# THE SPATIAL ECOLOGY AND HABITAT USE OF

# FREE RANGING BURMESE PYTHONS (*Python bivittatus*)

# IN THE SAKAERAT BIOSPHERE RESERVE

**Samantha Nicole Smith**

**A Thesis Submitted in Partial Fulfillment of the Requirements for the**

**Degree of Master of Science in Environmental Biology**

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# นิเวศวิทยาเชิงพื้นที่และการใช้พื้นที่อาศัยของงูหลามในธรรมชาติ (*Python bivittatus*) ในพื้นที่สงวนชีวมณฑลสะแกราช
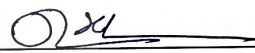
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Suranaree University of Technology has approved this thesis submitted in partial fulfillment of the requirements for a Master's Degree.
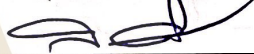
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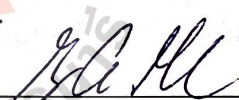(Dr. Colin Strine)

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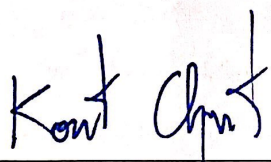(Director Surachit Waengsothorn)

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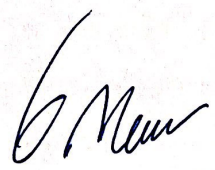
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ซาแมนต้า นิโคล สมิธ : นิเวศวิทยาเชิงพื้นที่และการใช้พื้นที่อาศัยของงูหลามในธรรมชาติ
(*Python bivittatus*) ในพื้นที่สงวนชีวมณฑลสะแกราช (THE SPATIAL ECOLOGY AND
HABITAT USE OF FREE RANGING BURMESE PYTHONS (*PYTHON BIVITTATUS*)
IN THE SAKAERAT BIOSPHERE RESERVE). อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน
โทมัส สไตร์น. 112 หน้า.

งูหลาม/ การใช้พื้นที่/ พฤติกรรมการเลือกใช้พื้นที่/ แบบจำลอง Dynamic Brownian Bridge
Movement (dBBMM) / การเคลื่อนที่

การศึกษาการเคลื่อนที่ของสัตว์เป็นแนวทางหนึ่งในการอธิบายแง่มุมของนิเวศวิทยาและ
ธรรมชาติวิทยาของสายพันธุ์สิ่งมีชีวิตจากการติดตามการเคลื่อนที่ของสัตว์ป่า นักวิจัยสามารถ
ตรวจสอบสัตว์กลุ่มเป้าหมายเกี่ยวกับการใช้ทรัพยากรภายใต้ลักษณะภูมิประเทศ พื้นที่และช่วงเวลา
ได้อย่างไร และทำความเข้าใจในการเลือกทรัพยากรที่จะส่งผลต่อการอนุรักษ์โดยเฉพาะอย่างยิ่งใน
พื้นที่ที่ลักษณะภูมิประเทศตามธรรมชาติได้รับการเปลี่ยนแปลงและถูกแยกส่วนออกมาจาก
กิจกรรมของมนุษย์ เช่น แปลงเกษตรกรรม การสร้างถนนและการตั้งถิ่นฐาน และการรบกวนอื่น ๆ
งูหลาม (*Python bivittatus*) เป็นงูขนาดใหญ่ที่พบได้โดยทั่วไปในภูมิภาคเอเชียตะวันออกเฉียงใต้
ถือเป็นผู้อยู่อาศัยทั่วไปและมักถูกพบเห็นได้ในพื้นที่ที่มนุษย์ครอบครอง โดยในบางกรณีอาจ
ก่อให้เกิดความขัดแย้งระหว่างมนุษย์กับงูได้ การศึกษานี้ใช้รูปแบบกรอบการทำงานมาตรฐานใน
การหาปริมาณการใช้พื้นที่ การเคลื่อนที่และการเลือกถิ่นที่อยู่อาศัยของงูหลาม (*P. bivittatus*) ใน
หย่อมของระบบนิเวศพื้น โดยการติดตามกลุ่มเป้าหมาย 7 ตัว ที่อาศัยในระบบนิเวศต่าง ๆ ของเขต
สงวนชีวมณฑลสะแกราชในช่วงระยะเวลา 22 เดือน และใช้แบบจำลอง Dynamic Brownian Bridge
Movement (dBBMM) ในการคำนวณหาพื้นที่การกระจายตัวในหน่วยเฮกตาร์ (Hectare: ha) พบว่า
*P. bivittatus* มีการเคลื่อนที่จำกัดในด้านความถี่และขนาดพื้นที่ (ค่าเฉลี่ย 98.97 ± 35.42 ha) และมี
ค่าเฉลี่ยความแปรปรวนของการเคลื่อนที่ต่ำ (2.66 ± 0.14 $\sigma^2$m)

ผู้วิจัยได้ใช้การวิเคราะห์แบบ step selection เพื่อสำรวจการเลือกใช้ถิ่นที่อยู่อาศัยของ*P.
bivittatus* โดยสัมพันธ์กับระยะทางไปยังลักษณะเฉพาะของถิ่นที่อยู่อาศัยในพื้นที่ศึกษาทั้งในระดับ
ประชากรและระดับบุคคล พบว่า *P. bivittatus* มีความชื่นชอบสภาพแวดล้อมที่มีแหล่งน้ำได้แก่
คลองชลประทานและพื้นที่การเกษตรที่มีแหล่งน้ำ (เช่น นาข้าว) และไม่แสดงท่าทีหลีกเลี่ยงพื้น
ที่ตั้งถิ่นฐานของมนุษย์อย่างชัดเจนซึ่งสนับสนุนแนวคิดการเกิดความขัดแย้งระหว่างมนุษย์กับงู
ตลอดระยะเวลาการศึกษายังมีการบันทึกข้อมูลเกี่ยวกับธรรมชาติวิทยา เช่น การผสมพันธุ์และการ

ทำรัง ซึ่งยังไม่เคยมีการรายงานการศึกษาในกลุ่มของสายพันธุ์พื้นเมืองมาก่อน ทำให้การศึกษานี้ถือ
ว่าเป็นรายงานฉบับแรกที่ให้ข้อมูลเกี่ยวกับนิเวศวิทยาของ *P. bivittatus* ที่เป็นสายพันธุ์พื้นเมืองมิใช่
สายพันธุ์รุกราน

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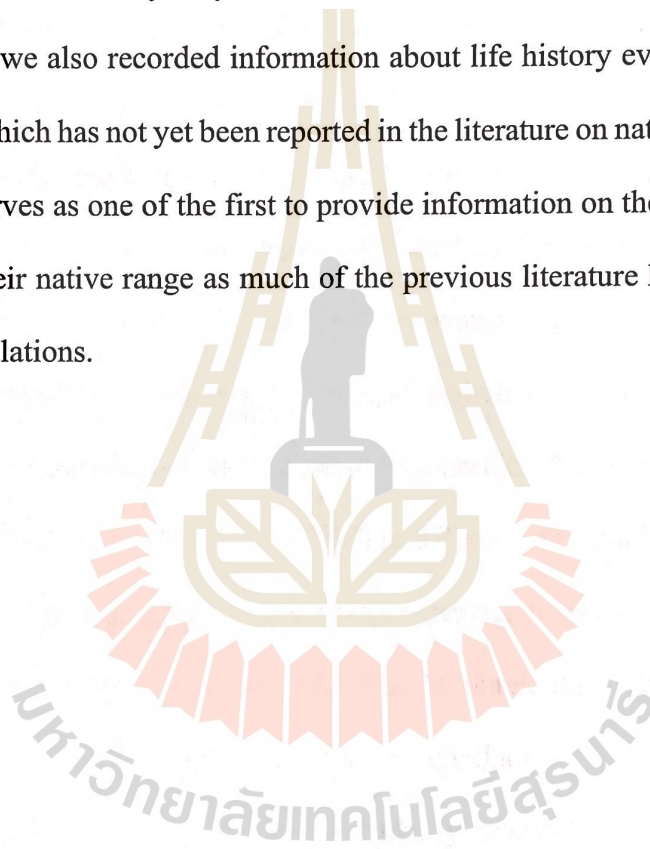ปีการศึกษา 2563                    ลายมือชื่ออาจารย์ที่ปรึกษา_____

SAMANTHA NICOLE SMITH : THE SPATIAL ECOLOGY AND HABITAT USE OF FREE RANGING BURMESE PYTHONS (*Python bivittatus*) IN THE SAKAERAT BIOSPHERE RESERVE. THESIS ADVISOR : COLIN THOMAS STRINE, Ph.D. 112 PP.

BURMESE PYTHON / SPACE USE / HABITAT SELECTION / DYNAMIC BROWNIAN BRIDGE MOVEMENT MODELS / MOVEMENT

Studying animal movement is one approach to elucidating aspects of species' ecology and natural histories. By tracking the movements of wildlife, researchers can investigate how animals utilize resources within landscapes across space and time. Understanding resource selection has conservation implications, especially in areas where landscapes have been modified and fragmented by agricultural conversion, the building of roads and settlements, and other anthropogenic disturbances. Burmese pythons (*Python bivittatus*) are large, constricting snakes found throughout much of Southeast Asia. Burmese pythons are habitat generalists and have been observed using human dominated areas which in some cases may initiate human-snake conflict. This study uses a standardized framework to quantify the space use, movements and habitat selection of Burmese pythons in a patchy land use matrix. Over the course of approximately 22 months, we tracked seven Burmese pythons through various habitat types in the Sakaerat Biosphere Reserve. We used dynamic Brownian Bridge Movement Models to quantify occurrence distributions (ha) and found that Burmese pythons restricted their movement by making infrequent moves and utilizing small areas (mean = $98.97 \pm$ SE 35.42 ha).

We used integrated step selection analysis to explore habitat selection for Burmese pythons in relation to distance to particular habitat features found within our study site. At both the population and individual level we observed a preference for aquatic environments such as water bodies, irrigation canals and aquatic agriculture (i.e., rice paddy). Burmese pythons did not show strong avoidance for human settlements, which supports the idea that they may initiate human-snake conflict. Throughout the course of this study, we also recorded information about life history events such as breeding and nesting which has not yet been reported in the literature on native Burmese pythons. This study serves as one of the first to provide information on the ecology of Burmese pythons in their native range as much of the previous literature has focused solely on invasive populations.

School of Biology       Student's Signature _____

Academic Year 2020      Advisor's Signature _____

# ACKNOWLEDGEMENTS

Special thanks goes to Ben Marshall for his willingness to answer questions about analysis and for trouble shooting many a script in R. I am grateful for Anji D'Souza for graciously sharing her equipment with me and for always being willing to give a helping hand. I cannot thank my field assistants, Joli Stavish and Shannon Thrasher enough. Their hard work, sense of humor and patience helped to make this research possible.

I have to thank my friends and family for supporting me and for at least trying to understand my desire to move across the world to study snakes. I thank my Nano for instilling a sense of adventure in me and for in some ways inspiring my interest in herpetology by teaching me how to hang anoles off of my ears in his backyard while I was growing up. I also thank my Grammie, who in addition to supporting me has also helped to foster my interest in herpetology by allowing me to spend hours catching frogs in her backyard during the summers. I thank my dad for supporting me and for teaching me the value of a strong work ethic from an early age. I thank my mom for being my biggest cheerleader throughout everything. Without her constant encouragement I'm not sure I would have stepped out of my comfort zone as many times as I have. Finally, I thank my better half, friend and husband, Max. He has truly been my greatest support system and has without a doubt made me a better scientist, friend and partner. I am very fortunate to have had his support throughout the good, bad and stressful times.

Samantha Nicole Smith

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# LIST OF ABBREVIATIONS

AIC     =     Akaike's Information Criterion

dBBMM   =     dynamic Brownian Bridge Movement Model

GPS     =     Global positioning system

IUCN    =     International Union for Conservation of Nature

MCP     =     Minimum convex polygon

PYBI    =     *Python bivittatus*

SBR     =     Sakaerat Biosphere Reserve

SE      =     Standard error

SERS    =     Sakaerat Environmental Research Station

SVL     =     Snout to vent length

TL      =     Tail length

# CHAPTER I

# INTRODUCTION

## 1.1    Background

Understanding an animals' spatial ecology or the way in which an animal moves through time, space and different habitat types can provide insight on the underlying patterns driving movement within the species, which can provide information about natural and life histories (Block et al., 2011; Dulau et al., 2017; Viana et al., 2018). One term or metric commonly used in spatial ecology is home range. The term home range was first defined by Burt (1943) as the area used by an individual animal for biologically important activities, such as hunting, sheltering, and reproducing (Burt, 1943). However, home ranges are likely more complex than described by Burt (1943) as home ranges may change as a result of availability of resources, or through increased movement during migration or dispersal, or change depending on the temporal scale that they are estimated over (Börger et al., 2008). Our estimates of home ranges for animals are only as good as the methods and technology used to arrive at those estimates (Powell and Mitchell, 2012). A more feasible measurement is calculating occurrence distributions, which can be used to quantify and predict space used by animals (Fleming et al., 2016). By understanding an animal's spatial ecology through studying their home range or occurrence distribution, scientists can make biological inferences about the species as well as potential threats to the species (Nathan et al., 2008).

With landscapes changing due to urbanization and habitat fragmentation worldwide, it is important to evaluate how animals utilize space within these modified landscapes. Reptiles are especially vulnerable to habitat loss in addition to other anthropogenic pressures and are suffering from population declines worldwide (Gibbons et al., 2000; Todd et al., 2010).

Typically, habitat loss due to urbanization is linked to a decrease in biodiversity (Sodhi et al., 2004, Sodhi et al., 2010). Southeast Asia is uniquely vulnerable to biodiversity loss due to the fact that it suffers from the highest rate of deforestation of any tropical region (Sodhi et al., 2004). In some cases, urbanization can homogenize biota, *i.e.* when select species resilient to landscape changes and urbanization become locally abundant within modified landscapes (McKinney, 2006). Species resilient to living amongst human disturbed areas may alter their behaviors to adapt to the changes in the landscape and avoid potential conflict with humans (Ditchkoff et al., 2006).

Burmese pythons (*Python bivittatus* KUHL, 1820) are large bodied, constricting, terrestrial snakes invasive in the Southeastern United States and native to Southeast Asia. Burmese pythons are habitat generalists and occur in forests, grasslands and coastal plains; additionally, Burmese pythons are also found in landscapes modified for human use such as agricultural land, plantations, and human settlements (Goodyear, 1994; Barker and Barker, 2008; Barker and Barker, 2010; Rahman et al., 2014). Results from our capture records of *P. bivittatus* in our site suggest that Burmese pythons are more commonly found in human modified areas than in the core, protected forest in the Sakaerat Biosphere Reserve (only two of 67 captured *P. bivittatus* were found in the protected area). Despite their apparent affinity for human disturbed areas, drivers of movement and habitat selection patterns in their native ranges remain largely unknown.

Thus, there are substantial knowledge gaps in their ecology. Successful management and mitigation strategies require a comprehensive understanding of the species' ecology, such as habitat selection patterns, spatial requirements, biologically relevant events (i.e., breeding seasons, nesting seasons), and threats to the species- all of which we provide information on as a result of our research.

This study is one of the first to quantify and provide estimates of native Burmese python movement and habitat selection using modern techniques and following a standardized framework. Furthermore, throughout the course of this research, we have observed several life history events that have not yet been recorded in the literature on native Burmese pythons. Ultimately, the findings from this research will help to begin fill the gaps in the literature on the ecology of native Burmese pythons.

## 1.2    Research Objectives

1.2.1    Estimate the seasonal home range size and space use of female *P. bivittatus* in the patchy land-use matrix of the Sakaerat Biosphere Reserve.

1.2.2    Determine habitat use preferences of *P. bivittatus* at the landscape scale.

1.2.3    Identify seasonal variance in movements of free-ranging *P. bivittatus* in the Sakaerat Biosphere Reserve.

1.2.4    Explore the reproductive ecology (breeding seasons, oviposition site selection, incubation periods) of free-ranging *P. bivittatus* in the Sakaerat Biosphere Reserve.

## 1.3 Research Hypotheses

1.3.1 *P. bivittatus* will maintain relatively small home ranges in comparison to the home range sizes from within their invasive range.

1.3.2 At the landscape scale, *P. bivittatus* will select for agricultural land and will non-randomly select for certain habitat features (distance to road, distance to water, distance to human settlement).

1.3.3 *P. bivittatus* movement will be correlated with the wet and dry seasons with *P. bivittatus* increasing movement frequency in the wet seasons, however variance in movement across seasons will differ between reproductive and reproductive individuals.

1.3.4 Breeding seasons of *P. bivittatus* will coincide with breeding seasons of invasive *P. bivittatus*.

## 1.4 Scope and Limitations of the Study

We began field work for this study in late September 2018 when my first study animal was captured and implanted with a radio-transmitter. We continued radio-tracking implanted individuals through July 2020. Radio-tracking was limited to the Sakaerat Biosphere Reserve where we tracked snakes across several different land-use types (protected forests, disturbed forest fragments, plantation forests, agricultural land, and land used for human settlements). By tracking snakes through a patchy land use matrix, we are able to identify habitat selection for particular features within our study site. However, we are not able to draw reliable inferences about habitat selection for snakes that were only tracked in a single habitat type (i.e., forest), which was the case for one individual.

