GPS accuracy when snakes sheltered underneath large buildings. During location checks I strived for an accuracy of < 5 m GPS accuracy. After locating a telemetered snake I recorded the time (dd/mm/yyyy hh:mm), location (UTM), the straight-line distance from the last known location to the new location (in the case that the individual relocated), and land-use type (mixed deciduous forest, settlement, semi-natural area, agriculture, or plantation).

Mixed deciduous forests (MDF) were essentially any large expanse of unmanicured vegetation which was generally dominated by deciduous trees. These forests were comprised of regrowth and disturbed forest fragments, and often had an understory dominated by tall grasses (particularly along the edges of forest patches; (Figure 3.5a). Agriculture was comprised of a variety of monocultures, including cassava, maize, sugarcane, rice, and small orchards, although the vast majority of agricultural land was used for cassava (Figure 3.5b). Agriculture land also included fallow fields and other idle land patches. Plantations consisted of eucalyptus, rubber, and teak tree plantation forests, as well as some palm oil plantations and large plots of mango tree plantations (Figure 3.5d). Settlement habitat covered a wide array of modified areas, including the properties of rural, suburban, and semi-urban housing, and university buildings and most of the areas surrounding the buildings. I determined the site to be settlement area if it was generally near anthropogenic structures, including frequently manicured lawns and fenced in yards and gardens. Thus, some areas are inherently more urbanized than others. To contrast the settlement and agriculture dominated habitats I determined smaller regions ($\geq$ 5 m across) of unmanicured vegetation which generally harbored dense understory vegetation and sparse tree cover as semi natural areas. These areas were not large enough to be considered a forest patch, and generally were elongated stretches of vegetation associated with irrigation canals, large agricultural field margins, water body edges, and expanses of non-forest densely vegetated patches running between some of the university buildings (Figure 3.5c).

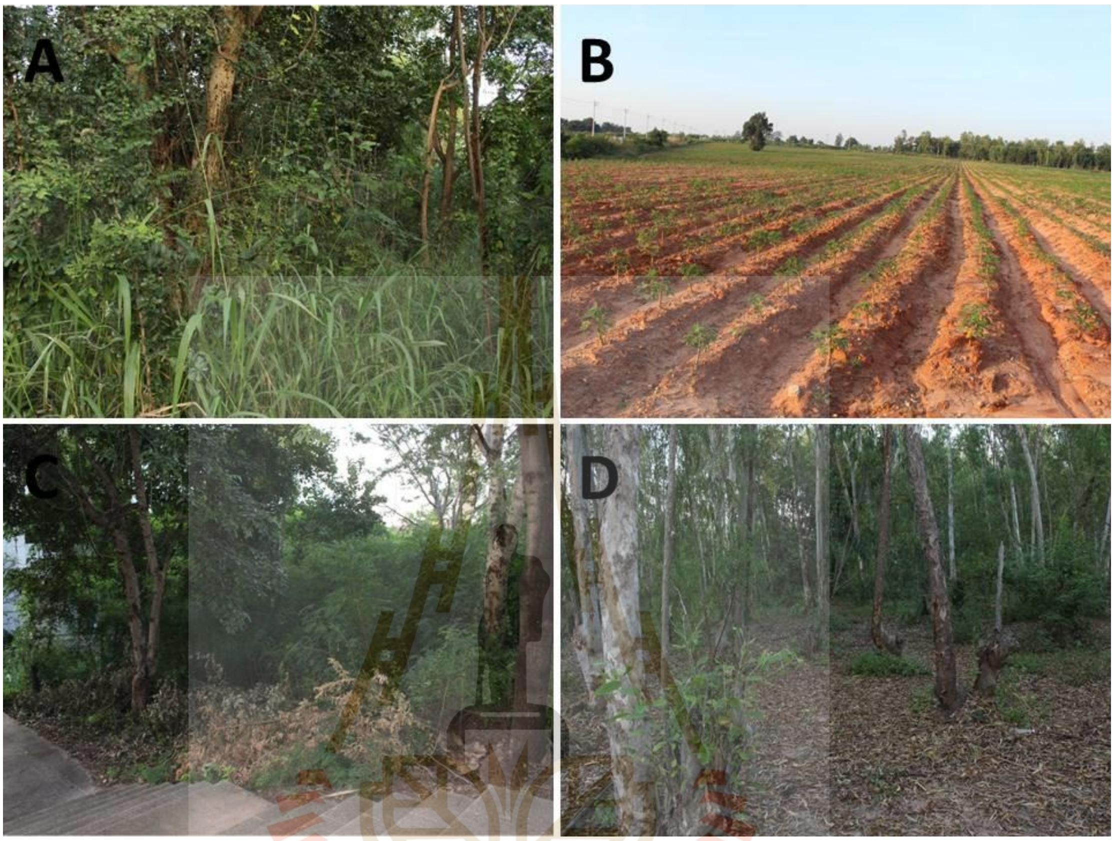

Figure 3.5 Photos of standard land-use types within the study site a) Mixed deciduous forest b) Agriculture (cassava) c) Semi-natural area d) Plantation forest (Eucalyptus).

While I was generally able to approach within 1 m of sheltering individuals during the daylight, I exercised more caution during nocturnal tracks, typically maintaining a minimum distance of approximately 5 m in attempt to lessen the chances of disturbing an active individual’s behavior, often using the described triangulation technique. During nocturnal tracks I attempted to gain visual of the snake if it appeared to be active if able to easily approach the snake, and when visual was obtained I recorded the animal’s observed behavioral state (moving, feeding, or foraging). When the radio signal was stable and visual was not obtained I determined the animal’s behavior to be “sheltering”.

Whenever feasible, I also positioned a Bushnell time-lapse field camera (Trophy Cam HD Essential E3, Model:119837) with infrared night capabilities on a tripod spaced approximately 2-5 m from an occupied shelter site (Figure 3.6). Cameras were positioned carefully so they may gather photos of the focal snake as it exits the shelter site. I hoped to capture novel behaviors which may be exhibited near shelter sites, and to gain information on their diel activity patterns. The cameras were programmed using a combined setting, including field scan, which continuously captured one photo every minute, along with motion sensor, which took photos upon movement trigger outside of the regular 1-minute intervals. While the movement of snakes didn’t trigger the camera to take photos, it was triggered by the movements of larger mammals, including dogs, cats, and humans that passed in front of the camera.

Figure 3.6 Camera trap positioned on a shelter site among a student dormitory.

3.5 Spatial Assessments

3.5.1 Space Utilization

Occurrence distributions were estimated for each telemetered individual using dynamic Brownian bridge movement models (dBBMMs; move package), as this is currently one of the better methods for estimating space use by free-ranging animals with course sampling resolutions, accounting for movement trajectories, time intervals between known locations, and GPS accuracy (Kranstauber et al., 2012; Silva et al., 2020). I selected a window size of 19 and margin size of 5, as these paired with my ~24 hour tracking regime seem to make biological sense, as the margin size is small enough to catch short resting periods, while a window size of 19 provides a time period long enough to get a decent estimate of motion variance when the animals exhibit activity. Additionally, these selections produced polygons which anecdotally seemed to fit each telemetered individual's movements by maximizing connectivity without overestimating the occurrence distribution. From the dBBMM occurrence distributions I extracted several contours (90%, 95%, and 99%) to represent space use (using R packages adehabitatHR and rgeos), however, I primarily focus on reporting the 99% and 95% contours for all individuals.

3.5.2 Space Use Predictors

Generalized Linear Models (GLM) were used to determine which covariates best predicted the 95% confidence area dBBMM occurrence distribution estimates of telemetered male *B. candidus* individuals. I examined the relationship between space use and individuals' corresponding snout-to-vent length (SVL), mass, number of days tracked, number of fixes, and proportion of fixes within human settlements. I ran

GLMs for each predictor variable independently, as well as models with multiple predictor variables together. Models were ran with both a Gaussian and Gamma distribution, but the Gamma distribution appeared to be better fit my occurrence distribution estimates based on the homoscedasticity of residuals and non-normality of residuals and outliers, therefore I only report model results using the Gamma distribution in the results. After running the models I compared AIC scores and looked at the R-squared values to distinguish which predictor variable best predicted total space use.

3.5.3 Site Fidelity

In order to examine the site re-use and time spent within different areas I used the R package "recurse". This helps to highlight areas which were revisited multiple times and total time spent in a given area. Sites can be defined by specifying a radius size for each site. I designated a site to be within a circular area with a radius of 5 m, as this was approximately my mean GPS accuracy. Revisits include when the animal was located within the designated circular area as well as when the animal was known to move through the site with the straight-line movement trajectories. I then assessed whether there were differences in site mean revisit frequency and mean time spent inside shelters between settlement habitat and less-disturbed (natural) areas with Bayesian tests of differences.

3.6 Activity Patterns

3.6.1 Movement Variance

I examined the motion variance, which is part of the output from the dBBMMs, in order to observe temporal shifts in an animal’s behavioral states. I set the window size as 19 and the margin size to 5, as 19 is nearly equal to three weeks, which allows us to get a decent enough estimate of motion variance when the animal is active, and 5 is short enough to catch the short resting periods (roughly 5 days). Low motion variance likely corresponds with periods of low activity, often due to behaviors associated with ecdysis and digestion. Motion variance peaks likely correspond to foraging movements. However, some extraordinarily larger peaks in motion variance may indicate movements associated with reproduction (i.e. mate searching), as seen in male snakes of other species.

3.6.2 Seasonality and Influence of Human Activity

Seasons were classified into three four month seasons, including wet season (01 June – 01 October), cold season (01 October – 01 February), and hot season (01 February – 01 June). The university has three annual semesters or terms which are approximately 98 (93-101) days, corresponding to when university staff and students partake in courses and activities on the university campus. The first term usually begins around March and finishes in early July, the second term usually begins early August and ends at the beginning of November, and the third semester begins in November and ends in late February. Between the semesters the number of residents and road traffic activity decreases, as during these brief periods the university is “closed”. The university is “closed” for 17 to 33 days each (mean = 20.83 days) between semesters each time.

I compared mean movement distance (MMD), mean daily displacement (MDD) between seasons using Bayesian Credible Intervals using flat priors. Distances were the straight-line distances between an individual's GPS locations from one day to the next (i.e. moves). All additional location checks were excluded so that there was only one location per individual per day. Using this same dataset I additionally calculated movement frequency for each season by dividing the number of moves by the total number of fixes. Differences in GPS locations were only considered a move if the new location was > 5 m from the previous location.

I used Bayesian regression models (BRM) with the brm package ((Bürkner, 2018) to assess the influence of season and academic session on motion variance. Season (hot, wet, and cold) and academic session (open or closed), which was used as a proxy for human activity levels, were used as experimental variables, and the individual ID was set as a random effect in both models. I used the bestNormalize package (Peterson, 2019) to render motion variance Gaussian, and to account for the autocorrelation in motion variance data, I used a third order autoregressive term matching my selected margin size (p = 5) in brms. The package's default priors were used, as I did not have prior information on this species' motion variance. I ran 5 chains of 5000 iterations, and determined the models achieved convergence using trace plots and when Rhat was equal to 1. I used the performance package to assess model quality (Ludecke et al., 2020) with R-squared regression metric to estimate the proportion of variation explained by the predictor variables. Model performance was evaluated using posterior predictor distribution plots (pp plot) and autocorrelation function plots (acf). BRMs were used instead of Fisherian methods, as assumptions for residuals are more relaxed and estimates are more conservative when using Bayesian methods.

3.7 Habitat Use and Selection

3.7.1 Habitat Use

Examining the proportions of use of different available land-use types can help us understand how the animals use different types of habitats. This may also help determine which land-use types are suitable or of particular importance to the study species. During tracking of each individual each location was determined as being within settlement, agriculture, plantation, semi-natural areas, or mixed deciduous forest while in the field. We then simply examined the proportion of locations within each land-use type in order to compare habitat use across different individuals.

3.7.2 Integrated Step Selection Function

We used Integrated Step Selection Functions (ISSF) models to examine the influence of land-use features on the movements of *B. candidus* at both the individual and population levels. I included movement data from all male individuals which had used more than one habitat feature (thus F16 and M29 were excluded) in my ISSF selection analysis. I used the package *amt* (Signer, 2018) to run ISSF for each individual, with distance to particular land-use features to determine association or avoidance of features. Land-use shapefiles were created in QGIS by digitizing features from satellite imagery combined with my local knowledge of the landscape. Semi-natural areas, plantations, mixed deciduous forest and water bodies were all combined into a single layer of less-disturbed habitats which we refer to as “natural areas”. These raster layers were then converted into layers with a gradient of continuous values of Euclidean distances to land-use features. As my study used manual VHF radio-telemetry tracking methods with a course temporal resolution, I opted to generate a large number of random steps (200) from each observed step, using similar to Smith et al. (2020), which may help guarantee that smaller and rarer features among my heterogeneous landscape were not missed.

I made nine different models testing for association to habitat features, with one being a null model which solely incorporated step-length and turning angle to predict movement, five examining land-use features individually (agriculture, buildings, settlement, natural areas, roads), and the other three being multi-factor models. Each model considers distance to a land-use variable, step-length, and turn-angle as an aspect of the model. Each of the nine models was ran for each individual. I then examined the AIC for each model, point estimates (with lower and upper confidence intervals), and p values in order to identify the best models for each individual and determine the strongest relationships and trends among the samples.

CHAPTER IV

RESULTS AND DISUSSION

4.1 Results

4.1.1 Captures and Biometrics

I captured a total of 24 *B. candidus* from within the study site between May 2018 and December 2020. Of these, 20 were captured through notifications from locals which found snakes among their homes and university buildings, while only three were found through non-standardized surveys and one was found opportunistically (Figure 4.1). Of individuals large enough to safely sex via cloacal probing (n = 21), 18 were males, while only three were determined to be female. I additionally processed some freshly killed *B. candidus* (n = 4) which were found dead on the roads within the study site shortly after being killed. Individuals were classified as juveniles if SVL < 800 mm, and adult if the SVL was greater than this. In total I processed a total of 12 juveniles (SVL 392-772 mm), 3 adult females (SVL 912-974 mm), and 13 adult males (SVL 904-1,456 mm; Table 4.1).

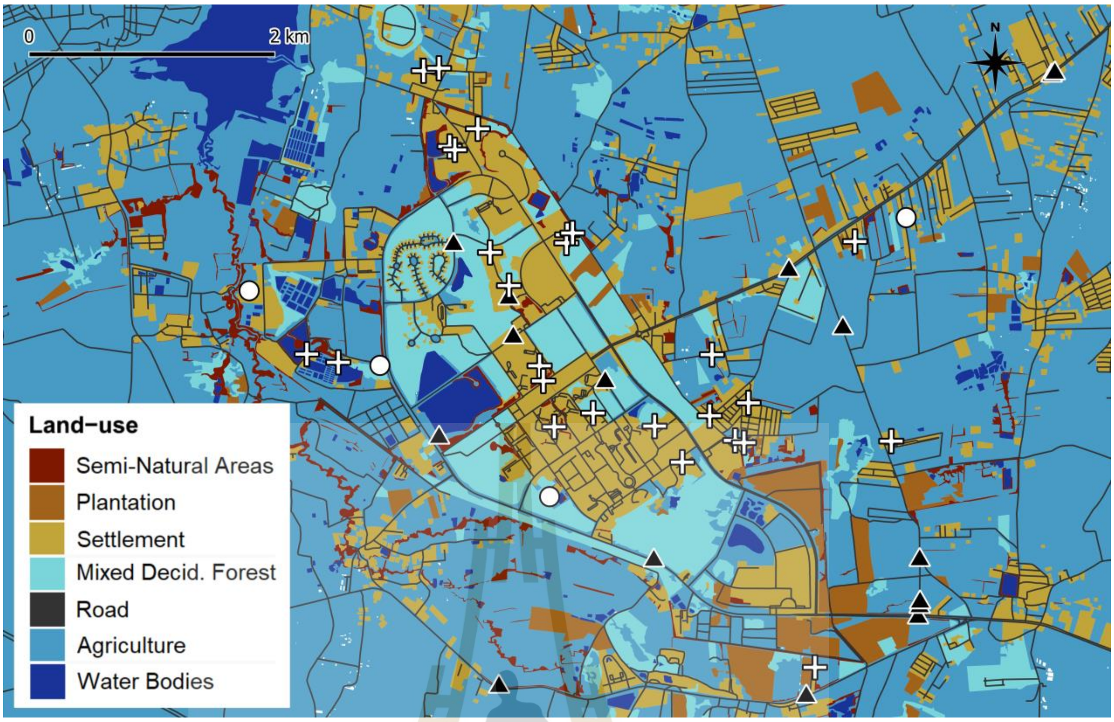

Figure 4.1 Land-use map showing locations where *B. candidus* encounters occurred within the study site. White circles indicate survey and opportunistic encounters. White cross-bars indicate notifications, and black triangles indicate road mortalities.

Table 4.1 Mean measurements of processed *B. candidus* with standard error. Head length (HL) and head width (HW) were only measured for 4 of the juveniles.

Group	N	SVL (mm)	TL (mm)	Mass (g)	HL (mm)	HW (mm)
Juvenile	12	556.1 ± 36	79.3 ± 5.3	40.9 ± 8.1	18.6 ± 1.7	9.1 ± 0.7
AD female	3	949.7 ± 19.1	125 ± 0.7	217.6 ± 0.6	29.2 ± 1.1	18.3 ± 0.7
AD male	13	1145.2 ± 45.8	142.1 ± 4.6	364.5 ± 37.7	34.6 ± 1.2	21.5 ± 0.9
Total	28	871.8 ± 59.6	113.4 ± 6.5	210 ± 34.2	30.6 ± 1.7	18.5 ± 1.2

Of the captured individuals, fourteen were implanted with radio transmitters. The average SVL of the implanted *B. candidus* was 986.9 mm, with a range of 645-1456 mm (Figure 4.2). Twelve of the snakes were implanted with the 1.8 g transmitters, while the two larger individuals (M12 and M32) were implanted with 3.6 g transmitters. On average implanted individuals were kept in captivity (i.e. from time of capture to time of release) for 129.5 hours before being released (22-322.8 h).

Table 4.2 Biometric data and capture method for each telemetered *B. candidus.*

Snake ID	SVL (mm)	TL (mm)	Mass (g)	Capture Method
M01	1130	152	339.5	Survey
M02	1081	151	287.7	Notification
M07	1013	141	248.4	Opportunistic
M12	1303	153	544.3	Notification
M14	914	128	218	Notification
F16	912	127	216.7	Notification
M22	650	94	63.6	Notification
M27	727	97	91.5	Survey
M28	772	114	91.2	Notification
M29	645	86	56.8	Notification
M32	1196	151	485	Notification
M33	904	126	176.7	Notification
M35	1113	139	450	Survey
M36	1456	103	500	Notification

4.1.2 Tracking Summary

The first telemetered krait was captured on 30 May 2018, and the last remaining telemetered *B. candidus* was lost on 24 March 2020 (Figure 4.2). Including initial capture locations, I gathered a total of 1,505 locations for telemetered *B. candidus*, with 1,381 being located during daylight, and 124 location checks during the nighttime. For the locations resulting from tracking locations, 752 locations were within the cold season, 445 within the hot season, and 308 within the wet season. The mean lag-time between location checks was 24.20 ± 0.41 h (0.17-410.0; Figure 4.3). Snakes were tracked for an average of 106.46 ± 15.36 days (28.5-222.77), during which I gained an average of 106.57 locations (25-232) per individual and they relocated an average of 23.29 ± 3.47 times (4-55). Most individuals were ultimately lost due to transmitter failures or other unknown reasons. The only known mortality among telemetered individuals was M01, which was a victim of road mortality. The individual M29 was only tracked for a total of 21 days before being lost to transmitter failure. During this time M29 only relocated three times. Therefore, I will not be using M29 in space use summaries or analyses.

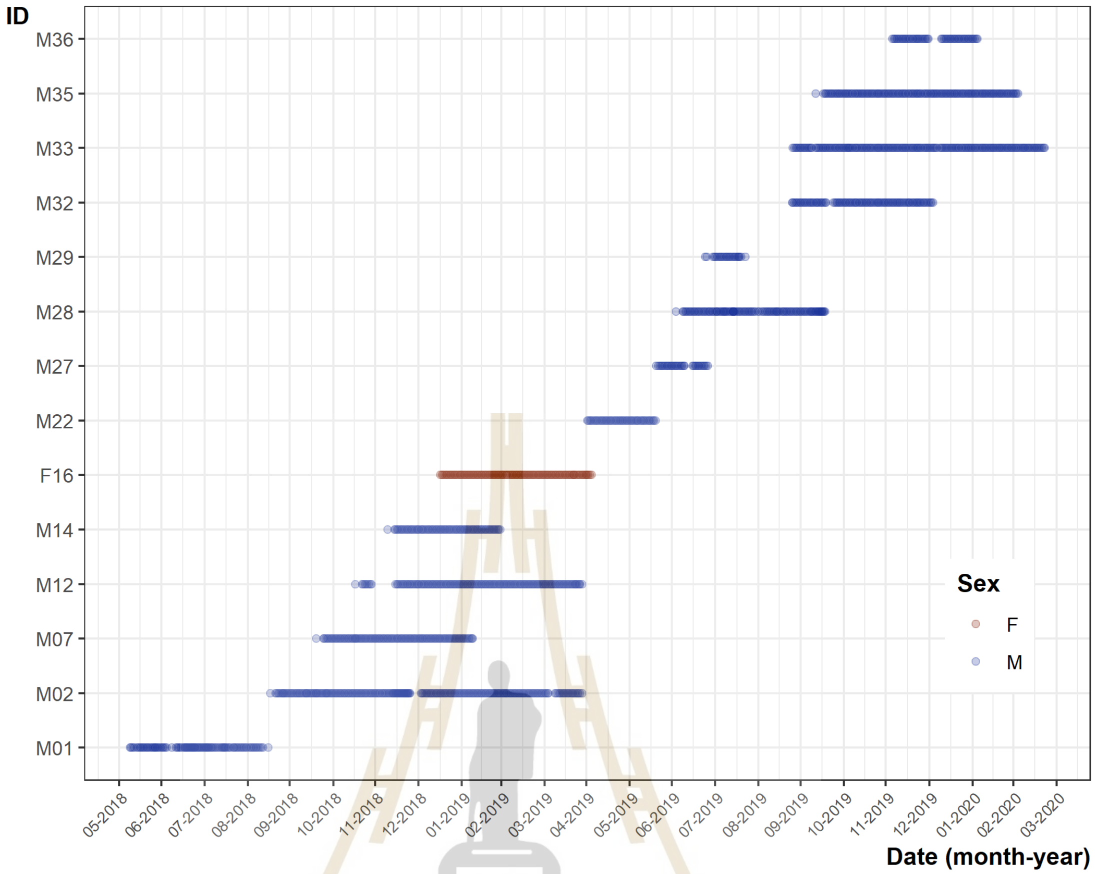

Figure 4.2 Completed location checks throughout the study period for males (semi-transparent blue) and the female (semi-transparent red), illustrating tracking durations and overlap of simultaneously tracked *B. candidus*.

The snakes were determined to be sheltering during the majority of diurnal and nocturnal tracks (1459 sheltering fixes total). Out of the 124 location checks during the nighttime, 40 locations were gained where telemetered *B. candidus* were found to be active (i.e. moving, foraging, or feeding) as well as two additional observations which occurred during the daylight. During another three nocturnal location checks the telemetered snake was thought to be active, however I did not gain visual of the snake, therefore the behavior was unknown. I determined snakes to be moving on 21 occasions, gained 19 locations where telemetered snakes were seen actively foraging, and gained two feeding observations on telemetered snakes.

