THE SPATIAL ECOLOGY, HABITAT USE, AND ACTIVITY OF BANDED KRAITS (*Bungarus fasciatus*) IN THE SAKAERAT BIOSPHERE RESERVE

Tyler Keith Knierim

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

Suranaree University of Technology

Academic Year 2018

นิเวศวิทยาเชิงพื้นที่ การเลือกถิ่นที่อยู่อาศัย และรูปแบบการดำเนินชีวิตของงูสามเหลี่ยม (*Bungarus fasciatus*) ในเขตสงวนชีวมณฑลสะแกราช

นายไทเลอร์ คีธ คิเนอร์ริม

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
สาขาวิชาชีววิทยาสิ่งแวดล้อม
มหาวิทยาลัยเทคโนโลยีสุรนารี
ปีการศึกษา 2561

THE SPATIAL ECOLOGY, HABITAT USE, AND ACTIVITY OF BANDED KRAITS (*Bungarus fasciatus*) IN THE SAKAERAT BIOSPHERE RESERVE

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

Thesis Examining Committee

____
(Asst. Prof. Dr. Duangkamol Maensiri)
Chairperson

____
(Dr. Colin T. Strine)
Member (Thesis Advisor)

____
(Mr. Surachit Waengsothorn)
Member

____
(Asst. Prof. Dr. Jacques Hill)
Member

____
(Dr. Santi Watthana)
Member

____
(Prof. Dr. Santi Maensiri)
Vice Rector for Academic Affairs and Internationalization

____
(Asst. Prof. Dr. Worawat Meevasana)
Dean of Institute of Science

ไทเลอร์ คีธ คิเนอร์ริม : นิเวศวิทยาเชิงพื้นที่ การเลือกถิ่นที่อยู่อาศัย และรูปแบบการดำเนินชีวิตของงูสามเหลี่ยม (*Bungarus fasciatus*) ในเขตสงวนชีวมณฑลสะแกราช (THE SPATIAL ECOLOGY, HABITAT USE, AND ACTIVITY OF BANDED KRAITS (*BUNGARUS FASCIATUS*) IN THE SAKAERAT BIOSPHERE RESERVE). อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน โทมัส สไตร์น. 141 หน้า.

งูสามเหลี่ยม/การเกษตร/การใช้พื้นที่/แหล่งอาศัย/ชนิดพันธุ์

เนื่องด้วยความสมบูรณ์ของระบบนิเวศทั่วโลกกำลังเผชิญกับปัญหาการถูกคุกคามจากมนุษย์อย่างต่อเนื่อง งานวิจัยหลากหลายขนาดจึงมีความสำคัญต่อความเข้าใจและการอนุรักษ์ระบบนิเวศเป็นอย่างมาก อย่างไรก็ตาม ข้อมูลพื้นฐานด้านชีววิทยาของสัตว์สายพันธุ์ที่แม้จะพบได้อย่างกว้างขวางและมีความสำคัญทางการแพทย์ก็ยังมีอยู่อย่างจำกัด โดยเฉพาะในสัตว์สายพันธุ์ซ่อนเร้นขนาดเล็กที่อาศัยอยู่ในเขตร้อนเช่นงู

จุดมุ่งหมายของงานวิจัยนี้คือการศึกษาถิ่นที่อยู่อาศัยของงูที่มีพิษร้ายแรงที่สุดชนิดหนึ่งในภูมิภาคเอเชียตะวันออกเฉียงใต้อย่างงูสามเหลี่ยม (*Bungarus fasciatus*) ในพื้นที่การเกษตร โดยการติดตามการเคลื่อนที่ด้วยคลื่นวิทยุและศึกษารูปแบบการดำเนินชีวิตของงูสามเหลี่ยมลักษณะตัวเต็มวัยอย่างใกล้ชิดจำนวน 4 ตัว แบ่งเป็นเพศเมีย 2 ตัว และเพศผู้ 2 ตัว ในเดือนสิงหาคมปี พ.ศ.2558 ถึงเดือนธันวาคมปี พ.ศ.2560 ทุกวันเป็นเวลาเฉลี่ย 379.25 ± 318.58 วัน จากการศึกษาพบว่าพื้นที่ออกหากินของงูสามเหลี่ยมอยู่ในช่วง 4.07 เฮกตาร์ (25.2 ไร่) ถึง 272.15 เฮกตาร์ (887.2 ไร่) มีค่าเฉลี่ยอยู่ที่ 103.58 เฮกตาร์ ± 141.95 เฮกตาร์ (95% ฟิกซ์ เคอร์เนล) โดยพื้นที่เหล่านี้ส่วนใหญ่เป็นนาข้าวซึ่งคิดเป็นร้อยละ 68.10 ของพื้นที่ศึกษา ทั้งนี้งูสามเหลี่ยมเลือกอาศัยในแหล่งอาศัยย่อย หลากหลายรูปแบบ ได้แก่ คันนา ขอบที่ดิน บ่อน้ำ และลำคลอง โดยงูสามเหลี่ยมหลีกเลี่ยงการอยู่อาศัยในบริเวณหมู่บ้านและที่อยู่อาศัยอื่นที่ได้รับการรบกวนสูง

พื้นที่ระหว่างขอบที่ดินและทางน้ำซึ่งเป็นพื้นที่ที่งูสามเหลี่ยมเลือกอยู่อาศัยมีลักษณะอุดมไปด้วยพืชล้มลุก ($r = 0.102$, $W = 1054.5$, $p < 0.05$) กลุ่มของต้นยูคาลิปตัส ($r = 0.404$, $W = 654.5$, $p = 0.281$) และเป็นบริเวณที่มีโพรงทางเข้าอยู่หนาแน่นมากกว่าบริเวณที่งูสามเหลี่ยมไม่ได้เลือกอยู่อาศัย ($r = 0.0327$, $W = 0.942$, $p < 0.05$) นอกจากนี้ยังพบว่างูสามเหลี่ยมที่ติดตามใช้พื้นที่บริเวณขอบที่ดินและคันนาในการผสมพันธุ์และสร้างรัง โดยงูเพศเมียทั้งสองตัวอาศัยอยู่ในรังตลอด

ระยะเวลาการฟักไข่ และจากการศึกษาเบื้องต้นพบว่างูสามเหลี่ยมออกหากินมากที่สุดในช่วงเวลา 21:00 - 22:00 23:00 - 01:00 และ 04:00 - 05:00 น.

ในระหว่างการศึกษาครั้งนี้ งูสามเหลี่ยมเพศผู้ทั้งสองตัวถูกฆ่าตายจากกิจกรรมทางการเกษตร โดยงานวิจัยนี้ได้ให้ข้อมูลเชิงลึกที่มีคุณค่าต่อชีวิตของงูสามเหลี่ยมที่อาศัยอยู่ในพื้นที่ที่มีการใช้งานโดยมนุษย์แม้จะเป็นเพียงการศึกษาในขั้นต้นก็ตาม และเนื่องจากการเลือกถิ่นที่อยู่อาศัยยังคงเป็นสิ่งที่ต้องคำนึงถึงในแง่ของการอนุรักษ์ การศึกษางูสามเหลี่ยมและสัตว์สายพันธ์ซ่อนเร้นอื่นๆ ในอนาคต การศึกษาจำนวนประชากรและรูปแบบการดำเนินชีวิตของสัตว์สายพันธุ์นี้ ทั้งในพื้นที่ที่ถูกใช้งานโดยมนุษย์และพื้นที่ที่ได้รับการคุ้มครอง จึงมีความจำเป็นต่อไปในอนาคต

สาขาวิชาชีววิทยา ลายมือชื่อนักศึกษา __________

ปีการศึกษา 2561 ลายมือชื่ออาจารย์ที่ปรึกษา __________

TYLER KEITH KNIERIM : THE SPATIAL ECOLOGY, HABITAT USE, AND ACTIVITY OF BANDED KRAITS (*BUNGARUS FASCIATUS*) IN THE SAKAERAT BIOSPHERE RESERVE. THESIS ADVISOR : COLIN THOMAS STRINE, Ph.D. 141 PP.

BUNGARUS/AGRICULTURE/SPACE USE/HABITAT/FOCAL SPECIES

As the integrity of our global ecosystems continues to face an onslaught of anthropogenic threats, the need for multi-scaled research approaches has become increasingly important. However, deficiencies in baseline life-history data remain for even widely distributed and medicinally significant species. These deficiencies are prominent for many small and cryptic species in tropical regions and are especially lacking for snakes.

The aims of this research were to investigate how one of Southeast Asia's most venomous snakes, the banded krait (*Bungarus fasciatus*), lives within an agricultural landscape. Between August 2015 and December 2017, the movement and activity of adult banded kraits (*n* = 4), 2 females and 2 males were intensively monitored using radio telemetry. Kraits were located daily, for 379.25 ± 318.58 days. The krait's occupied home ranges ranging from 4.07 ha (25.5 rai) to 272.15 ha (887.2 rai), with a mean of 103.58 ha ± 141.95 ha (95% fixed kernel). All home range estimate areas were dominated by race paddies, which comprised approximately 68.10% of the combined home range study area. However, kraits preferred to shelter amongst the less abundant micro-habitats such as paddy bunds, field margins, ponds,

and canals. Kraits avoided villages and other highly disturbed habitats within their home ranges. When sheltering within margins and waterways, shelter sites were characterized by taller dominant herbaceous vegetation (r = .102, W = 1054.5, p < 0.05), clumps of *Eucalyptus camaldulensis* trees (r = .404, W = 654.5, p = 0.281), and higher densities of burrow entrances (r = .0327, W = 942, p < 0.05) than similar unused locations. Field margins and patty bunds were also used by tracked kraits for mating and nesting. The two female kraits used a field bund to nest, which they were observed attending for the extent of the incubation period. Though inactive during the day, kraits became active at night, with preliminary hourly monitoring showing three peaks in nocturnal activity (21:00-22:00; 23:00-01:00; 04:00-05:00 hours).

Two kraits died during the study as the result of regular farming practices in the region. Although preliminary, this study provides valuable insight into the lives of banded kraits inhabiting an anthropogenic landscape. As habitat alteration continues to become a concern for conservation, future studies on banded kraits, and similarly cryptic species, should investigate population levels and essential life history events in both disturbed and preserved habitats.

School of Biology

Academic Year 2018

Student's Signature________________

Advisor's Signature________________

ACKNOWLEDGEMENTS

The field and research methods deployed in this study were approved by the National Research Council of Thailand (NRCT). Therefore, I would like to thank the NRCT and the Thailand Institute of Scientific and Technological Research (TISTR) for their approval of and financial support for the research that I conducted in the Sakaerat Biosphere Reserve. I would like to give a special thanks to the past superintendent of the Sakaerat Environmental Research Station, Dr. Taksin Artchawakom. His passion for conserving biodiversity through education, building friendships, and bridging gaps between a diverse array of friends from across the globe, played a tremendous role in my decision to study in Thailand. I am also grateful for the ongoing support and guidance from his successor, Surachit Waengsothorn. Director Surachit has provided ample assistance, serving as both the station's director as well as a committee member for this dissertation.

I sincerely appreciate the advice given by my thesis advisor, Dr. Colin Strine, as well as providing the opportunity to pursue research resembling what had once been merely a childhood dream. In this regard, I also thank Dr. Pongthep Suwanwaree for the opportunity to collaboratively study venomous snakes. I owe a big thanks to my additional thesis proposal and defense committee members: Dr. Jacques Hill, Dr. Santi Watthana, and Dr. Duangkamol for all their valuable insight.

The SERS staff have been undoubtedly supportive throughout the duration of my multi-year stay at the station. They have been inviting and accommodating despite the difficulties imposed by my slow progress to learn and speak Thai. I thank Dr.

Wironrong Changphet, a veterinarian of the Korat Zoo, who performed surgical transmitter implantation operations on the study animals, often on short notice.