Our sample size was comprised of almost entirely adult female Burmese pythons, so we are not able to confidently extrapolate our results to male Burmese pythons or individuals of other age classes. We suspect that by tracking snakes across a variety of land-use types that are found in other areas of their range, my findings will be applicable to understanding the ecology of Burmese pythons not only in the Sakaerat Biosphere Reserve, but in other parts of their distribution as well. With my sample size including mostly female *P. bivittatus* we are not able to make inferences about male *P. bivittatus* in our study site, however we suspect that male Burmese use resources similarly to female Burmese pythons.
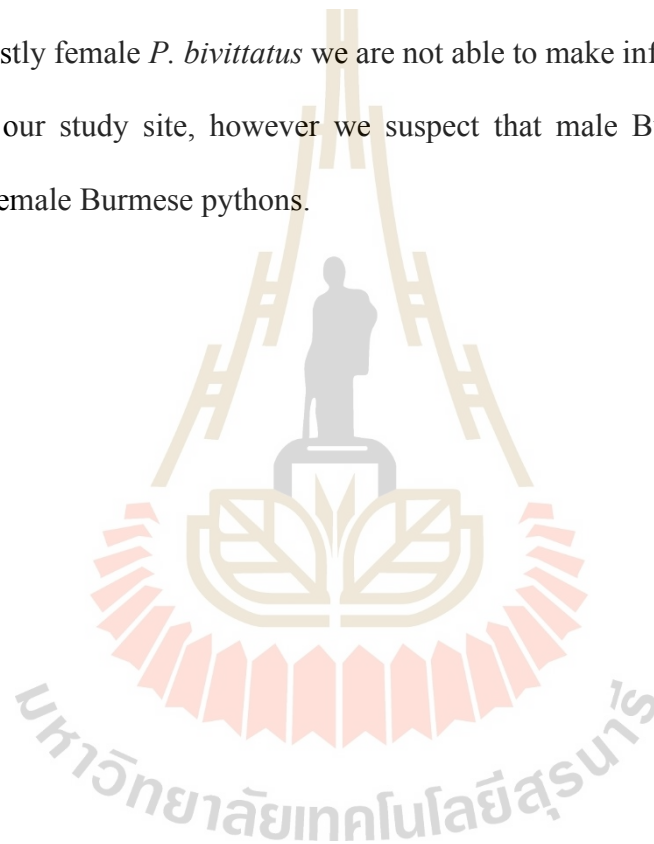
# CHAPTER II

# LITERATURE REVIEW

## 2.1    Study Species

### 2.1.1 Biology and ecology

*Python bivittatus* is a member of the Pythonidae family, which is made up by nine different genera composed of a total of 41 species (Uetz, 2020). Species in the Pythonidae family exist in Africa, Asia, and Indo-Australia, however most are found in Indo-Australia (Schleip and O'Shea, 2010).   All snakes in the Pythonidae family are non-venomous, relying on constriction to subdue their prey.

The Burmese python (*Python bivittatus*) is native to and broadly distributed throughout Southeast Asia (Figure 2.1). *Python bivittatus* has been known to occur in Bangladesh, Myanmar, Laos, in Thailand north of the Isthmus of Kra, Cambodia, Vietnam, Southern China and in disjunct populations in Northern and Northeastern India and in Southern Nepal (Barker and Barker, 2008; Barker and Barker, 2010).

**Figure 2.1** Distribution map of *Python bivittatus*. Adapted from Stuart et al., 2019.

*Python bivittatus* can reach 8.22 meters and are sexually dimorphic, with females growing larger than males (Table 2.1). The dorsal scales of *P. bivittatus* are yellow, light brown, dark brown and black and create irregular shaped dark brown blotches with black boarders. On the dorsal side of the head, there is a distinct arrowhead shaped, light brown marking with the point oriented towards the snout. Burmese python ventral scales are lightly colored, almost white, with small dark spots along the sides of the ventral scales. Additionally, spurs near the anal plate may be visible in adults with males typically having longer spurs than females (Cox et al., 2012) (Figure 2.2). Anal spurs are remnants of a vestigial pelvic girdle and have been observed in captive settings to stimulate copulation (Gillingham et al., 1982).

**Table 2.1** Average and maximum recorded measurements of male and female Burmese pythons. Table recreated from Reed and Rodda, 2009 and modified using estimates from Cox et al., 2012.

| Sex | Average size at hatching | | Average size at sexual maturation | | Largest size recorded | |
|---|---|---|---|---|---|---|
| | Total length (mm) | Mass (g) | Total length (mm) | Mass (kg) | Total length (mm) | Mass (kg) |
| Female | 500-700 | 75-165 | 2600 | 10 | 8220 | 182 |
| Male | 500-700 | 75-165 | 2000 | 5 | 4500 | 50 |

*Standard deviation, number of individuals, sampling method not available from literature.

**Figure 2.2** Coloration of Burmese python dorsal (A) and ventral (C) scales. Panel B highlights the arrowhead shaped markings that can be used to identify Burmese pythons. Panel D shows location of pelvic spurs.

Pythons acquire prey with assistance from their thermal pit organs, which detect thermal radiation from potential prey items and features within their environment (Goris, 2011). These thermal pit organs are located along the snout among the supralabial scales. While the foraging mechanisms of *P. bivittatus* have not been

extensively explored in the wild, studies on two Australian python species, Diamond pythons (*Morelia spilota*) and Green pythons (*Morelia viridis*) revealed that pythons acquired prey via ambush hunting, both in the wild and in a captive setting (Slip and Shine, 1988; Wilson, 2007). More information about the diet of Burmese python is available from their invasive range. A study from their invasive range in the Florida Everglades identified small to mid-sized mammals as primary prey items, however prey item size varied widely with prey items including items as large as a bobcat and one individual was discovered trying to ingest an alligator but died in the process (Snow et al., 2007). Pythons are thought to be dietary generalists and prey on mammals and birds (Luiselli et al., 2001; Kasterine et al., 2012; Natusch et al., 2016). Presumably, native Burmese pythons also predate upon birds and small to mid-size mammals depending on their relative size.

### 2.1.2 Reproductive Biology of *Python bivittatus*

From within their native distribution, there has been very little information shared about the reproductive biology of wild *P. bivittatus*. However, there have been several studies from the invasive range of *P. bivittatus* in the Florida Everglades that have shared findings about the reproductive biology of free-ranging *P. bivittatus*. Typically, Burmese pythons are solitary animals however, researchers from the invasive range of *P. bivittatus* have recorded that Burmese pythons form breeding aggregations, where two or more males will congregate around a female during copulation in the breeding season which is thought to be between December and April in their invasive range (Smith et al., 2016). Other species like Diamond pythons (*Morelia spilota*) also exhibit mating aggregations (Shine and Fitzgerald, 1995). Other

species of pythons may also form mating aggregations however they have yet to be observed.

      *P. bivittatus* are also capable of reproducing without fertilization from a male via parthenogenesis (Groot et al., 2003). Genetic analysis of the embryos from the captive Burmese python eggs revealed that all embryos were genetically identical to the mother (Groot et al., 2003). There are currently no known instances of wild, free-ranging Burmese pythons reproducing via parthenogenesis.

      Following oviposition, pythons provide some level of parental care to offspring by coiling around or 'brooding' their eggs (Stahlschmidt and DeNardo, 2011). Burmese pythons are also able to regulate clutch temperatures through facultative thermogenesis during brooding. Facultative thermogenesis is when *P. bivittatus* mothers rapidly twitch their muscles while coiled around their clutch to raise their body temperature (Brashears and DeNardo, 2013). Facultative thermogenesis has been displayed by mother Burmese pythons both in laboratory settings and free-ranging Burmese pythons in the Florida Everglades (Brashears and DeNardo, 2013; Snow et al., 2010).

      Incubation times are not well known for wild *P. bivittatus*, but observations of a captive individual found that a female laid a clutch of 35 eggs 114 days after breeding where the female remained coiled around the clutch for 56 days before the eggs hatched (Van Mierop and Barnard, 1976). Average clutch sizes of Burmese pythons in their native range have yet to be recorded but estimates from their invasive range suggest that Burmese pythons have large clutches with an average of 39 eggs per clutch but may lay as many as 107 eggs (Willson et al., 2011).

### 2.1.3 Burmese python conservation status

*Python bivittatus* is listed on the International Union for Conservation of Nature (IUCN) Redlist as 'Vulnerable' with decreasing populations, attributing the harvest of Burmese pythons for their skins, traditional medicine, and pet trade, as well as habitat loss to their decline (Stuart et al., 2019). In Thailand, Burmese pythons are protected by law under the Department of National Parks, Wildlife and Plant Conservation (DNP). Burmese pythons are also included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Species listed in Appendix II are not thought to be in immediate danger of extinction, but their trade must be regulated in order to protect and maintain populations. However, it is incredibly difficult to estimate snake population sizes due to their incredibly low detection rate (Dorcas and Wilson, 2009), meaning that there could be far fewer *P. bivittatus* in the wild than expected. It is likely best to give conservative estimates of snake population sizes rather than over-estimate population sizes considering snake populations world-wide are suffering from declines (Gibbons et al., 2000).

### 2.1.4 Burmese pythons as invaders

*Python bivittatus* occur outside of their native Southeast Asian range and are now an established invasive species in the Florida Everglades, USA. The Burmese python was first reported in the Florida Everglades as early in 1979 but was only recorded breeding in the Everglades 27 years later in 2006 (Dove et al., 2011). It is unclear how Burmese pythons became established in the Florida Everglades, but one hypothesis is that a large number of Burmese pythons escaped in 1992 during Hurricane Andrew when a trading facility suffered damage from severe winds and flooding.

Another, more biologically plausible scenario is that several mature individuals were released prior to 1985 and acted as founders to the population which was likely supplemented when large numbers were released during Hurricane Andrew (Willson et al., 2011). Burmese pythons are commonly kept as pets in the United States and are traded for their skins globally (Willson et al., 2011). Since their establishment in the Florida Everglades, researchers have focused on determining the effect of their introduction on the native fauna. Dorcas et al. (2012) discovered that gut contents of invasive Burmese pythons included remnants of 40 different native Florida species and suggest that a major decline in mammal populations is linked to the spread of Burmese pythons in the Florida Everglades. Dove et al. (2011) also analyzed gut contents of invasive *P. bivittatus* and found evidence of 25 different bird species consumed by Burmese pythons. Recently, scientists have discovered that Burmese pythons act as nest predators in wading bird communities and that predation rates by Burmese pythons at nest sites was 5 times higher than predation rates by native nest predators (Orzechowski et al., 2019).

Invasive Burmese pythons directly affect native fauna through predation but also affect native fauna indirectly by transmission of non-native parasites. Miller et al. (2017) used genetic sequencing to show that invasive Burmese pythons introduced a non-native lung parasite (*Raillietiella orientalis*) to native snake populations in the Florida Everglades. Furthermore, invasive pythons have affected the way that mosquitoes and native fauna interact, as invasive *P. bivittatus* have caused a severe decline in mid-size mammals that were once primary hosts for mosquitoes in the Florida Everglades (Hoyer et al., 2017). Since this decline in mid-size mammal populations, researchers compared data from mosquito blood meals from before and after the

invasion by *P. bivittatus* and discovered that mosquito bloodmeals from a single species, the hispid cotton rat (*Sigmodon hispidus)* have increased from 14.7% to 76.4% (Hoyer et al., 2017). The hispid cotton rat is a carrier of the zoonotic disease, the Everglades virus, which raises the concern of a potential increase in disease transmission as a result of increased host use by mosquitos.

Since their accidental introduction to the Florida Everglades, many studies have been attempted to assess Burmese pythons in their invasive range (Table 2.2). Yet, just two studies (Goodyear, 1994; Rahman et al., 2014) have focused on the ecology of native Burmese pythons. However, is worth mentioning that the paper by Rahman et al. (2014) did not appear in a peer-reviewed journal but in a published IUCN report.
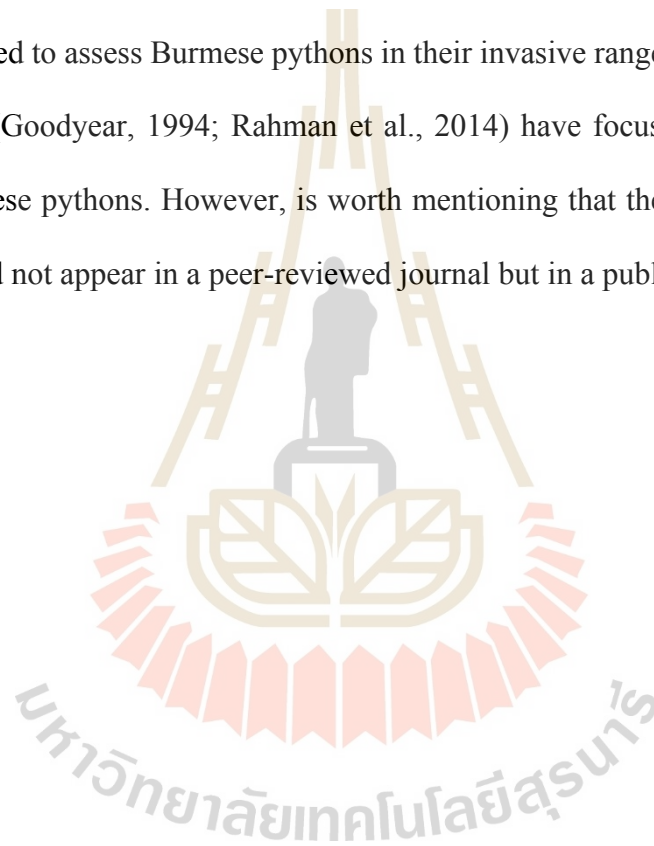
**Table 2.2** Summaries of studies conducted on *P. bivittatus* from their invasive range.

| Publication | Topic | Major Findings |
|---|---|---|
| Dorcas et al., 2012 | Effect of pythons on mammal populations | Introduction and spread of *P. bivittatus* coincides with declines in native mammal populations, especially mid-sized mammals. |
| Dove et al., 2011 | Predation of native avian species by pythons | Remnants of 25 native bird species found in the gut contents of invasive *P. bivittatus*. Burmese pythons have a potential to negatively impact bird populations. |
| Hart et al., 2015 | Spatial ecology and habitat use | Burmese pythons had large home ranges (mean 2250 ha) and showed low site fidelity. Majority of home ranges were from within slough and coastal habitats. |
| Hoyer et al., 2017 | Effects of invasive pythons on mosquito host use | Burmese pythons have been linked to decline in mid-sized mammals which has caused shift in host use of mosquitoes. Mosquito blood meals revealed that primary host is now a single species (Hispid cotton rat) and that diversity in host use has declined. |
| Hunter et al., 2015 | Using environmental DNA to detect pythons | eDNA analysis was used to detect Burmese pythons in 17 of 21 sites. Probability of detection using eDNA was between 0.59 and 0.87. |
| McCleery et al., 2015 | Mammal declines linked to invasive pythons | Experimental manipulation (translocation) of Marsh rabbits revealed that Burmese pythons were responsible for 77% mortality of study animals. Outside the experimental area, 71% of marsh rabbit mortality was due to mammalian predation. |
| Miller et al., 2017 | Parasite spread by invasive pythons | Burmese pythons have introduced a non-native lung parasite to native snakes in Florida Everglades. |
| Orzechowski et al., 2019 | Burmese pythons as nest predators in wading bird colonies. | Prior to 2017, no evidence of Burmese pythons at nesting sites of wading birds. Camera traps revealed that nest predation rate by Burmese pythons was 5x higher than native predators. |

**Table 2.2** (Continued).

| Publication | Topic | Major Findings |
|---|---|---|
| Pittman et al., 2014 | Navigational ability | Burmese pythons that were translocated far distances (21-36km) from their initial capture location via homing. Translocated snakes moved faster and in a more direct fashion towards their capture location than non-translocated snakes. |
| Reed et al., 2011 | Testing trap methods for invasive pythons | Trapping yielded in the capture of 3 individuals but was not considered successful as each trap had a capture rate of under 0.05%. |
| Smith et al., 2016 | Using Judas technique during breeding season | Tracking during breeding season resulted in 8 "betrayal" events where a tracked python led researchers to one or more non-tracked pythons in breeding aggregations. Mean daily movement for males was significantly greater than movement in females. |
| Snow et al., 2007 | Burmese python diet | Gut content analysis revealed that 50/56 pythons analyzed had remnants of 12 mammal species, five bird species, and one python was found attempting to consume an alligator. |
| Walters et al., 2016 | Habitat selection | Snakes selected habitat non-randomly. Snakes selected for broad-leafed and coniferous forest even though they were "less available" than other habitat types. |

## 2.2    Habitat Use of Burmese Pythons

Very little is known about the mechanisms that drive habitat selection and use for Burmese pythons. Within their native range, Burmese pythons occur in tropical lowlands, mangrove forests, rainforests, grasslands, and within human settlements (Barker and Barker, 2008). In a preliminary study done in Bangladesh, Rahman and others (2014) translocated and subsequently radio-tracked four Burmese pythons across a heterogenous landscape bordering Lawachara National Park. Burmese pythons appeared to use habitats differently depending on the individual, but as a whole Burmese pythons were found to use disturbed habitats such as degraded forest, tea plantations, plantations and orchards disproportionately to other habitat types available (Rahman et al., 2014). The Burmese pythons included in this preliminary investigation were captured in villages and amongst human settlements before being translocated, which suggests that Burmese pythons also use anthropogenically modified areas.

Scientists in the Florida Everglades explored the habitat use of radio-tracked Burmese pythons by comparing the habitat type selected by tracked animals vs. the habitat available to tracked animals via compositional analysis. Results showed that Burmese pythons used certain habitat types disproportionately to their availability, in other words, Burmese pythons actively selected certain habitat types even when other habitat types were more frequently available (Walters et al., 2016). Resource selection models revealed that habitat edge (HE), which was classified by forest land cover grid cells (50m) directly adjacent to marsh grid cells, and landcover type (LC) were the best predictors for habitat selection of tracked animals (Walters et al., 2016). Selecting for edges of habitats is not uncommon for snakes as edge habitats may provide optimal

thermoregulation opportunities (Blouin-Demers and Weatherhead, 2002) as well as foraging opportunities (Eskew et al., 2009; Wittenberg, 2012).