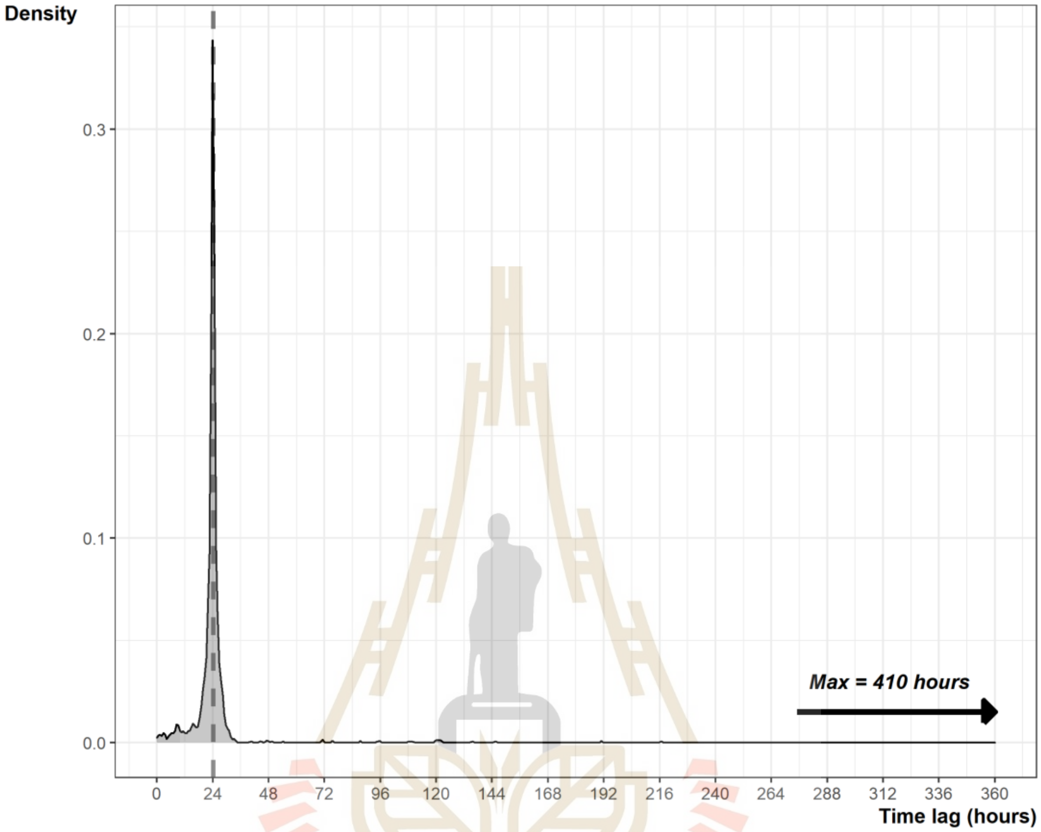

Figure 4.3 Density plot of time-lags between tracks for all telemetered individuals.

4.1.3 Movement Summary

I recorded a total of 326 relocations (> 5 m), covering a total distance of 36,603 m (includes all individuals). Overall mean movement distance was 112.62 ± 7.76 m (6–1130), and overall mean daily displacement was 24.57 m (Table 4.3). Mean movement distance for males (excluding M29) was 118.28 ± 8.32 m, and mean daily displacement was 27.42 ± 2.37 m (calculations exclude duplicate tracks per day). Also, males had relocated on 23.18% of the location checks. Overall mean motion variance was 2.20947 ± 0.2706609 (5.5278 x 10^{-05} – 160.401).

Table 4.3 Tracking and space use summary data for each telemetered *B. candidus*. Dates shown as yy-mm-dd, lag-time between location checks, number of relocations (moves), dBBMM at 90%, 95%, and 99% contours, and mean motion variance (σ^2m)

ID	Fixes	Start date	End date	Days	lag-time (h)	Moves	MMD (m)	MDD (m)	σ^2m
M01	116	18-6-9	18-9-15	99	20.58 ± 13.96	35	111.84 ± 25.7	38.96 ± 10.52	1.24 ± 0.17
M02	230	18-9-21	19-4-27	219	22.83 ± 13.71	62	85.33 ± 12.18	23.5 ± 4.26	1.23 ± 0.18
M07	130	18-10-25	19-3-13	140	25.73 ± 26.34	25	134.23 ± 26.27	23.25 ± 6.36	2.82 ± 0.61
M12	144	18-11-22	19-4-27	157	26.35 ± 32.30	24	165.39 ± 46.02	26.79 ± 8.94	3.98 ± 1.8
M14	77	18-12-15	19-2-28	76	23.89 ± 1.77	18	93.53 ± 16.76	20.92 ± 5.8	0.58 ± 0.06
F16	112	19-1-15	19-5-4	110	23.68 ± 3.04	15	47.57 ± 10.85	6.0 ± 2.01	0.16 ± 0.04
M22	51	19-5-1	19-6-19	50	23.94 ± 2.55	29	69.85 ± 16.03	36.32 ± 9.64	2.33 ± 0.34
M27	32	19-6-21	19-7-27	37	25.13 ± 13.45	9	80.86 ± 33.93	19.51 ± 10.11	0.62 ± 0.18
M28	116	19-7-9	19-10-18	102	20.99 ± 7.69	32	66.14 ± 10.65	18.62 ± 4.18	0.57 ± 0.09
M29	24	19-7-30	19-8-19	21	24.51 ± 11.38	4	91.67 ± 79.67	22.92 ± 20.78	0 ± 0
M32	99	19-9-24	20-1-3	102	24.68 ± 10.26	24	259.65 ± 57.67	60.94 ± 17.37	9.63 ± 2.34
M33	179	19-9-25	20-3-23	181	24.08 ± 5.42	32	85.53 ± 11.36	14.58 ± 3.09	0.76 ± 0.11
M35	141	19-10-17	20-3-4	140	24.11 ± 2.63	19	160.17 ± 19.66	20.89 ± 5.17	1.25 ± 0.21
M36	54	19-12-6	20-2-4	61	27.53 ± 26.36	17	185.44 ± 46.23	55.98 ± 18.04	4.31 ± 0.52

4.1.4 Space Use

4.1.4.1 Occurrence Distributions

Individual dBBMM occurrence distributions varied greatly, with the smallest being the single telemetered female *B. candidus*, F16, with a 99% confidence area (99% contour generated from the dBBMM occurrence distribution) of 0.42 ha, and the greatest being the 99% confidence area for M32, at 119.55 ha. Adequately telemetered male *B. candidus* (n = 12) had a mean 90% dBBMM confidence area of 6.88 ha (± 2.39, 1.23-29.81), 95% of 11.62 ha (± 4.33, 1.84-56.20), and a 99% of 22.85 ha (± 9.19, 3.21-119.55; Table 4.4). The excluded telemetered male individual, M29, which was only tracked for 21 days, with only 4 relocations had a 99% dBBMM of only 0.07 ha. My longest tracked *B. candidus*, M02 had a 99% confidence area of 26.76 ha, while the second-shortest tracked individual, M27 with only 32 fixes, had a 99% confidence area of 6.56 ha.

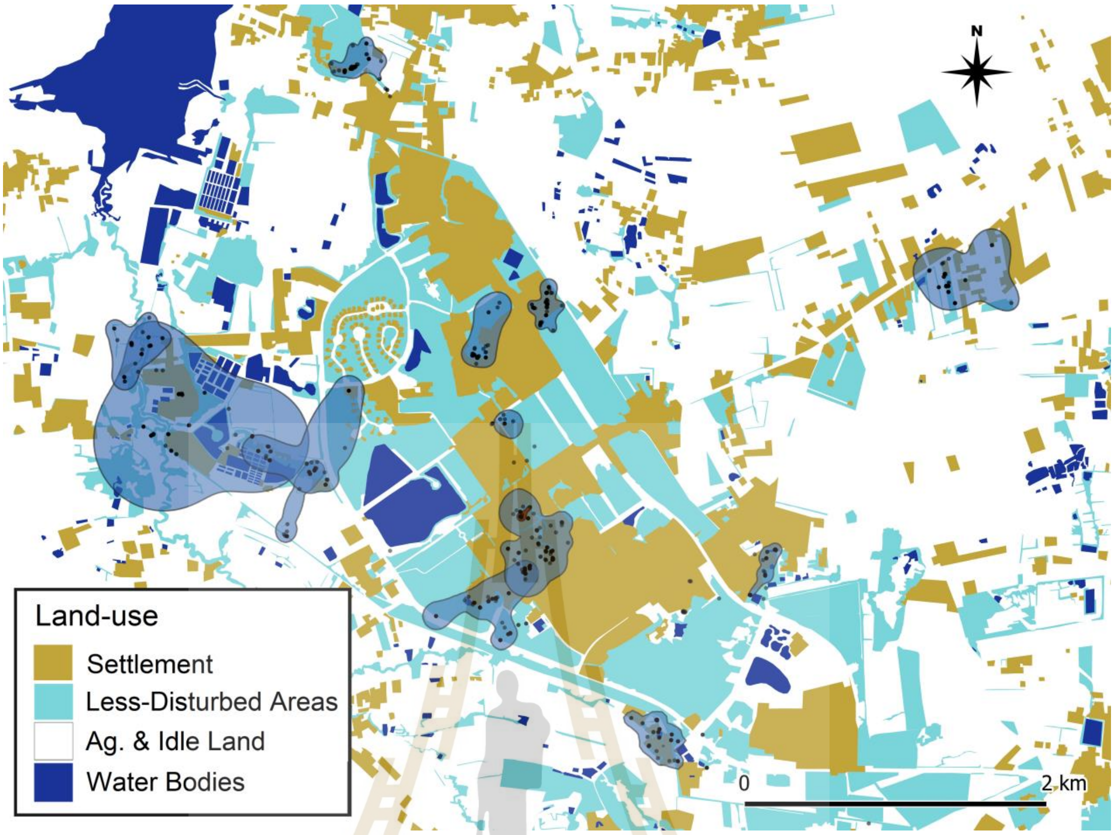

Figure 4.4 Land-use map illustrating the 99% confidence area dBBMM occurrence distributions for each individual (males in blue, female in red) and location fixes plotted as semi-transparent black dots.

Table 4.4 Area (ha) estimated for 90%, 95%, and 99% confidence area dBBMM occurrence distributions for each telemetered *B. candidus*.

Snake ID	Fixes	Mass (g)	90% (ha)	95% (ha)	99% (ha)
M01	116	339.5	6.67	10.47	18.72
M02	230	287.7	7.94	13.33	26.76
M07	130	248.4	3.00	7.94	25.95
M12	144	544.3	3.59	5.79	9.23
M14	77	218	1.23	1.84	3.21
F16	112	216.7	0.03	0.05	0.42
M22	51	63.6	3.96	6.05	10.07
M27	32	91.5	3.37	4.42	6.56
M28	116	91.2	1.86	2.74	4.79
M29	24	56.8	0.03	0.04	0.07
M32	99	485	29.81	56.20	119.55
M33	179	176.7	1.57	3.03	6.30
M35	141	450	3.49	6.83	13.10
M36	54	500	16.09	20.76	29.96

4.1.4.2 Space Use Predictors

Simple linear regression models reveal a small, but significant (p = 0.053) correlation between 95% confidence area occurrence distribution estimations and mass (R^2 = 0.2355, slope = 0.04552). However, there appears to be little to no noticeable correlation between the 95% occurrence distributions, as all other tested variables were not significant according to the linear regression models, including SVL (p = 0.084, R2 = 0.1783, slope = 0.02896), number of days tracked (p = 0.874, R2 = -0.0883, slope = 0.01229), number of fixes (p = 0.926, R2 = -0.09, slope = 0.007084), and proportion of fixes within settlement habitat (p = 0.688, R2 = -0.0743, slope = -5.527).

Using GLMs with a Gamma distribution I examined the relationship between an individual's corresponding mass, number of days tracked, and percentage of fixes within settlement habitat and the 95% confidence area (CA) occurrence distribution estimation. I ran six different models, three of which only examined one of the covariates individually, while the other three accounted for combinations of two or more of the covariates simultaneously. Overall, the models each performed fairly well with the exception of an outlier among the occurrence distribution estimates which resulted in non-normality of the residuals. Also, homogeneity in variance was not ideal. The model accounting for both snake mass and percentage of fixes within settlement habitat had the lowest AIC score (ΔAICc < 2), and had a high R^2 value of 0.86 (Table 4.5). However, my GLM results should be taken lightly as the model fit was not ideal due to the outlier, but it seems that both mass and proportion of time spent in settlement habitat both have some impact on the estimated occurrence distributions.

Table 4.5 R^2 values, AICc scores, ΔAICc, model weight, degrees of freedom, and model performance score resulting from each GLM predicting space use estimates (95% dBBMM confidence areas).

Model	R^2	AIC_c	ΔAIC_c	Model likelihood	w_i	df	Perform. score (%)
95% ~ Mass + Days + %Settle	0.86	86.920	5.541	0.063	0.053	5	77.80
95% ~ Mass + Days	0.68	89.843	8.465	0.015	0.012	4	31.41
95% ~ Mass + %Settle *	0.86	81.379	0.000	1.000	0.854	4	99.95
95% ~ Mass	0.56	88.679	7.301	0.026	0.022	3	17.53
95% ~ Days	0.44	90.941	9.563	0.008	0.007	3	0.00
95% ~ %Settlement	0.63	87.038	5.659	0.059	0.050	3	29.37

4.1.4.3 Site Fidelity

Overall, telemetered *B. candidus* exhibited relatively high site fidelity, with all but one of the telemetered snakes revisiting sites during the tracking duration at least once. For these individuals (excluding M29), the overall mean number of site revisits was 18.67 (range = 2–46), with an overall mean site revisit frequency of 370.87 ± 92.93 hours (28.37–1213.6), meaning they tended to return to a previously used shelter approximately every 15 days. Mean average time telemetered *B. candidus* remained within a shelter was 184.63 ± 47.63 hours (41.96–731.40).

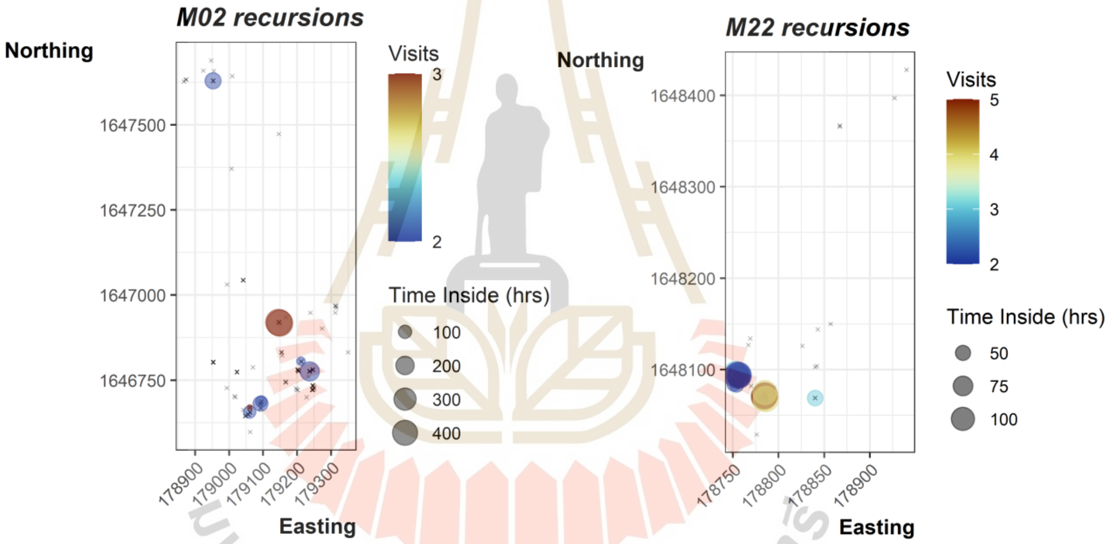

Figure 4.5 Spatial distribution between sites, showing the number of revisits to each site and time spent inside revisited sites for two individuals, M02 which resided in the center of SUT campus among the laboratory buildings; M22 which stayed within a small on-campus mixed deciduous forest fragment.

Table 4.6 Mean site revisit frequencies and time spent within a site for each individual when in natural habitats and settlement habitat.

Snake ID	Nat Time Inside	Nat Revisit Frequency	Settle Time Inside	Settle Revist Frequency	Overall Max Site Revisits
M01	5.27 ± 0.85	12.57 ± 0.08	4.53 ± 1.07	9.98	5 (15)
M02	24.53 ± 12.87	4.49	5.70 ± 0.99	12.78 ± 3.38	3 (21)
M07	9.86 ± 3.01	21.60 ± 3.95	8.19 ± 3.9	1.79 ± 0.06	6 (28)
M12	11.14 ± 3.48	15.44 ± 0.85	2.35 ± 0.72	NA	3 (11)
M14	13.96 ± 4.87	9.09 ± 7.59	5.66 ± 2.10	21.07 ± 2.68	3 (10)
F16	1.31	NA	1.73 ± 0.33	37.19 ± 22.95	6 (15)
M22	3.24 ± 0.35	5.27 ± 1.38	NA	NA	5 (46)
M27	7.50 ± 3.42	1.18	NA	NA	2 (2)
M28	17.29 ± 4.45	2.34 ± 0.01	6.68 ± 1.62	8.97 ± 1.78	3 (33)
M32	2.36 ± 0.42	6.07 ± 3.49	17.13 ± 4.04	NA	3 (12)
M33	2.57 ± 0.46	1.95	8.31± 2.19	69.64 ± 19.64	5 (29)
M35	34.12 ± 19.0	NA	8.81	11.54	2 (2)
M36	3.86 ± 1.5	NA	3.62 ± 0.95	NA	0

Mean time between site revisits for males was 213.13 ± 32.29 hours when among natural habitats (41 total revisits), while it was 590.53 ± 154.47 hours when among settlement habitat (30 total revisits). Bayesian tests of difference for revisit frequency and time spent inside between natural and settlement habitat types using Bayesian credible intervals (95% BCrI) revealed high levels of certainty that site fidelity between settlements and less-disturbed areas is different (Figure 4.6a). My data shows that there is a clear increase in the amount of time between site revisits when among settlement habitat, with 95% certainty that the true mean difference in time since last revisit is between is between 56.2 and 703 hours, thus sites were revisited among natural habitats more frequently than when among settlements.

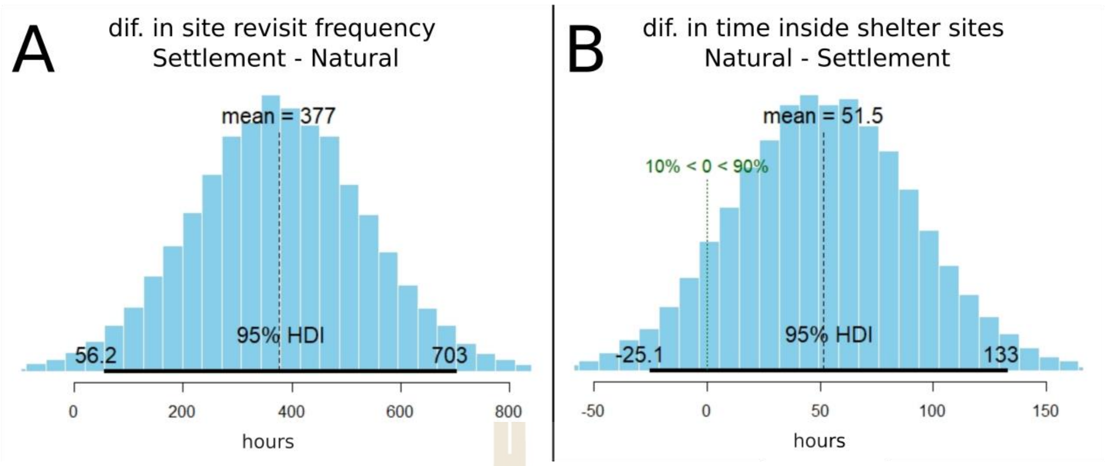

Figure 4.6 Bayesian credible intervals for the differences between site fidelity in settlement and less-disturbed habitats. a) Difference in site revisit frequency between the two different habitat categories. b) Difference in the amount of time spent within a shelter site between the two habitat categories.

In addition, 95% BCrI revealed a highly likely increase in the amount of time typically spent within shelter sites among natural areas than when among settlement habitat (Figure 4.6b). Based on my data, there is only a 10% chance of the time inside shelter sites among settlement habitat being the same or greater than when in natural habitats. After running the same tests including the single telemetered female, I found that both of the previously described trends are only strengthened.

4.1.5 Temporal Movement Patterns

4.1.5.1 Seasonality

Motion variance mean values were highest in the Cold season, when there notably were several particularly high peaks in motion variance from a few different individuals (M02, M07, M12, and M32) both years (Figure 4.7). These four highest peaks all coincided within the first two months of the cold season, October and November. Similarly, seven of the eight particularly large movements (> 400 m) documented occurred within late wet season or early cold season (September, October, and November), with the eighth occurring later in the cold season (early January).

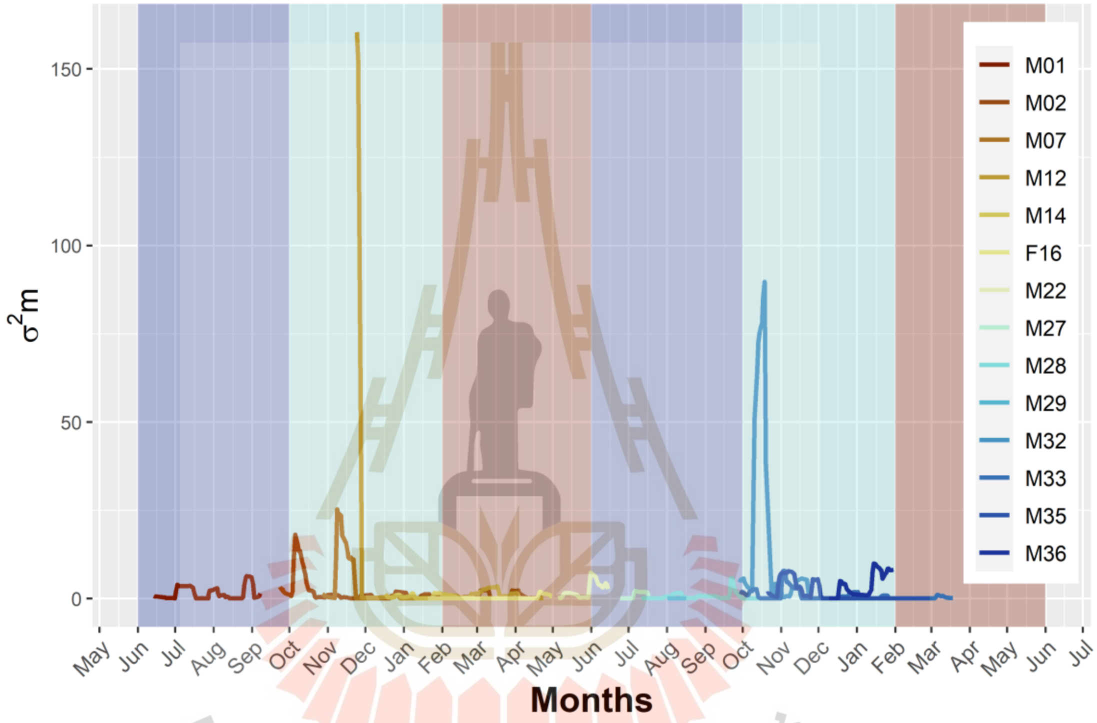

Figure 4.7 Motion variance for each individual throughout the study period, with background colors corresponding to season: blue = wet, light blue = cold, red = hot.

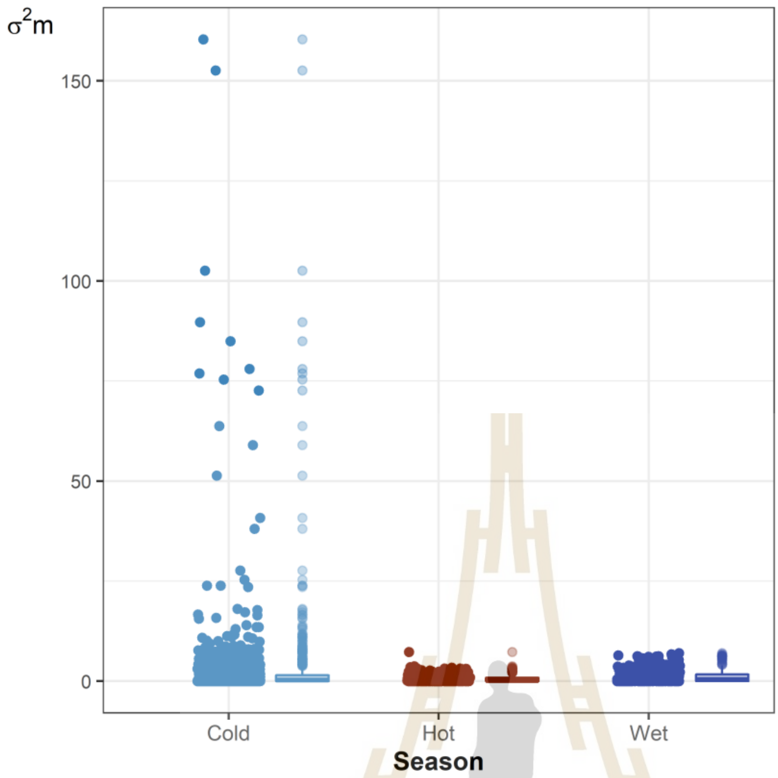

Figure 4.8 Total motion variance values for each season.

Overall mean movement distance was highest in the cold season (138.20 ± 13.75 m) and lowest during the hot season (77.06 ± 6.44 m), in contrast mean daily displacement was highest during the wet season (41.25 ± 6.26 m), and lowest during the hot season (12.46 ± 1.70 m; Table 4.7). Similarly, movement probabilities were highest for the wet season (0.3843) and lowest for the hot season (0.1617). These seasonal differences in MMD and MDD were then checked and verified with Bayesian credible intervals.