The Krait Team field technicians: Lindsey Pekurny, George Lonsdale, Wesley Dixson, and Lucy Hayes deserve a tremendous thank you. Their hard work played a tremendous role in the success of my project. Without their late nights and long, often solitary tracks spent out in boggy rice paddies, I would not be able to obtain the data that I present in this dissertation. I would also like to thank the numerous volunteers, researchers, and graduate students based at SERS for their valuable resources. Matthew Crane and Ines Silva's enthusiasm for innovative research and their guidance in my development as a researcher. Curt Barnes and Bartosz Nadolski's keen eye for finding and capturing a couple of the banded kraits used in this study. Matthew Ward, Anji D'souza, and Ysabella Montaño's comradery, and passion for conservation, even during the tough times

Tyler Keith Knierim

CONTENTS

CONTENTS (Continued)

CONTENTS (Continued)

LIST OF TABLES

Table **Page**

LIST OF TABLES (Continued)

LIST OF FIGURES

Figure **Page**

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF ABBREVIATIONS

AIC	=	Akaike's Information Criterion
BPM	=	Beeps per minute
BUFA	=	*Bungarus fasciatus*
K50	=	Fixed kernel 50% utilization area
K95	=	Fixed kernel 95% utilization area
GIS	=	Geographic Information System
GLM	=	Generalized linear model
GLMM	=	Generalized linear mixed models
GPS	=	Global Positioning Systems
HL	=	Head length
HW	=	Head width
IUCN	=	International Union for Conservation of Nature
MCP	=	Minimum convex polygon
MDD	=	Mean daily displacement
MMD	=	Mean movement distance
MRD	=	Mean relocation distance

LIST OF ABBREVIATIONS (Continued)

SBR	=	Sakaerat Biosphere Reserve
SE	=	Standard Error
SVL	=	Snout- to- ventral length
TBL	=	Total body length

CHAPTER I

INTRODUCTION

1.1 Introduction

The banded krait (*Bungarus fasciatus*) is a large, terrestrial snake belonging to the Elapidae family. Like many Elapids, kraits use potent neurotoxins to subdue their prey (Kerkkamp et al., 2015). Chanhome and colleagues (2011) suggest that banded krait's diet primarily consists of fish, amphibians, and reptiles, including other snakes. Banded kraits are widely distributed across South and Southeast Asia, from India and Nepal in the West, to coastal China and Taiwan in the East, while ranging South through much of Indochina and Indonesia (Chan-ard et al., 2015).

Despite their reportedly docile, secretive nature, banded kraits remain capable of inflicting potentially fatal bites to humans (Chanhome et al., 2011). Symptoms of krait envenomation usually include respiratory muscle paralysis, induced by the venoms effect on neuromuscular junctions via beta-presynaptic blockades (Ismail, 2013). Although little is known about the habitat requirements of banded kraits, they are thought to dwell in a variety of habitats including those disturbed by humans such as villages and farmland throughout their distribution (Stuart et al., 2013). Banded kraits have even been found during surveys of highly urbanized habitats, such as in Guwahati City, India (Purkayastha et al., 2011). Cohabitation with humans may lead to the rise for conflict between venomous kraits and humans throughout South Asia, a region undergoing rapid human population growth and development. There is an assortment of both direct and indirect ways in which humans kill snakes, including, vehicles collisions on roadways (Dutta et al., 2016), as a byproduct of agricultural activities (Knierim et al., 2018), through spiteful attacks by humans and mauling by feral animals (Whitaker and Shine, 2000). Banded kraits also face threats resulting from the unique cultural and socioeconomic contexts of regions within their range, such as being collected for skin trade and use in traditional medicine (Somaweera and Somaweera, 2010; Stuart, 2013).

Many studies have focused on the banded krait's potent venom, it's therapeutic potential, and the synthesis of anti-venom to treat bites (Gomes et al., 2017; Ratanabanangkoon et al., 2016; Rusmili et al., 2014). However, there remains a tremendous gap on the ecological habits and biology of this species. My study views banded kraits as a focal species, employing a range of field techniques to make in-depth observations on the species' spatial ecology, temporal activity, habitat usage, and behaviors. The kraits monitored in this study lived in the human-dominated Transitional Zone of the Sakaerat Biosphere Reserve. By intensively monitoring individuals, I hoped to gain information on their natural history, shedding light onto mechanisms underlying the population dynamics and ecology of banded kraits. These findings may then be applied towards reducing human-krait conflict and making informed conservation plans.

1.2 Research objectives

1) Quantify the home-range sizes of adult male and female banded kraits (*B. fasciatus*).

2) Measure the microhabitat features surrounding shelter sites used by banded kraits (*B. fasciatus*).

3) Identify temporal patterns in the nocturnal activities of radio-tracked banded kraits (*B. fasciatus*).

4) Document novel behaviors of banded kraits (*B. fasciatus*) at their shelter and nesting sites.

1.3 Scope and limitations

The first banded krait, we captured to implant with a radio transmitter and subsequently monitor at SBR was on August 16, 2015. In 2016, we added 2 more adults, which were captured during night surveys within the home range of the first study snake. We opportunistically captured an additional krait and implanted it with a radio transmitter in March 2017. All tracked kraits in this study were adult (2 female, 2 male) and had overlapping home ranges. Additionally, all radio tracked kraits were within the transitional zone of the SBR, with home ranges predominantly comprised of matrices of rice paddy agriculture. Due to the difficulty in locating new specimens within the SBR, our effort had been spent searching for individuals within the agricultural Transitional Zone where previous observations of the species had been reported. However, we also briefly (October – November 2017) surveyed disturbed forest fragments using drift fence trap arrays at the Suranaree University of Technology campus, but our efforts were to locate banded kraits were to no avail despite recently confirmed photographic reports of the species on a private property adjacent to the university.

CHAPTER II

LITERATURE REVIEW

2.1 Elapid snakes

Elapidae represents the largest family of venomous snakes, having more than 360 living species (Utez et al., 2017), and many of which considered medically significant to humans (Fry et al, 2009). Species in this clade produce potent neurotoxins which are administered through two tubular fangs fixed to the maxillary bone at the front of their mouth (Kerkkamp et al., 2017). The Elapidae family has undergone rapid evolutionary diversification (Sanders et al., 2008). This relatively young clade underwent rapid biogeographic expansion approximately 31 million years ago during the Oligocene Era (Kelly et al., 2009). Members of Elapidae are now distributed throughout much of the world's tropical and temperate terrestrial and marine zones. There remains much debate among herpetologists on the taxonomical breakdown and classification of many Elapids. However, modern herpetologists have generally divided Elapidae into three main lineages, including coral snakes (Castoe et al., 2007), the Australasian and marine elapids (Sanders et al., 2013; Sanders et al., 2008), and the Afro-Asian elapids (Slowinski and Keogh, 2000).

Many species take on unique morphological, physiological, and behavioral predatory defense strategies. For example, American coral snakes use vibrantly colored body bands as an aposematic warning sign to predators of their potent venom (Savage and Slowinski, 1992). Another example of elapid defense is the iconic hooding and venom spraying behaviors used by cobras of the *Naja* genus. Snakes of genera *Hemachatus* and *Ophiophagus* also employ defensive hooding, accompanied by aposematic body banding as a warning display (Panagides et al., 2017).

Kraits, of the *Bungarus* genus, currently comprise 15 species and represent a sister clade to Asian cobras, *Naja* (Utez et al., 2017). All but one species of krait, are generally characterized by distinctly colored body bands. Their banded patter also likely serves as an aposematic warning. This is further supported by the mimicry of several non-venomous genera which apparently mimic both krait behavior, morphological appearance, and body coloration to avoid predation. These impersonators have similar colorations and predator avoidance displays to kraits, while occupying overlapping zones of geographical distribution as their venomous counterparts (Karraker et al., 2014).

2.2 Radio telemetry of Elapid snakes

Elapidae represents the largest radiation of venomous snakes, and the second largest snake family, accounting for approximately 363 species (Utez et al., 2017) of the near 3,500 species of extent snakes (Figueroa et al., 2016). However, a quick search through scientific literature revealed that published ecological studies on the two largest Colubroidean snake families, Colubridae and Viparidae, far exceed the number from Elapidae. The ecology of Elapidae, particularly those taxa from tropical Asia and Africa remain scantly represented in literature.

The distribution of ecological research does not have an even representation across the globe, as highly biodiverse regions such as Southeast Asia remain severely underrepresented. Most of the ecological output is produced from only a few regions, including the wealthy countries of Australia and those in North America and Europe (Martin et al., 2012). This disproportionate trend also appears to be consistent within the limited ecological studies of Elapid snakes. By searching Google Scholar, I uncovered 12 studies published in peer reviewed journals, which used radio telemetry to study the spatial ecology, habitat selection, or activity periods of terrestrial Elapids (Table 2.1). Of these 14 publications, 11 were from Australia, and only 2 from Asia (Butler et al., 2005 a; Butler et al., 2005 b; Barve et al., 2013; Croak et al., 2013; Fitzgerald et al., 2010; Fitzgerald et al., 2003; Fitzgerald et al. 2002; Mohammadi et al., 2014; Shine, 1987; Shine, 1979; Webb and Shine, 1997 a; Webb and Shine, 1997 b; Whitaker and Shine, 2003; Whitaker and Shine, 2002).

Table 2.1 Review of scientific literature published on spatial ecology, habitat select, or activity period of terrestrial Elapid snakes between 1979-2017.

Region	***Elapid Species***	***Species Researched***	***Pub. #***	***Journals***	***Pub. Date***
Australia	104	*Hoplocephalus bungaroides* (Broad-headed snake)	3	PlosONE Biological Conservation Biological Conservation	2013 1997 1997
		Hoplocephalus bitorquatus (Pale-headed snake)	2	Australia Zoologist Journal of Thermal Biology	2010 2003
		Pseudonaja textilis (Eastern brown snake)	2	Herpetological Monographs Herpetologica	2003 2002
		Pseudechis porphyriacus (Red-bellied black snake)	2	Journal of Herpetology *Herpetologica	1987 1979
		Austrelaps superbus (Lowland copperhead)	1	*Herpetologica	1979
		Notechis scutatus (Tiger snake)	2	*Herpetologica Wildlife Research	1979 2005
		Hoplocephalus stephensii (Stephen's banded snake)	1	Copeia	2002
Americas	80	-	0	0	-
Asia	47	*Bungarus candidus* (Malayan krait)	1	Tropical Natural History	2014
		Ophiophagus hannah (King Cobra)	1	Hamadryad	2013
Africa	38	-	0	0	-
Total	293	9	14	***Average***	2005

2.3 *Bungarus fasciatus*

The banded krait (*Bungarus fasciatus*) is a large snake, reaching adult lengths of 2.12 m (Chan-ard et al., 2015). They are noted to feed on vertebrates, including small mammals, fish, amphibians, and reptiles, including other snakes and carrion (Chan-ard et al., 2015; Knierim et al., 2017). Kraits belong to the *Bungarus* genus within the family Elapidae, which currently includes 15 species with geographical distributions ranging from Iran in the west to China in the east, and Indonesia to the south. Banded kraits are perhaps the widest ranging species of krait, inhabiting much of South and Southeast Asia, sympatrically alongside other species of krait (Utez et al., 2017). They are nocturnal and thought to be associated with wetlands across a range of habitats from tropical evergreen forests to degraded areas near human inhabitation (Stuart et al., 2013). Like other krait species, the banded krait has characteristic dorsal body banding. However, their bodies are sharply triangular in cross section and their dorsal bands are yellow rather than white, with intervening black bands (Chanhome et al., 2011). All kraits possess potent neurotoxins, capable of causing human mortality via envenomation (Chanhome et al., 2011; Vongphoumy et al., 2016). Despite their potential health risk to humans, wide distribution, and IUCN listening as “Least Concern” (Stuart et al., 2013), there have yet to be any robust studies published on banded krait ecology.