## 2.3    Spatial Ecology of Burmese Pythons

The existing literature about the spatial ecology of free-ranging, native *P. bivittatus* is sparse at best. In 1992, a single Burmese python was tracked in Hong Kong for 24 days after a researcher was notified of a female Burmese python that had consumed a local persons' chicken. Over the course of the study, the individual maintained a home range of 12.3 hectares (Minimum Convex Polygon) (Goodyear, 1994). More recently, there has been one published study focused on understanding the spatial ecology of native *P. bivittatus* in Bangladesh by Rahman and others (2014). In the aforementioned study, four *P. bivittatus* were captured in a village bordering Lawachara National Park and implanted with radio transmitters before being released into the national park and subsequently radio tracked. Radio tracking revealed that the average home range sizes of tracked pythons averaged at 95.67 hectares (Kernel Density Estimate) and that *P. bivittatus* seemingly preferred areas modified by humans over natural forest within the national park. While the results gathered by Rahman et al. (2014) are useful to begin to bridge the gaps in the literature about the ecology of native *P. bivittatus*, the nature of the study likely does not allow for us to gather a complete picture of the spatial ecology of *P. bivittatus* due to the fact that the snakes were translocated from areas of human use into the national park. Translocation studies in the past have found that movements of translocated snakes are often irregular compared to the movements of non-translocated snakes (Reinert and Rupert, 1999; Plummer and Mills, 2000; Butler et al., 2005).

While *P. bivittatus* in their native range have been neglected in research, invasive populations of Burmese pythons in the Florida Everglades National Park have held the attention of researchers since their introduction and therefore have been the focal animals of several spatial ecology studies. Studies on the spatial ecology of invasive Burmese pythons have revealed that in the Florida Everglades, Burmese pythons use large amounts of space and show low site fidelity (Hart et al., 2015; Smith et al., 2016). The contrast in home range sizes between native and invasive radio-tracked *P. bivittatus* (Table 2.3) may be explained by the fact that within their introduced range they have no natural predators and a generalist approach allows for them to move through the Florida Everglades with very few biological constraints (Reed et al., 2012).
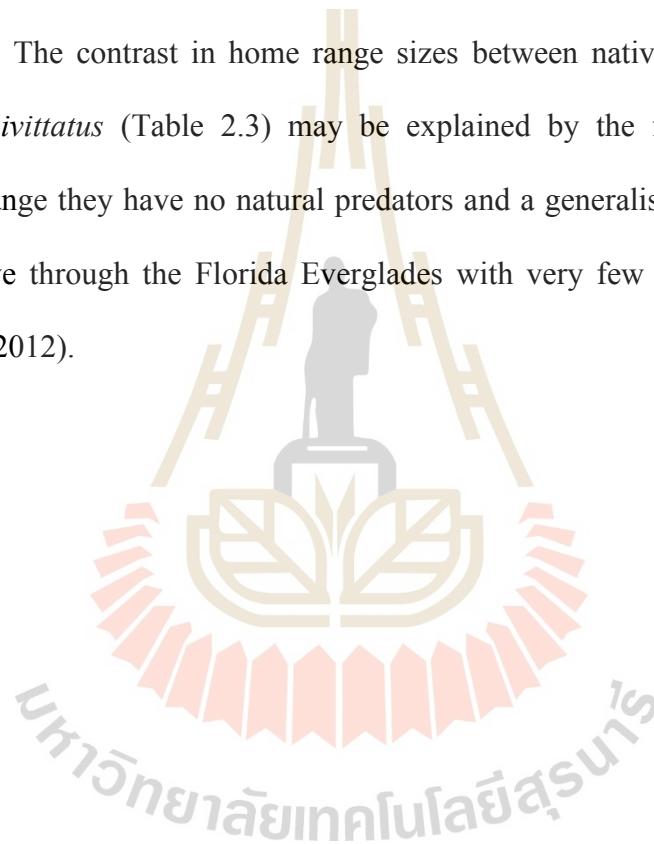
**Table 2.3** Summarized home range results from spatial ecology studies of both native and invasive *P. bivittatus* (Goodyear, 1994; Hart et al.*,* 2015; Rahman et al.*,* 2014, Smith et al.*,* 2016).

| Publication | Native or Invasive | Mean Home range size (ha) | Mean Number of days tracked | Tracking Regime | Estimation Method | Smoothing method | # of Individuals |
|---|---|---|---|---|---|---|---|
| Goodyear 1994 | Native | 12.3 | 24 | N/A | Minimum Convex Polygon | N/A | 1 |
| Rahman et al., 2014 | Native | 95.67 (SD= N/A) | N/A | 1x/day | Kernel Density Estimation | 55%-95% | 3 |
| Hart et al., 2015 | Invasive | 2250 (SD= 2130) | 319.9 (SD= 184.3) | 1x/week | Minimum Convex Polygon | N/A | 16 |
| Smith et al., 2016 | Invasive | 710 (SD= 1270) | 89 (SD= 30.2) | 1x/week | Minimum Convex Polygon | 100% | 33* |

*25 individuals were tracked, however 8 were tracked in consecutive seasons. Home range sizes were calculated seasonally, adding up to 33 home range estimates

## 2.4    Interactions Between Snakes and Humans

### 2.4.1 Snake-human Conflict

Human-wildlife conflict occurs as humans and native fauna compete for space, which has become increasingly more common with the expansion of human populations into spaces that were once habitat for wildlife (Barua et al., 2013). Human wildlife conflict is seen worldwide and involves species covering a wide variety of taxa (Seoraj-Pillai and Pillay, 2017). Human-wildlife conflict involving snakes is no exception, especially considering the fact that snakes are a widely held fear across cultures (Fredrikson et al., 1996; Öhman and Mineka, 2003). When animals, like *P. bivittatus* use human dominated landscapes, we can expect for conflict between humans and pythons to arise. Snake-human conflict likely has two underlying motivators, one being that venomous snakes may pose a potential human-health risk through snakebite (World Health Organization, 2019) and the other being that snakes may predate on livestock or commensal animals (Amador-Alcalá et al., 2013; Miranda et al., 2016). Pythons have been recorded consuming both livestock and pets (Goodyear 1994; Shine and Fitzgerald, 1996; Shine et al., 1998; Fearn et al., 2001; Luiselli et al., 2001; Goursi et al., 2012*;* Butler et al., 2013; You et al., 2013) and are therefore likely involved in snake-human conflict. Livestock loss due to wildlife predation poses a socio-economic issue, rather than a human health issue (Mishra, 1997; Barua et al., 2012). Domestic and livestock animals not only serve as primary sources of food for some, but in rural areas where people depend on domestic animals for their livelihood, livestock may be their primary economic asset (Romanach et al., 2007).

**2.4.2 Pythons in Human Modified Landscapes**

*Python bivittatus* have been recorded within their native range in areas of human use, such as agricultural land, plantations and in and around human settlements (Goodyear 1994; Barker and Barker, 2008; Rahman et al., 2014). Other species of the *Pythonidae* family have also shown a tendency to use areas of human settlements in suburban and rural areas of Australia (Shine and Fitzgerald, 1996; Fearn et al., 2002; Corey and Doody, 2010). It is not clear as to why large snakes such as pythons use areas disturbed by humans, however one possible explanation could be their prey preference of mammal and bird prey items (Luiselli et al., 2001; Kasterine et al., 2012; Natusch et al., 2016). Potential prey items such as rats, mice, and small livestock animals (e.g., chickens, ducks, geese) are often abundant in areas of human settlements (Brooks and Jackson, 1973; Langton et al., 2001). Throughout the course of our research we hope to elucidate the movements and subsequent habitat selection of Burmese pythons in a landscape that has been heavily transformed by human activities.

# CHAPTER III

# MATERIALS AND METHODS

## 3.1    Study Site

We conducted all fieldwork in the Sakaerat Biosphere Reserve (SBR) (Figure 3.1) in Nakhon Ratchasima Province, Thailand. The Sakaerat Biosphere Reserve is approximately 285 kilometers northeast of Bangkok Province in the Korat Plateau with elevations ranging from 250 to 762m above sea level (Trisurat, 2010). Annually, the SBR receives approximately 1260mm of rain with a mean yearly temperature of 26.0° (Silva et al., 2018). Using cluster analysis, Marshall et al. (2020) grouped the climatic conditions of the Sakaerat Biosphere Reserve into three seasons: hot (mean: 33.8 ± standard error [SE] 2.8°C; 2.5 ± 7.9 mm rainfall), wet (29.9 ± 2.2°C; 5.9 ± 11.1 mm rainfall) and dry (29.0 ± 3.5°C; 0.2 ± 0.8 mm rainfall). Hot season ranges from 16/03-30/09, the wet season is from 01/10-31/12 and finally the dry season runs from 01/01-15/03. The SBR is included in UNESCO's Man and Biosphere (MAB) program. The biosphere includes three main areas; a core area, buffer zone and transitional zone. The core area covers approximately 8,000 ha and consists of protected forests of varying types; dry evergreen forest (60%), dry dipterocarp forest (18%), and several small patches of reforested area, grasslands and bamboo patches which make up the remaining area (22%).

The core area enjoys increased protection as it regularly patrolled by forest rangers in effort to protect native flora and fauna. Outside of the protected area are an unprotected buffer and transitional zone that in total cover 36,000 ha. The buffer zone has fragments of unprotected or disturbed forests along with patches of plantation forest regrowth. The transitional zone is land almost exclusively used for agriculture, human settlements, and infrastructure (Figure 3.2). The agricultural area is used to produce mainly rice paddy, cassava, sugarcane and corn.
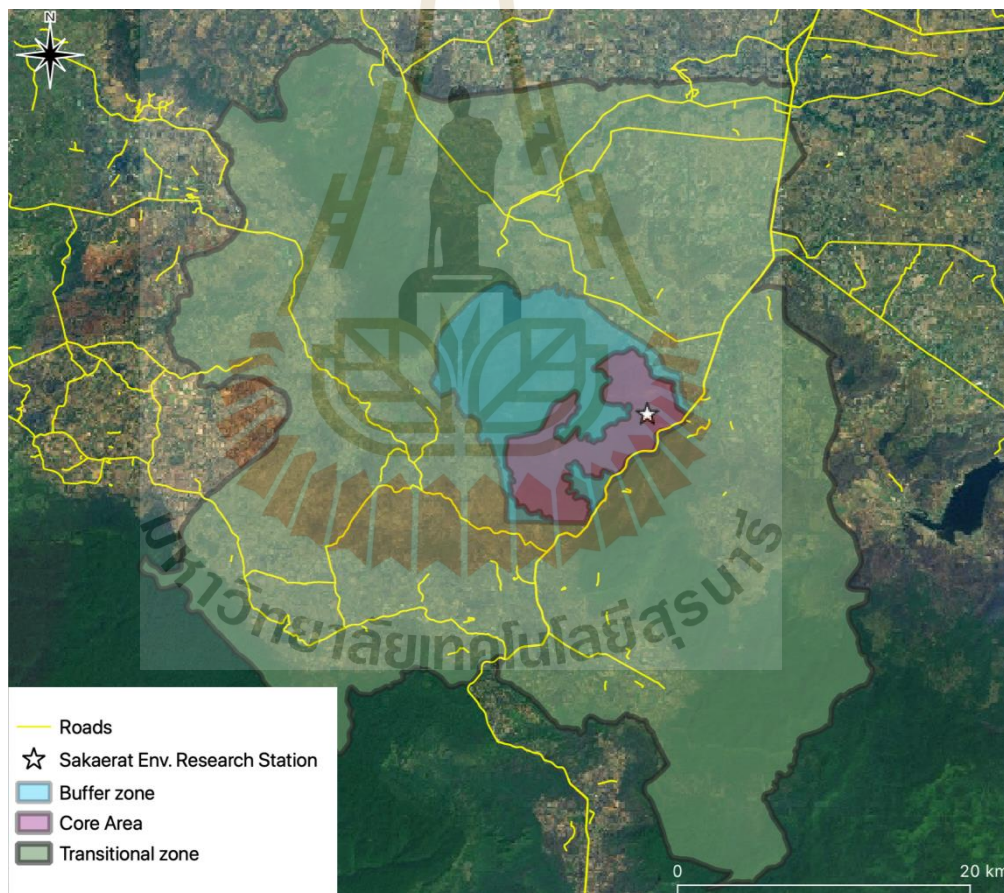


**Figure 3.1** Map of the Sakaerat Biosphere Reserve created using QGIS (Version 3.4) software.
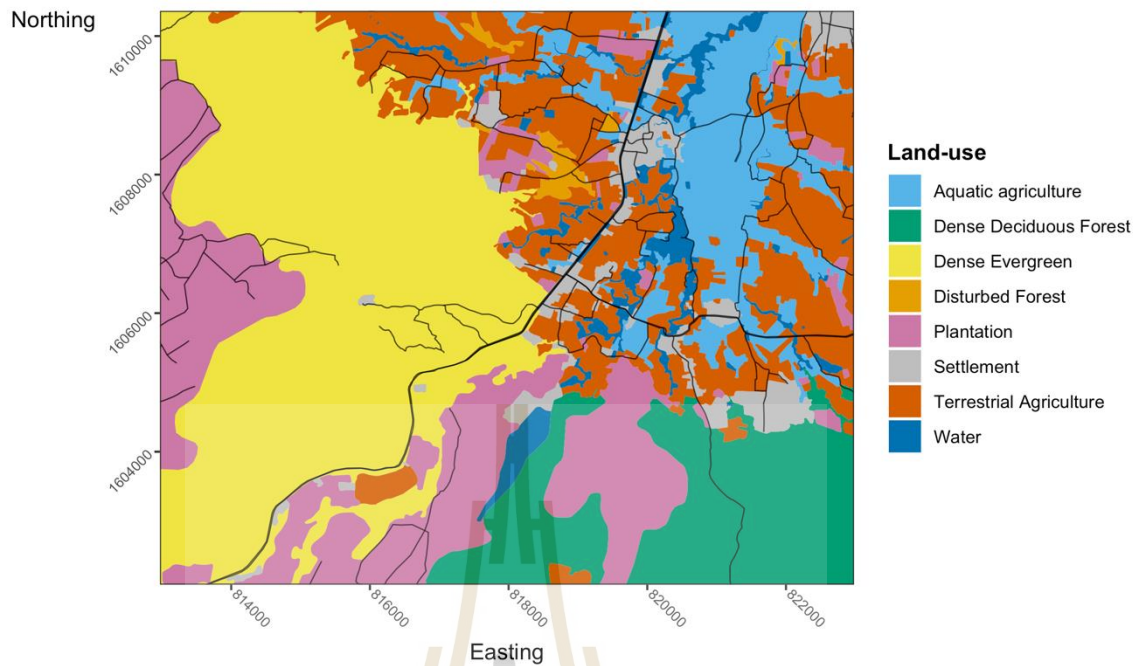
**Figure 3.2** Land use types found in study area. Roads are marked by black lines throughout the map. Figure recreated and modified from Smith et al. (2020).

## 3.2    Capture of Study Animals

We captured Burmese pythons through use of visual encounter surveys, notations from local residents, collaboration with rescue teams and through opportunistic encounters. Due to low detection rates of Burmese pythons, and snakes in general, we targeted our visual encounter surveys to areas where Burmese pythons had been observed before (mainly the agricultural area). We conducted visual encounter surveys both on foot and via road-cruise (i.e., searching for target animals while using a vehicle). To quantify survey effort, we recorded durations of surveys (hours), kilometers covered on foot and/or via road cruise.

We relied heavily on notifications from local residents and collaboration with the Udom Sab/Hook 31 Rescue team for assisting in the capture of many Burmese

pythons. We were fortunate to have several native speakers from the Sakaerat Environmental Research station help to facilitate snake calls and collaboration with the rescue team. On a few occasions, we located Burmese pythons opportunistically.

## 3.3 Morphometric Data Collection and Transmitter Implantation Surgery

Following the capture of Burmese pythons, we brought snakes back to our field laboratory at the Sakaerat Environmental Research station. We collected biometric measurements such as snout to vent length (SVL) (mm), tail length (TL) (mm), head length (mm), head width (mm) and mass (g). We also used this opportunity to determine the sex of Burmese pythons through the use of cloacal probing (Schaefer, 1934) as well as overall health and body condition of the animal. Prior to taking biometric measurements, we restrained snakes by placing their head in a clear, plastic tube. We used an inhalant anesthetic, isoflurane to temporarily anesthetize snakes. Using isoflurane allowed for us to minimize stress to the snakes during processing as well facilitate more accurate or standardized measurements. We collected all biometric data after the snake had lost muscle tone.

We intended to restrict radio-transmitter implantation to adult female Burmese pythons only, however due to human error we misidentified the sex of one adult male Burmese python and included him in our sample. We had a licensed veterinarian D.V.M Wirongrong Changphet of Nakhon Ratchasima Zoo complete all radio-transmitter implantation surgeries. We implanted Burmese pythons with Holohil model SI-2 11 gram or 13-gram very high frequency (VHF) transmitters to ensure that transmitter size did not exceed more than 5% of the animal's total body mass. D.V.M Wirongrong

Changphet completed surgeries following methodology outline by previous radio-telemetric studies (Reinert and Cundall, 1982; Hardy and Greene, 2000) and were in accordance with veterinary practices Act B.E. 2545.

Following processing and implantation surgeries, we intubated snakes via inspiratory ventilation using an endotracheal tube. We monitored implanted snakes for 12-24 hours before releasing them. When feasible to do so (i.e., snake tracked longer than 6 months) we recaptured study animals every six-eight months to collect biometric data and assess overall health.

## 3.4 Radio-Telemetry Tracking and Field Data Collection

We set out to radio-track all implanted snakes one time per day during daylight hours (06:00-18:30). We homed in directly on snakes in attempt to increase accuracy of our location data. However, in the event that snake locations did not allow for us to home in due to the snake being in water bodies or in otherwise inaccessible terrain, we used triangulation to locate snakes from the closest possible distance. Upon locating tracked snakes, we recorded location data (UTM coordinates), GPS accuracy (m), whether or not the snake moved (yes/no), distance moved (m) as well as habitat type used (Table 3.1). We also collected environmental data such as temperature at time of track (°C) and relative humidity (%). In the event that a snake was visible, we recorded any behaviors displayed (Table 3.2). We collected all data using the smartphone application (iOS and Android) Epicollect 5. The use of smart phone data forms allowed for us to upload data directly to a cloud database which lowered risk of potential data loss.