Table 4.7 Mean movement distance, mean daily displacement, movement probability (proportion of fixes that a snake moved), and mean motion variance for each season.

Season	MMD	MDD	Prop of fixes moved	Mean Motion Variance
Cold	138.20 ± 13.75	28.26 ± 3.49	0.2045	3.25 ± 0.476
Hot	77.06 ± 6.44	12.46 ± 1.70	0.1617	0.599 ± 0.055
Wet	107.35 ± 13.92	41.25 ± 6.26	0.3843	1.18 ± 0.102

Testing for probabilities of differences among the seasonal MMD and MDD data using Bayesian credible intervals (95% BCrI) revealed high levels of certainty of differences (Figure 4.9). Results show a 95% certain that the MDD for hot season is between 8.25 and 23.5 m less than the MDD in the cold season, and between 16.2 and 41.6 m less than the MDD in the wet season. Comparing MDD of wet season to cold season revealed that we are fairly certain that the MDD is about 10-16 m higher in the wet season than the cold season (95% BCrI = -0.637 – 27.7). Similarly, when examining MMD, results show the MMD is lower in the hot season than in the cold or wet seasons with a high level of certainty, though the difference in MMD is greater when comparing hot and cold seasons than the hot and wet seasons. However, comparing MMD of wet season to cold season revealed high certainty (~ 94% certain) that the MMD in the cold season is higher than the MMD in the wet season (95% BCrI = -69.3 – 8.2).

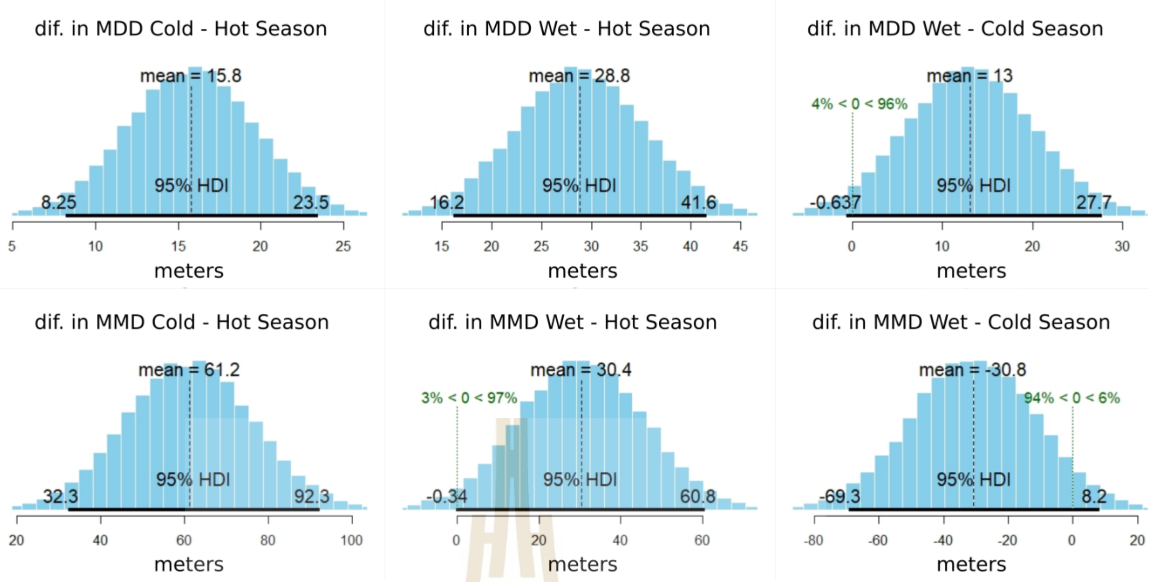

Figure 4.9 Bayesian credible intervals for the differences between mean daily displacement and mean movement distances between pairs of seasons.

In addition to there being a somewhat noticeable trend in when the unusually large movements occurred both years during the study, I also note some anecdotal trends in unusually long periods of inactivity among the telemetered male *B. candidus*. Six of the male *B. candidus* individuals remained inactive within the same shelter for > 20 days consecutively (mean = 37.57, range = 21-94) on at least one occasion (8 instances total). Three of these occasions occurred entirely within the Cold season (each began around mid to late November and lasted until mid-December), and another three similarly began in the Cold season (early December, late December, and late January) but didn’t relocate until early in the Hot season (2 relocated mid-February, and one hadn’t relocated even to the point of its recapture in early March). Two later instances where the telemetered individuals didn’t relocate for more than 20 consecutive location checks occurred entirely within the Hot season (end of January to late February and the other early April to late April). Interestingly, each of the six individual’s longest consecutive period of not moving occurred sometime after the individual had made an unusually large move, although this was often about a month or two thereafter.

Similarly, the single telemetered female remained within the same shelter complex (under the F1 building near the northern entrance) for a total of 85 consecutive days (25 January – April 20 2019), before leaving and sheltering about 85 m away for a single night and then returning and spending another six days back at this shelter site before beginning to ultimately move away and then being lost from the study due to transmitter failure.

4.1.5.2 Movement Variance and Seasonality

There was good convergence in the BRM according to trace plots, and the Rhat value was 1, thus the model has converged. However, the autocorrelation plots aren’t great looking, and the pp plot check was not ideal, as it showed possible zero inflation due to the large values, but overall the model appeared to fit the data well enough. The model had a high R^2 value for both the conditional R^2 (0.919) and the marginal R^2 (0.907). The point estimate for the wet season was just slightly higher than in the cold season, however, the 95% credible interval overlapped with 0, thus the difference is highly ambiguous with low levels of certainty (4.10).

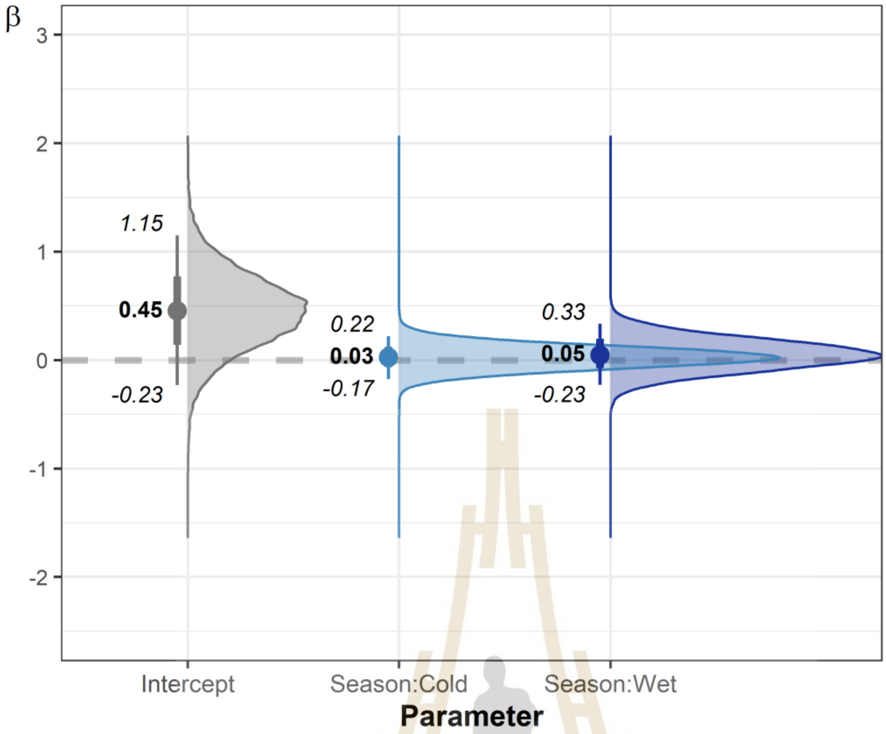

Figure 4.10 Seasonal changes in motion variance BRM results displayed with 95% credible intervals.

4.1.5.3 Movement Variance and Human Activity

Mean motion variance for solely when SUT was in session was 1.83 ± 0.247 (5.53 x 10^{-5}–103), while the mean was 3.89 ± 0.977 (5.53 x 10^{-5}–160) for when SUT was not in session (Figure 4.11). However, note the data is limited by the bias towards more days being "in session" than the short between term "out of session" periods, thus the in session sample (n = 1,135) was quite larger than that of the sample for out of session (n = 246).

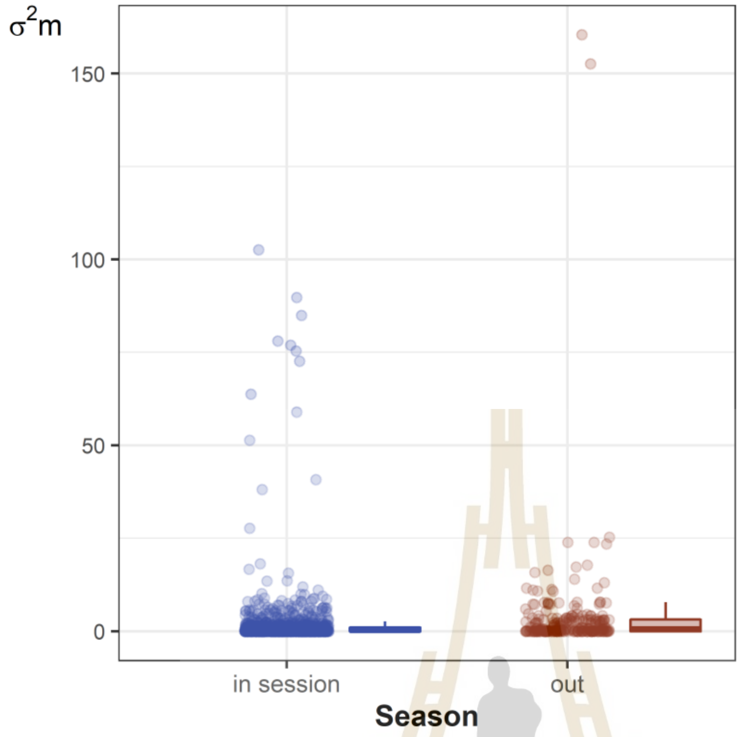

Figure 4.11 Plot of all the motion variance values for both during and between university semesters (in session vs. out of session).

The model performance, convergence, and fit were essentially the same as with the BRM examining seasons. Again, this BRM also had a high R^2 value for both the conditional R^2 (0.919) and the marginal R^2 (0.907), which seems to be largely due to the inclusion of the auto-correlation aspect to the model. The motion variance point estimate for when SUT was not in session was 0.11, with the upper 95% credible interval being at 0.22 and the lower at 0.00 (estimated error = 0.06; Figure 4.12). Thus it appears there may have been a slight increase in motion variance when the university was closed, although it is somewhat ambiguous since the lower 95% confidence interval ended directly on 0.00.

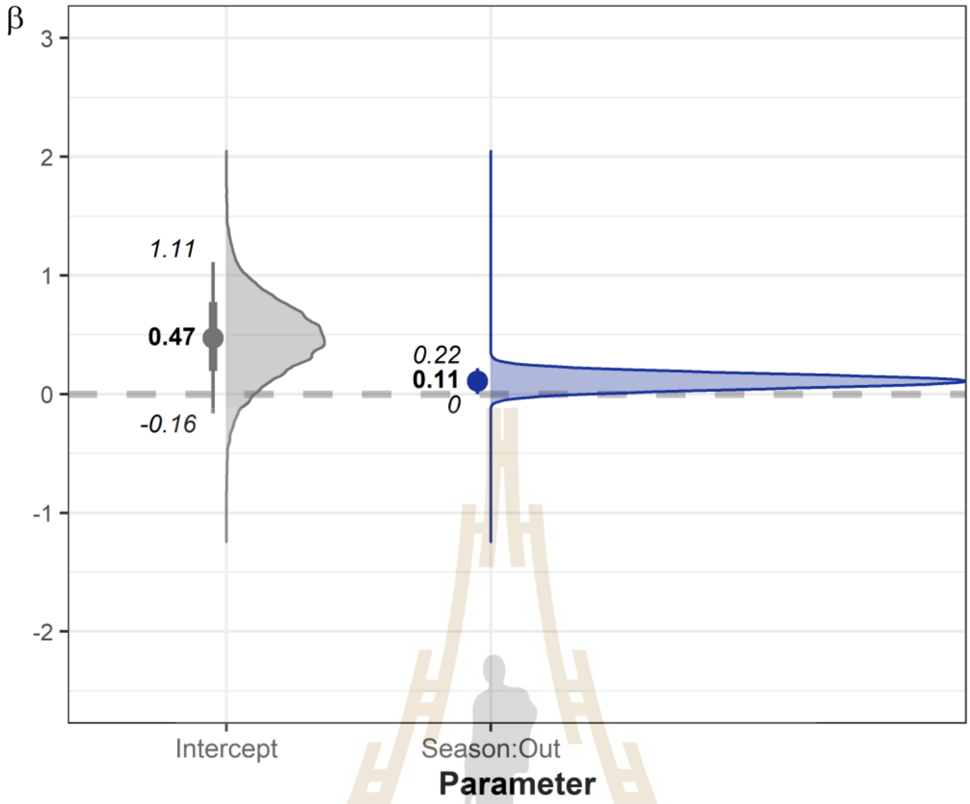

Figure 4.12 Results from the BRM examining differences in motion variance between when SUT was in session and out of session, with 95% credible intervals.

4.1.5.4 Diel Activity Patterns

I gathered a total of 1,160,970 photos from time-lapse camera trapping on ten of the telemetered individuals. Out of these, I was only able to identify focal animals as being within a total of 75 photos, from six different individuals, with a total of 14 different occasions (independent nights), with a mean of 5.36 (range = 1-18) photos per occasion. During these the snake generally peaked its head out and slowly exited the shelter site (n = 7), or simply just exited the shelter site and began moving away (n = 4), not to return again. However, on one occasion the snake was seen to pass back and forth and re-enter the shelter again through different burrow entrances several times as the individual foraged near the shelter before ultimately returning. Similarly M36 was also photographed to be active at night before returning to the same shelter. One other occasion an individual (M12) spent a few minutes lying just outside the shelter before moving off.

All snakes exited shelters under the cover of darkness. Most snakes were first photographed in the early night, with snakes becoming apparently active around 20:29 h on average (between 18:41 and 22:20 h). Times of activity above-ground around the shelter sites were found to be bi-modal, with the highest peak of activity taking place around 19:30 h, and the second, but smaller, peak at around 22:00 h (Figure 4.13). All photos of focal animals were between 18:41 h and 22:22 h. On average, snakes exited shelter sites 2.204 hours after sunset (range = 0.317 – 4.33 h, SD = 1.528 h).

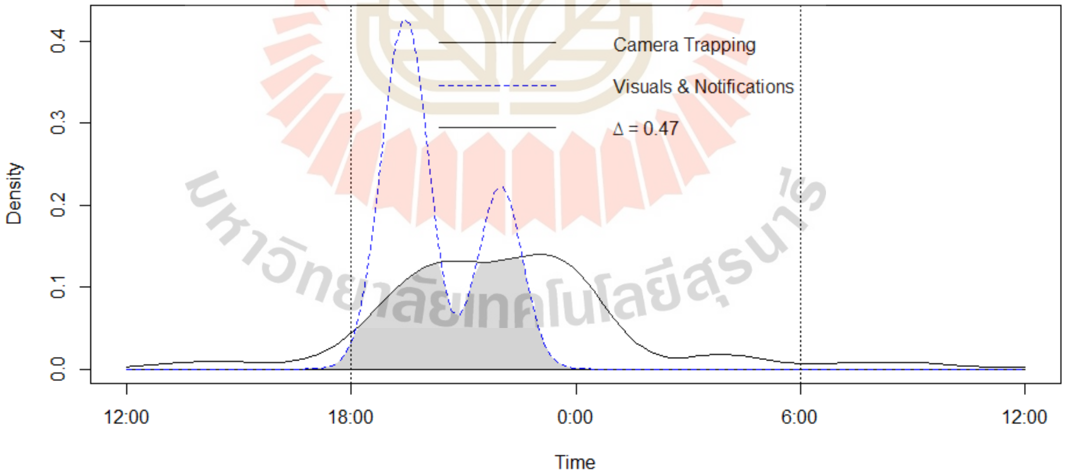

Figure 4.13 Density plot illustrating when *B. candidus* were found to be active via shelter site camera trapping, visual encounters, and sighting notifications (Δ = proportion of overlap).

Similarly, all of the visual encounters during surveys and tracking (n = 23) and each time an individual was deemed active via radio-telemetry signal without visual confirmation (n = 5) were during the nighttime. In total we received 30 notifications of *B. candidus,* of which the majority occurred between 18:00 h and midnight (n = 17). Another eight notifications occurred between midnight (00:00 h) and 06:00 h (at 00:00, 00:10, 00:12, 00:20, 00:23, 00:23, 3:30, and 4:30 h). Interestingly, one of the feeding observations which began at 00:20 h continued until 03:55 h, when it completed ingestion and began moving away. Another five notifications occurred during daylight (at 07:20, 09:20, 13:29, 15:10, and 17:45 h).

4.1.6 Habitat

4.1.6.1 Habitat Use

Habitat use varied widely across individuals (Figure 4.14), however, the overall most frequently used habitat was human settlements, with 51.2% of all fixes, with semi-natural areas being the second most commonly used habitat (25.2%), closely followed by mixed deciduous forests (22.8%; Table 4.8). The least used land-use types were agriculture (0.5%) and plantation forest (0.3%). Of the points among human settlement habitat 558 (72.47%) were associated with buildings and another 99 (12.86%) were associated with concrete drainage ditches, sidewalks, or other concrete structures.

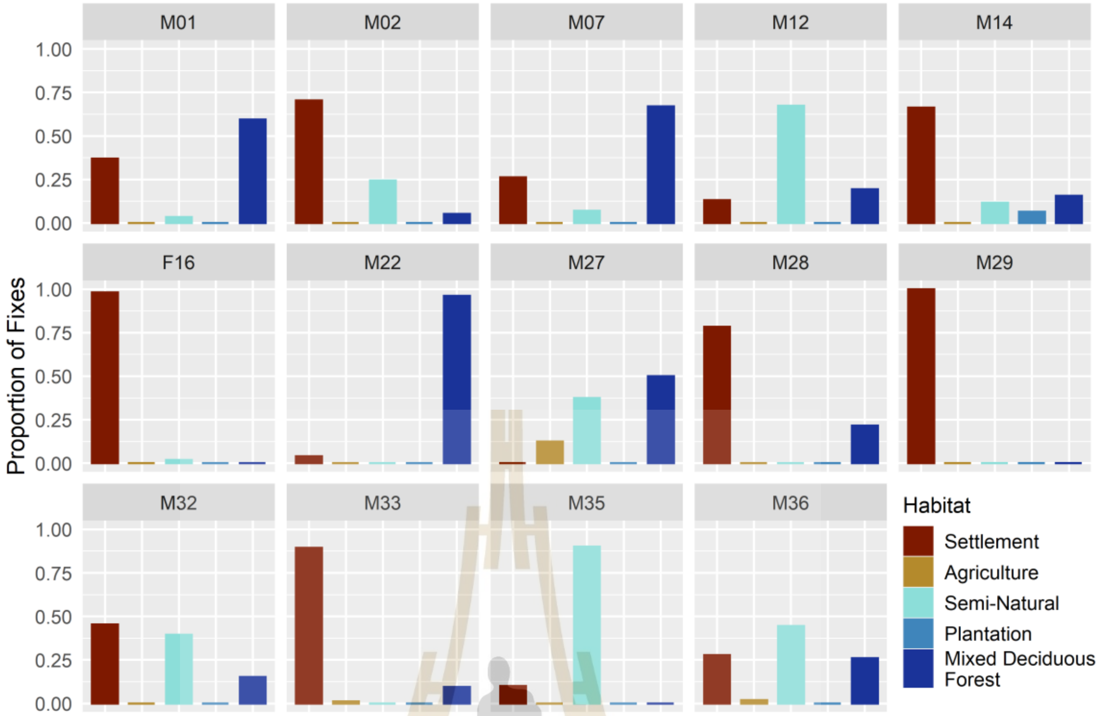

Figure 4.14 Habitat use proportions for each telemetered individual.

Table 4.8 Total number of fixes an individual was located in each land-use type.

Snake ID	Settlement	Semi-Nat	Agriculture	MDF	Plantation
M01	43	4	0	69	0
M02	162	56	0	12	0
M07	34	9	0	87	0
M12	19	97	0	28	0
M14	51	9	0	12	5
F16	110	2	0	0	0
M22	2	0	0	49	0
M27	0	12	4	16	0
M28	91	0	0	25	0
M29	24	0	0	0	0
M32	45	39	0	15	0
M33	160	0	2	17	0
M35	14	127	0	0	0
M36	15	24	1	14	0
Total	*770 (51.2%)*	*379 (25.2%)*	*7 (0.5%)*	*344 (22.8%)*	*5 (0.3%)*

4.1.6.2 Shelter Use

Telemetered snakes were determined to be sheltering in 1459 fixes. Out of these fixes, 560 were classified as anthropogenic shelters (Table 4.9), which included fixes where snakes were directly underneath buildings (507), sidewalks (2), concrete drainage ditches (37), or other anthropogenic structures. Many of the identified shelters however were burrows, with 497 fixes. Burrows included burrow systems and tunnels that were made by other animals, such as rodents, but which did not appear to be part of termite mounds or burrow systems. Termite mounds made up 280 of the shelter fixes. Lesser used shelter types included dense vegetation (48) and rocks (28). The shelter type was unknown in 46 of the fixes.

Table 4.9 Total number of fixes an individual was located within each shelter type.

ID	Burrow	Termite Md	Anthro	Rocks	Dense Veg	Unk
M01	27	27	40	0	5	8
M02	34	50	135*	0	2	0
M07	89	6	2	28	0	3
M12	67	62	8	0	0	6
M14	19	23	9	0	12	13
F16	0	0	109	0	0	1
M22	45	5	0	0	0	0
M27	27	0	0	0	0	3
M28	70	4	33	0	0	0
M29	0	0	20	0	0	1
M32	43	0	44	0	0	10
M33	23	5	148	0	0	0
M35	36	95	0	0	8	1
M36	17	3	12	0	21	0
Total	*497 (34.1%)*	*280 (19%)*	*560 (38.4%)*	*28 (2%)*	*48 (3.3%)*	*46 (3.2%)*

Interestingly, 114 of the shelters which were not “anthropogenic” were associated with concrete structures, such as drainage ditches and buildings, with 37 of the “burrow” and two “unknown” shelters within 1 meter of a building, 9 in or within a meter of a concrete drainage ditch, and another 19 within a meter of a paved sidewalk.

Figure 4.15 Examples *B. candidus* shelter sites among settlements. a) Overgrown concrete drainage ditch outside a laboratory building. b) Underneath the foundation or among the pipelines under a laboratory building. c) Under a concrete at a residency. d) Underneath a concrete floor of a gardening work-station.

4.1.6.3 Foraging Sites

Of the instances where telemetered snakes were observed to be moving, foraging, or feeding, 14 occurred within 1 meter of a paved sidewalk, 12 were associated with buildings (either inside or within 1 m to a building wall), and 8 occurred in or within 1 m of a concrete drainage ditch. In total, 26 of 43 observations were associated with concrete structures of some kind (Examples: Figure 4.16 and Figure 4.17). Five observations occurred within agriculture (two within cassava fields, one within fallow field, one among a fishery, and one on a road-side among a grass field). Several of the others were known to occur near the edge of a body of water. Another two telemetered individuals were observed moving within a meter of a chicken coup.