CHAPTER III

METHODS

3.1 Study area

The study was conducted within the Sakaerat Biosphere Reserve (SBR), in Nakhon Ratchasima, Thailand (14.44−14.55ºN, 101.88−101.95ºE, Figure 3.1). The SBR was established in 1967 as a UNESCO Man and Biosphere Reserve, nominated by the Thai government to facilitate biodiversity conservation (United Nations Educational, Scientific, and Cultural Organization; Tongyai, 1983). Biosphere reserves utilize three zones of land classification that fall along a gradient of management and human disturbance (Ongsomwang and Sutthivanich, 2014). At a biosphere's heart lies the Core Area, an area with enforced protection. The Core Area is surrounded by a Buffer Zone, managed to allow ecologically sound activities. A Transitional Zone surrounds the inner two and allows the highest level of human disturbance. Activities that foster sustainable socio-economic and cultural growth are encouraged within Transitional Zones (UNESCO [online] 2017). Sakaerat houses an 80 km² Core Area, predominately consisting of primary growth dry evergreen forest (60%), dry dipterocarp forest (18%), and secondary plantation forest (< 18%) (Tongyai, 1980). The surrounding Transition Zone represents nearly 82% of the reserve's total land area and is characterized by a patchwork of disturbed habitats including: fragments of native forest, plantation forests, upland and lowland agricultural fields, man-made reservoirs, irrigation canals, and settlements.

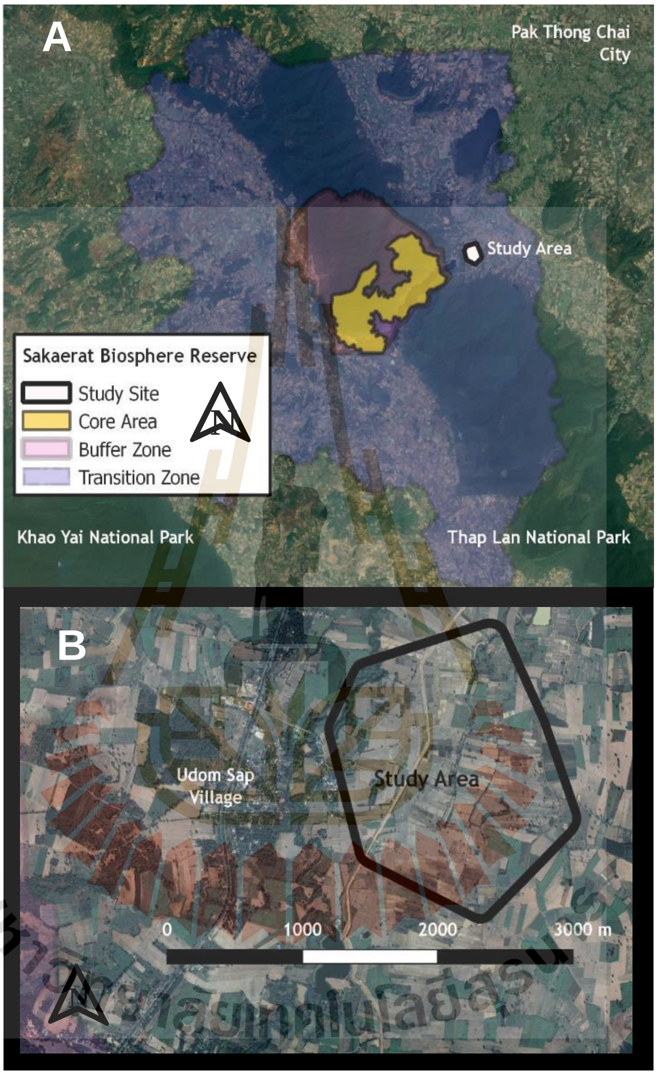


Figure 3.1 Map of the Sakaerat Biosphere Reserve with Core (orange), Buffer (pink), and Transition (purple) zones (A) (modified from Ongsomwang and Sutthivanich. 2015). The study area delineated by a minimum convex polygon around the outermost grouped krait locations (B).

The study area is an approximately 313 ha;1956 rai area within the Transition Zone, Northeast of the Core Area (Figure 3.1). The area is composed of heavily modified habitats such as: irrigation-fed rice paddies, sugar cane, maize, cassava fields, irrigation channels, small reservoirs, and villages. Elevation across the study site ranges from 227 m to 237 m above sea level. The region undergoes a unimodal rainy season, with peaks in precipitation normally occurring during May and September. However, the overall 'wet season' spans from May-November. The mean annual precipitation was 116.94 cm during the study period (2015- 2017). The mean annual wet season daily high was 29.17 ºC and low was 23.45 ºC. A dry season spans December-April and had a mean daily high of 28.38 ºC, and low of 19.20 ºC, during the study period (TISTR, 2018).

3.2 Surveys

With the help of various field assistants, I conducted opportunistic nocturnal surveys for kraits beginning at the onset of the study in 2016. At the beginning of each survey, surveyors recorded the ambient temperature, relative humidity, moon phase illumination, number of surveyors, and UTM coordinates at the location of their starting points. Surveyors left GPS devices turned on while surveying to record their distance covered and path walked. When a snake was observed, we recorded the species name and location. When surveyors encountered a krait, those who had been adequately trained to handle venomous snakes, captured it for biometric processing and subsequent radio transmitter implantation.

3.3 Processing and biometric measurements

We transferred captured kraits to the Sakaerat Environmental Research Station for processing and surgery. While at the station, kraits were housed in sterile plastic boxes, with secure lids following (Llewelyn et al., 2011; Llewelyn et al., 2009). When removing kraits from their boxes, we inserted the anterior portion of their bodies into a transparent acrylic tube (Figure 3.2A). Once secured in the tube, we administer isoflurane via a cotton filled vial placed into the end of the tube, which was then capped with a rubber bung. Isoflurane induced anesthesia which allowed for us to collect and record precise biometric measurements (Wilkinson and Leonatti, 2014). During processing, we measured: snout to vent length (SVL), tail length, mass, head length and width, body girth, sex, body condition, and too scale clips for potential later use as genetic samples. To determine sex, we used cloacal probing, which is considered standard methodology for snakes (Laszlo, 1975). A professional veterinarian from the Korat Zoo performed transmitter implantation surgeries on adult kraits while anesthetized either immediately following processing or during another anesthetization session the following day.

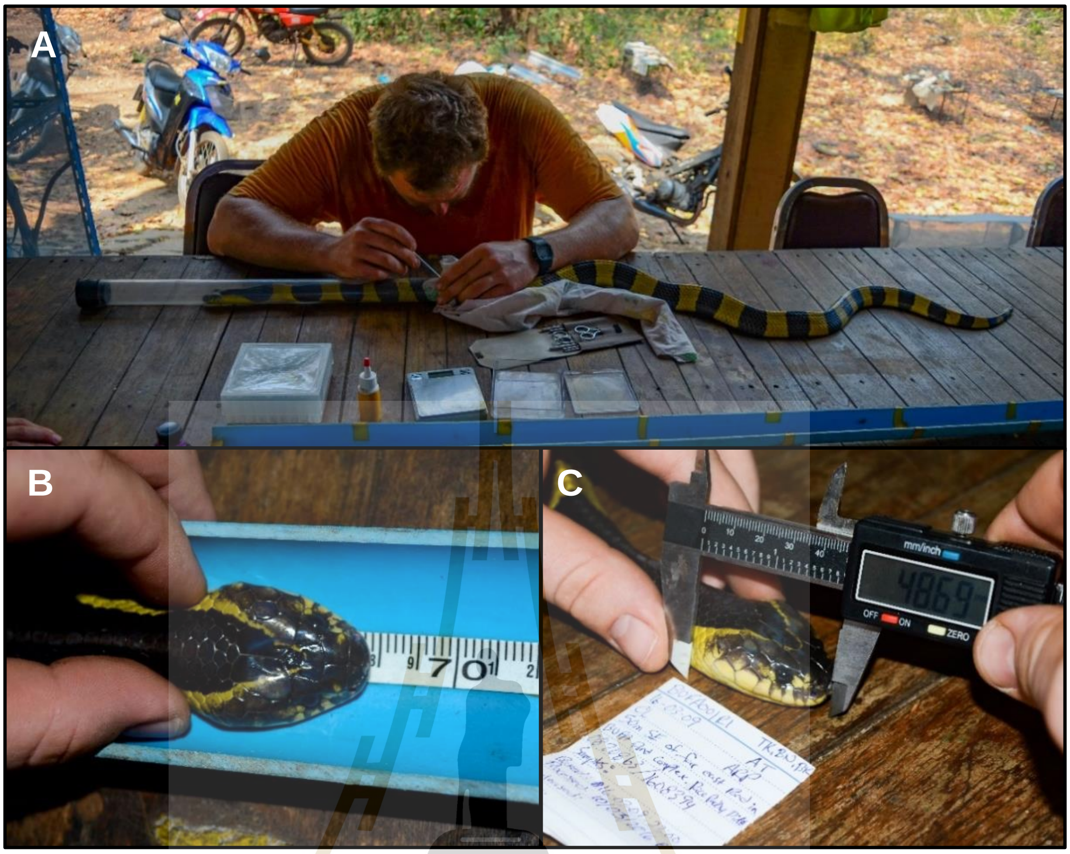


Figure 3.2 Colleague (Bartoz Nadolski) administering isoflurane and inspecting the body condition of an adult male *Bungarus fasciatus* (BUFA001) while inserted into a transparent snake tube (A), SVL head measurement (B), and head length (C).

3.4 Spatial ecology and radio telemetry

Captured kraits that were to be radio tracked underwent isoflurane induced anesthetization following the processing methodology. To ensure the animal’s safety and abide by local law, a certified veterinarian from the Korat Zoo, Dr. Wirongrong Changphet, lead operations and made all surgical incisions. Dr. Changphet followed the methodology described by Reinert and Cundall (1982; Figure 3.3A). To avoid adverse effects, only kraits large enough to be implanted with a radio transmitter weighing less than 5% of that animal's mass underwent operation. All tracked kraits were either implanted with one of two Holohil transmitter models, a 3.8 g SB-2 or 9 g SI-2 (Figure 3.3B and C) depending on the size of the snake and transmitter availability. The two models differentiated in size and battery life. However, the differences in size and mass were minuscule in relation to that of the snakes' body sizes and likely did not differentially affect the study animals. Following surgery, we intubated and monitored kraits until they became fully responsive. We then kept the kraits until nightfall when we then released them at their site of capture. Transmitters were removed following the same techniques as those used during incretion operations and all operations were carried out in accordance with Suranaree University of Technology's Animal Care and Use Committee Guidelines (ACUCG).

Figure 3.3 Author (T.K. Knierim) and veterinarian (Dr. Wirongrong Changphet) implanting a radio transmitter (A) and the two of Holohil radio transmitter models used in this study, an SI-2 (B) and SB-2 (C).

Primary spatial results were quantified using snake location data that we collected once per day, between 08:00 and 18:00. Daily tracks were avoided during early mornings, nights, and evenings to ensure that the presumably nocturnal kraits (Chanhome, 2011) were stationary and to collect data from their diurnal shelter sites. During day tracks, trackers followed the signal emitted from the internal VHF Holohil transmitters using an R410 ATS radio receiver in conjunction with an RA-23K

Teleonics antennae to the snake's location. When a krait had moved to a new location from the previous track, trackers did not approach closer than 6 meters, relying on triangulation to pinpoint the kraits location using the "draw line" feature on a Garmin 64S GPS unit. When a krait remained in that location until the next successive day track, trackers attempted to acquire an exact pinpoint by approaching within 1 m of the shelter site if the site was accessible by exposed soil, ruling out treading on a potentially unseen snake laying amongst dense vegetation. Trackers recorded data on the site's: global position, climatic conditions, surrounding habitat characteristics, and available macrohabitats within 30 m of each snake. Data was recorded digitally via smart phones, using Google's Open Data Kit (ODK). When able, trackers also stationed Bushnell field cameras at shelter sites which required daily battery and SD card maintenance.

3.5 Habitat preference

Duncan and Manly's habitat preference indices have been applied across a variety of radio telemetry studies (Gionfriddo et al., 1986; Knutson et al., 2018; Roy and Dorrance, 1985; Valeix et al., 2009), including those monitoring snakes (Knierim et al., 2018; Marshall et al., 2018; Silva et al., 2018). Manly et al. (2002) described three study designs in which habitat indices can be derived. In this study, I used a "Type III" design, where both "use" and "availability" were measured for each study animal individually. I classified used habitats as those that were diurnally occupied by tracked kraits, following my previous methodology in Knierim et al. (2018). Study areas were defined as the space within each krait's 100% MCP home range. I categorized habitats into 12 dominant types within each study area, including: cassava, canals, dikes (bunds), empty lots, field margins, human settlements, ponds, rice, roads, and sugar cane. The home ranges of BUFA001 and BUFA003 had two additional categories unavailable to BUFA002 and BUFA004, “plantation forest” and “vegetable field” (Figure 3.4; Table 3.1). Habitats were manually digitized across the study area using Google Satellite imagery in QGIS and were subsequently visited on the ground to resolve classification uncertainty.