We also used camera traps when they were available and when the snake was in an appropriate location for camera trap placement, such as areas without excess vegetations or other obstructions to the view of the snake's shelter site. We used camera traps in attempt to record behaviors such as ambushing, feeding, or mating (Table 3.2) in order to record natural history information.

**Table 3.1** Description of habitat types in study site.

| Habitat type | Description |
| --- | --- |
| Agriculture | Land used for crops, cultivation, irrigation, farming |
| Human Settlement | Area modified for man-made structure (house, restaurant, shed, store, etc.) |
| Ecotone | Area where two or more forest types meet |
| Pond | Man-made or natural body of still water |
| Plantation Regrowth | Old plantation forest with new forest growth |
| Plantation | Plot of land with planted trees such as eucalyptus, rubber, acacia, etc. planted in rows |
| Open | Land that has been cleared of vegetation, no canopy cover (i.e., construction areas) |
| Dry Evergreen Forest | Protected forest characterized by evergreen trees dominating canopy |
| Dry Dipterocarp Forest | Protected forest characterized by dipterocarp grass and single layer canopy |
| Mixed Deciduous Forest | Mix between DEF and DDF, bamboo grass absent |
| Heterogeneous Disturbed Forest | Mixed forest types, outside of core protected area, typically littered with anthropogenic waste |
| Bamboo Forest | Bamboo stands account for majority of canopy cover |
| Fragmented Dry Dipterocarp Forest | Patches of dry dipterocarp forest existing outside of core protected area |

**Table 3.2** Ethogram describing potential behaviors displayed by *P.* bivittatus. More than one behavior may be displayed at a time.

| Behavior | Description |
| --- | --- |
| Sheltering under cover | Majority of snakes' body is concealed |
| Moving | Snake is slowly moving in no distinct direction, repositioning |
| Fleeing | Snake is quickly moving away from observer |
| Tongue flicking | Snakes' tongue is extended and retracted repeatedly |
| Basking | >50% of snakes body is exposed to sunlight, sat still |
| Swimming | Snake is actively moving through water |
| Neutral position | Snakes' head is rested on body or ground, snake is not moving |
| Ambush position | Snakes' head is lifted off of ground and angled slightly upwards, snakes' body is coiled |
| Hissing | Audibly exhaling |
| Striking | Snake moves from ambush position and extends head and at least 1/3 of anterior part of body quickly before retracting head |
| Feeding | Snake is actively consuming prey item |
| Mating | Snake is in contact with male individual |
| Brooding | Snakes' body is coiled around egg mass |

## 3.5    Spatial Analysis

We quantified space use (occurrence distributions) and motion variance through the use of dynamic Brownian Bridge Movement Models (dBBMMs). Historically, many herpetology field studies focused on quantifying space use (or home range) have used Minimum Convex Polygons (MCPs) and Kernel Density Estimates (KDEs). Minimum convex polygons are calculated by taking the furthest most locations observed for the tracked individual and drawing the smallest possible polygon around these points and taking the area of the polygon (Powell, 2000). Kernel density estimates are used to identify areas of core use by placing a kernel over observed locations within

the distribution, which should highlight areas of core use with locations within close proximity of each other showing strong overlap of kernels (Seaman and Powell, 1996). In both of these more traditional estimation methods, movement and space use is only evaluated at the spatial scale whereas movement occurs at a spatiotemporal scale. Furthermore, MCPs and KDEs tend to vastly overestimate space use and are not adequate for modeling reptile movement (Silva et al., 2018; Silva et al., 2020).

In contrast, dBBMMs are more representative of animal movement and how it occurs over space and time. Dynamic Brownian Bridge Movement Models take into account the order of relocations and how much time an animal spends at each location and operate under the assumption that the animals' previous locations and future locations are related, whereas locations in traditional methods are treated independently of each other (Kranstauber et al., 2012). The use of dBBMMs also requires that users input the window and margin size during calculation which helps to explore the motion variance. Motion variance is essentially a measurement in changes or variation in movement intensity and can be used to identify behavioral changes. The window size acts as a snapshot of the animal's behavior while the margin size is the margin that is used to detect changes in motion variance. Both the window and margin size should be biologically relevant to the study animal. To determine window and margin size, I followed methodology similar to that outlined by Marshall et al. (2020). As we observed Burmese pythons remained stationary for long durations of time (~2 weeks), we used a window size of 15 data points. For margin size, we used a margin of 3 datapoints as we were able to detect differences in behaviors (movement vs. stationary) over the course of two data points. The model also requires that window and margin

size be odd numbers, which is why we selected a window size of 15 and margin size of three rather than 14 and two.

We were also interested in exploring site fidelity, or the reuse of shelter sites of our study animals. In their invasive range, Burmese pythons were observed to not exhibit site fidelity and rarely returned to areas previously used (Hart et al., 2015). We used recursive analysis in package *recurse* v.1.1.2 (Bracis et al., 2018) to investigate whether or not snakes in our study site would reuse shelter sites. To do this, we took the mean GPS error to determine the radius of sites to be used in our analysis for each individual. We classified revisits as any time an individual moved away from a site and then returned to the site at any point after 24 hours had elapsed (our targeted tracking lag). The output of recursive analysis provided us with residence times (h) that individuals spent at reuse sites as well as the frequency of which they returned back to shelter sites.

## 3.6    Seasonality

We used motion variance calculated via dBBMMs to detect differences in movement in relation to the hot, wet, and dry seasons. As we only tracked three individuals through all three seasons (PYBI021, PYBI022, and PYBI029), we were only able to detect seasonal differences for these three individuals. For these three individuals, we also calculated dBBMM occurrence distributions (99% confidence areas) for each season they were tracked for its entirety. In the event that a snake was tracked through an entire season multiple times (i.e., tracked in consecutive years) we took the average occurrence distribution (ha).

We also investigated the probability of movement (snake moved yes/no) using a Bayesian regression model with a Bernoulli distribution. For our predictor variables, we used seasons delineated from Marshall et al. (2020) (hot, wet or dry) and daily rainfall (mm), as well as individual ID as a random effect. We used rainfall data collected from the five weather stations at the Sakaerat Environmental Research station, where we used the average rainfall collected daily. There was missing rainfall data for portions of our tracking period meaning that we could only investigate movement probability from 09/01/2019-22/07/2020.
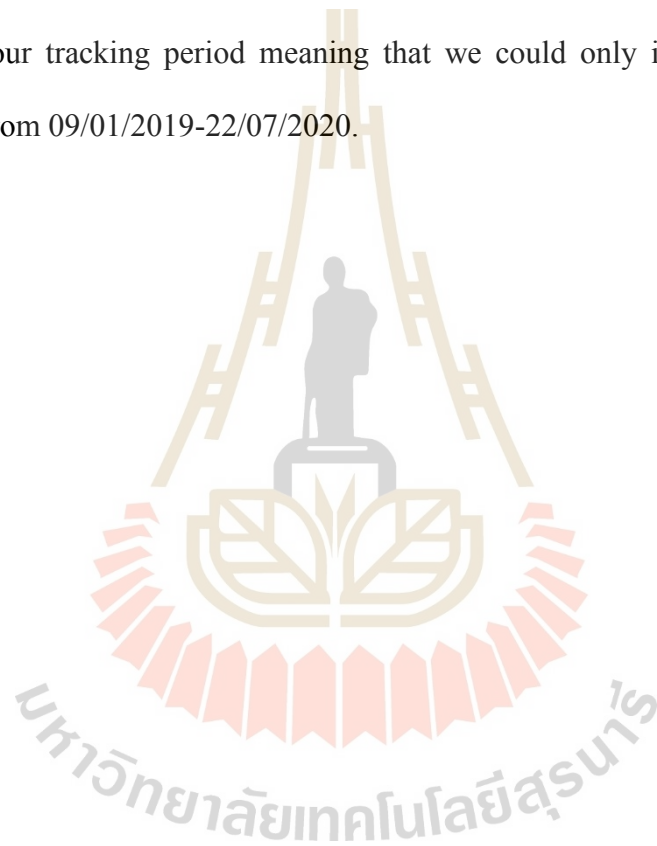
**Table 3.3** Packages used for data analysis in RStudio.

| Package | Author | Package used for |
|---|---|---|
| dplyr | Wickham et al., 2020 | Data manipulation |
| data.table | Dowle & Srinivasan, 2020 | Data manipulation |
| reshape2 | Wickham, 2007 | Data manipulation |
| readr | Wickham et al., 2018 | Reading data into Rstudio |
| lubridate | Grolemund & Wickham, 2011 | Working with dates/times |
| stringr | Wickham, 2019 | Reading data into Rstudio |
| pracma | Borhers, 2019 | Calculating means/SE |
| rgdal | Bivand et al., 2010 | Reading in shapefiles into Rstudio |
| raster | Hijmans, 2020 | Create and work with rasters |
| sp | Bivand et al., 2013 | Work with shapefiles |
| ggplot2 | Wickhham, 2016 | Data visualization |
| scales | Wickham & Seidel, 2020 | Manipulating plot/map scales |
| ggthemes | Arnold, 2019 | Color palettes for visualization |
| ggspatial | Dunnington, 2018 | Visualizing spatial data |
| cowplot | Wilke, 2019 | Data visualiztion |
| move | Kranstauber, 2020 | Calculate occurrence distributions and motion variance |
| adehabitatHR | Calenge, 2006 | Extract occurrence distribution |
| rgeos | Bivand & Rundel, 2020 | Calculate occurrence distribution areas |
| recurse | Bracis et al., 2018 | Revisit analysis |
| amt | Signer et al., 2018 | Individual level integrated step selection analysis |
| INLA | Rue et al., 2020 | Population level integrate step selection analysis |
| brms | Bürkner et al., 2020 | Bayesian regression modeling |

## 3.7    Habitat Selection

To investigate habitat selection of Burmese pythons at the landscape scale, we used integrated step selection analysis at both the individual and population level. Integrated step-selection functions are a way to understand habitat used by tracked individuals vs. habitat that is perceived to be available to the individual and to predict habitat use (Thurfjell et al., 2014). Understanding an animals' habitat selection can also be used to understand animal movement as animal movement and habitat use are closely linked (Van Moorter et al., 2016). This method incorporates animal movement throughout landscapes, where each observed location (obtained through telemetry data) is treated as a step. For each observed step, there are several random steps calculated where the animal could have gone or used habitat "available" to the animal, which represents habitat actually used by the animal vs. habitat available to the animal. Random steps are sampled from the distribution of the animals' previous observed steps and the step characteristics (distance between steps, direction) (Avgar et al., 2016). In step-selection functions, predictor covariates (e.g., habitat type, vegetation type, distance to relevant landmarks such as roads or open water) may be taken into account and weighed against each other to determine which habitat features help to characterize animal movement via habitat selection.

We included all snakes in our integrated step selection analysis that used more than one habitat feature. We used package *amt* (Signer, 2018) to create integrate step selection functions (ISSFs) at the individual level. We used the distance to particular habitat features to determine selection versus avoidance. We used a shapefile provided by the Thai Land Development Department (2017) that contained land use data for our study site. We separated the land use categories to create raster layers.

We created continuous raster layers by taking the Euclidean distances to certain habitat features (water bodies, forest, terrestrial agriculture, human settlements, roads and aquatic agriculture). We inverted our raster layers (i.e., inverted Euclidean distances) to avoid zero-inflation of distances to our habitat features of interest. By inverting our raster layers, this also allowed for easier interpretation of our results (i.e., an association for habitat feature is represented by a positive estimate). We selected top models for predicting habitat selection using Akaike's Information Criterion (AIC) where models within $\Delta$ AIC < 2 were considered to be the top performing models.

In order to account for the coarseness of VHF data, we generated 200 random steps for each observed step (i.e., relocation). For individual level ISSF, we created ten models including the step length (i.e., distance between relocations) and turn angle for each step. One of these ten models was a null model which included only step length and turning angle to predict movement. We created six models that used a single habitat feature to predict selection and an additional three multi-factor models which included a combination of the three different habitat features to predict selection.

To explore habitat selection at the population level, we used modified code provided by Muff et al. (2019). We created Poisson models with stratum-specific effects to create population level ISSFs using a Bayesian framework. For population level analysis we created six single factor models using the same habitat features and rasters we used for investigating individual level habitat selection. Similar to creating individual level ISSFs, we randomly generated 200 steps for each observed location. Following methodology from Muff et al. (2019), we used a weak prior of 0.0001 for our fixed effects. We fitted our Bayesian models using integrated nested Laplace approximations in package *INLA* (Rue et al., 2020).

## 3.8    Reproductive Biology

As we radio-tracked one male Burmese python, we examined his motion variance during the perceived breeding season (November-February) based off of breeding seasons for Burmese pythons in their invasive range. Breeding seasons for native Burmese pythons have not been identified in the literature. We captured and began tracking our male, PYBI028 in January 2019 which did not allow for us to examine his movement through the entirety of the perceived breeding season. However, following his release, he exhibited steep peaks in motion variance, potentially in pursuit of females.

Furthermore, we placed a camera trap at the shelter site of one of our females during the breeding season as she remained in the same burrow for an extended period of time (>30 days). We used camera trap images to observe copulation as well as the presence of other snakes (presumably males) around the burrow.

As Burmese pythons provide an increased level of maternal care and stay with their eggs following oviposition up until hatching, we were able to infer when a female was with a nest via observations made during tracking (i.e., snake had been in the same location for an extended duration). We confirmed presence of nests after a snake had been in a site for 30 days following the breeding season. We then monitored nests closely in attempt to estimate approximate incubation periods. Following hatching, we collected neonates to collect morphometric parameters and to determine nest success. We determined nest success by comparing number of hatched individuals (via counting number of vacant eggs) and the number of eggs laid total. We were also able to gather incubation temperatures for one nest through placing a datalogger (recording at 15-minute intervals) into a nest laid by PYBI055.

# CHAPTER IV

# RESULTS AND DISCUSSION

## 4.1 Results

### 4.1.1 Captures

Throughout the course of our study, we captured 67 individuals through various capture methods (Figure 4.1). The individuals captured represented Burmese pythons of all age classes and of both sexes. Aside from capturing hatchlings from our monitored nests, the most fruitful method of capturing Burmese pythons was through notification from local residents within our study site and through collaboration with the Udom Sab/Hook 31 rescue team, which resulted in the capture of 25 individuals. Opportunistic encounters of Burmese pythons led to the capture of six Burmese pythons. Visual encounter surveys resulted in the capture of five individuals. We recorded visual encounter survey effort between 27/07/2019 and 09/04/2020, where we covered 1707.98 km via road cruise and 96.4 km on foot over the course of 177 hours and 34 minutes (Figure 4.2). The remaining 31 individuals were neonates from the nests of two of our tracked individuals.
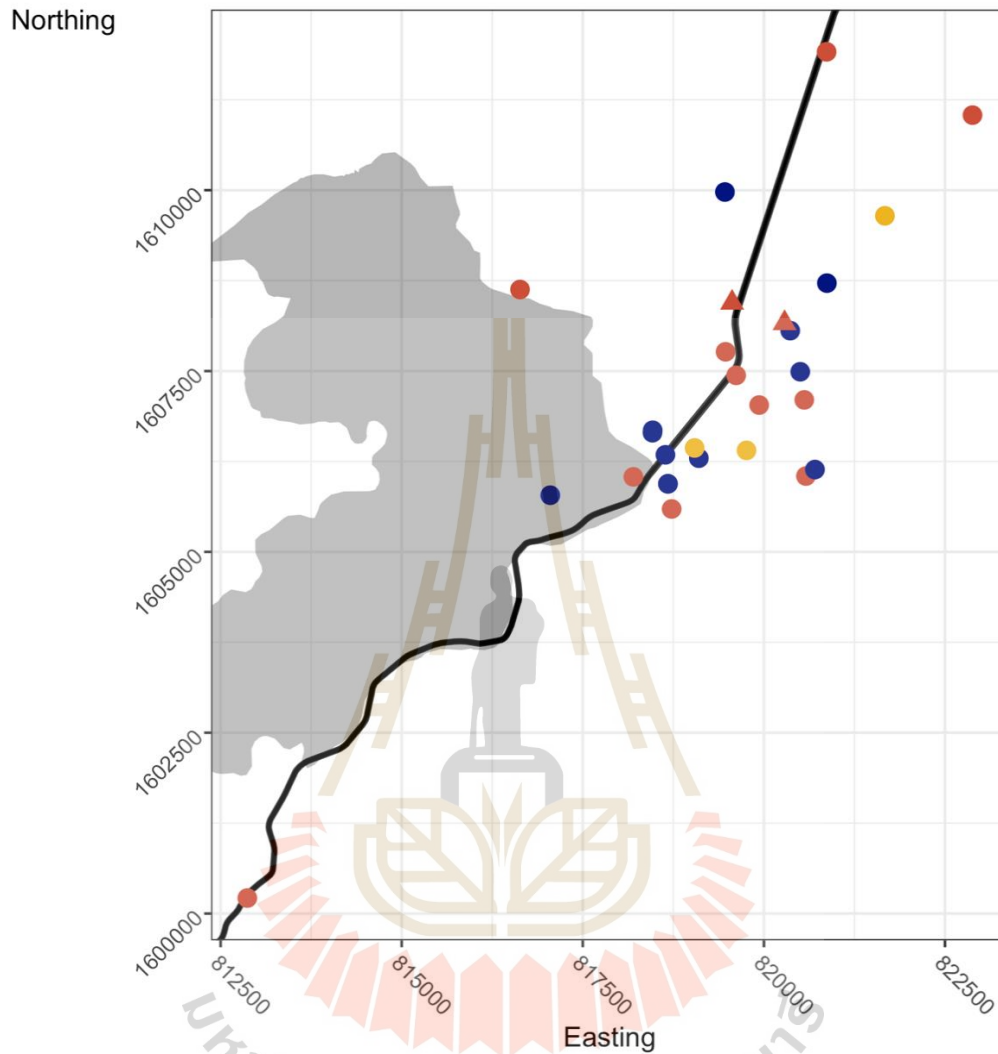
**Figure 4.1** Capture locations of Burmese pythons. Blue circular points represent Burmese pythons captured during the wet season, orange circular points indicate capture locations during the hot season, and Burmese python capture locations during the dry season are marked by yellow circular points. Two nest locations are marked by orange triangles. The core area of the Sakaerat Biosphere Reserve is shown by the grey shaded area and the Highway 304 is displayed by the darkened line across the map.
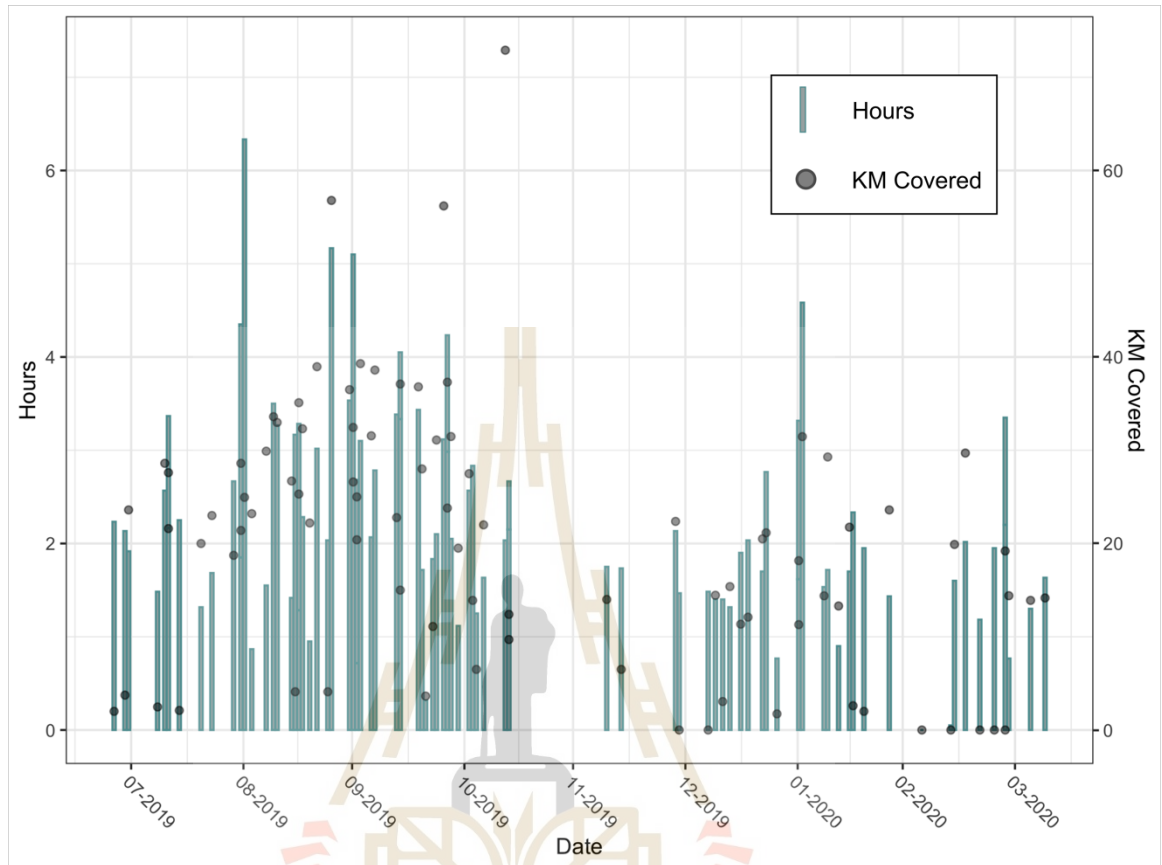
**Figure 4.2** Recorded visual encounter survey effort. Effort hours are measured on the left Y axis and plotted with blue bars. Total kilometers covered (includes KM covered on foot and via road cruise) are measured using the right Y axis and illustrated by grey points on the plot.