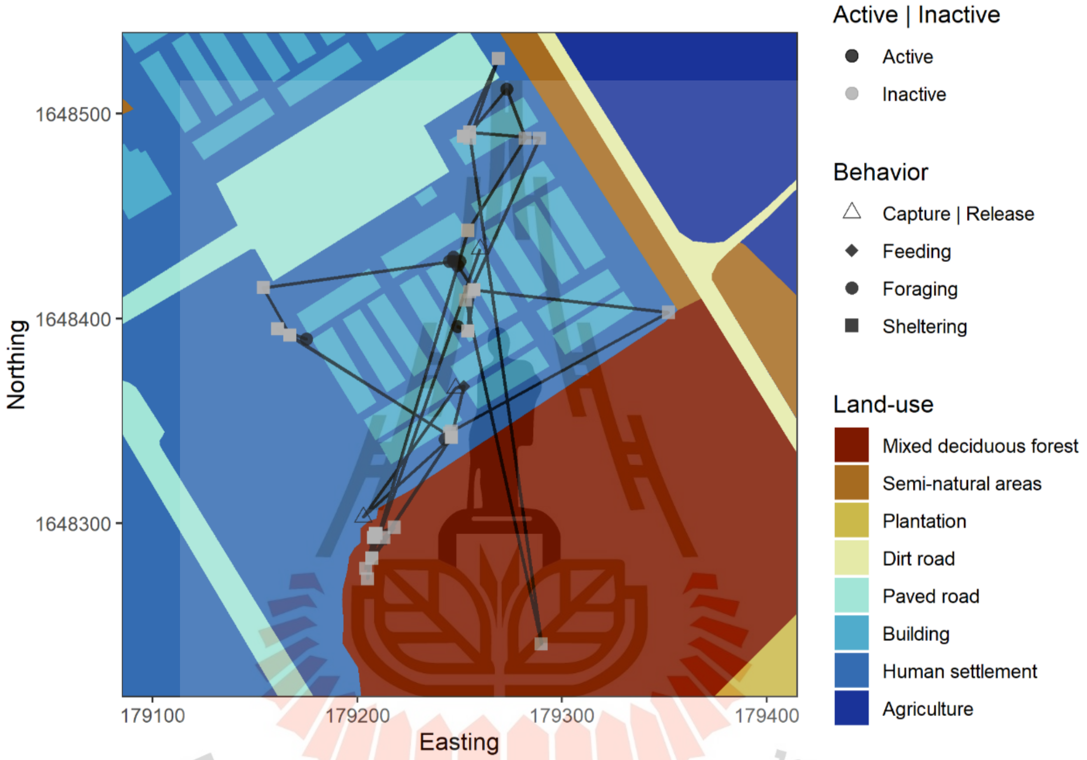

Figure 4.16 Land-use map with locations where M28 was found sheltering, foraging, feeding, and even came into conflict with humans among a densely populated SUT dormitory (S-15; Hodges et al., 2021).

Of the feeding observations made, two were within concrete gutters running adjacent to a dormitory sidewalk and only about two meters away from dormitory rooms. Another occurred in a dirt road-side ditch about ten meters from a house, and the final observation took place within a building.

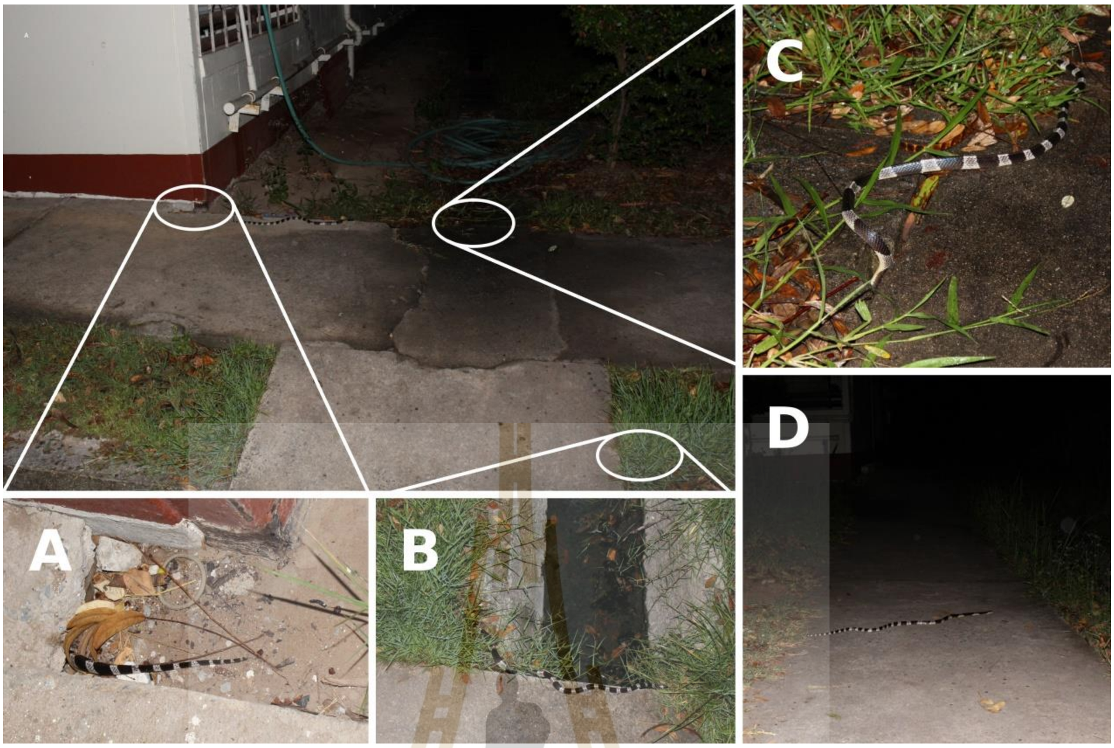

Figure 4.17 Observations of M28 foraging among a busy sidewalk and buildings at a student dormitory a) Forging in holes under sidewalk b) Foraging along drainage ditch and sidewalk c) Probing his head into burrows and crevices which may harbor prey species d) The *B. candidus* crossed over the sidewalk a total of four times during a two hour period (Hodges et al., 2021).

4.1.6.4 Integrated Step Selection Functions

When examining habitat selection at the individual level, results revealed that several individuals which had unambiguous positive relationship/attraction for both buildings and natural areas. All individuals appeared to be indifferent (neither attracted towards nor avoided) both agriculture and roads. There was high variation/error bars for the relationship with the distance to settlements.

Table 4.10 Model formulas and AIC scores for individual ISSF models. * indicates AIC scores within < 2 Δ AIC of the model that best predicts selection for an individual.

model	F16	M01	M02	M07	M12	M14	M22	M27	M28	M32	M33	M35	M36
model1 (null)	**171.77***	344.97	630.74	249.51	238.97	175.35	300.1	84.34	357.76	270.95	331.35	185.62	164.1
Settlement	**170.54***	346.2	636.42	254.11	225.66	180.48	300.83	82.8	357.36	270.56	315.42	190.92	160.46
Road	**172.36***	350.22	624.8	251.75	239.23	180.63	305.41	85.13	359.84	272.38	323.27	190.49	168.71
Building	**172.17***	346.51	621.69	249.57	231.45	180.9	305.31	85.58	**351.58***	266.5	309.21	191.07	**158.01***
Agriculture	176.99	349.78	635.61	239.95	244.37	180.36	302.14	88.8	362.25	275.3	334.06	190.49	169.3
Natural	173.68	341.05	629.29	238.88	228.64	173.3	277.04	83.2	363.54	**258***	330.46	**158.25***	163.44
Ag + Nat +Build	174.06	**337.02***	619.02	**235.65***	**206.56***	**168.93***	**272.75***	81.51	**350.65***	264.86	312.54	**158.14***	**158.2***
Rd + Build + Nat	173.06	**337.57***	**609.01***	240.63	**207.46***	**167.4***	**273.39***	**79.13***	**350.43***	265.42	**304.42***	**158***	**157.66***
Rd + Ag + Nat	175.26	343.81	622.02	**236.57***	226.34	171.29	**274.08***	82.92	360.08	273.28	310.44	**157.93***	163.79

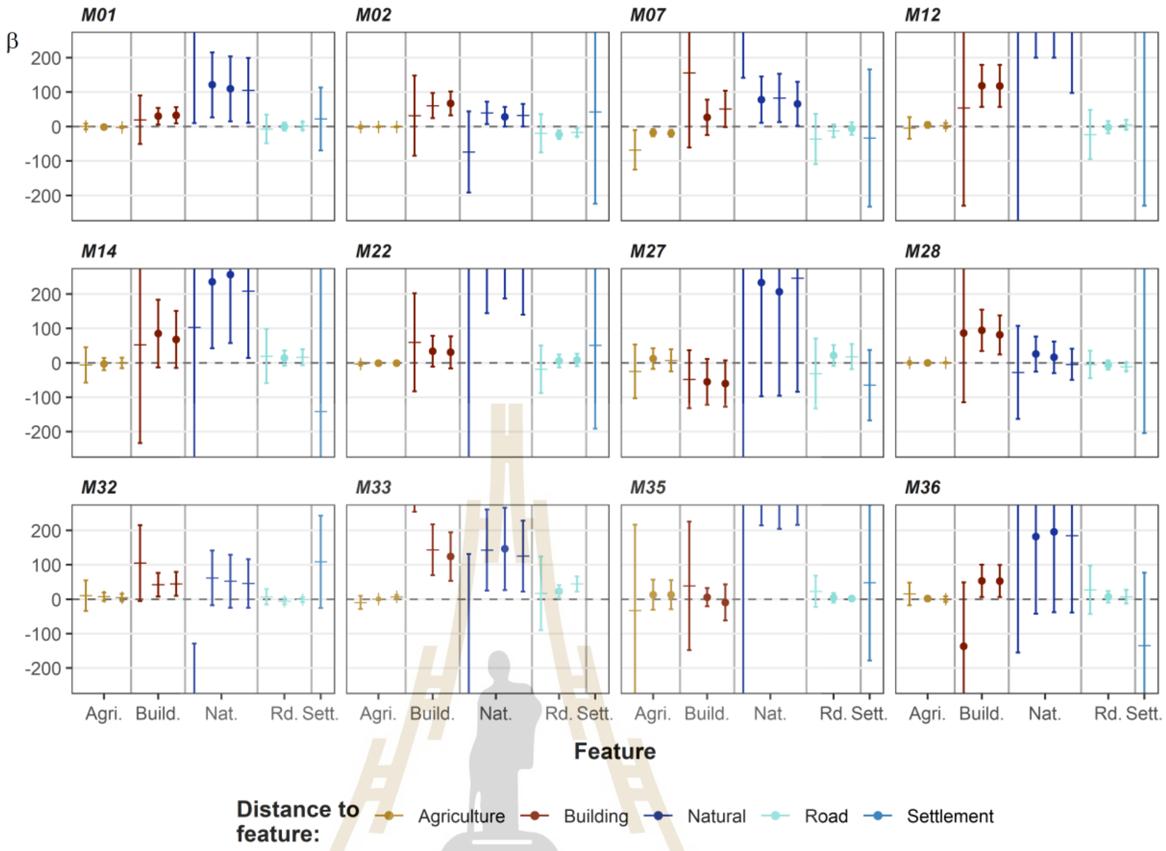

Figure 4.18 Individual ISSF model results based on distance to habitat features. Positive estimates suggest association with habitat feature, error bars indicate 95% confidence intervals, and circles mark the habitat features that were included in models with AIC scores within < 2 D AIC of top performing models.

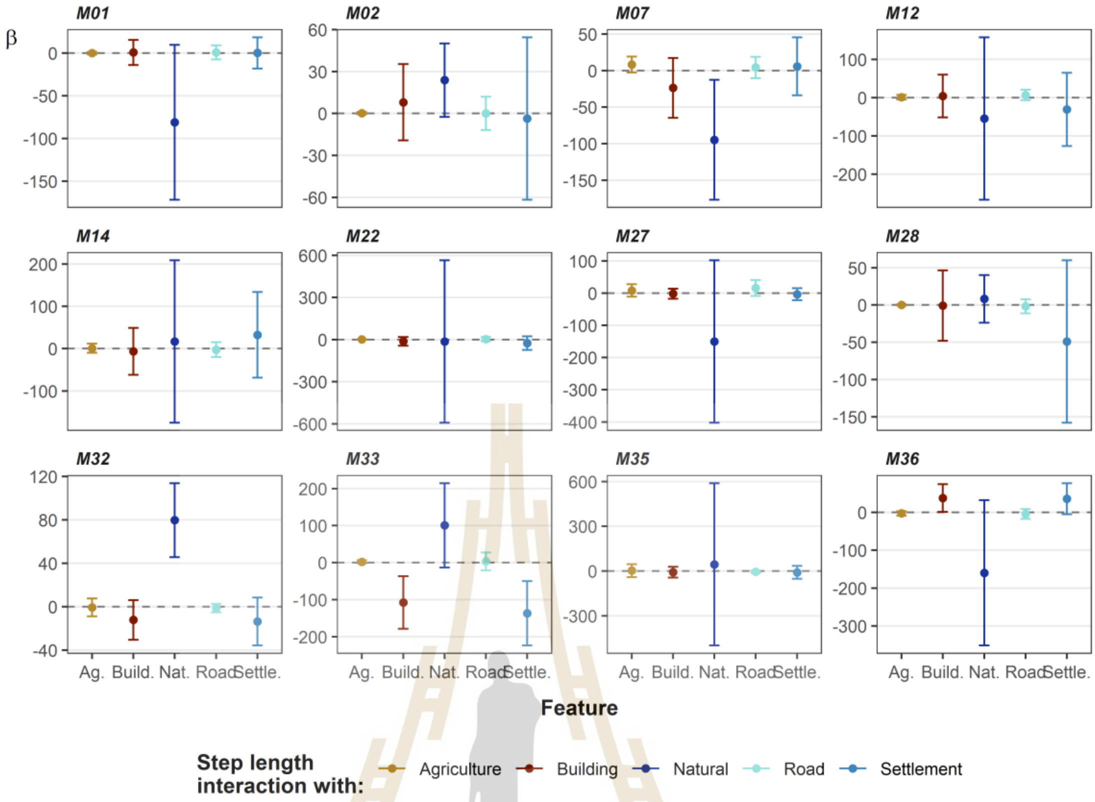

Figure 4.19 Individual ISSF model results based on the interaction between land-use features and step length. Error bars indicate 95% confidence intervals.

Out of the 9 models ran for each individual, there were 50 cases where distance to a land-use feature was found to be significant ($p \leq 0.05$) in a model (n = 7). These included model 2: Settlement (n = 1), model 4: Building (n = 1), model 5: Agriculture (n = 1), model 6: Natural (n = 3), model 7: Agriculture + Natural + Building (n = 16), model 8: Road + Building + Natural (n = 17), and model 9: Road + Agriculture + Natural (n = 11). These most notably included distance to buildings, with 16 models showing significant positive association to buildings for eight different telemetered individuals (M01, M02, M07, M12, M28, M32, M33, and M36), and distance to natural areas, with 24 models showing significant positive association from eight different individuals (M01, M02, M07, M12, M14, M22, M33, and M35), and one model for M32 showing negative association with distance to natural areas. Also among the distance to features found significant in models were distance to agriculture, with three models for M07 showing unambiguous avoidance, and one model for M33 showing attraction, distance to road, with two models for M02 showing clear negative association and two models for M33 showing positive association with roads. Lastly, distance to settlement was only found significant in one model for M33, showing an unambiguous positive association with settlements.

4.1.7 Mortality and Threats

4.1.7.1 Human Killings

I documented one unintentional killing of a juvenile *B. candidus*, which was hit by a lawnmower near SUT campus in 2019. While I did not document any intentional killings of *B. candidus* within the study site during the study period, I have documented an intentional killing that occurred in early (3 May 2019), Nakhon Ratchasima, by a local which was hunting frogs (though I was told the snake was killed out of fear rather than for food). I also documented an intentional killing that occurred within the study site, but before the study began, in 2012, as SUT Security staff killed an adult *B. candidus* which was encountered among a university building. In addition to these killings I recorded 12 intentional killings and 1 unintentional killing (agriculture machinery) out of the 19 supplemental *B. candidus* mortalities found through Facebook snake identification pages.

Table 4.11 Total numbers of *B. candidus* mortalities corresponding to the cause and dataset type; number of notifications or individuals encountered, number of telemetered individuals, and anecdotal (non-standardized sampling, gathered haphazardly) number of individuals posted on social media (Facebook groups, namely "Snakes of Isaan" and "Snakes of Laos").

Type	No. Individuals through Study	No. Telemetered Individuals	Social Media Supplemental
Road Mortality	16	1	2
Intentional Killing	2	0	12
Unintentional Killing	1	0	1
Killed by Dog	0	0	4
Wounded by Dog	4	1	0

4.1.7.2 Road Mortalities

I recorded a total of 16 road mortalities within my study site between May 2018 and January 2020. Twelve of the road mortalities were adults, of these only three were confirmed to be males and one was confirmed to be a female, however, the sex was unknown for the remaining eight adult *B. candidus*, though three of which were believed to be likely females. Four of the road mortality victims were juveniles. Five of the road killed *B. candidus* were killed on a paved roads on campus, one was killed on a paved walking path, while the remaining ten were found dead on roads surrounding the university campus. Most of the road mortalities both years occurred within the Cold season (n = 10), particularly between the first two months of the Cold season, October (n = 5) and November (n = 4). In contrast, five *B. candidus* were found dead on roads in the Hot season months, and only one road mortality was detected during the wet months. The majority of road mortalities were recorded during the first year of the study period (May 2018 – April 2019), and only two road mortalities have been observed since, both of which were found serendipitously in November of 2019.

4.1.7.3 Free-ranging Domestic Carnivores

In addition to *B. candidus* mortalities due to direct and indirect human killings, I also documented domestic carnivores (i.e. domestic dogs and cats) to be a potential threat to *B. candidus* living among a human dominated landscape. While none of my telemetered or captured individuals were killed due to dog attacks, I did confirm four of the rescued *B. candidus* to have been wounded by domestic dogs through notification by the resident/home owner. Additionally, I documented several other captured *B. candidus* which had healed wounds and scars which resembled the known dog bites, however, I am unsure as to the actual cause of the wound in these cases. Out of my 19 supplemental mortality data gained from social media, I also documented four *B. candidus* which were killed by dogs.

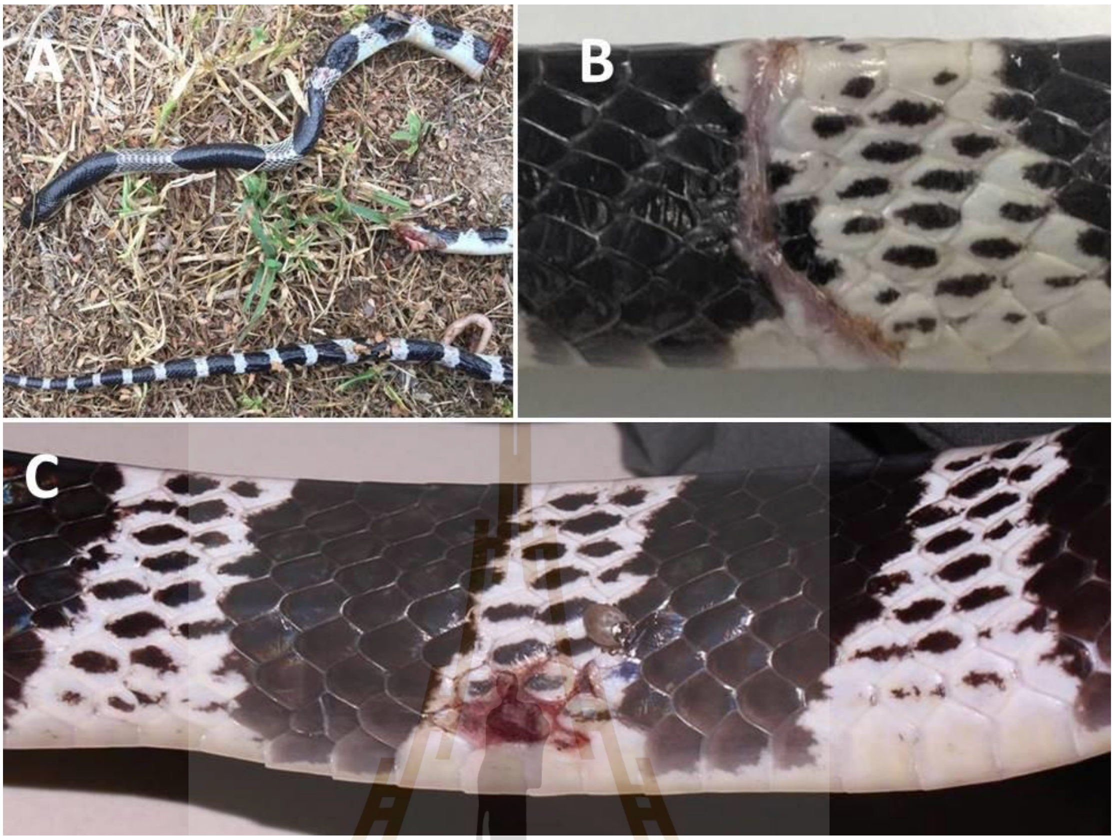

Figure 4.20 *B. candidus* wounded by domestic animals a) An individual which was killed by a dog and posted on social media b) M02 which had new healed wound a few weeks after the camera trap photos taken of the cat stalking it c) Dog bite wound to M12.

While I did not document any attacks on *B. candidus* by cats, I did gather photos of an interaction between one of my telemetered adult male *B. candidus*, M02, and a free-roaming cat though camera trapping at a shelter site (Figure 4.21). About one month after briefly recording this interaction, I recaptured M02 in order to replace his radio-transmitter, during which I found him to possess a new large scar, which seemingly resembles a long cut or scratch wound (Figure 4.20b).

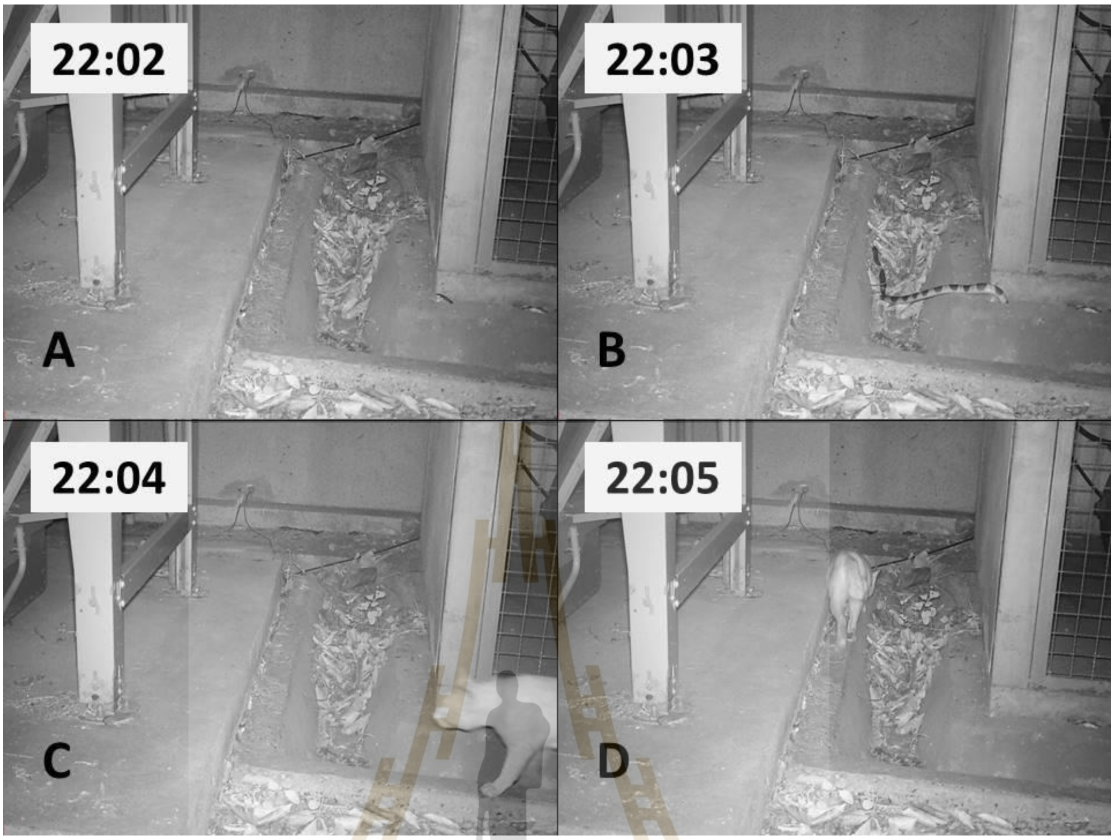

Figure 4.21 Camera trap photos of M02 as he exits his shelter site a) M02 peaks his head out from shelter entrance b) He exits his shelter at 22:03 h c) at 22:04 h a cat appears d) The cat is crouched down clearly staling the snake.

4.1.8 Natural History

4.1.8.1 Diet

I were able to gather information on the diet of *B. candidus* through both observations of predation events and identifying prey in fecal samples collected from captured *B. candidus* (Table 4.12). I documented four predation events by *B. candidus* through my study. Two occurred in concrete drainage gutters just a couple of meters from student dormitory rooms (S-15), one occurred inside a laboratory building (F2), and one occurred in a roadside ditch just 10 m away from a house where a late-night student party was happening. Three of the observations were of *B. candidus* individuals preying on colubrid snakes (2 *Oligodon fasciolatus*, 1 *Chrysopelea ornata*), while the other was a B. candidus preying on a large caecilian (*Ichthyophis sp.*). In addition to these predation events, I also observed *B. candidus* which was dead on a road just a few cm away from a roadkill *Hypsiscopus plumbea*.

Figure 4.22 *B. candidus* predation observations a) Predation on a caecilian b) Predation on a golden tree snake inside a university building c) Predation on a banded kukri snake in a drainage gutter at a dormitory d) A second predation on a kukri snake at a dormitory.

Table 4.12 Number of observations of prey taxa identified through predation observations and fecal samples.