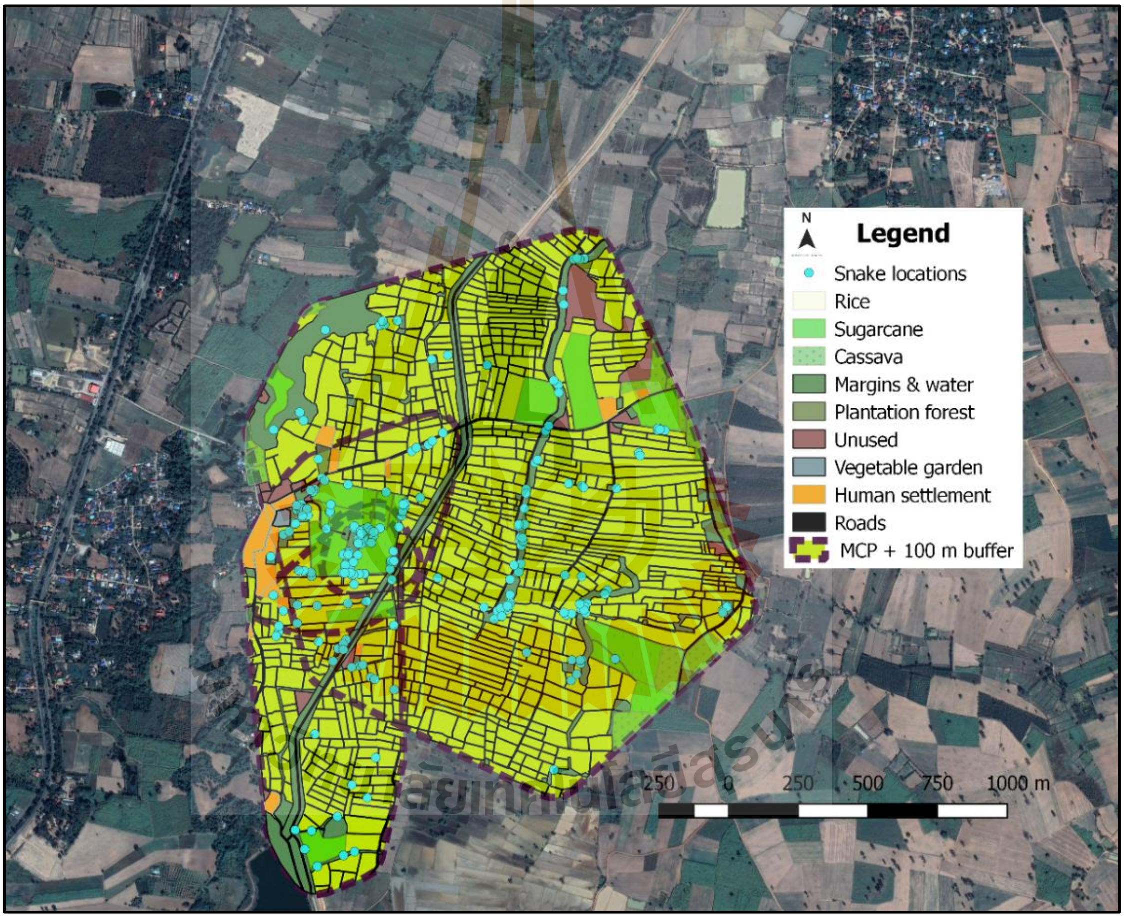


Figure 3.4 Digitized habitats within each of the four overlapping MCP home ranges and diurnal snake locations (blue circles).

Table 3.1 Description of habitats used in analyses and percent composition of the total study area. Study area is defined by the area within an MCP traced around the outermost points of all overlapping 100% MCP home ranges.

Habitat	Description	Total Study Area
Rice	Seasonally flooded rice paddies harvested 2/year	68.10%
Sugar cane	Sugar cane fields harvested 1/year	7.45%
Canal	Irrigation canals and artificially channelized streams (> 3m diameter)	6.85%
Dike	Narrow, embankment subdividing rice fields (< 2m diameter) and (91 cm ± 53 cm) high	5.37%
Cassava	Cassava field	2.36%
Pond	Retention and fish ponds	2.05%
Empty	Unused lots that remained in fallow throughout study period	1.97%
Margin	Either a depression or embankment dividing habitat types (> 2 m diameter)	1.89%
Settlement	Actively used buildings and surrounding lot	1.83%
Roads	Paved and dirt (3 – 5 m diameter)	1.51%
Plantation	Plantation forests of *Eucalyptus camaldulensis*, or mixed fruit orchards (> 10 m at minimum diameter)	0.50%
Vegetable	1 large vegetable garden apx. 100 m diameter, receiving regular maintenance	0.10%

3.6 Habitat Selection

Habitat selection was additionally assessed at the microhabitat scale to infer how banded kraits may have selected their diurnal shelter sites. Herein, microhabitat is defined as the habitat features within a 3-meter radial encircling a retreat site or as diurnal radio-telemetry location of a stationary krait. Habitat characteristics were recorded during daily tracks once kraits had been determined stationary and then located at their shelter site locations. However, data was collected inconsistently throughout the study period because of variation in radio tracker's interpretation of field protocol. Additional shelter site surveys were conducted at the end of the radio-tracking study period.

Habitat plots were generated within a GIS vector comprising the top four preferred habitats ranked by Duncan's Index of preference: ponds, field margins, canals, and paddy dikes (Figure 3.4). I restricted the analyses to the top four habitats because less preferred habitat types were subject to regular disturbance. Therefore, the state of site covariates was likely to change frequently through time. The study area for each snake was determined by creating a 100-meter buffer around each krait's 100% MCP home range (Knierim et al., 2018). A random sample of 15 previously used (selected) shelter sites (diurnal radio-telemetry locations) without replacements were generated for each krait using the Rand and Rank functions in Microsoft Excel 2016. Thirty-five random plots were also generated, representing locations of available shelter sites, using Quantum GIS (QGIS). Sample sizes for selected and available plots were validated using power simulation analyses with the R package, simr. Once grouped, the three snake's microhabitat plots totaled 45 selected (previously used) and 35 available (random) plots. (Figure 3.5).

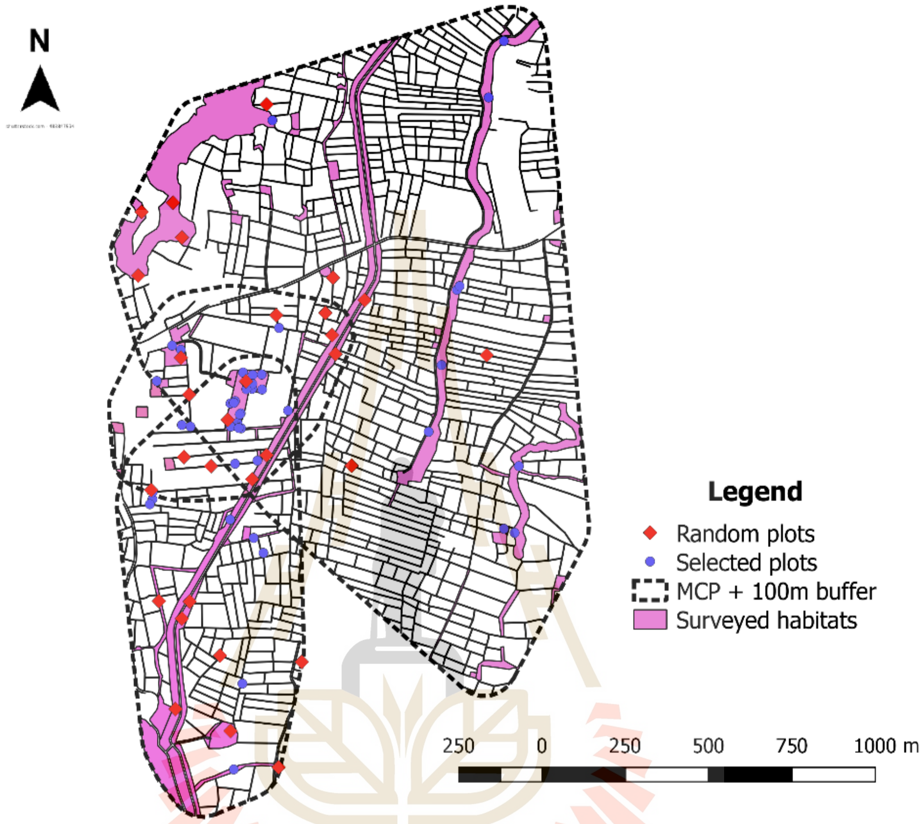


Figure 3.5 Habitat selection plots delaminated from krait MCP home range estimates.

3.7 Nocturnal activity

Trackers conducted night tracks between March 23th to July 13th, 2017 to monitor the activity and movements of the kraits. Night tracks were carried out on a cyclic schedule with each krait being monitored for 1 hour per night. The monitoring hour rotated to the next subsequent hour in time sequence each subsequent night. Monitoring periods were between (18:00 and 08:00), with the cycle repeating at 18:00 the day after a morning track ending at 08:00. Trackers spent the first 15 minutes of each hour period attempting to locate the kraits by making wide-arc triangulations. During wide-arcs, trackers avoided approaching closer than 30 meters to the snake estimated location to reduce disturbance. Kraits were monitored for movement at 15-minute intervals throughout each hour period. We inferred movement by fluctuations in the signal while counting the number of beeps per minute (BPM), while holding the tracking equipment stationary and the receiver set to the lowest audible gain. We recorded temperature, humidity, and moon phase during each 15-minute breaks. During the last 15 minutes of the hour, trackers again wide-arced the snake's location to reconfirm whether the snake had moved or not, allowing us to measure the distance moved from its shelter site.

During the nesting period of BUFA003 and BUFA004, trackers additionally employed 1 to 2 field cameras (Bushnell Trophy Camera HD Essential), set on time laps (i.e. field scan) to capture activity. Cameras were placed 1-3 m away from the shared burrow entrances used for while nesting. Activity was classified by generalizing non-moving behaviors from the ethogram in the following section (Table 3.2), including: "Moving", "Part_out", "Part_in", "Exit_frame", and "Enter_frame." Field camera deployment is discussed in greater detail in the following section (3.8 Behavior Behavior).

3.8 Behavior

During daily tracks, trackers positioned field cameras (Bushnell Trophy Camera HD Essential) at krait shelter sites to monitor capture behaviors and monitor their activity. Camera traps are commonly used in ecological studies to capture large endotherms, as their large warm bodies easily trigger motion sensor field cameras by creating a heat differential. However, snakes are ectothermic and therefor rarely set off camera's motion triggers. To compensate, we set cameras to "motion trigger" and "field scan" to capture photos at one-minute intervals, as well those triggered by the motion of endothermic animals interacting with the shelter site. These sequential images provide us with continuous snapshots of activity or lack thereof. Herein, I report the behaviors and activity captured from the combined shelter site of BUFA003 and BUFA004 between April 2017 – June 2017). I define behavioral states as those with clear distinctions and then generalized into 8 categories detailed in my ethogram (Table 3.2).

Table 3.2 General activity and behavioral ethogram for BUFA003 and BUFA004 at nest site.