### 4.1.2 Morphometrics

Of these 67 we were able to collect morphometric information for 65 individuals (Table 4.1) as well as re-collect morphometric data for four of our radio-tracked individuals on recaptures (Table 4.2). We have broken up average estimates between adult males, adult females and juveniles which include measurements from both males and females. We considered any male individuals with a total length (snout-vent length plus tail length) of 2000mm or less are considered to be juveniles while females with a total length of 2500mm or less.

**Table 4.1** Mean biometric measurements from captured *P. bivittatus* captured in study area. SVL: Snout to vent length; TL: tail length

|  | SVL (mm) | TL (mm) | Mass (g) | N |
|---|---|---|---|---|
| Males | 2199.67 (SE = 32.6) | 333.08 (SE= 5.9) | 6239.58 (SE = 612.4) | 12 |
| Females | 2595.09 (SE= 141.9) | 338.09 (SE = 15) | 8910.57 (SE= 2433.7) | 11 |
| Juveniles | 1355.67 (SE = 157.5) | 192.33 (SE = 22.2) | 2073.57 (SE = 684.2) | 9 |
| Neonates | 534.91 (SE = 7.3) | 74.85 (SE = 1.8) | 110.94(SE = 2.9) | 33 |

**Table 4.2** Biometric measurements from all radio-tracked individuals from their first processing and most recent processing as well as total growth.

| ID | Sex | SVL (mm) | TL (mm) | Mass (g) | # of recaptures | SVL at most recent capture (mm) | TL at most recent capture (mm) | Total growth (mm) |
|---|---|---|---|---|---|---|---|---|
| PYBI021 | Female | 2732 | 320 | 12635 | 4 | 2744 | 330 | 22 |
| PYBI022 | Female | 2331 | 314 | 8355 | 2 | 2360 | 318 | 33 |
| PYBI028 | Male | 2306 | 355 | 8425 | 1 | 2314 | 352 | 5 |
| PYBI029 | Female | 2312 | 297 | 7330 | 3 | 2423 | 300 | 114 |
| PYBI033 | Female | 2214 | 296 | 6780 | 0 | NA | NA | NA |
| PYBI055 | Female | 3085 | 401 | 19485 | 0 | NA | NA | NA |
| PYBI060 | Female | 2472 | 340 | 7815 | 0 | NA | NA | NA |
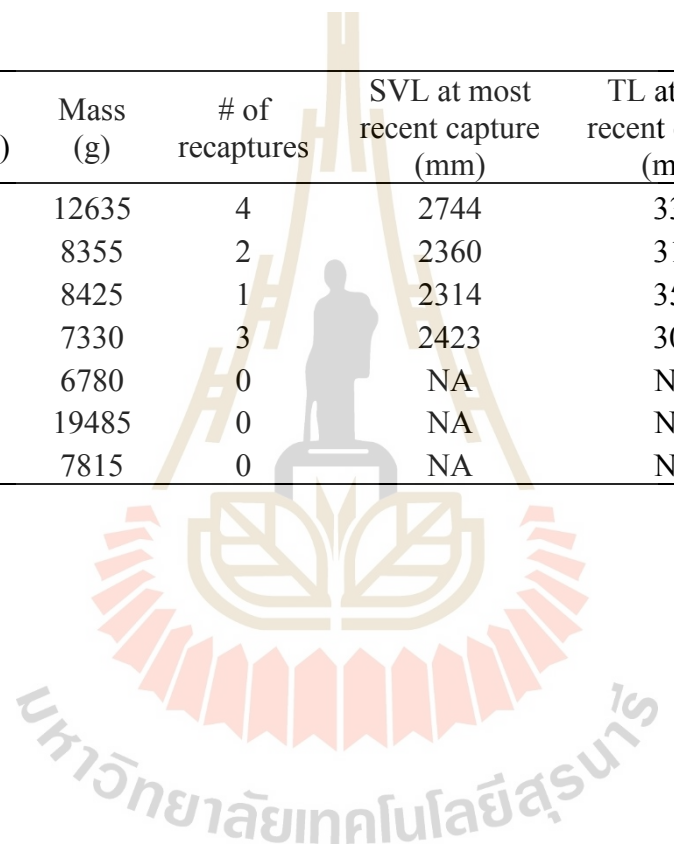
### 4.1.3 Radio-tracking

We captured, implanted and radio-tracked seven adult Burmese pythons (6 females, 1 male). Our study period lasted approximately 22 months from 2018-09-29 to 2020-07-22. On average, we tracked snakes for $327 \pm$ SE 85 days (range $= 41 - 662$ days) (Table 4.3). During the radio tracking period, we located snakes on average 310 $\pm$ 80 times (range $= 41 - 631$ times). Our target time lag, or time between consecutive data points for individuals was 24 hours, however there were several instances when snakes were not tracked every day (Figure 4.3). Despite these events, our mean tracking lag was $25.43 \pm 0.32$ hours (range $= 8.55 - 452.77$ hours). The results in this section have been used to produce a preprinted manuscript which is available at: https://doi.org/10.1101/2020.09.17.302661.
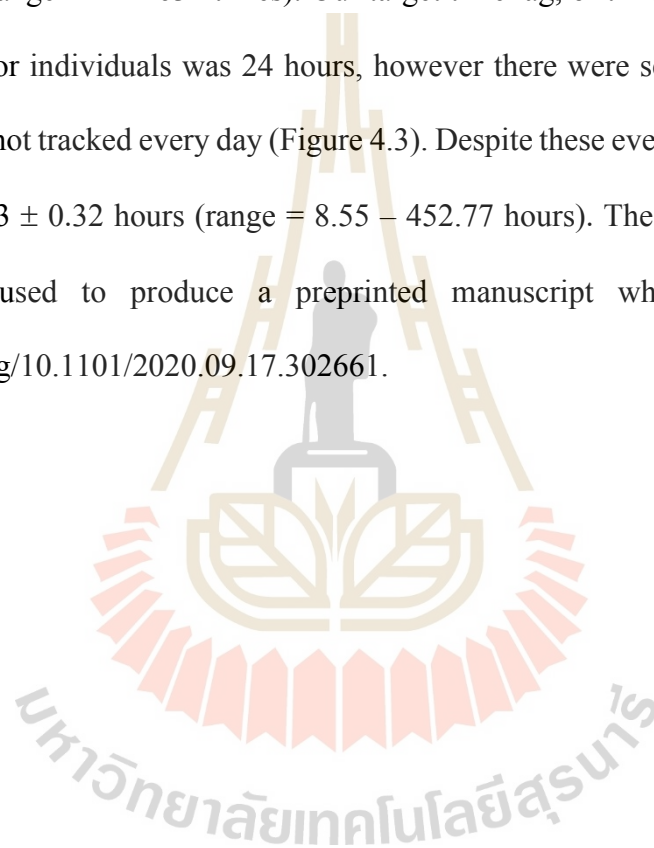
**Table 4.3** Tracking summary for radio-tracked individuals as well as occurrence distributions (90%, 95%, 99% ha) and mean motion variance. Table recreated from Smith et al. (2020).

| ID | Fixes | Start | End | Days | Lag (h) | Relocations | 90% | 95% | 99% | $\sigma^2 m$ |
|---|---|---|---|---|---|---|---|---|---|---|
| PYBI021 | 631 | 2018-09-29 | 2020-07-22 | 662 | 25.22 ± 0.33 | 216 | 25.27 | 46.81 | 94.94 | 1.74 ±0.12 |
| PYBI022 | 438 | 2018-10-25 | 2020-02-23 | 486 | 26.69 ± 1.11 | 151 | 17.7 | 28.83 | 53.64 | 1.24 ±0.1 |
| PYBI028 | 176 | 2019-01-09 | 2019-07-16 | 188 | 25.76 ± 0.79 | 70 | 23.66 | 44.87 | 88.38 | 6.27 ±1.19 |
| PYBI029 | 486 | 2019-02-23 | 2020-07-22 | 515 | 25.48 ± 0.83 | 234 | 59.16 | 82.01 | 139.54 | 3.67 ±0.32 |
| PYBI033 | 41 | 2019-05-18 | 2019-06-28 | 41 | 24.65 ± 0.61 | 23 | 4.81 | 6.27 | 9.05 | 1.09 ±0.17 |
| PYBI055 | 205 | 2019-11-12 | 2020-06-06 | 207 | 24.37 ± 0.33 | 27 | 0.08 | 0.76 | 21.71 | 0.63 ±0.15 |
| PYBI060 | 191 | 2020-01-05 | 2020-07-14 | 191 | 24.12 ± 0.25 | 64 | 116.87 | 176.93 | 285.56 | 6.06 ±0.69 |
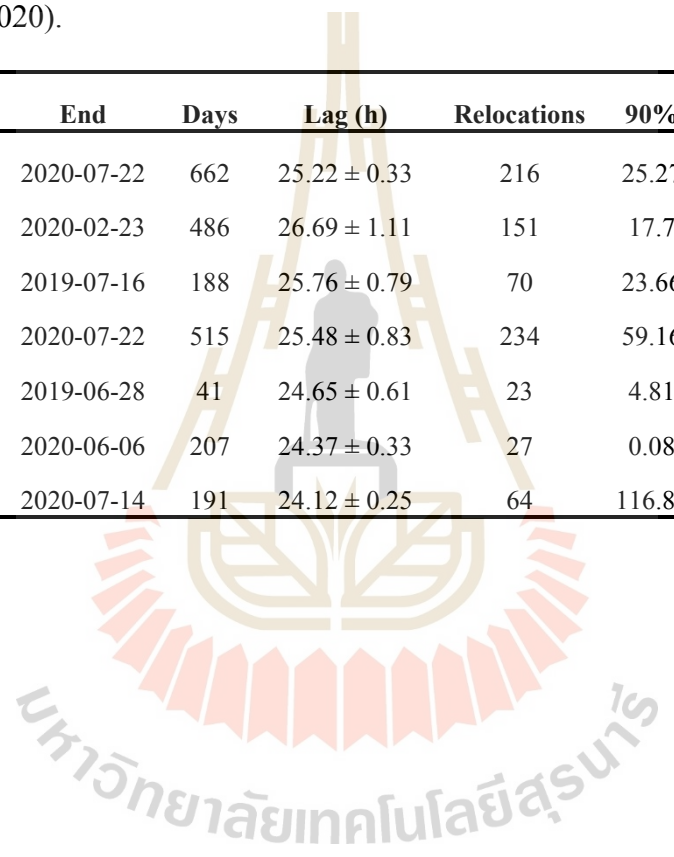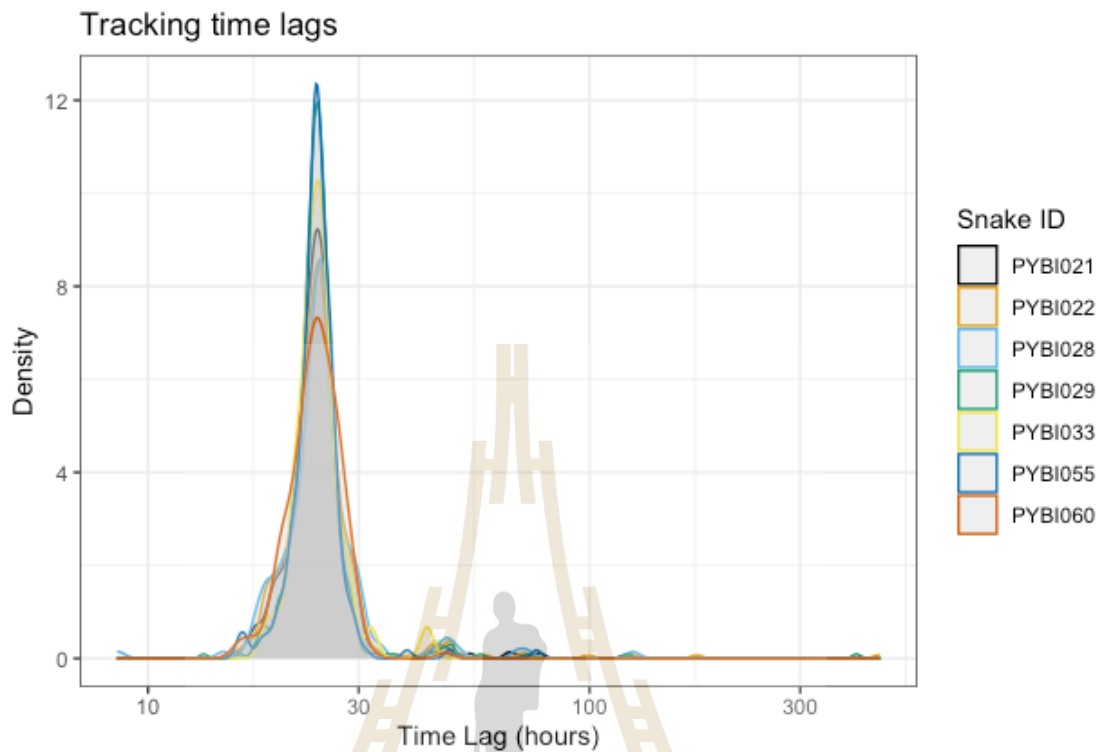
**Figure 4.3** Tracking time lags, or duration between consecutive data points for all radio-tracked snakes. Figure recreated from supplementary figures provided by Smith et al. (2020).

### 4.1.4 Spatial Analysis

We used dynamic Brownian Bridge Movement Models to calculate the occurrence distribution for all of the radio-tracked snakes included in our study. We calculated 99%, 95% and 90% confidence areas for all snakes (i.e., contours generated from dBBMM occurrence distributions) (Table 4.3). Radio-tracked Burmese pythons, including our tracked male, in our study site had a mean 99% occurrence distribution of 98.97 ± 35.42 ha. Female Burmese pythons had a mean 99% confidence area of 100.74 ± 41.86 ha. The snake with the largest 99% confidence area (285.56) was

PYBI060 who was our only snake to be tracked exclusively within the forested core area of the biosphere reserve. In contrast, our snake with the smallest 99% confidence area (9.05 ha), PYBI033 was tracked for the shortest duration of all of our snakes (41 days).