Taxa	Prey	No. Individuals	Diet Composition (%)
Mammal	Small mammals	2	11.8
Amphibian	Caecilian	1	5.9
Reptile	Snakes	8	47.0
	Skink	1	5.9
	Squamate (unk)	2	11.8
Unidentified	Unknown	3	17.6

I also collected fecal samples from 12 of the captured *B. candidus*. Of these fecal samples I was able to visually identify prey to some level of taxa in nine of the samples. Of the identified prey, two samples contained fur from small mammals of some kind (likely order Rodentia), one contained scales from a large scincid lizard (*Eutropis multifasciata*), four contained scale remains from small snakes (suborder Serpentes), and two of the samples contained numerous small scales either from scincid lizards or snakes of the species *Cylindrophis jodiae* (order Squamata), as there were no elongated ventral scales present, as would be seen in any other native snake species.

4.1.8.2 Reproduction

Although I did not observe mating or other behaviors associated with mating in *B. candidus*, such as male combat, I did observe a pair of *B. candidus* which were both killed by vehicular collision right next to each other. This occurred in late October (24-10-2018). Additionally, the telemetered female, F16, became inactive and remained in the same general area under the northern entrance to the F1 building for essentially 95 consecutive days (25 January – April 30 2019).

4.2 Discussion

4.2.1 Space Use

4.2.1.1 Occurrence Distributions

My study provides the first in-depth investigation of the movements and ecology of *Bungarus candidus*, providing baseline data and important information on the ecology of a medically significant snake species living among a human-dominated landscape. I found *B. candidus* occurrence distributions (dBBMM 99% confidence area) to be highly variable among individuals, ranging from 3.21 to 119.55 ha, with the average being 22.85 ± 9.19 ha. Results from GLMs revealed some of the observed variation in space use can be explained by the snake's body size and the dominant landscape where the snake resides, as there appears to be a positive relationship between space use and mass, and a negative relationship between space use and the proportion of fixes within settlement habitat. However, caution should be taken, as the relationships were fairly weak, but also the presence of the outlier in occurrence distribution (M32) may be skewing the slope to be higher than the true change in area use due to body mass.

Previously, only two past studies have reported the movements of *B. candidus*, although both were based on a single telemetered individual each and did not utilize more current and accurate methods of analyses (Knierim et al., 2018; Mohammadi et al., 2014). The only other past study of the spatial ecology of kraits was the investigation of the spatial ecology of banded kraits (*Bungarus fasciatus*) by Knieirim et al. (2020). Each of these three krait studies were based at the Sakaerat Biosphere

Reserve (SBR), Thailand, approximately 84 km south of my more semi-urban-agriculture study site.

Drawing comparisons in the total space use observed in my telemetered *B. candidus* to findings from other studies is not easily done. As previously discussed in the literature review, the majority of studies on the spatial ecology of snakes have used older and more inaccurate methods of estimating space use, such as MCPs and KDEs, which are not comparable to dBBMM (Silva et al., 2020). Additionally, caution should be taken even when making comparisons between studies which both used dBBMM to estimate space use, as differences in sampling regimes and selected window and margin size will affect the occurrence distribution estimates.

Thus far, only two other studies have used dBBMMs to estimate space use of other elapid snakes. Both happen to be Southeast Asian active foraging elapids which were studied at the SBR. Knierim et al. (2019) found that telemetered banded kraits, *Bungarus fasciatus*, had an average dBBMM 99% confidence area estimate of 61.72 ± 51.88 ha (20.28-134.88; n = 3; ws = 15, mrg = 3; tracks every ~24 h), while Marshall et al. (2020) found that king cobras, *Ophiophagus hannah*, had an average dBBMM 99% confidence area estimate of 750.30 ± 139.52 ha (149.28-1081.54; n = 7; ws = 25, mrg = 5; tracks every 8.5 ± 0.1 h). While both studies used a different window size and margin size and had a different sampling regime from my study, it appears clear that these two larger active foraging elapid species used larger areas of space than my telemetered *B. candidus*, which had an estimated 99% dBBMM occurrence distribution of only 22.85 ± 9.19 ha (n = 12, 3.21-119.55).

The observed differences in overall space use is consistent with what may be expected based simply on the differences in body size of these species, with *B.*

candidus being the smallest, and *O. hannah* being the largest, as studies have shown there tends to be a positive relationship between overall area use and the animal's body size (Carfagno and Weatherhead, 2008; Mech and Zollner, 2002; Ofstad et al., 2016; Perry and Garland, 2002; Reiss, 1988). Thus, my findings showing a weak positive relationship between individual mass and occurrence distribution are also consistent with this idea. Previous studies have suggested that larger bodied animals have higher energy demands, thus resulting in overall larger home ranges or areas of general space use (McNab, 1963; Tufto et al., 1996). However, body size is only one of many variables which influence space use by animals, as even larger snakes from other taxa and which exhibit different foraging strategies and behaviors but that lived in similar habitats, such as *Python bivittatus*, actually occupied smaller areas of space (average dBBMM 99% estimate 98.97 ± 35.42 ha, n = 7) than the average *O. hannah* (Smith et al., 2020).

Though I was limited to estimating the space use of only a single adult female *B. candidus*, I found that the female had a much smaller occurrence distribution than all telemetered males (excluding inadequately tracked M29). As seen in my study, numerous other studies have observed male snakes to have larger occurrence distributions and home ranges than conspecific females (Bauder et al., 2016; Blouin-Demers and Weatherhead, 2001; Hyslop et al., 2013; Marshall et al., 2019; Whitaker and Shine, 2003). For example, the smallest occurrence distributions area estimations for both telemetered *O. hannah* and *B. fasciatus* were observed in among the telemetered females (Knierim et al., 2019; Marshall et al., 2018). This trend has also been documented in other herpetofauna, including tortoises (Lue and Chen, 1999; Ward et al., 2020) and lizards (Lewis and Saliva, 1987; Perry and Garland, 2002;

Schoener and Schoener, 1982), and is often attributed to differences in reproductive movements, such as increased male movement distances during mate searching in order to maximize access to females (Gregory et al., 1987), and reproductive condition and related thermoregulation needs for gravid females (Blouin-Demers and Weatherhead, 2001; Whitaker and Shine, 2003). However, this trend in snakes may be partly due to the male-biased sexual size dimorphism exhibited in some snake species, where males are larger than females, including *B. candidus* (Shine, 1978), and the increased energy consumption requirements associated with having a greater mass (McNab, 1963; Tufto et al., 1996). Although I was limited to comparisons between only a single female and a relatively small sample of males, my data appears to suggest that intersexual differences, rather than differences in resource needs for larger individuals, affected the overall space use by *B. candidus*, as the telemetered female *B. candidus* had a smaller occurrence distribution estimate than even smaller males which were tracked for shorter durations of time (such as M22 and M27), similar sized males tracked for less time (M14), and smaller males which were tracked for comparable amounts of time (M28). However, in order to know if female *B. candidus* actually do utilize smaller areas of space than males, and in order to better understand the drivers of movement distance and overall space use area, future studies with larger sample of both males and females are required.

In order to better compare the space use of *B. candidus* from other studies with my results I ran dBBMMs for the two previously published, and one unpublished dataset, movement data from *B. candidus* telemetered at the SBR, using the same window size and margin size as used in my study (ws = 19, mrg = 5). The adult male which spent its time in the protected dry Dipterocarp forest of the SBR and which had

20 locations, and was tracked every 38.63 ± 11.2 hours over a period of 30.58 days described in Mohammadi et al. (2014) had a dBBMM 99% confidence area estimate of 28.18 ha. The juvenile male which was tracked about every 50.19 ± hours for 66.91 days (33 fixes) among the settlement and agriculture habitats in the SBR transitional zone described in Knierim et al. (2018) had a dBBMM 99% confidence area estimate of 11.96 ha. Lastly, the unpublished male *B. candidus* which was tracked within the dry evergreen forest of the SBR roughly every 27.8 ± 0.99 hours over 103 days, with 90 datapoints, had a 99% dBBMM confidence area estimate of 11.98 ha. These findings are consistent with my space use estimates at the SUT study site (where the average occurrence distribution 99% confidence area estimate for males was 22.85 ± 9.19 ha), despite the differences in tracking regime and total number of fixes. This lends support to the resilience of this method, where dBBMM are able to handle tracking infrequencies and short tracking durations (Silva et al., 2020).

Though some studies have found that an animal's space use tends to increase when living among a heterogenous landscape with patchily distributed resources (Mueller and Fagan, 2008; Owen-Smith et al., 2010), I found a seemingly weak negative relationship between the amount of time spent in settlement habitat and the individual's overall space use. This may be due to the limited availability of suitable habitat for the snakes among the lands dominated by settlements, thus restricting their space use. O'Donnell and delBarco-Trillo (2020) and Tucker et al. (2018) show that home ranges of terrestrial vertebrates tend to be reduced when among increasing levels of urbanization. Additionally, there are generally more roads and more heavily trafficked roads bisecting land among settlements which may act as semi-barriers to the snakes (Shepard et al., 2008). Experiments by Andrews and Gibbons (2005) found that some snakes, particularly smaller species appeared to avoid crossing roads during staged encounters, while Shepard et al. (2008) found that radio-telemetered eastern massasauga rattlesnakes, *Sistrurus catenatus*, avoided crossing roads, crossing roads significantly less often than predicted. Marshall et al. (2020) found that *O. hannah* movements were reduced among more heavily modified areas, with movements being restricted to the limited less-disturbed areas and increased movement when within the protected forest of the SBR. The authors suggest this may be an attempt to avoid threats among more disturbed areas as well as due to foraging, as the limited semi-natural areas likely also serve as refuges for prey items living among the agriculture dominated landscape (Marshall et al., 2020). Additionally, snakes are ectothermic, and thus must also consider temperature suitability of areas, though the importance of this as a driver for snake space use is ambiguous in the tropics (Luiselli and Akani, 2002).

Though my comparisons are anecdotal, and extreme caution should be taken when making comparisons due to the extremely small sample size, estimated occurrence distributions for *B. candidus* living in the more continuous forests of the SBR appears to lend support to the idea that their space use area does not depend heavily on the availability of large continuous natural habitats, as the two males which lived entirely within the protected SBR forests did not appear to have a clear overall increased space use when compared to *B. candidus* at SUT. When comparing the space use of the three SBR *B. candidus*, it appears more likely that overall space use area was influenced by the individual’s size, as the individual tracked in the village had a nearly identical occurrence distribution estimate as the individual tracked for an even longer duration solely within the forest, with a similar body size, while the larger telemetered individual in the SBR forest utilized larger area. However, each of these three individuals were tracked during different seasons, thus they are not ideal for drawing comparisons.

Although the LM and GLM results show a positive relationship between space use and mass, caution should be taken, as the relationships were fairly weak, and also due to the presence of the outlier in occurrence distribution (M32), which may be skewing the slope to be higher than the true expected change in area use with an increase in body mass. Furthermore, results and extrapolations were greatly limited due to the small sample size. Lastly, while I did run dBBMM with the same window and margin size for snakes tracked within the SBR as I used in my study, the comparisons are less than ideal, as tracking regimes and consistency was not identical, as each individual was tracked in a different season, two of the three SBR *B. candidus* were tracked irregularly, with generally longer periods of time between location checks, and the low number of overall location fixes. Due to these issues, I decided not to include the space use estimates and movement summaries in comparative analyses. Thus, all comparisons and reasoning drawn from these comparisons between sites should be taken with extreme caution.

4.2.1.2 Site Fidelity

The telemetered *B. candidus* in my study exhibited relatively high site fidelity, revisiting sites approximately every 15.45 ± 3.87 days. Despite the relatively short tracking durations (106.46 ± 15.36 days) and infrequent tracking regime (once every ~24 hours) the mean number of site revisits for individuals was 18.67 (range = 2–46). My study found that *B. candidus* revisited sites more frequently than did telemetered

P. bivittatus where the same methods of assessing site revisits as in my study, as the *P. bivittatus* revisited sites on average every 43.47 ± 14.64 days (Smith et al., 2020). Despite Smith et al. (2020) having much longer tracking durations (mean = 327 days, range = 41-662) than the snakes in my study, the total number of *P. bivittatus* site revisits observed was seemingly fewer (range 4-35 revisits), with two of the seven *P. bivittatus* never returning to a single previously used site throughout their entire tracking durations. Thus, *B. candidus* exhibited higher site revisit frequency relative to *P. bivittatus*, suggesting that individual sites are highly important and carefully selected by *B. candidus*.

I had expected the telemetered *B. candidus* to revisit sites more frequently among settlement habitat than among less-disturbed areas, as there was likely a limited availability in suitable shelters among more heavily disturbed habitats, as well as an increased risk of conflict with humans arising, which may result in the snake limiting its movements to the few areas it had previously resided and deemed as safe. Limited movements and site fidelity exhibited by *P. bivittatus* among disturbed areas have been attributed to similar ideas and explanations (Smith et al., 2020). However, opposite to what I had expected, my findings reveal *B. candidus* revisit frequency was generally higher among less-disturbed habitats. Although this seems unlikely, as thermoregulation in the tropics is ambiguous (Luiselli and Akani, 2002), this could be due to a limited availability of thermally suitable shelter sites among natural habitats. The resulting trend could be due to spatial resource hotspots, such as sites near available water or higher prey densities, within the natural habitats. I observed some of the telemetered *B. candidus* to forage for prey near and even within shelter sites, sometimes returning to the same shelter after foraging among the nearby surrounding area (Hodges et al., in press.), *B. candidus* may be more likely to return to shelters near particularly favorable foraging sites. Whitaker and Shine (2003) found that telemetered *Pseudonaja textilis*, an Australian active foraging elapid, selected shelter sites where prey was more abundant, and also found that most individuals exhibited site fidelity to some degree, favoring areas with supposed greater prey availability.

While the aforementioned explanations may be part of the reason for the found results, I think it is far more likely to be due to one of two, or a combination of both, additional explanations. One alternative explanation for there being higher site revisit frequency in shelters among natural habitats could simply be due to there being limited natural areas among the landscape, which is dominated by more heavily disturbed lands such as agriculture and settlements, thus increasing the chances of overlap and site reuse among the available natural areas. The other likely potential reason for there not being higher site revisit frequencies among settlements may be due to the presence of large and cave-like shelter systems available underneath many of the university's large buildings, which were used frequently by the telemetered snakes. This means that snakes may move freely through these continuous cave-like tunnel systems which span far greater areas than typical shelters among natural habitats, such as termite mounds or rodent burrow systems, which easily fit into a given area with a 5 m radius (as I used to define sites in my study), thus allowing the snakes to move out of "sites" while still remaining within the same shelter or refuge system when among settlements.

I did not account for individuals in this analyses, thus individuals which had higher revisit frequencies but also spent more time in one particular habitat may skew the results of the test. Another potential limitation to my study's findings is that identifying site revisits is entirely based on GPS locations, as site revisits are defined as a return to or a pass through a given area with a radius of 5 meters. The accuracy of the GPS is often reduced when near large buildings, therefore, GPS accuracy tends to be worse for locations where snakes were underneath or adjacent to large anthropogenic structures among settlement habitat. Additionally, through camera trapping I was able to see that while the snakes generally move to a new shelter site after emerging after the sun has set, on some occasions I found the snakes exited and foraged among the shelter site before ultimately returning to the same shelter before sunrise. Thus, site revisit frequency would be higher if tracking resolution allowed for the detection of such movements during the night.

4.2.2 Temporal Activity Patterns

4.2.2.1 Seasonality

Comparing movement distances across different seasons using Bayesian credible intervals revealed with high levels of certainty that snakes were least active in the hot season, tended to move less often but covered greater distances when moving in the cold season, and tended to make more frequent but generally smaller moves in the wet season. Similarly, motion variance was lowest in the hot season, though BRMs revealed motion variance to not be significantly different between cold and wet seasons, despite there being distinct peaks in motion variance which occurred in the cold season.

The telemetered *B. candidus* exhibited an overall reduction in activity during the hot season, which is generally the driest period in my study site, receiving the smallest amount of rainfall particularly during the early months of the hot season.

This trend to have reduction in movements in the drier seasons has also been documented in other species of reptiles in this region of northeast Thailand, including the tortoise *Indotestudo elongata* (Ward et al., 2020), and snakes *Python bivittatus* (Smith et al., 2020) and *Ophiophagus hannah* (Marshall et al., 2020). This reduction in activity during particularly hot and dry periods is commonly attributed to the need to conserve water and energy, as resources, such as water and prey availability are likely limited during this period (Loehr, 2012; Peterson, 1996). Further accentuating this idea, this period also corresponded with the majority of the observed extraordinarily prolonged periods of inactivity in telemetered *B. candidus* of my study, which were likely a behavioral response to conserve water and energy, though it may have also been driven by reproductive behaviors, as this dry period also appears to correspond with when they have been reported to mate in Thailand by Chanhome et al. (2011). However, little is known about mating behavior of *Bungarus* species.

In contrast to the hot season, resource availability would likely be highest during the wet season due to the increase in and generally more regular rainfall (Collins et al., 2014). Many vertebrate species have been documented to become more active following rainfall (Hau, 2001; Loehr, 2012; Mazerolle, 2001; Palis, 1997; Todd and Winne, 2006; Vickery and Bider, 1981), including some snake species (McDonald, 2012; Spence-Bailey et al., 2010). According to optimal foraging theory, animals can theoretically reduce movement distances required to obtain resources during foraging when resources are abundant and readily available (Doherty and Driscoll, 2018; Wasko and Sasa, 2012). The telemetered *B. candidus* in my study may have increased movement frequency while reducing movement distances during the wet season in order to take advantage of the abundant resources without needing to move greater distances in order to locate food and water.

Interestingly, telemetered snakes tended to be most active during the wet season, which is when the majority of bites (ca. 49%) by *B. candidus* were found to have occurred in Thailand (followed by the cold season, which accounted for ca. 31% of bites; Tongpoo et al., 2018). While we notifications of B. candidus sightings from locals living in the study site appeared to occur fairly evenly across the months and seasons, I found that most of the conflicts between *B. candidus* and humans within my study site tended to occur within the wet season, as this season had the highest average number of notifications per month during the two year study (hot = 0.75, wet = 1.25, cold = 1.0), with the highest number of rescues per season in 2019 (n = 9). Interestingly, this did not coincide with when I found *B. candidus* dead on the roads among the study site. Rather, *B. candidus* road mortalities were more commonly encountered during the cold season, and seemingly correspond to the spikes in motion variance of telemetered male *B. candidus* (Figure 4.23), which resulted from unusually large movements which may be related to mate searching in males. It makes sense that an animal would be more at risk of coming into conflict with humans or road mortality when moving greater straight-line distances, as in theory the animal would be required to cross more roads. In fact, the sole mortality among telemetered *B. candidus* was a male (M01) which fell victim to vehicle induced mortality while crossing a road during the individual’s largest straight-line move to date in the last fifteen days of the wet season in September.

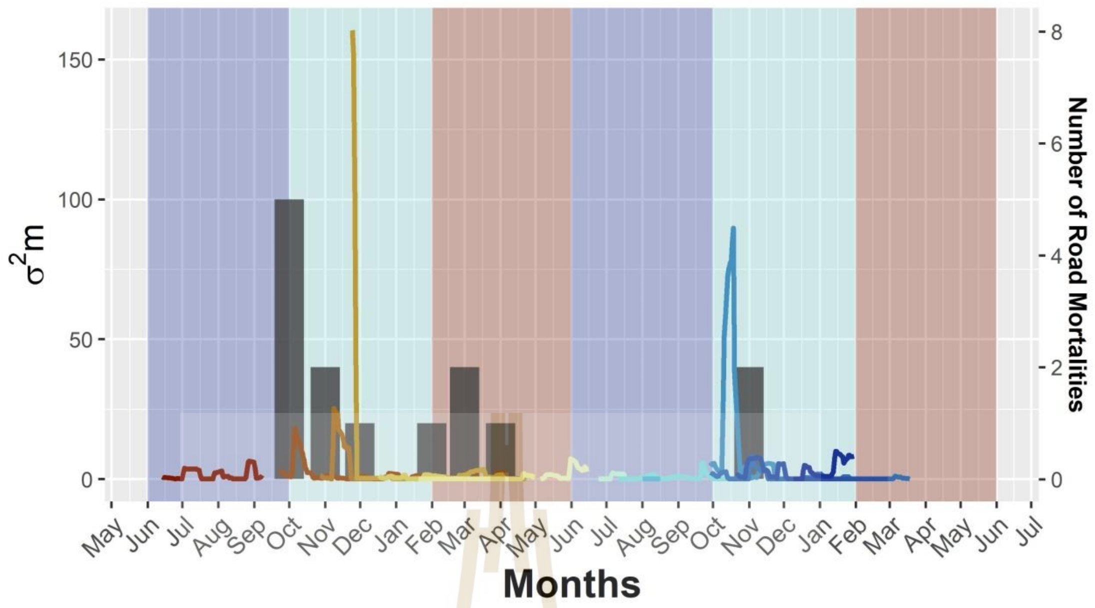

Figure 4.23 Number of monthly road-induced mortalities plotted with motion variance of individual's throughout the study period.

Surprisingly, even though the snakes appeared to be most active during the wet season, and most sighting notifications occurred in the wet season (especially in September), no road mortalities (aside from the telemetered M01) were detected within the wet season during the two year study. This may further support the idea that increased movement distances result in higher risk of road mortality. Perhaps the snakes are able to forage more easily in a given area without the need to cross roads during the wet season. However, one inconsistency with this idea was that there were surprisingly more road mortalities detected in the hot season, when snakes were moved less frequently and didn't tend to move particularly large distance, than in the wet season.

The findings from this should be taken lightly, as all road mortalities were detected serendipitously during daily location checks of telemetered individuals and non-standardized active surveys. Potential alternative explanations for the variation in road mortality detections could be changes in detection rates, as road-kill may deteriorate more rapidly or be more likely to be washed away or carried away by scavengers during the wet season than in other seasons. Additionally, differences in vehicular traffic on roads among the study site may have also influenced the number of mortalities.

4.2.2.2 Reproduction Patterns

Males had highest peaks in motion variance in the cold season. These peaks were more than five times larger than the individual’s other independent peaks in motion variance. As seen in males of other snake species, these exceptionally high peaks in motion variance associated with large movements are likely related to reproductive movements, namely mate searching (Marshall et al., 2020). If these movements do indicate male mate searching, then mating likely occurs soon thereafter. The eight recorded exceptionally large movements (> 400 m) occurred between late September and early January, thus breeding may occur over earlier and over a broader period of time in my study site than previously has been reported by Chanhome et al. (2011), which stated that mating occurs in December and January, and nesting between February and March.

Assuming that breeding does occur within the hypothesized range for *B. candidus* living within my study site during my study period, I can assume that females would nest between December and early March, which largely overlaps with when the telemetered female was suspected of nesting underneath a building due to her prolonged inactivity (late January to late April) and strong fidelity to this particular site, which may indicate nest attendance, as has been observed in several other snake species (Hill et al., 2006; Whitaker et al., 2013), including the sympatric krait species *B. fasciatus* (Knierim et al., 2019).

Despite my efforts through camera trapping, we did not obtain visual evidence of mating or other conspecific interactions associated with mating, such as male combat (Shine, 1978), from my study individuals. My only evidences of potential reproduction activities, aside from the already discussed movement patterns exhibited by adult male *B. candidus*, were a few anecdotal observations. These observations included the observed pair of *B. candidus* in late October which were found dead on a road next to each other, which does fit within the hypothesized mating period. Additionally, while the telemetered female which was suspected of nesting was not noticeably gravid during processing on 14 January 2019, she appeared to be in exceptional health, and later when I gained a visual observation of her during tracking on 1 May 2019 she appeared rather emaciated, having more prominent vertebral ridge and skin folding, which could indicate recent oviposition.

While multiple aspects of my findings appear to suggest mating occurring within the cold season, the limitations in my findings cannot be ignored. My interpretation of these large movements as indicating the onset of mating is largely speculation based on movement data from a small sample of male *B. candidus*, where individuals were not telemetered across all seasons. Thus I am unsure whether individuals not included in my study or even telemetered individuals would make similar large movements during other seasons. Furthermore, I did not obtain actual evidence of the female nesting, nor do I know the true reason for why two adult *B. candidus* were found dead on the road next to each other.