Behaviour ID	**Description**
Peak	Head and neck (heads apx. length of neck) protruding from or visible in burrow entrance
Scope	Head to end of anterior half of body length protruding from burrow
Moving	Entirely out of burrow and moving between photo intervals
Stationary	Entirely out of burrow and stationary for at least 2 consecutive photos
Part_out	> first anterior half of body protruding from burrow (i.e. exiting burrow)
Exit frame	Image of exterior body crossing frame
Part_in	> last exterior half of body protruding from burrow (i.e. entering burrow)
Enter frame	Image of anterior body entering frame

3.8 Data Analyses

3.8.1 Spatial ecology analyses

For ease of comparison between kraits and similar taxon in other studies, I estimated home ranges using two methods: 95% Minimum Convex Polygon (MCP) and fixed kernel density estimates. All home range estimates are reported in hectares (Ha) unless stated otherwise. Minimum convex polygons are perhaps one of the simplest and historically widely used estimations methods and have been used in previous reports on related taxa (Croak et al., 2013; Mohammadi et al., 2014; Stiles et al., 2017; Vanek and Wasko, 2017). However, MCPs often overestimate areas of core activity, and may contain empty space that was not utilized by the study animal (Wasko and Sasa, 2009). I performed both MCP and kernel estimates using R Studio packages: ctmm, move, sp, ggplot2, adehabitatHR, and rgdal. As a result of sample size limitations, the power of robust statistical comparisons was limited, therefor many spatial results are presented only as descriptive statistics (mean ± standard error).and discussed as focal observations. Direct comparisons are made from means of grouped sexes as home range size is well known to differ substantially between female and male snakes (DeGregorio et al., 2011; Hart et al., 2015; Marshall et al., 2018; Strine et al., 2018; Whitaker and Shine, 2002).

Fixed kernel density estimates rely on smoothing factors to estimate area of utilization by the study animal and weight give to animal locations (Blouin-Demers and Fox, 2006). Several smoothing factor methods have been commonly used by spatial ecologists. The first, H_{ref}, may not be adequate for banded kraits as krait relocations (daily shelter sites) are often clumped, probably resulting in overestimated home ranges as described by (Worton, 1989). Another method, H_{LSCV}, which has generally been used with small or infrequently moving species (Seaman and Powell, 1996), delaminates tight-fitted utilization areas around animal locations. H_{LSCV} predicted 95% kernel utilization areas that were widely disjunct from one another, especially for the wide ranging BUFA001.

The kraits in this study varied widely in their movement length's shelter site distributions, with one individual, BUFA001, who regularly rotated use between areas measuring approximately 1.8 km apart. Therefore, I chose to use custom smoothing factors that were objectively fitted to each krait, following the methodology used by Marshall et al. (2018) with king cobras, also in the SBR. This method uses the smallest whole numbered H smoothing factor that creates a contiguous range around all snake locations. To allow comparability to other reptile spatial studies, I opted for 50% kernel contours to indicate "core area" use and 95% contours to represent more generalized areas of utilization (Laver and Kelly, 2008; Marshall et al., 2018). Although home range estimates from the entire study period are initially presented, I decided to remove individuals whose home ranges did not pass bootstrap analyses (i.e. none-asymptotic) for in-depth comparisons between individuals. I performed a bootstrap analysis on both 95% MCPs and 95% kernels estimates and considered a home range asymptotic when the average home range size derived from 90% of randomly ordered krait shelter site locations were within 10% of the home range estimate derived from all krait shelter sites.

When appropriate, I used straight line distances between successive shelter sites and mean distances moved between daily tracking periods to estimate mean daily displacement (MDD). However, when individual kraits were radio located less than 20 days per month, I opted for primarily using mean movement distance (MMD), calculated by the straight-line distance between subsequent locations for movement summaries.

3.8.2 Habitat preference

I calculated habitat preference ratios to examine the banded krait's use of various agricultural habitats. Habitat ratios were calculated by dividing the proportion of all observations recorded in a habitat type by the proportion of available area covered by that habitat. Duncan (1983), formulates the ratio as $P_{1i} = \frac{U_i}{A_i}$, where P = preference, U_i = the percentage of all observations recorded in habitat i, and A_i as the proportion of the study area composed of habitat i. Habitat preference ratios have been similarly applied to ecological studies by Manly et al. (2002). In both cases, the resulting preference values fall along an index: 0 (total avoidance), to 1 (used proportional to availability), and > 1 (preference for said habitat) (Duncan, 1983; Manly et al., 2002). Preference scores can be transformed and displayed as log normalized indices (P becomes P_2), in which preference is occurs when ($P_2 > 0.3$) (Duncan, 1983). If test assumptions are met, selection may then be tested across each animal in the study, as well as between habitat types using Pearson Chi-square tests (Bryson-Morrison et al., 2017; Manly et al., 2002). However, I present only preference ratios (Duncan's, P_i), or W_i, coined by Manly et al. (2002), to avoid violating Chi-square test assumptions stemming from small and non-independent samples (Sabo and Boone, 2016).

3.8.3 Habitat selection

Both random and used microhabitat plots were demarcated by a 6-meter diameter circle to account for the minimum GPS accuracy in the field (3-meter). Variables recorded at each of the 45 selected and 35 available plots included: HEIGHT, WIDTH, BURROW DENSITY, ORIENTATION, VEGETATION, WETNESS, TREES, the presence or absence of EUCALYPTUS, TERMITE MOUNDS, EROSION, and the distances to ROAD, WATER, and SETTLEMENT (Table 3.3). Variables that were correlated with each other greater than R = 0.70 were eliminated from final models. WIDTH was removed, as it was strongly correlated with HEIGHT (R = .80).

Generalized linear mixed models (GLMM) with binomial error distributions were used to evaluate potential shelter site selection with snake ID as the random effect and shelter site selection as the binomial response variable. I considered all possible model combinations as candidate models. Models were ranked by Akaike Information Criterion corrected for small sample size (AICc), using R package AICcmodavg. For multiple models having value rankings below 2 AICc units, I performed model averaging (Arnold 2010; Burnham and Anderson, 2003). Covariates were assessed by their confidence intervals and removed from the final models accordingly. To validate each model, I used Kolomogrov-Smirnov test to assess the deviance of model residuals from predicted estimates using R package DHARMa. Marginal R^2 and conditional R^2 values were used to assess variance resulting from the either only fixed or both random and fixed effects (Nakagawa and Schielzeth, 2013). Significance thresholds for statistical results are set at 0.05, unless otherwise stated.

Table 3.3 Covariates used in generalized mixed modeling and their measurement descriptions.

Variable	Definition	Data
BURROW	Count of burrow entrances > 2.5 cm in diameter (diameter of smallest krait's head)	Count
HEIGHT	Mean height (side 1 & side 2) of raised or depressed land feature	Length (m)
WIDTH	Width across land feature at center of plot	Length (m)
ORIENTATION	Directional lengthwise orientation of elevated linear land feature	Linear direction (0-180º)
TREE	Density of mature woody trees (> 10 cm DBH)	Count
VEGETATION	Height of dominant vegetation composing plot area	Categories: (> 50cm, 50-100cm, > 1 m)
CROP	Type of adjacent agricultural crops (all growth phases/management phases)	Categories: (*e.*g. Rice)
WETNESS	Wetness category determined by combinations of adjacent agriculture along a gradient of ephemeral - permanent water regimes	Categories: (1 – 6)
EUCALYPTUS	Agricultural *Eucalyptus camaldulensis* clumps	Presence/absence
TERMITE MOUND	Elevated termite or ant mounds (> 50cm)	Presence/absence
EROSION	Sink holes, tunnels, depressions resulting from the flow of water	Presence/absence
WATER	Distance to nearest permanent body of water	Distance (m)
ROAD	Distance to nearest road	Distance (m) & road type (primary, secondary)

3.8.4 Nocturnal activity and behavior

Nocturnal activity data acquired from night monitoring using radio telemetry and photographic camera monitoring provides hourly and by minute estimates of individual krait activity states. However, the small number of individuals (n = 2 females, 1 male) severely limits the applicability of robust statistical analyses or modeling, so I primarily use means ± standard deviation to summarize descriptive statistics. In this manuscript, I primarily report the activities and behavioral state of the nesting females as the two were monitored nightly with both methods throughout their nesting period. Although lacking in statistical power, I do report several in-depth descriptions of life history events which have important implications in our understanding of the reproductive biology of kraits.

CHAPTER IV

RESULTS AND DISCUSSION

4.1 Results

4.1.1 Surveys

Only 5 individual banded kraits were located during surveys, much fewer than the total number of non-target snake species (55). Two kraits (BUFA001, BUFA002) were captured during active surveys, while the other 2 were opportunistically located during the nocturnal monitoring of currently tracked individuals (Table 4.1).

Table 4.1 Night surveys in and around the site that later became designated as the "study area". Only surveys from adjacent habitats (> 1 km) or from habitat similar in land use character to that of BUFA001's home range (i.e. rice paddy dominant) is summarized here.

Surveyor	Surveys	Man hours	Non-Target Snakes	Krait Encounters	Krait encounters / manhours
Krait Team	18	39	13	1 (neonate)	0.0256
Green Pit Viper *	7	16	4	0	0
Common Cobra Team	29	173	24	0	0
King Cobra Team	29	126	14	2	0.0158
Total	83	354	55	3	0.0085

* Survey targets arboreal species, representing lower detection probabilities for terrestrial kraits

4.1.2 Biometrics

The first four kraits (BUFA001-BUFA004) were the radio tracked focal group of adult kraits. The two females had a mean SVL = 1,236 mm; however, mass was is only known for BUFA003, 642.8 g. The mean SVL and mass for the 2 males was greater, SVL = 1,503 mm, mass = 1,439.5 g. Three neonates (BUFA005, BUFA006, BUFA007) were captured as they emerged from the linked nesting chamber attended by BUFA003 and BUFA004 and were therefore impossible to determine which of the two nests they originated without further genetic analyses. The hatchling's mean SVL = 337 mm and mass = 15.53 g. An additional juvenile, BUFA008, was captured on a rice bund during an active night survey outside the home range areas of all tracked kraits.

Table 4.2 Basic biometric attributes of all processed banded kraits during study period.

Snake ID	Sex	Age Class	SVL (mm)	Mass (g)	Capture Method
BUFA001	Male	Adult	1576	1449	Survey
BUFA002	Male	Adult	1626	1430	Survey
BUFA003	Female	Adult	1341	642.8	Track
BUFA004	Female	Adult	1131	UK	Track
		Mean	1418.5	1173.9	
BUFA005	Male	Hatchling	332	15.9	Nest Monitoring
BUFA006	Male	Hatchling	342	16	Nest Monitoring
BUFA007	Male	Hatchling	UK	14.7	Nest Monitoring
BUFA008	Female	Neonate	424	21.5	Survey
		Mean:	366	17	

4.1.3 Spatial ecology and movement

Between August 8, 2015 and November 30, 2017, I acquired 902 unique diurnal datapoints (225.50 ± 189.40) from 4 *B. fasciatus*, that were radio tracked for 1517 days (379.25 ± 318.58 per individual) using Holohil SI-2 and SB-2 radio transmitters (Table. 4.3). Radio tracking duration varied greatly among individuals due to all individuals being initially captured at sporadically during the study period, premature transmitter failure (BUFA003, BUFA004), and mortality (BUFA001, BUFA002). The two mortalities caused by the unintended result of a brush fire ignited by farm workers (BUFA002), and the mechanical harvesting of a rice field by a combine harvester (Figure 4.1).

Table 4.3 Summary of radio transmitter use and tracking period.

Snake ID	Transmitter type 1	Transmitter type 2	Start Date	End Date	Days tracked	Number of Fixes
BUFA001	Holohil SI-2: 11g, 40 x 11 mm	Holohil SI-2: 9g, 33 x 11 mm	2015-08-16	2017-11-22	829	475
BUFA002	Holohil SI-2: 9 g, 33 x 11 mm	N/A	2016-05-13	2016-08-26	107	17
BUFA003	Holohil SB-2: 3.8 g, 14 x 9.5 mm	Holohil SI-2: 9g, 33 x 11 mm	2016-11-26	2017-11-30	369	228
BUFA004	Holohil SB-2: 3.8 g, 14 x 9.5 mm	Holohil SB-2: 3.8g, 14 x 9.5 mm	2017-03-14	2017-10-12	212	182
				Mean	379.25	225.5

Figure 4.1 A1) The charred body of BUFA002, whose mortality resulted from a fire set by farm workers to clear a dry pond bed of unwanted vegetation in preparation to the on-coming rice growing season. A2) Site of BUFA002 mortality. B1) Body of BUFA001 at the edge of a rice paddy hours after being dismembered by a combine harvester.