In addition to calculating occurrence distributions, we also calculated the mean motion variance of our individuals (Figure 4.4). Mean motion variance was low (2.66 $\pm$ SE 0.14 $\sigma^2$m; range= $5.53^{-05}$ – 98.45 $\sigma^2$m). Two individuals exhibited higher mean motion variances, our male (PYBI028) and our female that was tracked exclusively in the forest (PYBI060). Their mean motion variances were 6.27 $\pm$ 1.19 $\sigma^2$m and 6.06 $\pm$ 0.69 $\sigma^2$m respectively. We observed a very low mean motion variance for one individual, PYBI055 who remained stationary throughout the majority of her tracking duration during breeding season and nesting (0.63 $\pm$ 0.15 $\sigma^2$m).

Overall, Burmese pythons tended to have somewhat small and confined occurrence distributions which is illustrated in the visualization of the contours generated by the dynamic Brownian and Bridge Movement Models (Figure 4.4). We saw considerable overlap between two of our snakes, PYBI021 and PYBI022 who at one point were tracked within 10 meters of each other for several days in a row. The occurrence distribution of PYBI033, an individual that was only tracked for 41 days also shows some overlap with the occurrence distribution of PYBI021 and PYBI022, however seeing as she was tracked for a short period of time, it is unclear whether or not we would see this overlap expand or not. The occurrence distribution of PYBI055 shows a large linear movement corridor between her locations following her implantation and several locations around her nest site. Despite tracking her for just over 200 days, we recorded relatively few relocations. We also saw a fairly linear

movement corridor in the occurrence distribution of PYBI028, our male. During the breeding season, we saw spikes in motion variance, characterized by large (~600m) movements in short succession as he moved in the forested area. Almost immediately after moving into the forest he retreated back to the agricultural land where he greatly restricted his movement.

Our tracked snake, PYBI029 had the second largest occurrence distribution. She maintained a fairly refined area, and her movements were somewhat predictable. Her occurrence distribution occurred almost entirely over agricultural land, however she infrequently used plantation as well as disturbed forest, but human settlements were sparse throughout her occurrence distribution (Figure 4.5). PYBI060 had the largest occurrence distribution which illustrates large, linear movements throughout the forested cored area of the biosphere reserve.

Our recursive analysis revealed that certain individuals exhibited shelter site fidelity within their occurrence distributions. Five out of the seven snakes that were tracked returned to shelter sites that they had previously used, and the degree of site fidelity or number of site revisits varied between individuals (range 4-35 revisits). On average, those snakes shown to exhibit shelter site fidelity revisited sites once every 43.47 ± 14.64 days. Residence times spent in shelter sites ranged from 24.1 – 2010 hours, and on average Burmese pythons spent approximately five days in a single shelter site (125 ± 11.6 hours). The results in this section have been used to produce a preprinted manuscript which is available at: https://doi.org/10.1101/2020.09.17.302661.
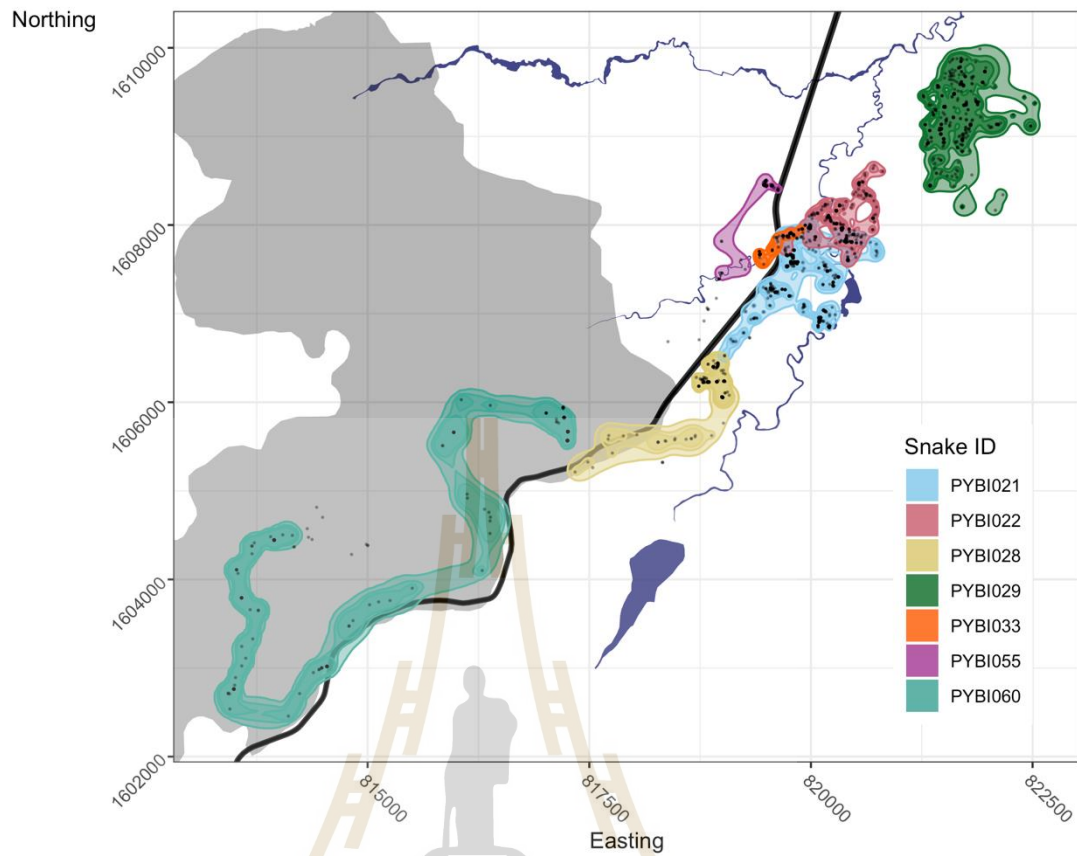
**Figure 4.4** Contours generated from dynamic Brownian Bridge Movement Models for tracked individuals. The core area of the SBR is highlighted by the grey area while major irrigation canals and water bodies are highlighted by dark blue. The Highway 304 is depicted by the emboldened black line. Figure recreated and modified from Smith et al. (2020)
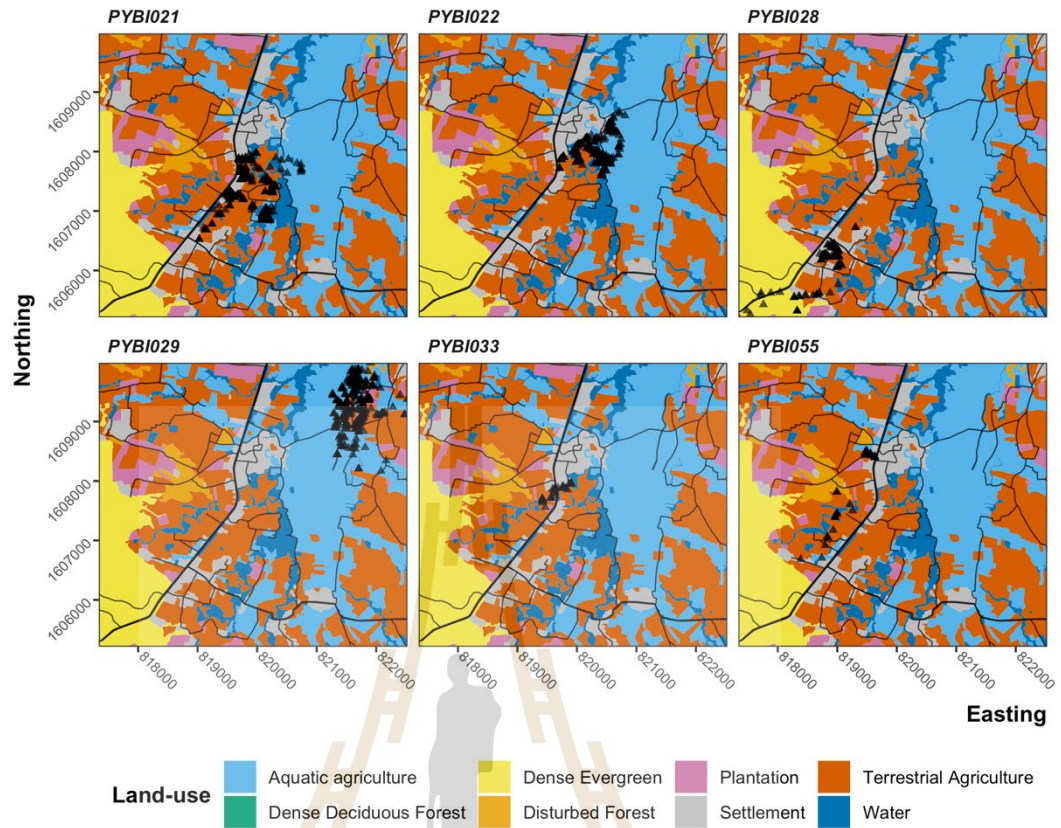
**Figure 4.5** Relocations across study site and different land-use types for snakes tracked within the agricultural matrix. Animal locations are marked by black triangle icons. Roads are marked by black lines on the map.
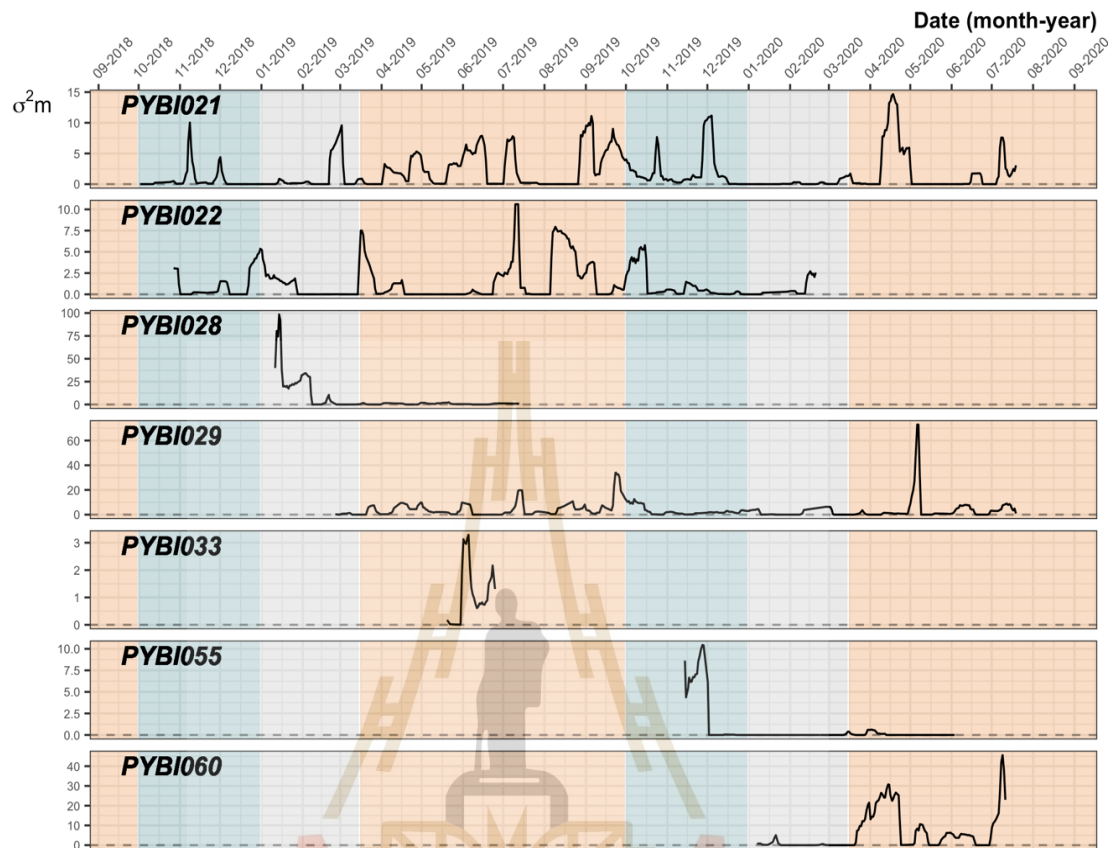
**Figure 4.6** Motion variance for tracked individuals for entirety of tracking duration. The hot seasons are highlighted by orange areas, the wet seasons are highlighted by blue areas, and dry seasons are highlighted by grey areas. Figure recreated from Smith et al. (2020).

### 4.1.5 Seasonality

We investigated seasonal differences in motion variance for the three individuals that were tracked for one year or longer and therefore were tracked throughout all three seasons (PYBI021, PYBI022, and PYBI029). There was slight variation in motion variance depending on the seasons with hot season exhibiting the

highest mean motion variance (3.12 ± 0.21 $\sigma^2$m). The dry season was linked to the lowest mean motion variance (0.76 ± 0.09 $\sigma^2$m) (Figure 4.6).

We calculated seasonal occurrence distributions for these individuals (PYBI021, PYBI022, PYBI029) for the seasons that they were tracked through the entirety of the season. For all three snakes, the hot season was linked to the largest mean occurrence distribution (74.21 ± 11.69 ha) (Table 4.4).

**Table 4.4** 99% occurrence distributions (ha) for snakes tracked for one year or longer and included in seasonal analysis.

| ID | OD Hot | OD Wet | OD Dry |
|---|---|---|---|
| PYBI021 | 74.01 | 18.97 (SE = 8.65, N =2) | 11.61 (SD= 10.79, N= 2) |
| PYBI022 | 54.05 | 14.63 | 3.14 |
| PYBI029 | 94.57 | 23.81 | 40.18 |
| Mean | 74.21 (SE = 11.69) | 19.14 (SE = 2.65) | 18.31 (SE= 11.21) |

Despite the fact that the hot season was linked to the highest mean motion variance and highest mean seasonal occurrence distribution, the probability of movement was highest during the wet season (Table 4.5). During the wet season, movement probability was 53.7% while in the hot season movement probability was 38.5%. Movement probability was lowest during the dry season (23.7%). The probability of movement following rainfall was 38.7%.

**Table 4.5** Results from Bayesian regression model used to predict movement probability across different seasons and following rainfall.

| Variable | Estimate | Movement probability | Est. Error | Lower CrI | Upper CrI |
|---|---|---|---|---|---|
| Hot Season | -0.47 | 38.50% | 0.29 | -1.12 | 0.14 |
| Rainfall | -0.01 | 38.70% | 0.01 | 0 | 0.03 |
| Wet Season | 0.62 | 53.70% | 0.13 | 0.36 | 0.88 |
| Dry Season | -0.72 | 23.30% | 0.12 | -0.97 | -0.48 |

### 4.1.6 Habitat selection

We tracked six snakes through a patchy, land-use matrix found in our study site (Figure 4.5). Only one snake, PYBI060 was found to use a singular habitat type, which in this case was dense evergreen forest. We found that snakes in the agricultural matrix used several different habitat types. We quantified the number of relocations per habitat or land-use type and saw a skew towards aquatic habitats, whether that was water bodies or aquatic agriculture (Figure 4.7). Aside from PYBI060, only one snake, PYBI028 did not appear to use aquatic habitats, however it is worth noting that our results from further analysis do not suggest a strong avoidance of aquatic habitats.

We used 10 models (including one null model) to further investigate habitat selection at the landscape scale on an individual basis (Table 4.6). We used distance to forested areas, water bodies, aquatic agriculture, roads, human settlements and terrestrial agriculture to predict selection. We excluded PYBI060 from our integrated step selection analysis as she was only tracked in the forested areas and therefore did not have the opportunity to display attraction/avoidance of habitat features included in our models. There were four different models that best illustrated habitat selection, Model 5, Model 6, Model 9 and Model 10. Model 5 was a single factor model that

incorporated distance to water bodies and was the top performing model for PYBI022. Model 6, the top model for PYBI028 was another single factor model including aquatic agriculture. Model 9, a multi-factor model included roads, terrestrial agriculture and water and was the top model for PYBI055. Model 10 was the best performing model for three individuals (PYBI021, PYBI029, and PYBI033) and illustrated a positive association for the multiple habitat features in the model. Model 10 incorporated water bodies, human settlements and aquatic agriculture. Several of our models exhibited very broad confidence intervals for certain individuals and in some cases overlapped zero. This uncertainty is likely attributed to the fact that our dataset was coarse and that Burmese pythons relocated relatively infrequently.

Estimates from our integrated step selection analysis suggested that only three out of the six snakes included in the analysis were associated with forested areas, however this association was minimal. Habitat features found within the agricultural matrix appeared to be better predictors for habitat selection. PYBI028 and PYBI055 showed a positive association with human settlements ($\beta$ 99.94 95% CI [Confidence interval] 29.12 – 170.75, and $\beta$ 68.89, 95% CI -31.78 – 169.57, respectively). All snakes showed a positive association with aquatic environments (i.e., water bodies or aquatic agriculture) (Figure 4.8).

At the population level, we observed low mean estimates for habitat selection range: $-1.37^{-04}$ – 0.003) (Table 4.7). Consistent with selection at the individual level, our study animals were positively associated with water bodies ($\beta$ 0.003, 95% CrI [Credible interval] 0.001 – 0.004) (Figure 4.9). We did not detect avoidance of more anthropogenic features (i.e., roads and human settlements). We observed low individual variance for each model which is not entirely surprising with the coarseness of our data.