4.2.2.3 Movement Variance and Human Activity

Anthropogenic activities have been shown to influence wildlife activity and behavior (Boydston et al., 2003; Ordiz et al., 2017). Results from my BRM appear to suggest that the telemetered *B. candidus* activity was influenced by human activity levels among the study site, indicating that *B. candidus* are adapting to life among human-dominated landscapes, seemingly exhibiting caution by reducing movements during periods when more humans are present and exhibit higher activity levels. Some studies have found a negative relationship between human activity levels and some wildlife species activity among (Manenti et al., 2020; Ordiz et al., 2017). For example, Ordiz et al. (2017) found that bears appear to shift diel activity and foraging behaviors in response to increased human activity, appearing to avoid coming into conflict with humans by hunting predominately nocturnally in areas with larger human populations, while being more diurnal in areas with fewer humans. Additionally, Manenti et al. (2020) found that numerous animal species appear to have become more active and are using habitats differently following a rapid and dramatic decrease in human activity due to COVID-19 lockdowns in Italy. Similarly, my findings also appear to demonstrate a rapid behavioral response to human activity levels in *B. candidus* at SUT. The observed difference in *B. candidus* motion variance during and between SUT terms may be a behavioral response to human activity, attempting to reduce their chances of coming into conflict with humans, which do pose a clear threat to the snakes.

However, the BRM results are somewhat ambiguous due to the small “SUT out of session” sample, the presence of some outliers of high motion variance within out of session sample period, the overall weak relationship, as well as the model fit not being ideal. Thus these results should be taken lightly. Additionally, this model depends on the use of a proxy for human activity, in or during session representing periods when the university is more heavily used and lived in by a large number of people. This also lends to a much higher increase in the amount of traffic on roads. In contrast, when the university is out of session or between terms, this should demonstrate a significant drop in human activity on the campus, as most students return home to be with their families and many of the university buildings and facilities close during this period. When the university is between terms I have noticed that it even impacts the local businesses which often temporarily close until the next term begins and students and staff return to the university. However, this trend in activity levels would be less significant further from the university campus, among some of the other nearby villages, where some of the telemetered snakes lived.

4.2.2.4 Diel Activity Patterns

My study found *B. candidus* to be highly nocturnal through the use of radio-telemetry, camera trapping, active survey effort, and sighting notifications. During location checks of telemetered *B. candidus*, none were found to be active during daylight, while despite the much smaller sample of nocturnal tracks, individuals were found active during nighttime on 28 occasions. Camera trapping revealed that *B. candidus* tend to exit their shelters to begin moving shortly after sundown, with most individuals leaving shelter sites around 19:30 h (ca. 2.2 hours after sunset). In contrast, I found that most opportunistic sightings of *B. candidus* by residents occur around 23:30 h, and then after midnight the number of these observations begins to decline. However, this likely doesn’t indicate that the *B. candidus* stop moving after midnight, but rather is a result of a detection bias, as most people in the area go to sleep during the night, thus resulting in a steady decline in human activity as the night gets later. Despite this obviously lower detection probability in the late night and early morning, I still received notifications throughout the night and into the early morning, therefore, I feel confident to that *B. candidus* within this study site likely remain active throughout the entire night.

Despite being active at night when it is dark, the telemetered B. candidus exhibited caution when exiting shelters, generally peering out from the burrow opening for several minutes before beginning to move out slowly. This appears to be a predator avoidance behavior, and could be a response to the presence of humans as well as nocturnal predators such as owls and cats, which are present within the study site. Due to the small sample I was unable to examine if differences in exhibited caution levels are related to the time of night the snake is exiting, habitat type or other general environmental conditions, or even the individual's body size, but these could be interesting questions which could be examined by future studies.

While none of the telemetered snakes were found to be active during diurnal location checks, I did receive a few sighting notifications during the daylight hours. The early morning predation observation likely resulted due to the fact that it often requires long periods of time for snakes to subdue and ingest prey, even up to several hours as seen by the *B. candidus* depredation on the caecilian, and the *B. candidus* likely had begun the depredation on the *C. ornata* at some time before sunrise. The other three diurnal observations however each appear to have clearly resulted from the snake being disturbed from a refuge by anthropogenic activities, as one was hit by a lawn mower while sheltering under leaves, one was seen moving adjacent to a field which was presently being harvested, and one was found by students as they were collecting leaves and other natural items from a semi-natural area. There was only one occasion where it was unclear as to whether a *B. candidus* I was notified of had been active during the midday or if it had been disturbed from a shelter, as it was found under bleacher styled seating of an outdoor covered boxing training gym. These occasional diurnal sightings reflect the findings of Tongpoo et al. (2018), which found that nearly 27% of bites by kraits in Thailand occurred during the daylight, with the vast majority of the bites in the dataset resulting from *B. candidus*.

My diel activity study was not standardized, and I did not account for human activity levels throughout the day and night and the resulting probabilities of sightings occurring by people. Most notifications of observations that occurred later than midnight coincided with weekend nights, or midterm or final exam weeks, when people, namely students, tended to remain active much later into the night, therefore seemingly demonstrating the impact the number of people active during the night has on the detection of snakes. Therefore, my results from notifications are largely anecdotal. Camera trapping was effective in identifying the times that the snakes first exited shelter sites and became active, but they were not able to reveal much beyond that. Furthermore, my sample resulting from nocturnal location checks of telemetered snakes is limited to a small and biased sample, as rarely located snakes during the night, and nearly all took place before midnight. I recommend future studies implement a standardized nocturnal tracking regime with a finer temporal resolution for radio-telemetered *B. candidus* in order to better determine their nocturnal activity patterns and identify if there is a peak in diel activity throughout the night.

4.2.3 Habitat

My study reveals that *B. candidus* are habitat generalists, able to use a variety of habitats, including semi-urban and highly disturbed areas with large population of humans. While there was variation among individuals in how they reacted to different land-use types, there were some pretty clear trends among some individual. Telemetered *B. candidus* tended to exhibit some level of association with both buildings and natural areas.

Attraction to buildings may be due to environmental conditions they provide. It appears that the snakes were able to move freely underneath the concrete foundation of the old large university buildings (likely through empty cavities, areas eroded away, and animal burrows), and may resemble the conditions provided by subterranean cave systems, with more stable temperatures and moisture even during periods of weather extremes (i.e. dry, wet, cold, or hot). Reptiles generally select shelters which will keep them safe while also providing suitable temperatures, selecting shelters that provide protection from the high temperatures and evaporative water loss in hot and dry climates (Davis et al., 2008; DeNardo et al., 2004; Kerr and Deguise, 2004; Melville and Ii, 2001). Other studies have also shown that during colder periods reptiles may rely on artificial refuges, as the natural shelters have less than optimal thermal conditions (Martín, 2001). Additionally, these shelter types may potentially offer safe places where the snakes are at less risk of predation and less likely to be disturbed by human activities when among settlement habitat. Lastly, these artificial cave systems under the buildings may provide suitable habitat and refuge for a variety of other animal species which are commonly seen on the university campus (such as rodents, other snakes, lizards, and sub-fossorial and terrestrial amphibians), and may in effect, harbor their own ecosystem. Though the data is lacking, it could be that prey abundance is higher among large and old buildings than elsewhere among the highly disturbed habitats. Thus, large and older buildings appear to act as large artificial refuges, with extensive burrow systems and crevices throughout, which may provide both important shelter sites, which maximize thermal and predator-avoidance benefits, and act as foraging sites for *B. candidus* on the university campus.

Association of *B. candidus* with natural areas was expected, as this most closely represents their unaltered natural habitat. These patches of natural areas among urban and degraded landscapes often act as refuge for wildlife species (Choosai et al., 2009; Hughes, 2017a), including snakes, such as *Ophiophagus hannah*, which predominately used natural areas among the landscape dominated by agriculture and settlements (Marshall et al., 2018a, Marshall et al., 2020). These less-disturbed patches of natural areas contain dense vegetation and likely harbor more potential prey (Marshall et al., 2020). As a predator avoidance strategy, snakes generally prefer to move through areas with cover and avoid wide-open areas (Andrews and Gibbons, 2005; Marshall et al., 2020; Shepard et al., 2008). My findings suggest that natural areas are important to habitat for *B. candidus* and must be maintained in order to allow these snakes, as well as numerous other species, to persist among human-dominated landscapes.

When snakes were among areas dominated by agriculture they were limited to using less-disturbed areas for shelter sites. This may be largely due to the lack of burrows within the actual fields which experience higher levels of disturbance and frequent crop rotations. Knierim et al. (2018) similarly reported that the *B. candidus* tracked in an agrarian landscape relied heavily on less disturbed areas, including field margins, attributing this largely to the presence of available shelters. However, telemetered *B. candidus* did not avoid agriculture land, and were occasionally found moving through and potentially foraging within monoculture fields of cassava and fallow fields during the night.

My results suggest that telemetered *B. candidus* tended to show indifference to (not avoiding nor associating with) roads. Snakes did cross roads, however, some of these crossings had culverts present nearby which the snakes may have used. On two occasions I observed a telemetered snake moving cautiously towards a roadside, but when cars passed as they drew nearer to the road edge they both turned around and went back the direction they had come from. Though the snakes exhibited caution in crossing roads, and may have occasionally used culverts, I know that the tracked snakes did cross over roads and sometimes even sheltered within a few meters of a roadside. This apparent indifference to roads may help explain the relatively high number of vehicle induced mortalities I documented on roads throughout the study site.

Telemetered *B. candidus* used a variety of shelter types, though artificial anthropogenic refuges, rodent burrows, and termite mounds appear to be the most important. Previous studies had found that both termite mounds and burrows appear to be frequently used as shelters by wild *B. candidus* in both natural and agricultural land-use types (Mohammadi et al., 2014; Knierim et al., 2018). Both provide networks of tunnels underground which not only provide protection from many potential threats and provide refuge from less-suitable environmental conditions, they also may harbor potential prey which the snakes could hunt or opportunistically feed on while sheltering (Mohammadi et al., 2014). My study provides the first evidence of concrete anthropogenic structures, such as concrete drainage ditches, sidewalks, and buildings as being used by *B. candidus* as shelter sites.

While several other studies have examined the movements and habitat use by snakes in human-dominated landscapes (Anguiano and Diffendorfer, 2015; Butler et al., 2005), few have mentioned the use of concrete anthropogenic structures as refuges. However, Wolfe et al. (2018) reported that telemetered *Pseudonaja affinis*, a large elapid species from Australia, was quite adapted to life in urbanized settings, with some individuals occasionally sheltering underneath housing and paving stones. In contrast, Lelièvre et al. (2010) found that telemetered snakes living in colder temperate areas frequently used anthropogenic structures as refuge sites, as they provided thermal qualities which were more suitable for the snakes than the available cooler natural shelters; even utilizing anthropogenic refuges regularly inside protected natural areas (Lelièvre et al., 2010). However, my study is on the first to demonstrate that some snake species use large concrete structures as shelters, even more frequently than available natural shelters, in a warm tropical climate.

While snakes must invest a relatively large amount of effort into thermoregulatory behaviors in temperate regions (Peterson et al., 1993), where the temperatures tend to fluctuate greatly, thermoregulation often requires little to no effort by snakes living in tropical areas, where temperatures are generally more stable and warm (Luiselli and Akani, 2002; Shine and Madsen, 1996; Slip and Shine, 1988). However, some studies have shown that thermoregulation is still important to snakes living in the tropics, though it is more subtle and often only utilized during certain circumstances (Anderson et al., 2005; Luiselli and Akani, 2002). Studies on the nocturnal elapid snake, *Hoplocephalus bungaroides*, from sub-tropical Southeastern Australia -where temperatures vary more drastically than in my study site- selected for microhabitats based on their thermal suitability, selecting for rock shelters with less canopy cover overhead during the cooler months, while tree shelters were used more frequently during the hot summer months (Webb and Shine, 1997; Pringle et al., 2003). Research by Anderson et al. (2005) suggests that there are likely few thermal constraints on the behavior of active foraging nocturnal snakes living in the tropics, such as *B. candidus*, thus there are likely other variables driving *B. candidus* to shelter under large artificial refuges than simply the thermal and water retention benefits provided alone.

Pandey et al. (2020) suggested that perhaps kraits use household structures as shelters more frequently in the rainy season (when the majority of bites occur) due to the heavy rainfall during the monsoon which may displace snakes from shelters and drive them to dry refuges, such as households. In contrast, Marshall et al. (2018a) hypothesized that king cobras use anthropogenic structures more frequently in the hot season due to thermal benefits, which lead to an increase in contact with humans (Shine and Madsen, 1996).

Kraits may also be drawn to anthropogenic structures –even sometimes entering them- in search of prey (Hodges et al., 2020; Pandey et al., 2020), as prey abundance is known to influence snake movements and habitat use (Shine and Madsen, 1996; Wasko and Sasa, 2012; Whitaker and Shine, 2003), and it appears that my telemetered *B. candidus* did tend to forage near and sometimes even within utilized shelter sites. Pandey et al. (2020) noted that most of the *Bungarus caeruleus* individuals encountered among households had empty stomachs, potentially indicating they entered in homes in search of prey. Some rodent species are considered synanthropic, and commonly occur among households and old buildings, which may then attract snake predators (Fearn et al., 2001; Shankar et al., 2013; Pandey, 2015). Pandey et al. (2020) also discovered that *Bungarus caeruleus* occurring among settlements commonly fed on rodent prey, though they were previously found to feed predominately on snake prey (Slowinski, 1994b). Roadside drainage ditches can provide local conditions which are suitable for a wide variety of herpetofauna (Homyack et al., 2016; Mazerolle, 2001). Despite being dry much of the year, the drainage ditches at SUT do retain water temporarily. I have observed a variety of fauna living in these drainage ditches, including freshwater crabs, freshwater eels, numerous frog species, caecilians, skinks, and other snake species (such as *Fowlea flavipunctatus, Xenopeltis unicolor, Cylindrophis jodiae, Hypsiscopus plumbea*, *Oligodon fasciolatus*, and *Ptyas mucosa*), many of which are known prey of *B. candidus* or other *Bungarus* species (Van Hoesel, 1959; Kuch and Schneyer, 1991; Grossmann and Schafer, 2000; Mao et al., 2010; Siow and Figueroa, 2016; Knierim et al., 2017, Hodges et al., 2020). Concrete drainage ditches and old concrete buildings may be important foraging sites for *B. candidus*, as we observed individuals foraging and feeding among these anthropogenic structures.

While it appears that the use of these structures as shelters and foraging sites is largely driven by prey availability and potential thermoregulatory benefits, it could also be due to predator avoidance. Although it appears that the *B. candidus* followed along the edges or move within drainage ditches in search of prey, it may be that the ditches simply facilitate movement through otherwise open and manicured areas, offering protection from potential predators. For example, Mazerolle (2001) found that drainage ditches provided frogs with continuous linear habitats which facilitated their movements through an otherwise hostile landscape, and Marshall et al. (2020) found similar results regarding *O. hannah* using vegetated irrigation canals to move through an agrarian landscape.

While thermal and water retention benefits available from artificial shelters are likely partly responsible for the resulting association, it may be more that the snakes prefer to shelter near optimal foraging sites, and often forage along and among anthropogenic structures. Lastly, it should be considered that snakes are known to follow along barriers, such as fence-lines or sides of buildings, thus the telemetered *B. candidus* may have similarly been moving along the edges or within the concrete drainage ditches. My results are not conclusive in determining the primary force driving *B. candidus* towards anthropogenic structures. It may be a combination of all of these variables; sheltering and foraging among and underneath anthropogenic structures may maximize predator-avoidance and thermal benefits while simultaneously having needed resources, such as food and water, available. Further research is needed to better understand the importance of both roadside ditches and large anthropogenic structures to *B. candidus* and other herpetofauna at SUT.

4.2.4 Mortality and Threats

My study revealed a variety of potential threats to *B. candidus* living among human-dominated landscapes. Road induced mortality appears to be the largest threat *to B. candidus* living among areas heavily modified by humans, as this was the only known source of mortality for my radio-telemetered *B. candidus*, and I documented an additional 15 *B. candidus* dead on the roads within my study site during the two year period. Though there were only a few occasions each, unintentional killings from land management and agricultural activities, and attacks from domestic animals were also identified as potential threats to *B. candidus* through my study. While intentional direct killings of snakes is known to be a common threat to snakes living among humans (Dodd, 1987; Meek, 2012; Pandey et al., 2016; Miranda et al., 2016; Marshall et al., 2018b), I was unable to document any direct killings of kraits within my study site during my two year study period (though I know of some that occurred at neighboring locations or at out study site before the study began). The resulting lack of direct killings of *B. candidus* in my study may partially be due to the decresed detection and encounter rates due to kraits being active during the night when people are generally sleeping (Viravan et al., 1992). I did document a few (n = 6, 4 species) direct killings of other snake species which were found and killed by people during daylight. While it is possible that fewer *B. candidus* were killed within my study site as a result of my ongoing snake education and conflict mitigation efforts (Balakrishnan, 2010), the effectiveness of my efforts have not been quantified. It seems more likely that persecutory killings of the snakes were likely just underreported in my study site, as not everyone knew about my research on *B. candidus*, and many people would presumably not want to implicate themselves for killing of snakes which I was actively working to study and conserve.

Kraits exhibit several defensive behaviors which may make them more susceptible to certain threats. For example, when first approached with a flashlight at night *B. candidus* tended to become motionless, seemingly in attempt at crypsis so that the potential predator would not detect their presence. This defensive strategy could become particularly lethal for kraits crossing the roads at night, which would presumably stop moving as a motor-vehicle with headlights approaches. Similarly, the typical head-hiding defensive strategy exhibited by krait species (Tan and Ponnudurai, 1990) could make them more susceptible to attacks by dogs and cats.

Road-induced mortality was found to be the most common source of mortalities among *B. candidus* living among a human-dominated landscape, and it appears that there may be a seasonal trend in when *B. candidus* are killed on roads which coincides with when the telemetered male *B. candidus* of my study exhibited highest motion variance due to exceptionally large movements, with the majority of *B. candidus* found dead on the roads being males. Additionally, the only road induced mortality of the tracked individuals occurred during the individual's largest straight-line distance movement. Thus, it appears that male *B. candidus* are most susceptible to road-induced mortality during larger movements, which tend to occur in the early cold season and are likely attributed to mate searching behaviors.

4.2.5 Diet and Role in Ecosystem

My findings suggest that *B. candidus* are opportunistic active foragers and generalist predators, taking a variety of prey even among a small sample size. However, based on my limited observations, it appears that squamates, namely snakes, may make up the largest dietary component, as has been reported in other *Bungarus spp*. (Slowinski, 1994b). I only witnessed one *B. candidus* preying on an amphibian, a caecilian, but no fecal samples were found to have remains of amphibian prey. This may be due to my study's limitations, as I relied on visual identification of prey among the digested remains in feces and detections of predation events in the field. While scales from squamate prey and fur from mammalian prey tend to be difficult to digest completely, and thus are often visually identifiable from the snakes' feces, small anuran prey items would more likely have little or no surviving diagnostic features due to digestion of the soft tissues and small bones (Egeter, 2014). Also, most anuran prey, would likely be devoured rapidly in comparison to the prey handling time necessary to ingest large and elongated prey, such as snakes. I therefore believe my study is biased towards finding *B. candidus* feeding on snakes and other larger bodied prey which would require longer periods of time to ingest and potentially more of a physical struggle to subdue. Due to these clear limitations in study design, I am unsure of the actual prey composition of wild *B. candidus* within my study site, though I know they feed on a variety of prey.

Polyphagous and generalist predators can often adjust to conditions within a given environment, as they can take advantage of a variety of prey resources, thus feeding on whatever may be available. Studies have shown that generalist predators often play an important role in controlling populations of prey, including pest populations in agricultural ecosystems (Symondson et al., 2002). Results of a study using a single marine model ecosystem which examined the influence of changes in abundance of an apex generalist predator (cod fish) suggest that increasing numbers of a given generalist predator reduces spatial beta diversity in the ecosystem (Ellingsen et al., 2020), however, this is likely not the case for all generalist predators, and may only pertain to voracious apex predators, such as the cod. Predators, which are an integral part of an ecosystem, are predominately polyphagous, as truly specialized monophagous predators are rather uncommon (Welch et al., 2012). Generalist predators tend to have less dramatic and direct influence on prey populations since they utilize a broad array of prey, and as populations of a given prey species decline and thus become less abundant, generalist predators then tend to shift their diet composition and resort to feeding on more easily available prey (Symondson et al., 2002; Welch et al., 2012).

4.2.6 Krait Bite and Conflict Prevention

While no bites by *B. candidus* occurred within the study site throughout the duration of the study, despite the frequent space use overlap, this is not unusual, as bites by *B. candidus* appear to be quite uncommon. In Thailand, *B. candidus* are responsible for relatively few bites, especially when compared to the number of bites by other similarly widespread and common venomous snake species, such as *Naja kaouthia*, *Trimeresurus macrops*, *Trimeresurus albolabris*, and *Calloselasma rhodostoma* (Viravan et al., 1992; Buranasin, 1993). However, *B. candidus* appears to have the highest mortality rate among bite victims, even rivaling the total number of mortalities by other highly venomous species which contribute to far more envenomations (Looareesuwan et al., 1988). Thus, there is a great need to better prevent these bites from occurring in order to save lives. Understanding the habits and ecology of venomous snakes can be useful in helping develop conflict prevention management strategies in attempt to reduce snakebites.

Results from this study revealed that telemetered *B. candidus* were associated with anthropogenic structures, highlighting potential for conflicts with humans to arise, and thus the need for preventative measures and education programs to build awareness among the community in attempt to reduce the chances for snakebites to occur. Due to the association with anthropogenic structures, it would be difficult to deter the snakes completely from residential and university buildings within the study site. Since the majority of bites by *B. candidus* tend to occur to victims inside their homes, special effort should be made to limit their ability to enter buildings. Telemetered *B. candidus* were found to enter buildings through PVC drains which emptied outside, and both floor drains and gaps under doors or walls seem to be common points of entry for snakes to enter households and dormitories within the study site. Thus, pipelines and floor drains should be covered and gaps under doors and building walls should be eliminated and maintained. As an additional precaution, I suggest the use of bed-nets, which appear to be an effective method for preventing bites by kraits, even when sleeping on the ground, as most bites by *Bungarus* species tend to happen to people while sleeping (Chappuis et al., 2007).

My results also demonstrated potential for bites to occur to people outdoors, particularly when walking among dark sidewalks near old buildings and vegetated areas. Educational programs are likely among the most effective methods of preventing snakebites by building general awareness to the potential risks and the need to exhibit caution when walking or working outdoors (i.e. use a flashlight at night, wear footwear and clothing that covers feet and ankles, and watch where putting hands and feet when outdoors). However, educational programs often require high levels of effort and resources, especially if held on a remotely large scale, thus posting of signage among areas where both the snakes and people frequently occur may be a more feasible alternative method to help build awareness. Additional measures which may reduce chances of snakebites among residential areas include installation of snake-proof fencing around housing and keeping areas around homes clean and clutter free (i.e. moving wood piles, building materials, trash, grain stores, and other clutter away from the house, keeping food properly contained, and removing understory vegetation) in order to not attract snakes or their prey (Parkhurst, 2009; WHO, 2016).

For locations similar to my study site, I suggest examining the costs and effectiveness of adding sections of fencing to help discourage snakes from actually crossing onto sidewalks among the university campus (Laidig and Golden, 2004). This method could be particularly beneficial if placed among the student dormitory walkways, where students live in high densities and are also more likely to be active after nightfall, though if not done correctly could lead to snakes entering and becoming stuck within the fenced areas (Baxter-Gilbert et al., 2015). Additionally, I documented several *B. candidus* individuals to cross and forage among sidewalks at these dormitories on multiple occasions. Furthermore, I documented four snakebites by other snake species which all occurred to students which were walking among the on campus student dormitories in the dark without a flashlight or closed-toe footwear.

Since the telemetered *B. candidus* in my study tended to shelter under or near older structures which had more crevices, cavities, or burrows which perforated underneath the structure's foundation and individuals exhibited site fidelity, it may also be worth investigating the effectiveness and feasibility of sealing and maintaining such openings along the edges of buildings if attempting to discourage the snakes from utilizing this area. In theory, this process would limit the availability of shelters among buildings, thus hopefully negating the association with buildings observed in my dataset. However, this would need to be studied extensively in order to better understand the effect it would have on resident *B. candidus*, and other fauna, and to evaluate the potential costs and benefits of this method, as this may be detrimental to species persistence among heavily modified habitats.

Lastly, while m study solely focused on the movements and ecology of *B. candidus*, it is likely that other active foraging elapids which live among similar human-modified matrix landscapes behave similarly, thus recommendations and extrapolations from my study may also be applicable to other species. For example, based on my observations, it seems likely that the sympatric *N. siamensis* may use habitats similarly to *B. candidus*. Additionally, findings from my research on *B. candidus* could be useful in understanding the ecology of other krait species, such as the closely related *B. caeruleus*, which is responsible for thousands of deaths in the Indian subcontinent (Kularatne, 2002; Suraweera et al., 2020), and appears to share some similarities with *B. candidus*. Both *B. candidus* and *B. caeruleus* commonly occur among settlements, where they feed on similar prey (Kuch and Schneyer, 1991; Slowinski, 1994b; Grossmann and Schafer, 2000; Kuch, 2001; Hodges et al., 2020; Pandey et al., 2020) and are known to bite people within homes, often while the person is sleeping (Kularatne, 2002; Warrell, 2010; Tongpoo et al., 2018; Pandey et al., 2020). Furthermore, bites by both species tend to occur predominately in the wet season (Tongpoo et al., 2018; Pandey et al., 2020). However, I am not claiming that *B. caeruleus*, or even all *B. candidus*, behave like the individuals in my study. Movements, behaviors, and habitat use may vary greatly in other areas with different weather conditions or different land-use types and anthropogenic structures available. While the suggestions presented here are derived from observations and findings from my study, none of these suggestions have been evaluated.