Based on the 902 unique diurnal locations (i.e. shelter sites), I generated home range estimates using two variations of two methods for each krait: 95% MCP, 100% MCP, 50 kernel, and 95% kernels (Table 4.4). Home range estimates using 95% MCPs varied from 0.39 ha (BUFA002) to 149.55 ha (BUFA001), averaging 48.36 ± 34.26 ha for the four kraits. Average 95% kernel estimates were larger (103.58 ± 141.95), ranging from 4.07 ha (BUFA002) to 272.15 ha (BUFA001).

Table 4.4 Movement and home range size from entire tracking period for each krait. "MMD" is the mean movement distance. "MCP" is the minimum convex polygon calculated from 95% and 100% of locations in hectares "Kernels" fixed kernel density estimate in hectares. "H value" is the optimal smoothing factor used to estimate kernel home ranges.

Snake ID	Relocations	MMD	MCP		Kernel		H value
			95%	100%	50%	95%	
Total Study Period							
BUFA001	164	298.79	149.55	197.63	60.77	272.15	200
BUFA002	9	77.56	0.39	1.26	0.88	4.07	30
BUFA003	70	126.87	13.67	21.20	13.62	57.20	127
BUFA004	47	129.82	29.83	30.95	13.75	80.91	124
Simultaneous BUFA001 & BUFA002							
BUFA001	3	558.84	20.47	20.47	22.03	87.26	130
BUFA002	9	77.56	0.39	1.26	0.88	4.07	30

All four of BUFA002's range estimates failed to reach an asymptote using bootstrapping analysis. Additionally, during the six month period in which BUFA002 (SVL = 1626 mm, mass = 1430 g) was simultaneously tracked with the other similarly sized adult male, BUFA001 (SVL = 1576 mm, mass = 1449 g), his 95% MCP estimate was 0.39 ha, 98.08% smaller than BUFA001's (20.47 ha) and therefore removed from future analyses and comparisons unless stated otherwise (Table 4.4). The asymptotic home range estimate for the single male (BUFA001) was 149.55 ha (95% MCP) and 272.15 ha (95% kernel); whereas the average for the two females (BUFA003, BUFA004) was smaller, 21.75 ± 08.08 ha (95% MCP) and 69.06 ± 11.85 ha (95% kernel).

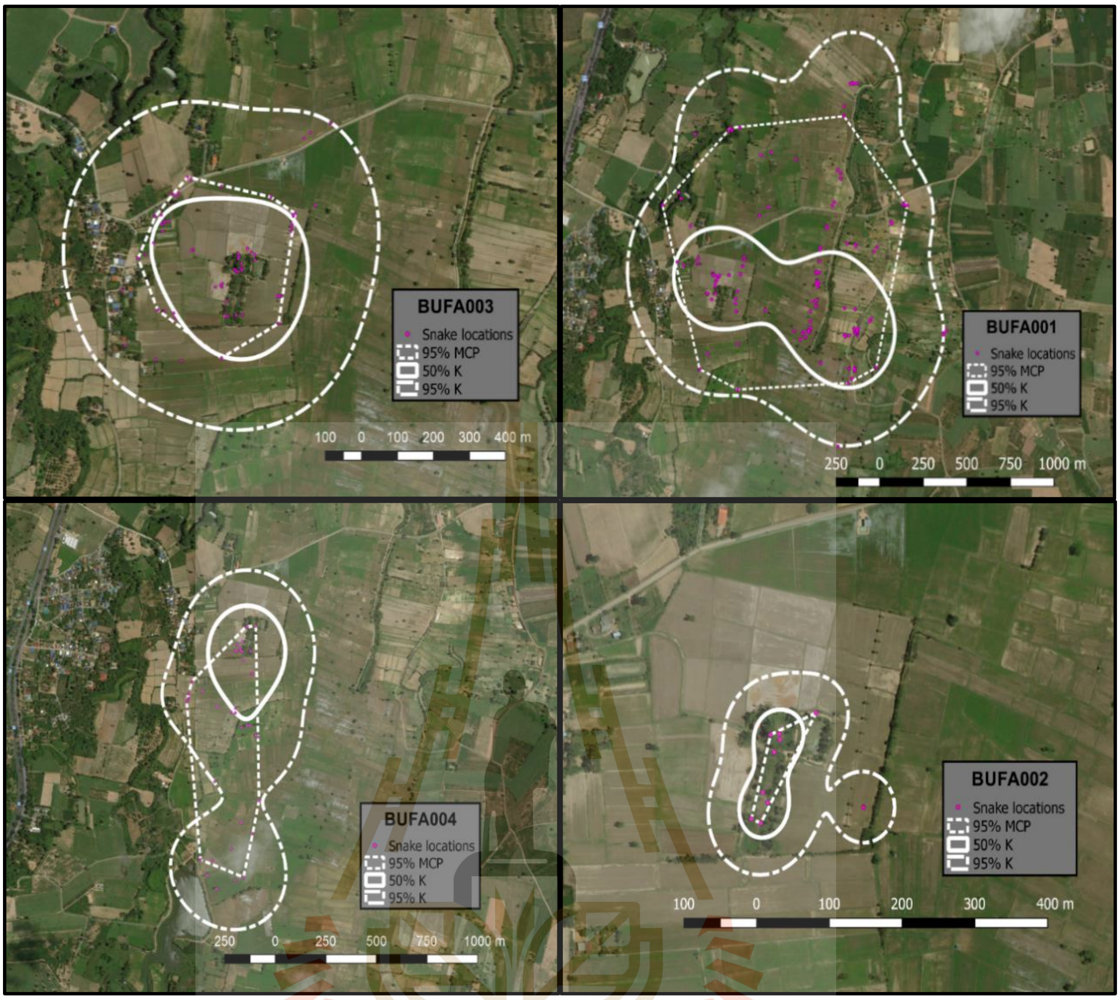


Figure 4.2. The total home ranges for A.) BUFA001, B.) BUFA002, C.) BUFA003, D. BUFA004 from all unique locations between 2015-2017. Dashed line shows the 95% MCP, two-dashed is boundary of 95% kernel, thick solid lines corresponds to the 50% kernel boundary of core activity areas. Small purple circles mark unique diurnal krait locations.

Three of the kraits (BUFA001, BUFA003, BUFA004), were simultaneously radio tracked between April 2017 and September 2017. I located kraits once a day for at least 20 days per month during each of the six months in the period. Home range estimate means varied between (55.67 ± 50.46 ha) for 95% MCPs, (16.71 ± 11.98 ha) for 50% kernels, and (86.56 ± 54.59) for 95% kernels, while each home range estimate for the three snakes shared varying degrees of spatial overlap (Table 4.5 B, Figure 4.3; see Appendix A for graphical visualization).

All home range estimates were asymptotic (> 95%) for each snake and for the entire six-month period. Estimates reached an 90% asymptote when broken down by each month, except for BUFA003, for the months of May and June while movement was substantially reduced during nesting (Table 4.6) and the single month of April for BUFA004, when frequency of relocations (i.e. "moves") was also reduced as the possible result of nesting (Table 4.6). On average, mean daily displacement (MDD) of kraits between April 2017 – September 2017 was 47.20 ± 23.54 m. BUFA001, the single adult male had the greatest MDD (79.69 m) during this time period, while the two females averaged 30.96 ± 6.29 m per day (Table 4.5). Due to some irregularity in diurnal tracking fix intervals, (26.7 ± 1.6 days tracked/month), I also report mean movement distances (MMD) summarized in (Table 4.5).

Table 4.5 A) Movement and home range sizes from simultaneous tracking period (April 2017 – September 2017). "MMD" is the mean movement distance. "MCP" is the minimum convex polygon calculated from 95 of locations in hectares "Kernels" fixed kernel density estimate in hectares. "H value" is the optimal smoothing factor used to estimate kernel home ranges. B) Percent overlap home range overlap (95% MCP, 50% kernel, 95% kernel) between the 3 kraits.

A.	**Relocations**	**MMD**	**MDD**	**95 % MCP**	**100% MCP**	**50% K**	**95% K**	**H value**
Simultaneous Tracking Period: Apr-Sep. 2017								
BUFA001	58	221.21	79.69	126.20	127.55	32.88	157.57	110
BUFA003	36	110.35	24.67	10.99	13.62	4.23	24.83	57
BUFA004	46	128.75	37.25	29.83	30.99	13.01	77.29	120

B.	**95mcp**			**50k**			**95K**		
Krait_ID	**B.1**	**B.3**	**B.4**	**B1**	**B.3**	**B.4**	**B.1**	**B.3**	**B.4**
BUFA001	-	5.90	1.06	-	10.80	23.14	-	14.94	18.07
BUFA003	65.30	-	20.20	83.92	-	81.60	94.80	-	86.15
BUFA004	4.49	27.67	-	58.50	26.52	-	36.85	7.16	-

Home range sizes differed between the second 6-month dry season (December 2016 – April 2017) and the adjoining 3rd 6-month rainy season (May 2017 – October 2017) for BUFA001. During the dry season, BUFA001 utilized a 40.18 ha 95% MCP and relocated between shelter sites 40 times, while having an MMD = 268 m, and MDD = 74 m. In contrast rainy BUFA001 used a 128.28 95% MCP and relocated 54 times, while having an MMD = 168.03, and MDD = 90.22 during the following rainy season.

Kernel home range estimates give much different results than MCPs between these two seasons. The 95% kernel estimate for the dry season was 241 ha, much greater than the 217-hectar estimate for the following rainy season. See Table 4.6.

Table 4.6 Movement and home range sizes across comparative seasons. "MMD" is the mean movement distance. "MCP" is the minimum convex polygon calculated from 95 of locations in hectares "Kernels" fixed kernel density estimate in hectares. "H value" is the optimal smoothing factor used to estimate kernel home ranges and "Asy." indicates whether. MCP home range estimates reach asymptote (T = True) or failed to stabilize (F = False).

	Days	% Daily Fixes	Moves	MMD	MDD	95 % MCP	95% K	H value	Asy.
BUFA001 Seasonality									
2nd Dry Nov.- Apr 2017	144	81	40	268.72	74.64	40.18	241.55	276	T
3rd Rainy May -Oct. 2017	177	86	54	168.03	90.22	128.28	217.52	143	T
BUFA003 Seasonality									
Dry Dec. – April 2017	141	79	27	124.28	30.23	8.49	28.87	88	T
Rainy May – Nov. 2017	211	83	44	125.7	31.6	13.38	29.63	65	T
Nesting April 14 – July 1, 2017	78	88	4	164.15	11.90	0.00	27.93	113	F
BUFA004 Nesting									
Nesting April 3 – June 17, 2017	75	88	10	81.65	12.56	0.08	1.87	24	T

While nest attending, the two females simultaneous shared the same burrow complex for 95 days, BUFA003 (April 14, 2017 – July 1, 2017; 109 days) and BUFA004 (April 4, 2017 – June 17; 105 days). During the nesting period (April 4, 2017 – July 1, 2017) the movement of both females was greatly reduced from non-nesting periods. BUFA003's MDD = 11.90 m, a 38.5 percent reduction in meters, from the non-nesting period (dry and rainy season 2017) mean (Table 4.6). Movement frequency was also reduced for both snakes from non-nesting period. However, MMDs were greater as the few moves made from the nesting site to other shelter sites, that were briefly visited for no more than 1 night, were greater than the MDDs during non-nesting periods (Table 4.6). The distance both females spent away from the nest was not significantly different from one another, Two-sample Kolmogorov Smirnov (D = 0.108, p = 0.593). See Figure 4.3 for detailed summary of proximity to one another and to their nesting site during the nesting period.