The results in this section have been used to produce a preprinted manuscript which is available at: https://doi.org/10.1101/2020.09.17.302661.
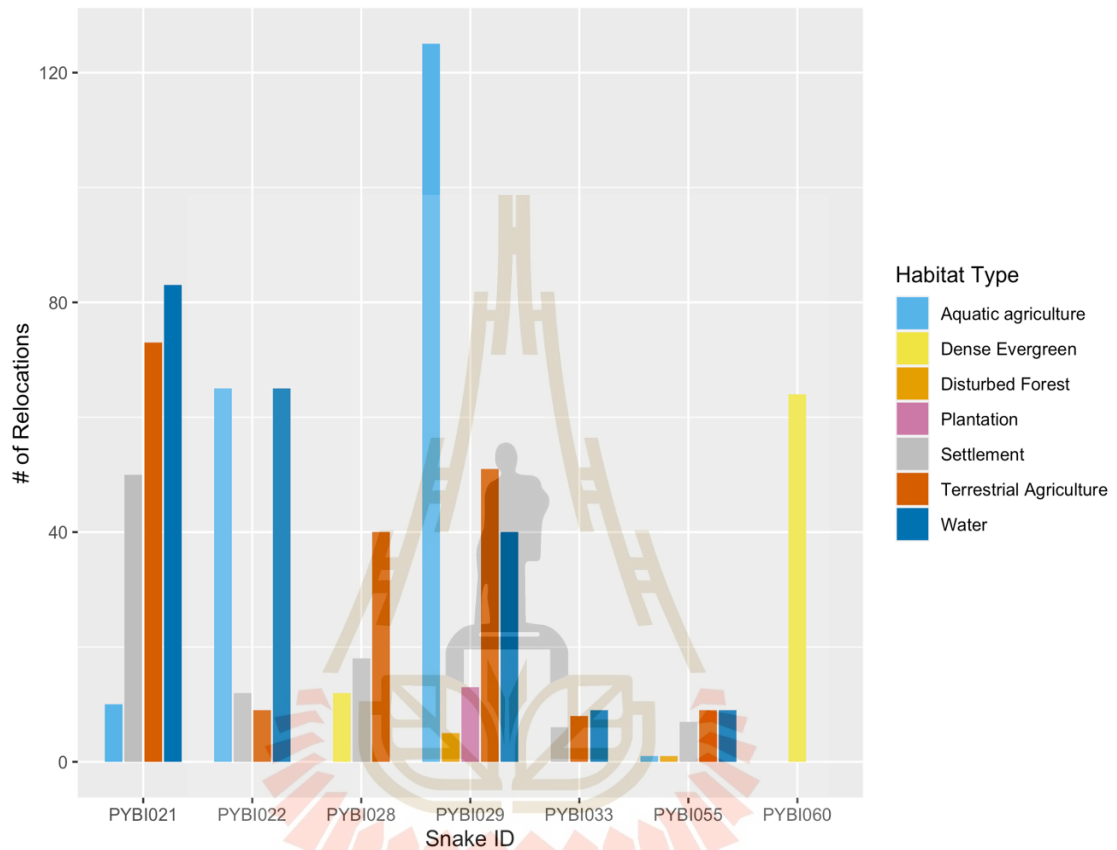


**Figure 4.7** Number of relocations for all radio-tracked snakes within land-use types throughout the study site.

**Table 4.6** Model formulas and AIC scores for integrated step selection functions. Table recreated from Smith et al. (2020).

| Model | Model formula | PYBI021 | PYBI022 | PYBI028 | PYBI029 | PYBI033 | PYBI055 |
|---|---|---|---|---|---|---|---|
| model1 | log_sl*cos_ta+strata(step_id_) (null model) | 2238.4 | 1564.92 | 725.44 | 2456 | 228.63 | 269.39 |
| model2 | Model1 + forest + forest:sl + forest:ta | 2235.6 | 1569.43 | 721.25 | 2452.23 | 232.58 | 273.9 |
| model3 | Model1 + settle + settle:sl + settle:ta | 2233.67 | 1570.53 | 720.7 | 2458.89 | *228.09* | 269.77 |
| model4 | Model1 + road + road:sl + road:ta | 2234.94 | 1564.77 | 726.27 | 2456.14 | *227.85* | 267.63 |
| model5 | Model1 + water + water:sl + water:ta | 2221.18 | *1556.79* | 718.98 | *2438.1* | 228.75 | 258.01 |
| model6 | Model1 + aq.ag + aq.ag:sl + aq.ag:ta | 2236.23 | 1566.62 | *713.66* | 2460.39 | *227.18* | 268.8 |
| model7 | Model1 + terr.ag + terr.ag:sl + terr.ag:ta | 2237.94 | 1565.76 | 724.98 | 2453.68 | 230.82 | 272.42 |
| model8 | Model1+ road + forest + settle | 2240.91 | 1567.83 | 728.49 | 2444.86 | 232.65 | 271.58 |
| model9 | Model1+ road + terr.ag + water | 2219.99 | 1563.62 | 717.28 | *2439.77* | *227.46* | *252.34* |
| model10 | Model1 + water + settle + aq.ag | *2216.48* | 1562.47 | 723.76 | *2437.96* | *226.24* | 258.73 |

sl: step length, ta: turn angle, settle: human settlement, aq.ag: aquatic agriculture, terr.ag: terrestrial agriculture. * indicates AIC score within < 2 Δ AIC of model that best predicts selection for individual.
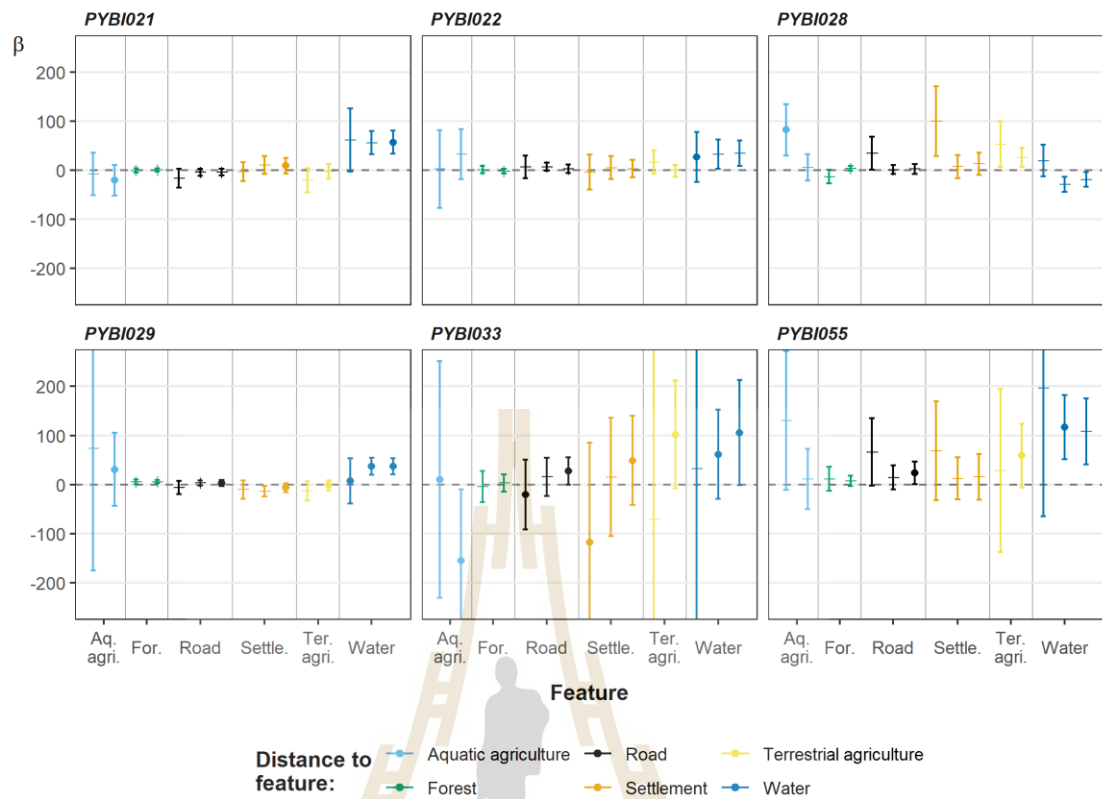
**Figure 4.8** Habitat selection in relation to distance to habitat features at the individual level. A positive estimate indicates selection while negative estimates suggest avoidance. Error bars are used to display 95% confidence intervals. Circles are used to mark habitat features that were included in top performing models. Figure recreated from Smith et al. (2020).

**Table 4.7** Model formulas, mean estimates, and amount of individual variation of habitat selection at the population level. Table recreated from Smith et al. (2020).

| Model | Model formula | β | Individual Variance |
|---|---|---|---|
| 1 | Step_id + forest + forest:sl + forest:ta | 8.04E-04 | 4.91E-06 |
| 2 | Step_id + settle + settle:sl + settle:ta | 5.66E-04 | 4.83E-06 |
| 3 | Step_id + road + road:sl + road:ta | 0.001419404 | 9.34E-06 |
| 4 | Step_id + water + water:sl + water:ta | 0.002720069 | 6.10E-12 |
| 5 | Step_id +  aq.ag + aq.ag:sl + aq.ag:ta | -1.37E-04 | 1.18E-05 |
| 6 | Step_id + terr.ag + terr.ag:sl + terr.ag:ta | 0.004166886 | 8.17E-06 |

sl: step length, ta: turn angle, settle: human settlement, aq.ag: aquatic

agriculture, terr.ag: terrestrial agriculture
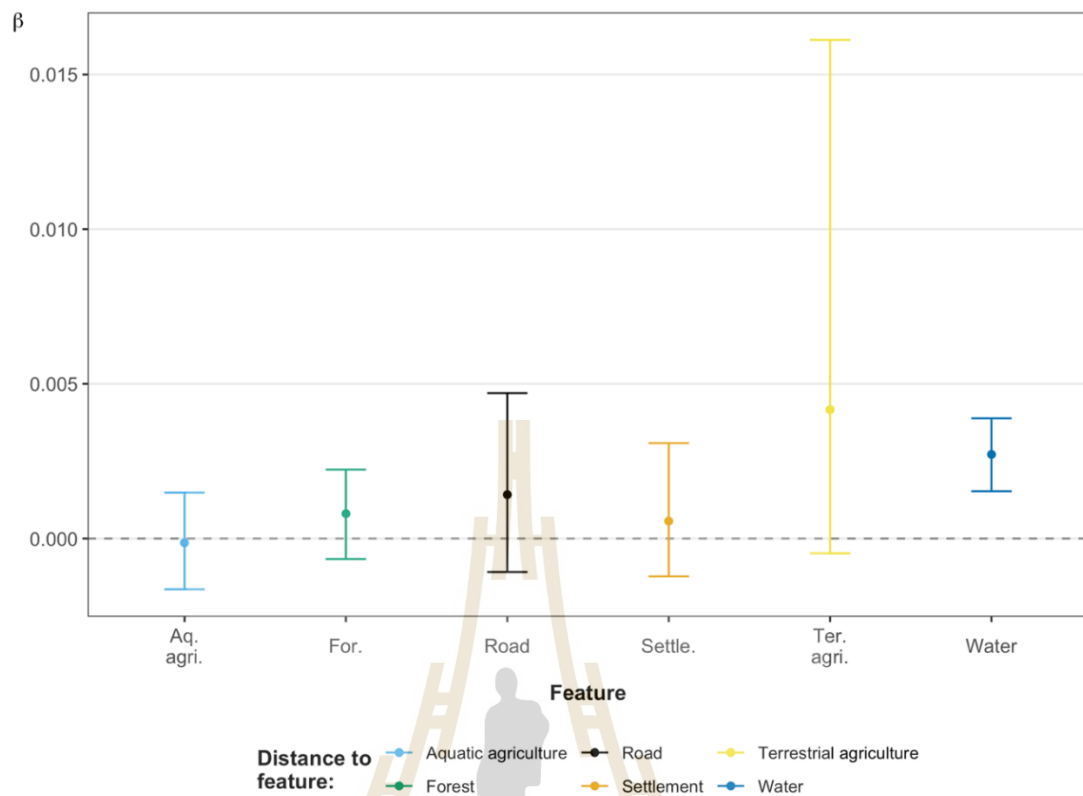
**Figure 4.9** Population level selection in relation to distance to habitat features. Positive estimates indicate selection for habitat features. 95% credible intervals are illustrated by the error bars. Figure recreated from Smith et al. (2020).

### 4.1.7 Reproductive Biology

We monitored the nests of two individuals, PYBI022 and PYBI055. These two individuals were the only snakes in our sample believed to have nested during our tracking period. On 17/04/2019, PYBI022 relocated to a burrow in a field margin. We tracked PYBI022 to this burrow for one month before confirming the presence of a nest by placing a phone camera into the burrow she was sheltering in. PYBI022 spent a total of ~56 days in this burrow. Sometime between ~12:00 on 8/06/2019 and ~11:00 on 9/06/2019, relocated and left the burrow, at this time we did not observe any hatchlings.

In attempt to capture emerging neonates, we built a small mesh fence around the burrow. We periodically checked on the fence two to three times a day until we discovered the first hatchling that had emerged on 11/06/2019. Hatchlings continued to emerge periodically up until 16/06/2019. We discovered PYBI022 had laid 15 eggs, 11 of which successfully hatched.

We did not observe PYBI022 in contact with any males prior to nesting. Using gestation period estimates (~114 days) stated by Van Mierop and Barnard (1976), we suspect that fertilization occurred sometime around 22/12/2018. As we did not confirm the presence of nest until 30 days had passed since PYBI022 moved to the burrow, we are not able to definitively determine incubation time, however presuming that she deposited her eggs within the first 24 hours of relocating to the burrow, we suspect the incubation period was ~56 days.

Our other individual to nest, PYBI055 behaved differently to PYBI022 prior to nesting. On 23/12/2019, we located PYBI055 in a large burrow surrounding an exposed root system. PYBI055 remained in this location for ~84 days. During this time, we placed a camera trap in front of the entrance to the burrow in attempt to capture breeding events. We observed several males entering and exiting the burrow, sometimes several entering within hours of each other. We observed one copulation event on 21/02/2020 when PYBI055 and one other snake had moved out of the burrow to breed.

PYBI055 moved to her nest site sometime between ~09:00 on 11/04/2020 and ~09:00 12/04/2020, which was in a brush pile along an overgrown field margin, only meters from a road. As we had observed males entering and leaving the burrow, we assumed that PYBI055 was gravid and therefore monitored her movements closely. The day after she had moved to her nest site, we visually confirmed the presence of her

nest, allowing for us to get a more precise estimate of incubation time. PYBI055 left the nest sometime between ~13:00 on 06/06/2020 and ~11:00 on 07/06/2020, putting the incubation time at approximately 55 days. When we arrived at the nest on 07/06/2020, we discovered that at least four neonates had already hatched and left the nest. PYBI055 laid 32 eggs, two of which did not successfully hatch. The mean nest temperature for PYBI055's nest was 31.96°C ± 0.2 (range 24.24°C – 35.16°C) (Figure 4.10).
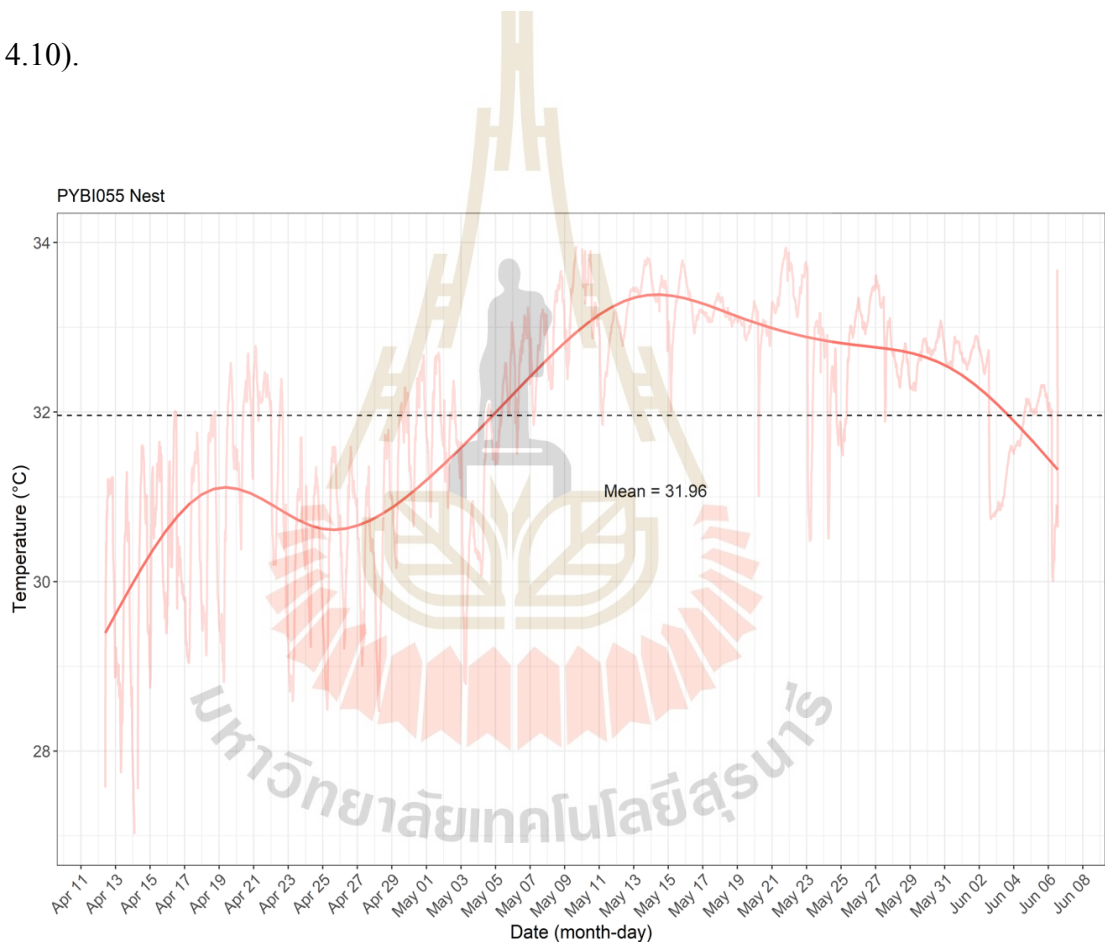


**Figure 4.10** Incubation temperatures for the nest of PYBI055. Temperatures recorded every 15 minutes.

## 4.2    Discussion

### 4.2.1 Surveys and Captures

The nature of our captures and combined survey effort speaks to the difficulty of finding Burmese pythons in our study site. Over the course of over 177 hours, covering a total of 1,804.38 kilometers, we only managed to find and capture two Burmese pythons. However, we suspect survey effort to be much greater as we did not record all survey hours and we collaborated with other research teams in attempt to capture study animals and their effort was not recorded. We only captured two Burmese pythons during recorded visual encounter surveys, both of which did not meet tracking criteria (i.e., sex, age class).