CHAPTER V

CONCLUSION AND RECOMMENDATION

5.1 Objectives and Hypotheses

The research objectives established for this project were; 1) Estimate space use of male *B. candidus* among a human-dominated landscape, 2) Identify the best predictors of *B. candidus* space use area, 3) Determine what factors influence site fidelity in *B. candidus* living among a human-dominated landscape, 4) Identify temporal patterns in movement variance, and 5) Determine if land-use features influence *B. candidus* movements. Space use was estimated through the use of dynamic Brownian Bridge Movement Models which created occurrence distributions for each telemetered individual. I was then able to test the influence of individual-specific variables, such as body size, number of days tracked, and proportion of fixes within settlement habitat, on the individuals' dBBMM occurrence distributions with the use of Generalized Linear Models. I used the R package recurse in order to analyze site revisit frequency, and compared seasonal differences in dBBMM derived motion variance along with mean movement distance, mean motion variance, and movement probabilities in order to identify temporal patterns in movements. Lastly, Integrated Step Selection Functions were used to evaluate the influences different land-use features had on the movements of telemetered *B. candidus*.

The first hypothesis states that male *B. candidus* will have a larger utilization distribution than previously reported by the past study by Mohammadi et al. (2014). I then compared dBBMM 99% confidence area occurrence distributions made for Mohammadi et al.'s single telemetered male *B. candidus* to the mean occurrence distributions of this study's telemetered males, and found that the mean for all males was smaller than the single adult male *B. candidus* from the past study, however, when using only values from telemetered adult *B. candidus* the mean was only 0.09 ha smaller than the occurrence distribution estimate for the individual telemetered by Mohammadi et al. (2014). Therefore, the estimate from Mohammadi et al. (2014) appears to be consistent with my occurrence distribution estimations, thus I fail to reject the null hypothesis.

The second hypothesis suggested that the snake's body size would be the best predictor out of the tested variables for dBBMM 95% confidence area occurrence distributions. After running the simple linear regression models and GLMs, I found that the value which contributed the most to the observed variation on space use was indeed the snake's mass. Therefore, I reject the null hypothesis.

The third hypothesis stated that male *B. candidus* will exhibit higher site revisit frequency among settlement habitat than when among less-disturbed habitats. However, I found that site revisit frequency is in fact higher among natural habitat with high levels of certainty. There was an estimated difference in mean revisit frequencies between the two habitat categories of about 377 h (15.7 days), thus I fail to reject the null hypothesis.

My fourth hypothesis stated that male *B. candidus* motion variance peaks would coincide with their supposed breeding season between the months of December and January in the cold season (Chanhome et al., 2011). While there were clear peaks in motion variance which were substantially higher than the rest of their usual motion variance, as well as pretty clear trends in when these peaks occurred, these motion variance peaks fell between the months of October and November, in the early cold season. Since there were prominent peaks in motion variance which were so near to the expected time (beginning just two months before being expected to start and within the same season), I consider this to support my hypothesis, and I reject the null hypothesis. I feel these peaks are most likely attributed reproductive movements (i.e. mate searching), and there is likely variation year-to-year as climate and other variables which likely trigger these behaviors are not always temporally consistent. Similarly, the data which the reproductive time frame was estimated from was collected from unknown locations in Thailand, and mating may take place in different months across different regions.

My fifth hypothesis stated that *B. candidus* movements would be influenced by habitat features, and I had expected telemetered snakes to be associated with forested areas. Testing for association with ISSF revealed that many of the individuals showed clear association with less-disturbed habitats including mixed deciduous forests and semi-natural areas. In addition, ISSF also showed a number of individuals to exhibit clear association with buildings among settlement habitat. As I did find land-use features to affect *B. candidus* movements, as well as finding an association with natural areas, I fail to reject the null hypothesis.

5.2 Conclusions and Recommendations

My study is among the first to investigate the movements and ecology of a medically significant snake living among a largely semi-urban human-dominated landscape, and the first study on *B. candidus* to track multiple individuals using a standardized framework and modeling analyses. Though sample sizes were limited in all aspects of this study (i.e. n = 14, mean no. fixes = 106.57), this study provides important baseline data on the ecology and natural history of a little-studied but medically significant snake species. This study also acts as a preliminary study adding to our limited knowledge on how snakes, particularly nocturnal active foraging species from the tropics, live when closely sharing space with humans, and provides an example study framework which could be duplicated in order to examine the ecology of other medically significant snakes living among human-dominated landscapes.

Bungarus candidus are able to tolerate highly disturbed habitats as long as adequate sections of vegetated and less-disturbed areas persist among the landscape. Telemetered *B. candidus* from my study occupied relatively small areas consistent with previous studies' space-use estimates from protected areas, thought space use appears to be weakly linked to both the individual's body size and the amount of time spent within settlement habitat. Movement activity was seasonal, finding that male *B. candidus* reduce activity in the hot season, increased movement frequency in the wet season, and exhibited peaks in motion variance during the early cold season (between October and November), seemingly indicating the onset of the breeding season. Snakes in my study appear to show some level of attraction to both less-disturbed natural areas and buildings. Lastly, results from my study also suggest that *B.*

candidus may react to changes in human activity levels by altering their movements in attempt to avoid conflict with humans.

My study is the first to demonstrate that a snake may alter its behavior and movements in response to changes in human activity in a human-dominated landscape via radio-telemetry. Additionally, the finding that telemetered *B. candidus* spent the majority of their time sheltering under anthropogenic structures, such as buildings and concrete drainage ditches, and exhibited attraction to buildings is significant for multiple reasons. Firstly, it is the first study within the tropics to show this result, which seems to suggest snakes likely gain more than thermal benefits alone from the utilization of artificial refuges. Secondly, it demonstrates just how common it is for *B. candidus* to share space closely with humans. Lastly, this frequent use of anthropogenic structures as shelters and association with buildings provides insight into why most of the bites by kraits occur to people within their homes.

Since the results of my study suggest that *B. candidus* are associated with buildings, it would likely prove ineffective and costly to attempt to deter *B. candidus* from settlements. Instead, recommend more effort be made to increase awareness among residents through education programs and posted signage. Such programs can teach the important precaution measures, such as using flashlights when outdoors at night and covering drains and eliminating gaps along housing where snakes could potentially enter. Alternatively, snake-proof fencing could be added along the perimeter of residential areas where *B. candidus* are known to occur, or even along the sides of paved sidewalks in order to limit their presence among homes and sidewalks, though this could lead to snakes entering and becoming stuck within the fenced areas if not done properly or well maintained (Baxter-Gilbert et al., 2015).

It appears that artificial shelters, such as buildings and concrete drainage ditches, along with remaining natural and semi-natural areas are important for the survival of *B. candidus* among heavily modified human-dominated landscapes. Linear semi-natural areas, such as irrigation canals, field margins, and strips of unmanicured vegetation, as well as roadside ditches may facilitate movement and provide important foraging sites for telemetered *B. candidus*. These features are likely particularly beneficial to herpetofauna and other wildlife remaining in highly disturbed and urbanized areas, where there is little suitable habitat. Additionally, remaining forested areas likely provide some protection from human activities, which are generally detrimental to snake populations and often cause direct mortality.

In contrast, the combined association with anthropogenic structures and apparent lack of avoidance of roads and agriculture reveals great potential for *B. candidus* mortality. While the snakes are susceptible to persecutory killings by people when among human habitations, my findings suggest that road-induced mortality is among the greatest threats to *B. candidus* which live among human-dominated landscapes. Due to the limited nature of my data, I suggest future studies further evaluate threats and survival of *B. candidus* living among similarly unprotected and highly disturbed human lands. It may be worth examining the effectiveness of culverts which pass underneath roads and the addition of roadside snake crossing signage as methods of reducing mortalities on roads.

Despite the fairly consistent findings from my study, regarding space use, movement and habitat selection, and temporal activity patterns, inferences are limited by my small sample size. Due to low capture rates I only tracked a total of 14 *B. candidus* individuals, with all but one being male. Furthermore, individuals were only tracked for a mean of 106.46 days (106.57 fixes) due to transmitter issues. These limitations reduced my ability to examine temporal patterns in space use and movements, and to make statistical comparisons between conspecific sex and age class groupings. I recommend future studies use larger samples, with more representatives of both sexes, and examine movement patterns among different study sites in order to help elucidate widespread trends in the species. Future research should investigate survival and reproduction of the species among human-dominated landscapes in order to better determine whether such populations are actually viable. Lastly, I recommend implementation of more studies like this, examining movements, habitat selection, and activity patterns, on other medically significant snake species among human-dominated landscapes within regions where snakebites are known to occur in attempt to develop better management techniques for snakebite prevention.

APPENDICES

APPENDIX A

DBBMM SPACE USE ESTIMATES

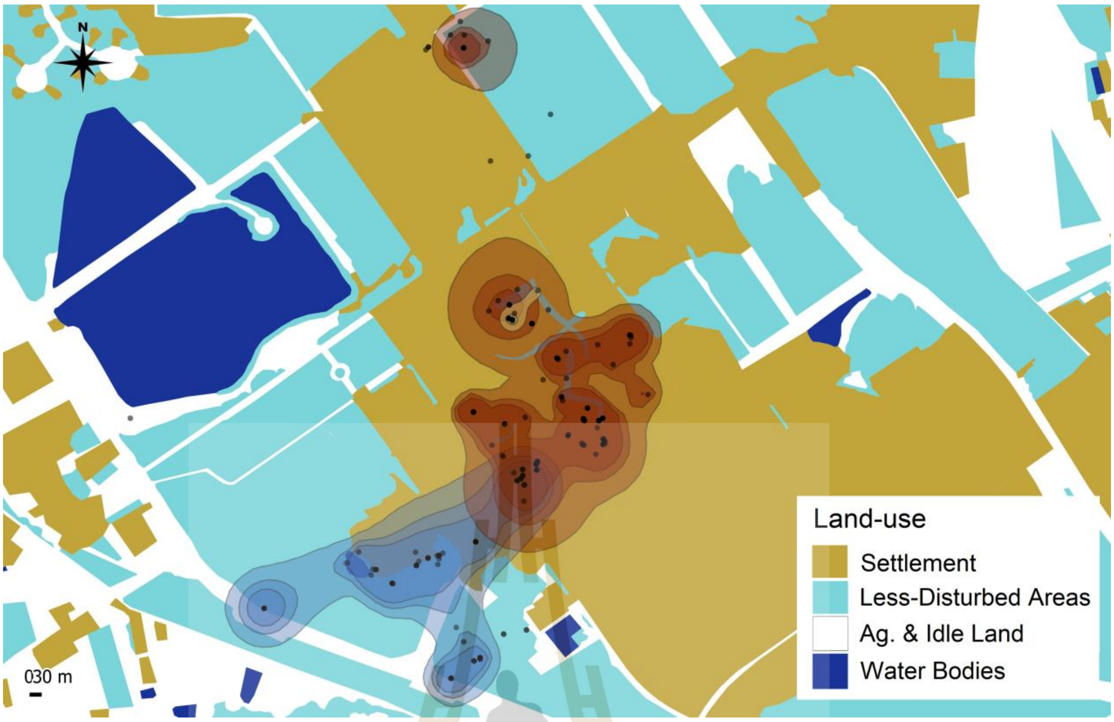

Figure A-1 dBBMM occurrence distribution estimates for individuals M01 (blue), M02 (red), and F16 (tan), with 99%, 95% and 90% confidence area estimates.

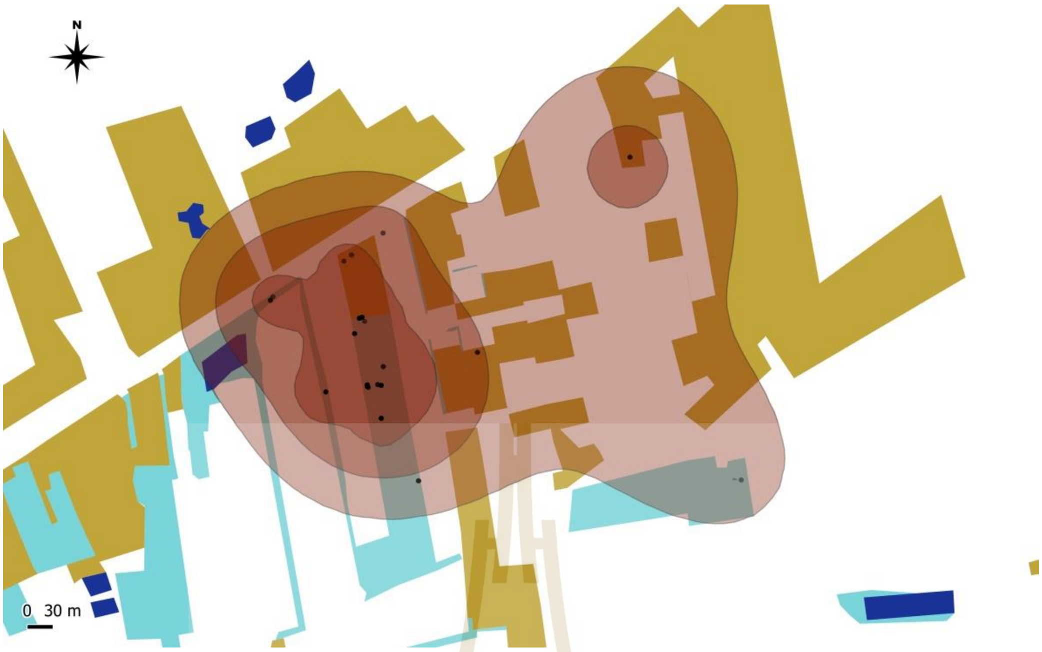

Figure A-2 dBBMM occurrence distribution estimates for M07 (red) with 99%, 95% and 90% confidence area estimates.

Figure A-3 dBBMM occurrence distribution estimates for M12 (red) with 99%, 95% and 90% confidence area estimates.

Figure A-4 dBBMM occurrence distribution estimates for M14 (red) with 99%, 95% and 90% confidence area estimates.

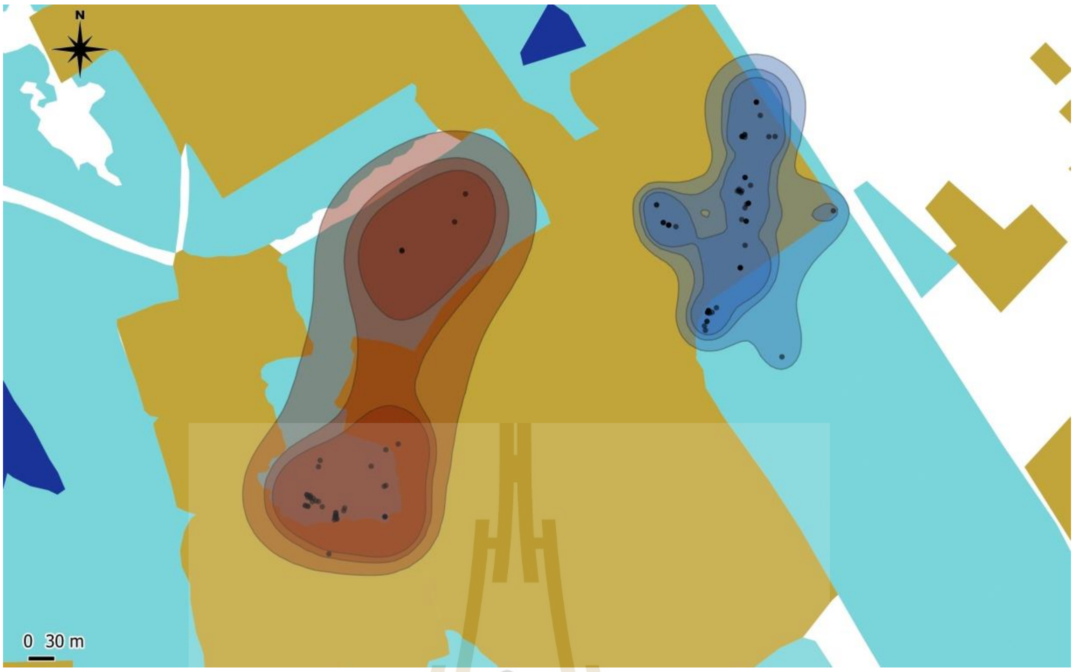

Figure A-5 dBBMM occurrence distribution estimates for M22 (red) and M28 (blue) with 99%, 95% and 90% confidence area estimates.

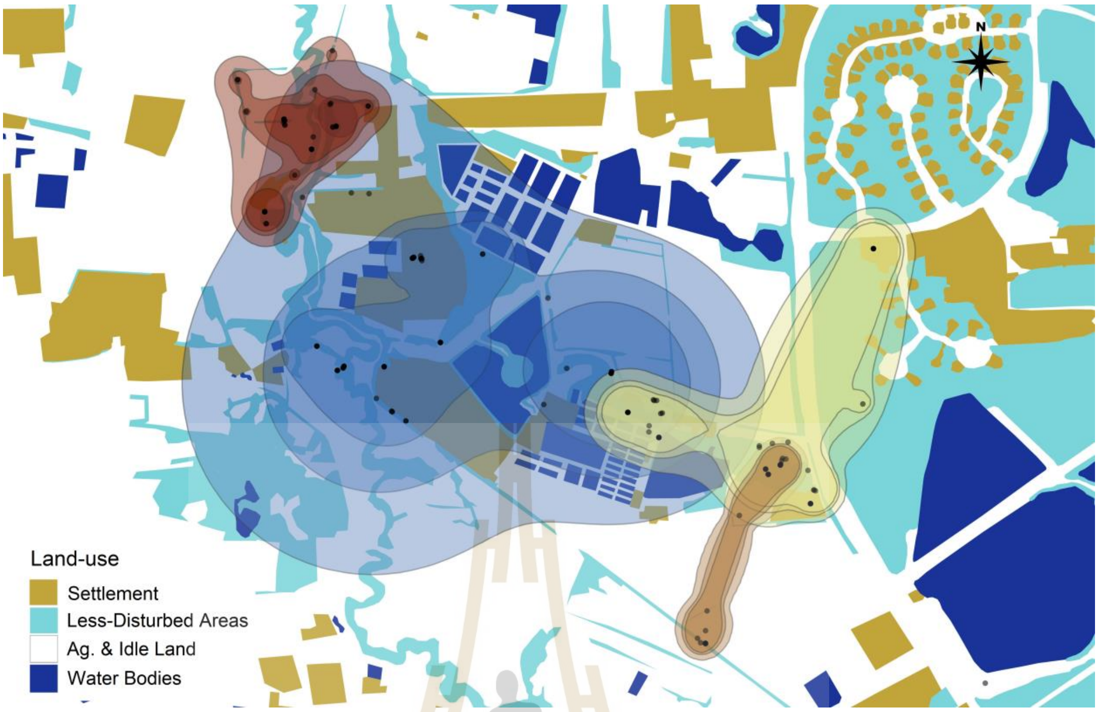

Figure A-6 dBBMM occurrence distribution estimates for M27 (orange), M32 (blue), M35 (red), and M36 (yellow) with 99%, 95% and 90% confidence area estimates.

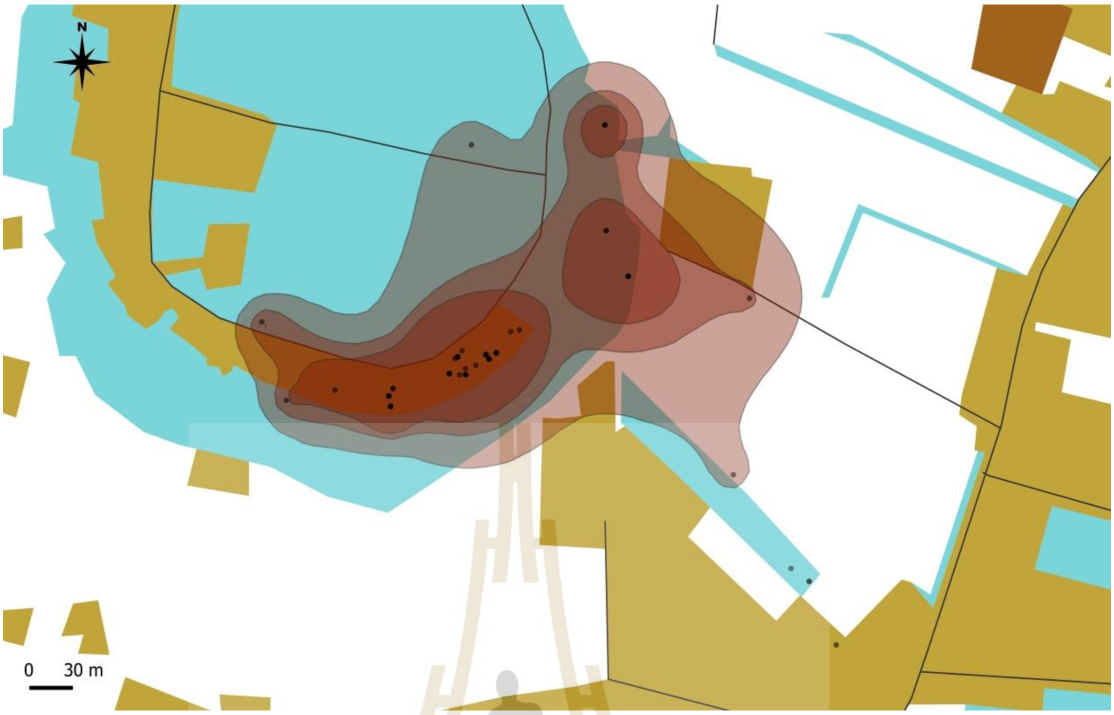

Figure A-7 dBBMM occurrence distribution estimates for M33 (red) with 99%, 95% and 90% confidence area estimates.

APPENDIX B

GLM VALIDATION AND RESULTS

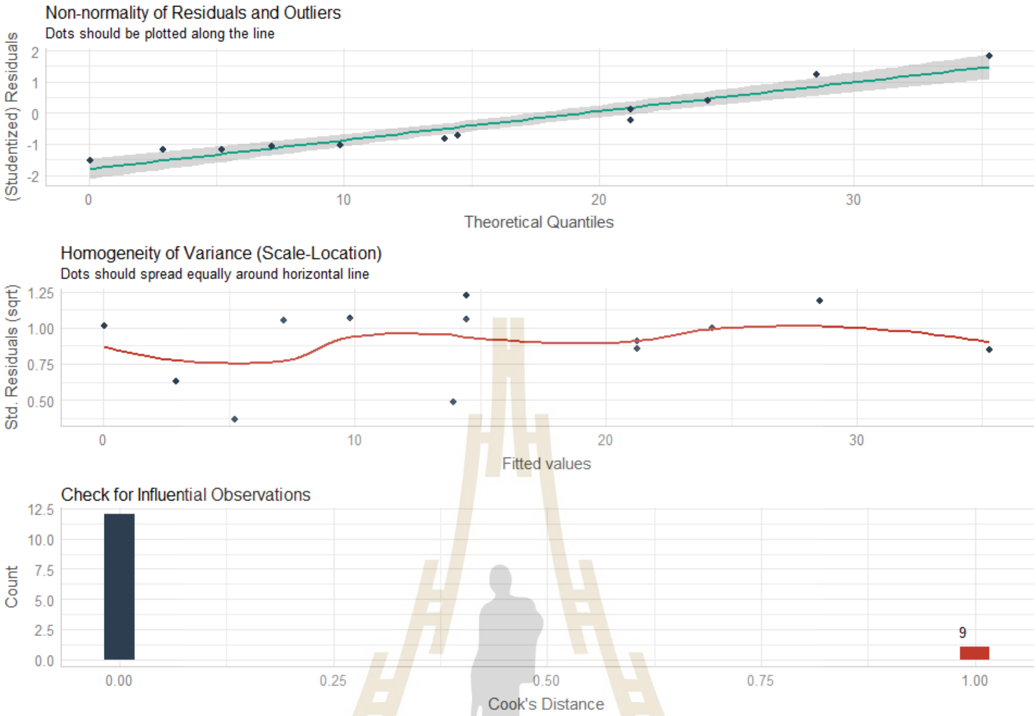

Figure B-1 GLM performance check glm(dBBMM95 ~ days tracked, family = Gamma (link = identity)).