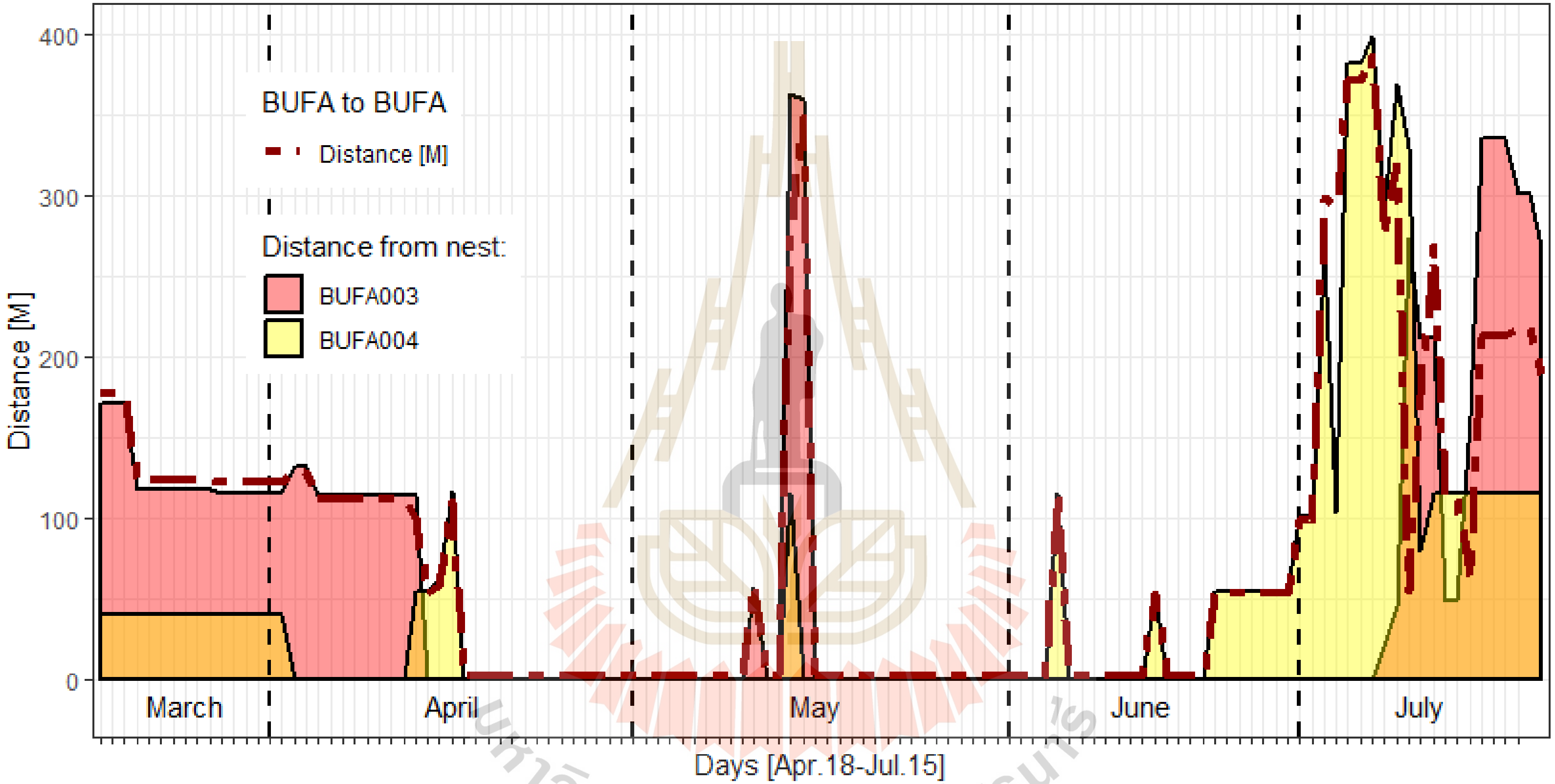


Figure 4.3 Summary of BUFA003 and BUFA004's proximity to shared nest site and to each other. Dark-red dashed line indicates the distance between the daily diurnal locations of the two snakes. The light red and light-yellow colors represent the two kraits proximity to the nest site along a daily scale.

4.1.4 Habitat preference

The most abundant habitat within three of the four study areas was rice (51.00% ± 20.82%), followed by sugar cane across all four study areas (21.50% ± 17.02%). The total study site spanned the width (apx. 1000 m) of a rice dominated riparian lowland tracing the Mun Drainage (Figure 4.6). Variation in the proportion of available rice between BUFA002 (24%) and the other three snakes may be attributed to the BUFA002's significantly smaller home range (Table 4.4), centered around a cluster of retention ponds, estimated from a short tracking period of infrequent fixes. Although BUFA002 failed the bootstrapping analyses of home range stability and had been removed from further comparisons between kraits, I report habitat ratios for this individual as descriptive statistic.

Figure 4.4 Seasonally flooded rice paddies dominate the study region, accounting for the highest percentage of landcover in BUFA001, BUFA003, and BUFA004 home ranges. while upland agriculture, seen in the background composed. Upland agriculture (seen in back ground) characterized by cassava and maize dominate the adjacent habitats outside snake home ranges.

The kraits varied in their habitat preference indices (Figure 4.5). However, the top three ranked habitats for BUFA001, BUFA003, and BUFA004 were field margins (9.79 ± 3.18), ponds (8.08 ± 2.94), and dikes (4.73 ± 2.56). Additionally, BUFA001 frequently sheltered in three canals that bisected his home range, resulting in strong preference (P_{1i} = 6.86) for canal. One canal available, extended into BUFA004's study area. However, it was avoided (P_{1i} = 0.71), as a likely consequence of recent construction. The trenching of the canal and construction of a paired roadway had only recently been finished within months of BUFA004's initial capture (March 2017). The sloped banks of this canal were scarcely vegetated and received periodic disturbance by heavy machinery throughout the study period (Figure 4.6E). Duncan's index of preference scores for each habitat are summarized in log normalized form (P_2), following (Duncan, 1983) in Figure 4.5.

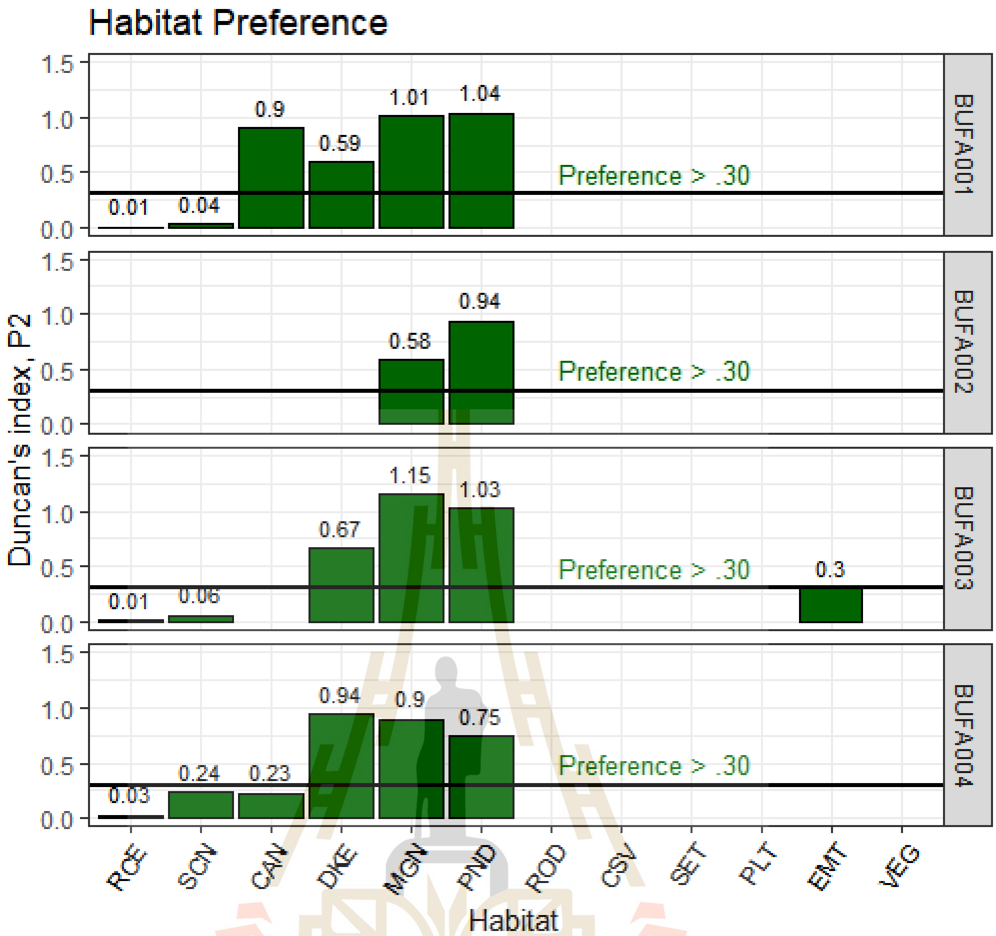


Figure 4.5 Habitat preference indices for all tracked kraits using log-normalized Duncan's Index. Preferences calculated from 100% MCP home range estimates. Habitat codes: CAN – canal, CSV – cassava, DKE – paddy dike/bund, EMT – empty/unused land, MGN – field margin, PLT – plantation forest, PND – pond, SCN – sugar cane, SET – settlement/village, RCE – rice paddy field.

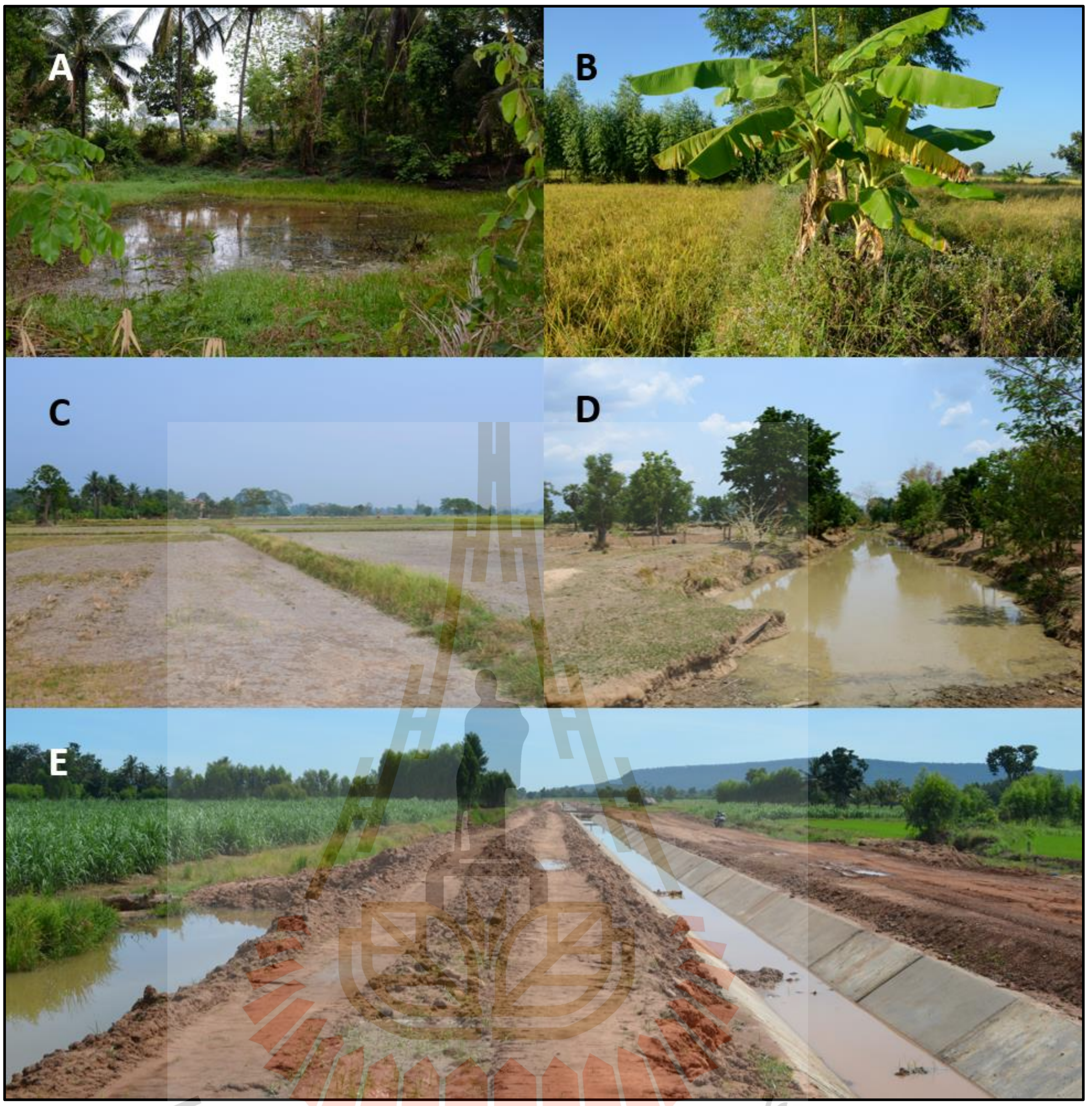


Figure 4.6 Top ranked habitats in habitat preference index. A) Retention pond, B) Field margin, C) rice paddy bund (i.e. dike), D) banks of irrigation canals, except for E) a recently constructed canal which was sparsely vegetated and underwent periodic mechanical work, was avoided by the three kraits.