These low encounter rates are not entirely unexpected. Snakes with cryptic life histories often have low detection probabilities (Steen, 2010) making capturing them difficult, and thus has implications for field study design. Aside from capturing neonates from the two nests that we were actively monitoring, the majority of captures were a result of notification from local residents and by working the rescue team. The fact that many of the snakes that we were notified about were found in or near people's homes is significant from a human-wildlife conflict angle. Several of the Burmese pythons we received notification for had been seen eating livestock such as ducks and chickens, therefore causing economic loss for the livestock owners.

We also responded to snake calls (i.e., notifications) where Burmese pythons had become entangled in fishing nets or mesh fencing. In these instances, we were required to cut netting and fencing materials at the expense of the owners of the nets or fences. These events suggest that Burmese pythons do in fact initiate snake-human conflict in our study site.

**4.2.2 Space Use, Movement and Seasonality**

In general, Burmese pythons in our study site tended to have small occurrence distributions and restricted their movements. On average, Burmese pythons exhibited low mean motion variances where there were periodic peaks in motion variance followed by long stationary durations. Burmese pythons can be classified as ambush predators (Ross and Winterhalder, 2015) and the peaks in motion variance could be related to Burmese pythons locating new ambush sites and then remaining there to digest any captured prey.

The largest occurrence distribution belonged to our female, PYBI060 who was tracked exclusively within forested habitats. Within these forested habitats she showed large, linear movements which were not consistent with our other snakes, aside from the male, PYBI028 who moved briefly into a patch of forest during the breeding season. We also saw the highest mean motion variance for PYBI060 and PYBI028. The high mean motion variance of PYBI028 are likely attributed to the steep peaks in motion variance exhibited during the perceived breeding season (January-February) as after the breeding season (March- onwards) he maintained very low motion variance. This is not entirely surprising as male snakes may move differently, making large, linear movements during breeding season in pursuit of females (Duvall and Schuett, 1997; Waldron et al., 2006; Jellen et al., 2007). Despite his high mean motion variance, PYBI028 had one of the smallest occurrence distributions. Excluding his breeding season movements, PYBI028 spent much of his time in an area heavily modified by human settlements and terrestrial agriculture.

In contrast, PYBI060 maintained high motion variance throughout most of her tracking duration, aside from when she was tracked during the dry season. While she

was not included in analysis to detect seasonal difference in mean motion variance, this trend is consistent with our findings that mean motion variance was lowest in the dry season. Average occurrence distributions for individuals tracked for a year or more were smallest in the dry season. Additionally, we found that probability of movement was lowest during the dry season, further supporting the idea that female Burmese pythons restrict movement during the dry seasons in comparison to the hot and wet seasons.

The large occurrence distribution and high motion variance of PYBI060 in comparison to snakes tracked in the agricultural land elicits discussion about animal movement and space use in undisturbed versus disturbed or fragmented habitat. Animals in human modified landscapes may alter their space use and behaviors as a way to anthropogenic avoid pressures (Ditchkoff et al., 2006; Doherty et al., 2019: Wang et al., 2017). While our inferences are limited about how Burmese pythons utilize forested or more undisturbed habitats, the behaviors and movements of PYBI060 in comparison to her agricultural counterparts do seem to imply that Burmese pythons in an anthropogenic landscape may use space differently. Additionally, PYBI029 had the second largest occurrence distribution and was tracked throughout agricultural land and otherwise disturbed habitats. That being said, there were very few human settlements within PYBI029's occurrence distribution. If Burmese python movement is affected by the presence of human settlements, we would expect for snakes in areas with few human settlements to utilize larger areas and move more frequently, which is what we observed with both PYBI029 and PYBI060.

Results also suggested that most of our snakes returned to previously used shelter sites, thus exhibiting site fidelity. The only two snakes to not show site fidelity

were PYBI033, an individual that was only tracked for 41 days and PYBI060, our forest female. The frequency of which snakes in the agricultural land returned to previously used shelter sites suggests that these snakes may carefully select and reuse shelter sites in a modified landscape. Findings from previous studies have found that animals may return to suitable refuge sites in areas or seasons when there are few shelter sites available (Beck and Jennings, 2003; Whitaker and Shine, 2003; Young et al., 2017).

Previous studies from the invasive range of Burmese pythons (Southern Florida, USA) have used more "traditional" estimators of space use (i.e., MCPs and KDEs), which do not allow for estimates to be reliably compared across studies (Silva et al., 2018; Silva et al., 2020). Furthermore, these studies have also lacked clarity in their methods (i.e., sampling regime, data collected), making it especially difficult to compare our space use estimates with other studies. Despite these drawbacks, we are able to make some broad comparisons between our findings and those of studies on invasive Burmese pythons. In their invasive range, for instance, Burmese pythons appear to use large very large areas, typically do not exhibit site fidelity and make large, linear movements (Hart et al., 2015).

Invasive Burmese python movement and space use is likely different due to the fact that in their invasive range there may not be the same pressures that are present in our study site. Specifically, our study site has been fragmented by agricultural conversion and the placement of roads and human settlements. Agricultural conversion has been known to influence space use and activity of animals in these modified landscapes (Doherty and Driscoll, 2018; Marshall et al., 2020; Tucker et al., 2018). The Florida Everglades on the other hand, is characterized by large areas of interconnected wetlands with forest patches throughout. Furthermore, invasive Burmese pythons face

low risk of predation, especially after reaching maturity (Reed et al., 2012). In our study site, Burmese pythons face anthropogenic pressures and risk of predation by native predators such as King cobras. In attempt to avoid predation, animals may alter their movements (Doherty et al., 2019; Rettie & Messier, 2001; Sih, 1984).

### 4.2.3 Habitat Selection

Consistently we saw that Burmese pythons in our study site were positively associated with aquatic habitat features, whether this association with aquatic agriculture such as rice paddy or water bodies (i.e., ponds and irrigation canals or klongs). Despite there being large areas of terrestrial agriculture, only three of our snakes showed an association with terrestrial agriculture, although for all three snakes this association was slight. Terrestrial agriculture, such as cassava and orchards often lack suitable refugia or microclimates for ectotherms (Frishkoff et al., 2015; Gallmetzer and Schulze, 2015) and therefore may be avoided by the Burmese pythons in our study site. Researchers studying grass snakes (*Natrix* natrix) in an agricultural landscape found that snakes used terrestrial monocultures, but also showed affinity for less prevalent habitat types, including riparian zones (Wisler et al., 2008). The affinity for aquatic features is consistent with findings in the Florida Everglades, as Burmese pythons regularly utilize aquatic environments and have even been considered semi-aquatic (Mazzotti et al., 2011; Hunter et al., 2015).

Another possible explanation for Burmese pythons' associations with aquatic habitats could be that these aquatic habitats have may high densities of potential prey items. Rice paddy fields can act as wetland like habitat and are often home to communities of wading birds (Fujioka et al., 2010; Lawler, 2001) which we often

observed during radio-tracking. We suspect that the vegetation that grows along irrigation canals and along ponds provides shelter for Burmese pythons in these agricultural matrices. Throughout our study site, there are also irrigation canals which have been known to be used by other snakes in our study site (King cobras) as movement corridors (Marshall et at., 2019; Marshall et al., 2020). It is possible that Burmese pythons also use these irrigation canals to traverse through agricultural areas.

Of the snakes that we tracked in the agricultural matrix, we observed a strong avoidance for human settlements for only one snake, which could have implications for conflict between humans and pythons in our study site. In areas where humans and wildlife compete for space and other resources, or when wildlife is responsible for economic loss due to damages or livestock loss, human wildlife conflict is likely to occur (Barua et al., 2013; Dickman, 2010). Many residents in the human dominated areas of our study site keep livestock like chickens, ducks and geese. There were several occasions when we were notified of a Burmese python either consuming or had obviously just consumed (visible bulge in the gut) livestock. Two of our radio-tracked snakes, PYBI021 and PYBI033 were captured after being observed eating ducks or chickens. Luckily, these instances did not lead to the persecution of these individuals, however there are accounts of snake mortality in our study site as a result of conflict between snakes and humans (Marshall et al., 2018).

While we did not observe any direct persecution of Burmese pythons in our study site, we did encounter road mortalities, Burmese pythons becoming entangled in mesh fencing material, and even Burmese pythons in fishing traps. All of these threats are unique to anthropogenically modified areas, highlighting the risks of these areas for Burmese pythons.

Roads in particular can act as a barrier of movement for some reptiles (Shepard et al., 2008), which could be the case for two of our individuals (PYBI021 and PYBI022) that would in some cases shelter less than 30 meters from a major road (Highway 304), but never actually crossed. On the other hand, we tracked two of our individuals, PYBI028 and PYBI033 on either sides of the Highway 304, meaning that they either crossed over the road or utilized culverts that go under the road throughout our study. Roads can also be a contributing source of mortality for reptiles (Gibbs and Shriver, 2002; Rosen and Lowe, 1994, Row et al., 2007) which we observed along the Highway 304. Despite these risks, our sample of Burmese pythons in the agricultural areas did not tend to avoid roads. Given that our sample size was limited, we are not able to make strong inferences about the impacts of roads on Burmese pythons, but their indifference to roads prompts further investigation on interactions between Burmese pythons and roads.

### 4.2.4 Reproductive Biology

We are able to make limited inferences about the reproductive biology of Burmese pythons in our study site. We only observed two of our tracked females to nest, both of which differed greatly in their motion variances and behaviors prior to nesting and therefore complicate our attempts to understand the reproductive biology of wild, native Burmese pythons. However, in their invasive range Burmese pythons are thought to reproduce biennially (Willson et al., 2011), which we did not observe in our site. Two of our radio-tracked snakes PYBI021 and PYBI029 were tracked for two consecutive nesting periods (April-June) and neither nested during our study period,

suggesting that in our study site Burmese pythons may reproduce every third year or more.

Both of our nesting snakes remained with their eggs for nearly the entire incubation period, which for PYBI022 was ~56 days and for PYBI055 was ~55 days. These incubation periods are consistent with incubation periods observed in captive individuals (Van Mierop and Bernard, 1976). As to be expected, nesting periods can be illustrated by our motion variance plot where during nesting we see and absence of peaks in activity. However, prior to nesting and during the breeding season, PYBI022 exhibited periodic peaks in motion variance, while PYBI055 restricted her movement and spent nearly 84 days in a burrow.

By examining the motion variance of our tracked male, PYBI028 as well as using gestation periods provided by Van Mierop and Barnard (1976) to estimate gestation durations and approximate fertilization dates, we are able to make inferences about breeding seasons for Burmese pythons in our study site. We suspect that Burmese pythons in our study site breed from December to March, which is similar to what is seen in their invasive range. In their invasive range, Burmese pythons are known to mate between December and April (Smith et al., 2016). Due to our low sample size of reproductive females, our observations can realistically only serve as a preliminary investigation into the reproductive biology of native Burmese pythons. However, as there is virtually no information about the reproduction of native Burmese pythons, these observations can help to prompt further investigation and begin to lay the foundation of a better understanding of Burmese python reproduction.

# CHAPTER V

# CONCLUSION

This study serves as one of the first investigations of native Burmese python space use, movement, habitat selection and overall natural history. To the best of our knowledge, this study is the only to follow a standardized framework (i.e., use of dBBMMs, structured tracking regime) to quantify the space use and movements of Burmese pythons, both in their invasive range and native range. The findings detailed in this dissertation help to elucidate the natural history of native Burmese pythons, as the overwhelming majority of information available is from the invasive range of Burmese pythons.

We found that Burmese pythons utilized small areas, which is inconsistent with findings from their invasive range. However, in order to make reliable comparisons, we urge that other researchers working with Burmese pythons be more transparent about their methods and even go so far as to make their data available, if feasible (i.e., journal policies allow for data to be made accessible). Motion variance of Burmese pythons was consistently low. We saw the highest mean motion variance from our tracked male and a female tracked through a more pristine environment, which may be related to the absence of anthropogenic pressures that our snakes tracked in the agricultural areas were subjected to.

Burmese pythons showed an attraction for aquatic environments which has been observed in invasive populations in the Florida Everglades. The tendency for Burmese pythons to select for these aquatic environments could help to explain their invasion success in their introduced range which consist of interconnected wetlands. Burmese pythons did not show a strong avoidance for anthropogenic habitat features, including human settlements and roads which raises concern from a snake-human conflict angle. In our study site we observed Burmese pythons engaged in various forms of conflict (i.e., road mortality, entanglement in fencing and fishing traps, caught in agricultural burning, and consuming livestock) which prompts further investigation into how anthropogenic pressures may influence a large, free ranging snake such as the Burmese python in human dominated landscapes.

Despite our fairly consistent observations of space use, movement and habitat selection, our inferences are limited by our small sample size. Burmese pythons proved to be difficult to find and we often relied on notification from local residents to add individuals to our sample size, meaning that our sample was not randomly selected. Our sample could have been biased towards Burmese pythons that were more likely to enter human settlements. We tracked mainly females, meaning that our results cannot be extrapolated to trying to understand the movements and habitat selection of male Burmese pythons. All snakes included in our sample were of sexual maturity, therefore limiting our interpretations to a single age class.

Our study site being a patchy land use matrix allowed for us to explore habitat selection of native Burmese pythons. However, we only tracked one snake exclusively in a forested area which does not allow for us to make conclusive interpretations about how snakes in forested areas select habitat and move through these habitats. Moving

forward, we suggest that future studies attempt to include individuals tracked through both pristine and disturbed areas. Additionally, future studies should investigate the movements and habitat selection of male Burmese pythons as well as explore the ecology of individuals from different age classes. As Burmese pythons appear to show indifference for anthropogenic features and we have observed them to act as initiators of snake-human conflict, further studies should be focused on understanding interactions between pythons and humans in a modified landscape. The conservation status of the Burmese python (vulnerable with decreasing populations) urges that investigating the ecology and potential threats to Burmese pythons is both worthwhile and necessary.
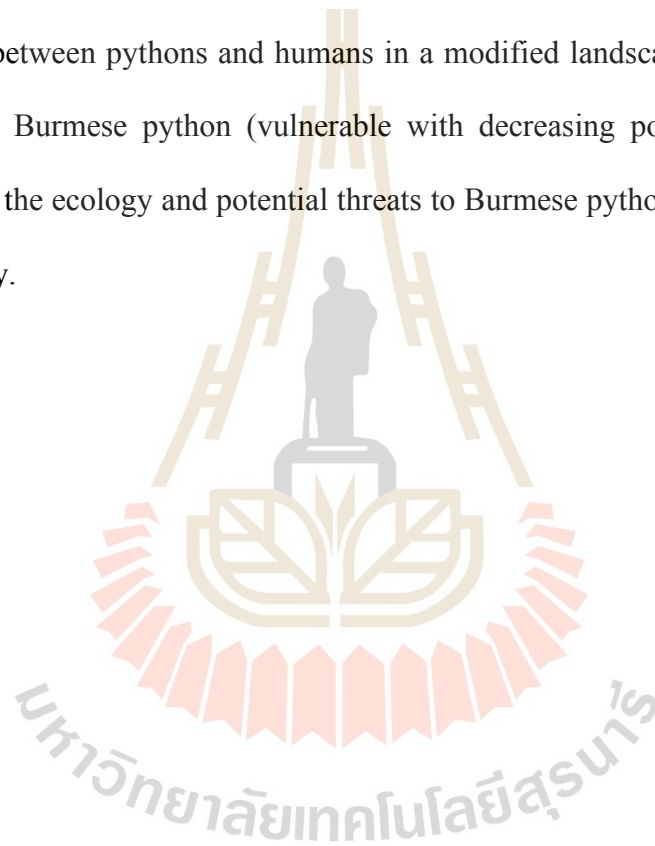
# REFERENCES
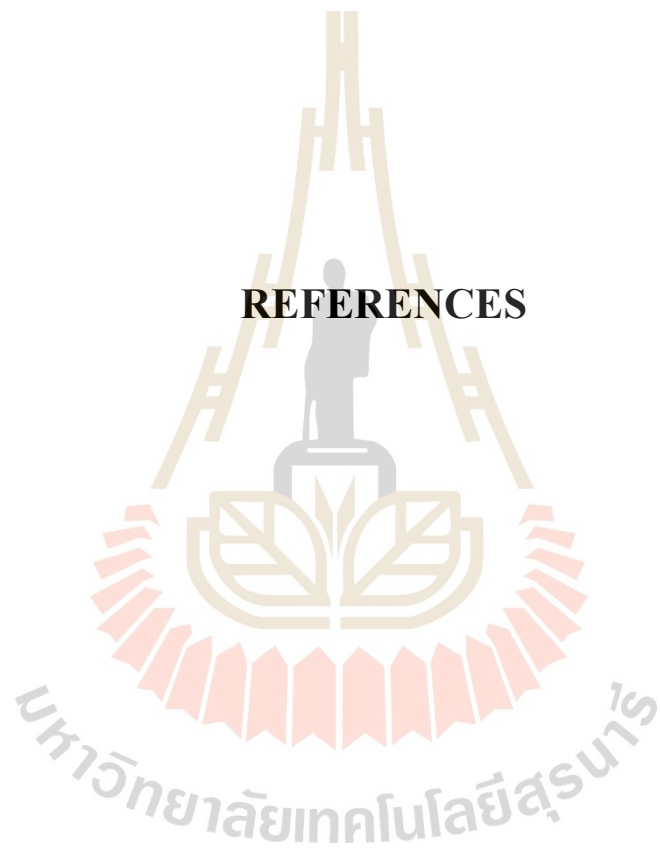
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# CURRICULUM VITAE

**Name**                Samantha Nicole Smith

**Date of Birth**       July 8th, 1994

**Place of Birth**      Kodiak, Alaska, USA

**Education**           2017 B.Sc., Animal Behavior, University of New

England, Biddeford, Maine, USA

## Publications

**Smith, S. N.**, Jones, M. D., Marshall, B. M., Waengsothorn, S., Gale, G. A. and Strine, C. T. (2021). Native Burmese pythons exhibit site fidelity and preference for aquatic habitats in an agricultural mosaic. **Scientific Reports.** doi: https://doi.org/10.1038/s41498-021-86640-1.

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