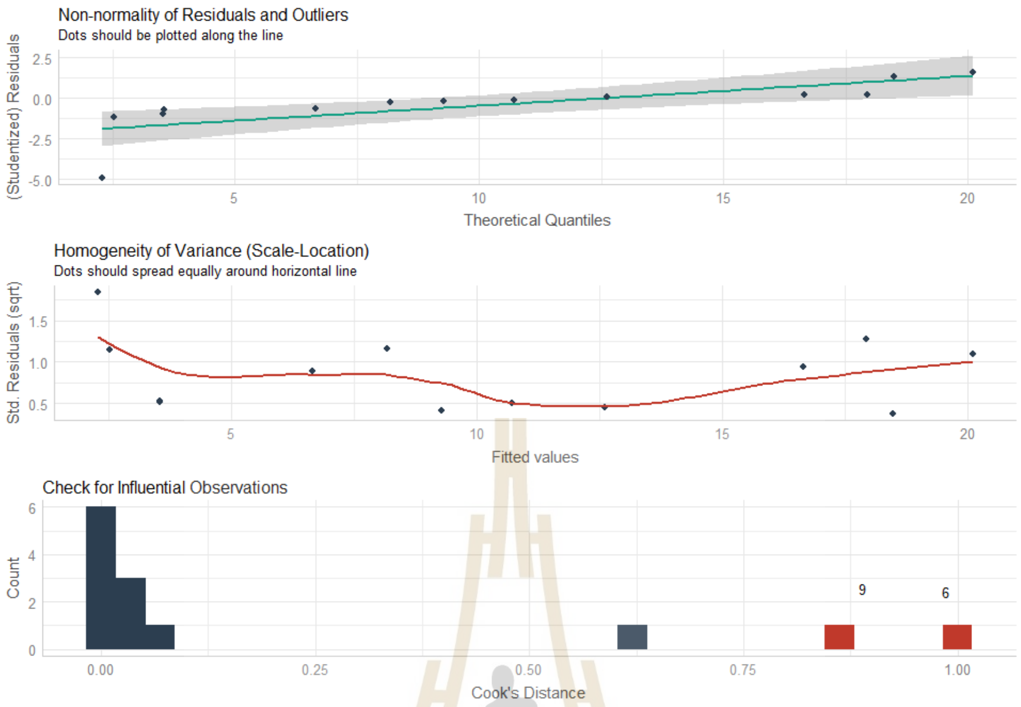

Figure B-2 GLM performance check glm(dBBMM95 ~ mass, family = Gamma (link = identity)).

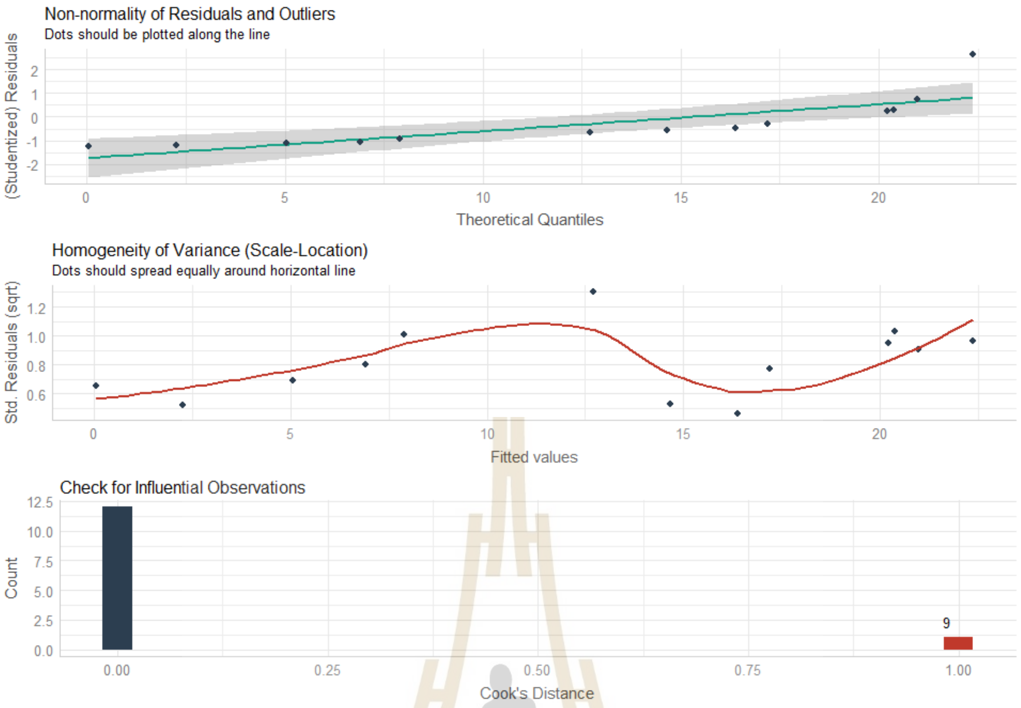

Figure B-3 GLM performance check glm(dBBMM95 ~ proportion of fixes in less-disturbed areas, family = Gamma (link = identity)).

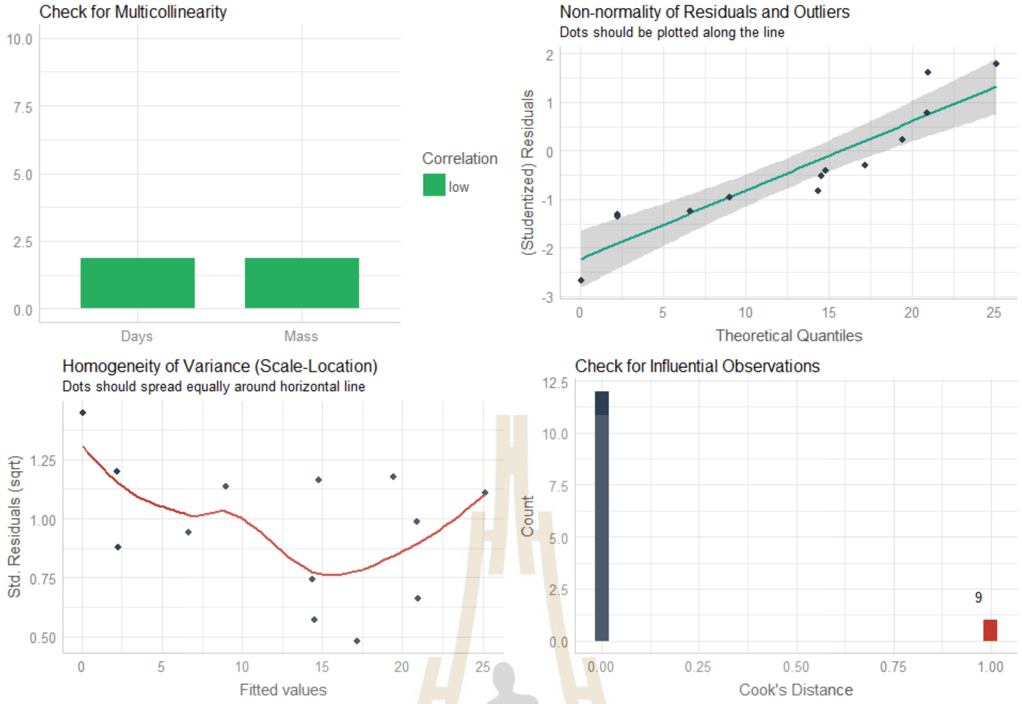

Figure B-4 GLM performance check glm(dBBMM95 ~ mass + days, family = Gamma (link = identity)).

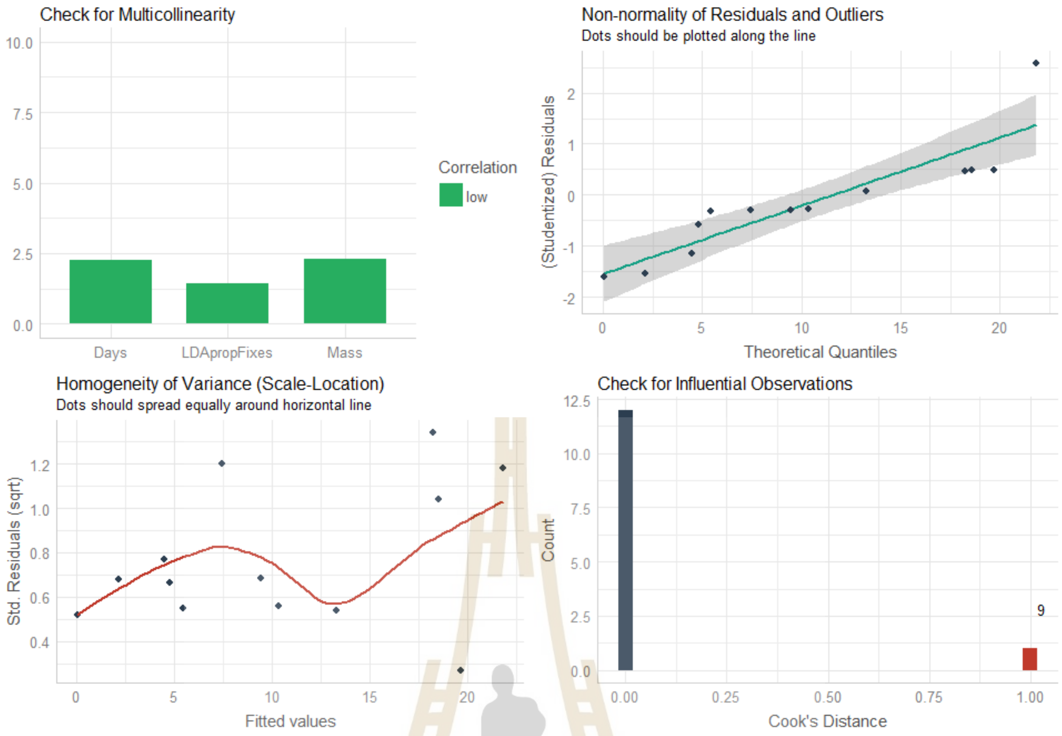

Figure B-5 GLM performance check glm(dBBMM95 ~ mass + days + proportion of fixes in less-disturbed areas, family = Gamma (link = identity)).

APPENDIX C

BRM VALIDATION AND RESULTS

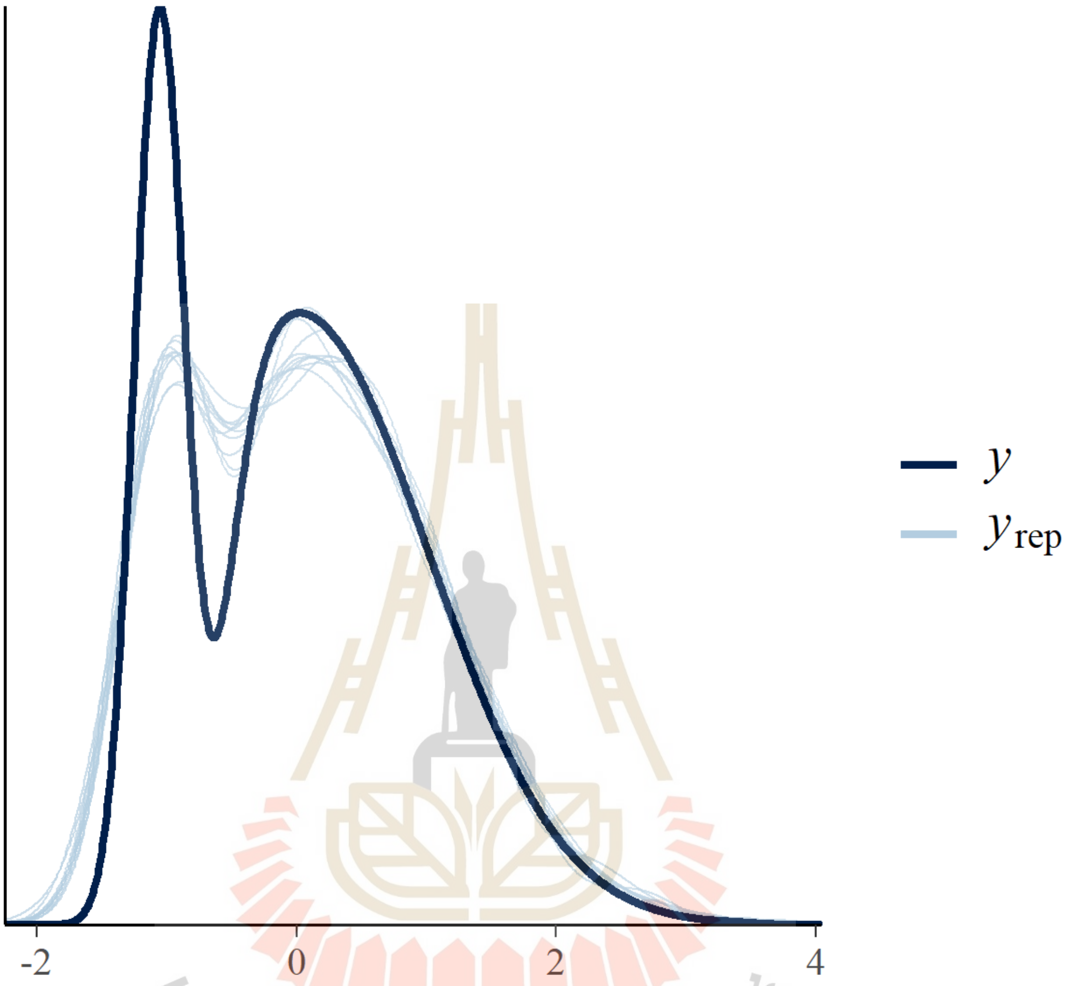

Figure C-1 BRM posterior predictor distribution plot.

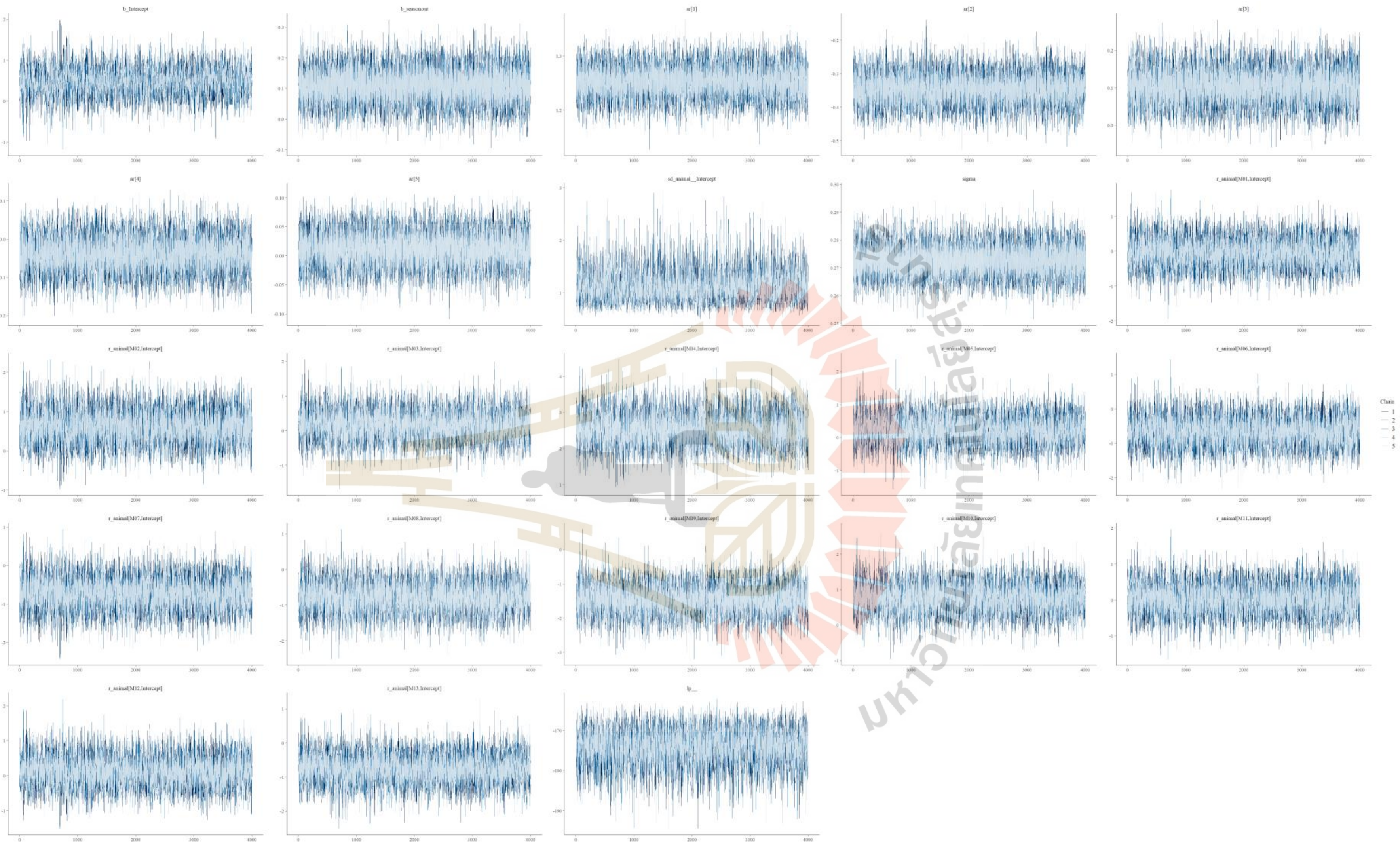

Figure C-2 BRM trace plots.

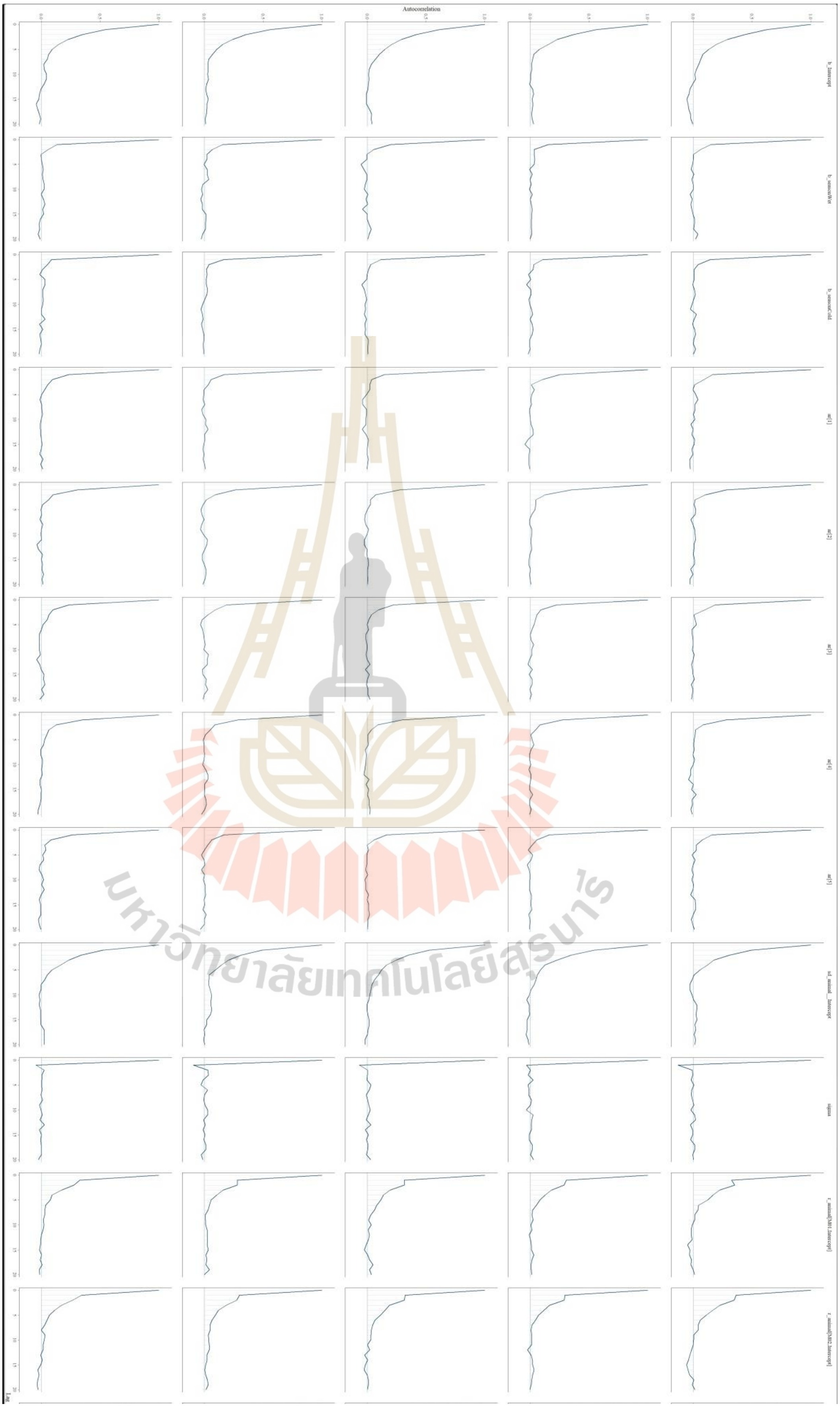

Figure C-3 BRM autocorrelation function plots (part 1).

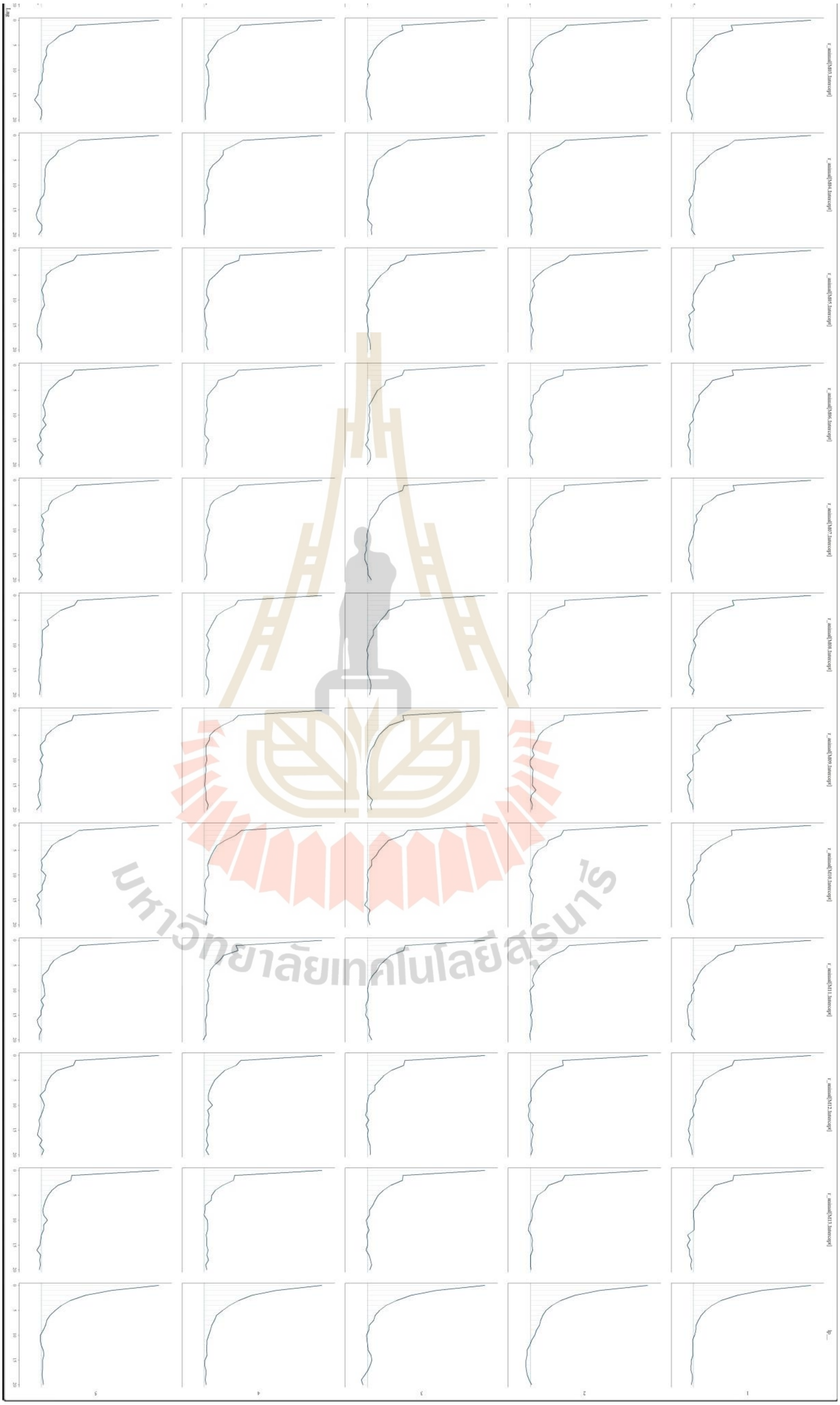

Figure C-4 BRM autocorrelation function plots (part 2)

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