4.1.5 Shelter site selection

The top model explaining differences between the previously used and available sites for the three radio-tracked kraits included BURROW, VEGETATION, EUCALYPTUS (Table 4.7). Confidence intervals for each of the variables in the best fit model did not range below zero (Table 4.7). The random effect (SNAKE_ID) of the top model had equivalent marginal (R^2 = 0.64187) and conditional (R^2 = 0.6418) R^2 values, indicating no affect from similarity in selection between kraits. The best fit model was additionally validated using a Kolomogrov-Smirnov test to assess the deviance of model residuals from predicted (*p* = 0.7054).

Table 4.7 Generalized linear mixed model results influencing krait shelter selection.

Model	Covariates	K	AICc	ΔAIC	AICc weight	LL
Model 1	BURROW + VEGETATION + EUC. (present)	5	68.69	0.00	0.99	-28.94
Model 2	BURROW + VEGETATION + EROSION (present)	5	73.04	4.35	0.1	-31.11
Model 3	BURROW	3	84.85	16.15	0.0	-39.26
Model 4	VEGETATION	3	95.94	27.24	0.0	-44.81
Model 5	Eucalyptus(present)	3	98.34	29.64	0.0	-46.01
Model 6	Erosion (present)	3	99.31	30.62	0.0	-46.50
Model 7	HEIGHT	3	105.19	36.50	0.0	-49.44
Model 8	TREE	3	108.71	40.02	0.0	-51.20
Model 9	ROAD TYPE	3	111.20	42.51	0.0	-52.44
NULL	Intercept	2	112.14	43.45	0.0	-53.99
Model 10	WATER	3	112.27	42.58	0.0	-52.98
Model 11	TERMITE	3	113.05	44.36	0.0	-53.37
Model 12	ROAD	3	113.42	44.73	0.0	-53.55
Model 13	ORIENT	3	114.27	45.58	0.0	-53.98

Table 4.8. Breakdown of variables from top two candidate models (Model 1, Model 2) for predicting selection of shelter. Bold confidence bound scores indicate violations.

Model	Explanatory variable	Coefficient estimate	Standard error	Lower confidence bound (2.5%)	Upper confidence bound (97.5%)
Model 1	Intercept	-3.882	1.013	-6.135	-2.096
	BURROW	1.024	0.297	0.504	1.681
	VEGETATION	1.099	0.380	0.398	1.915
	EUCALYPTUS	2.028	0.800	0.564	3.777
Model 2	Intercept	-3.588	0.927	-5.613	-1.927
	BURROW	0.902	0.291	0.387	1.540
	VEGETATION	1.150	0.360	0.481	1.914
	EROSION	1.629	0.965	**-0.127**	**3.799**

Kraits used certain agricultural habitat features in higher proportions than they were available. These habitats included a vast network of raised field bunds, subdivided ephemerally flooded rice paddies and larger margins, separating fields from adjacent habitats. Kraits also used depressed peripheral agricultural features including the banks of irrigation canals and retention ponds. Kraits used shelter sites amongst raised and depressed features having certain microhabitat characteristics in greater proportion than their availability. Specifically, canal and pond banks and dike and field margins having greater differences in height from that of adjacent fields or waterways (r = .0108, W = 909, p = 3.33e-05). Amongst these field margins and waterways, kraits selected shelter sites characterized by having taller dominant herbaceous vegetation (r = .102, W = 1054.5, $p < 0.05$), clumps of *Eucalyptus camaldulensis* trees (r = .404, W = 654.5, p =

0.281), and higher densities of burrow entrances (r = .0327, W = 942, $p < 0.05$). So, I inferred that banded kraits are nonrandomly selecting for certain habitat features, including high burrow density, and higher dominant vegetation heights (Figure 4.7).

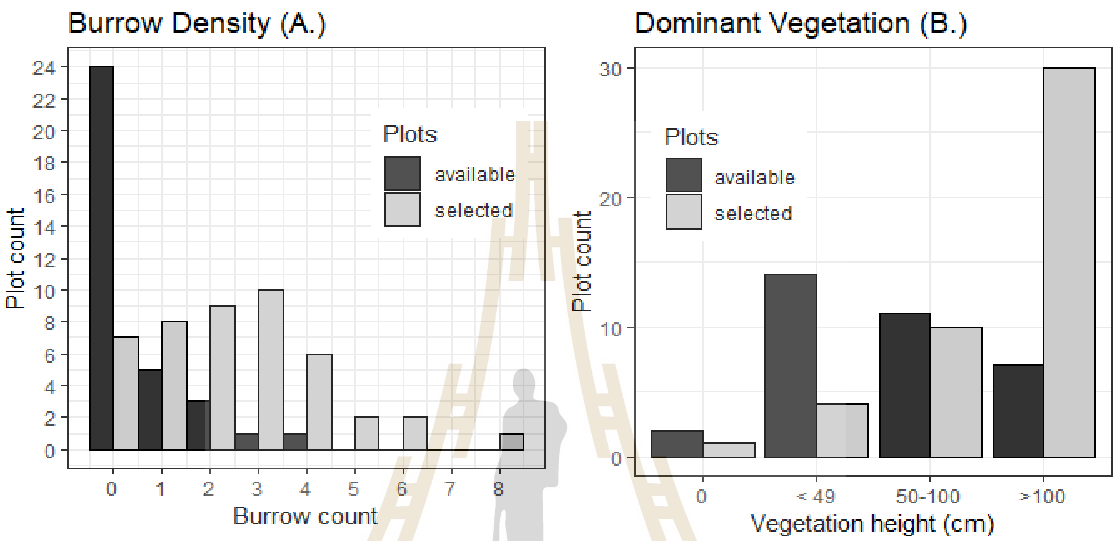


Figure 4.7 The top two influential expletory variables, A) burrow density and dominant B) vegetation height from the best fit model.

4.1.6 Nocturnal activity

I obtained a mean of 70.33 ± 2.36 unique hourly monitoring events per krait between Mar 22,.2017 – July 13,2017 across a 14-hour temporal scale (18:00 – 07:00). The three kraits were monitored had similar hourly monitoring effort between one another. BUFA001 had a mean of 4.79 ± 1.21 monitoring tracks per hourly period, while BUFA003 had 5.14 ± 1.06 and BUFA004, 5.14 ± 1.19. BUFA001 was ‘Active’ during at least 1 of the 3 BPM sampling periods within a monitoring period, during 20 monitoring periods (29.85% of night tracks). While the two females were active for a mean of 18.50 ± 1.50 out of 72-night tracks, approximately 25.69% (Table 4.9).

Combined, the 3 kraits had the highest proportion of activity between the hourly periods beginning at 20:00, 21:00, 00:00, 02:00. Hourly activity and distances kraits movement distances during the hours are summarized further in Table 4.9 and Figure 4.8. Movement lengths could not always be determined in the field due to the logical challenges of obtaining signal, and triangulating krait locations prior to the cyclic BPM sampling periods. Sample sizes of both study animals sampling periods with movement observations, I do not report environmental variables assessed as predictors using generalized models.

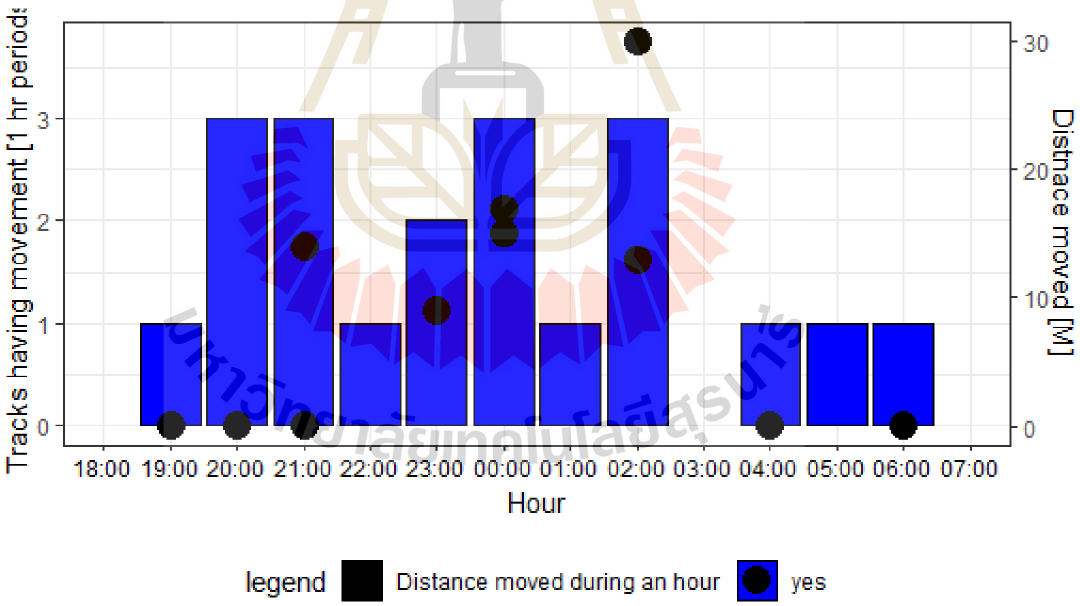


Figure 4.8 Counts of hour-long tracks (monitoring periods), having krait activity during at least 1 of the 3 BMP checks for the 3 kraits. Known distances moved during hourly periods are plotted as black circles, summarizing individual events.

Table 4.9 Summary of night tracks between March 3, 2017 and July 13, 2017. "Movement nights" is the percent of night monitoring periods where movement was observed for each hourly period. "MMD" are mean distance moved during hourly periods. "MRD" is mean distance between relocations. "Temp." is mean ambient temperature. "Hum." is mean ambient humidity.

Time	BUFA001		BUFA003		BUFA004		Movement nights	MMD male	MMD female	Relocations male	Relocations female	MRD male	MRD female	Temp.	Hum.
	moves	total	moves	total	moves	total									
18:00	1	5	0	4	0	4	8%	uk	0	2	3	133	189	28.58	76%
19:00	1	5	2	5	0	4	21%	27	0	1	2	227	122	27.51	82%
20:00	1	6	1	5	**3**	5	31%	11	0	1	4	56	129	26.95	86%
21:00	2	4	**3**	6	2	5	**47%**	209	5	1	2	111	7	27.17	87%
22:00	**3**	5	1	4	1	5	36%	uk	Uk	3	0	71	0	26.98	86%
23:00	2	7	**3**	6	**3**	6	**42%**	uk	76	0	2	0	139	26.86	85%
00:00	**4**	7	**3**	6	**3**	7	**50%**	35	12	0	2	0	141	26.37	87%
01:00	2	4	**3**	7	1	7	33%	257	Uk	0	2	0	149	25.95	89%
02:00	0	3	1	4	2	7	21%	0	37	0	2	0	32	25.61	91%
03:00	1	3	0	4	0	4	9%	uk	0	1	0	53	0	25.57	88%
04:00	**3**	5	2	4	1	4	**46%**	26	10	3	1	89	110	24.93	91%
05:00	0	4	1	7	0	4	7%	0	Uk	2	3	131	109	24.85	91%
06:00	0	5	0	5	1	6	6%	0	0	1	3	70	269	25.57	92%
07:00	0	4	0	5	0	4	0%	0	0	2	2	64	187	27.56	84%

Activity states inferred from monitoring the two female kraits, BUFA003 and BUFA004 using time-lapse photography suggest peaks in external nest activity (viewable movement and stationary resting) earlier in the night (18:00 – 22:00), and again after midnight, (00:00 – 02:00). Some activity was observed during 04:00 – 06:00, when kraits were seen returning to their nests. However, I am unsure whether absences in activity result from the kraits moving out of camera frame and becoming active further away from the nest site. Further examination of photographic data is required before statistical testing. Activity at the nest site is further summarized in Figure 4.9.

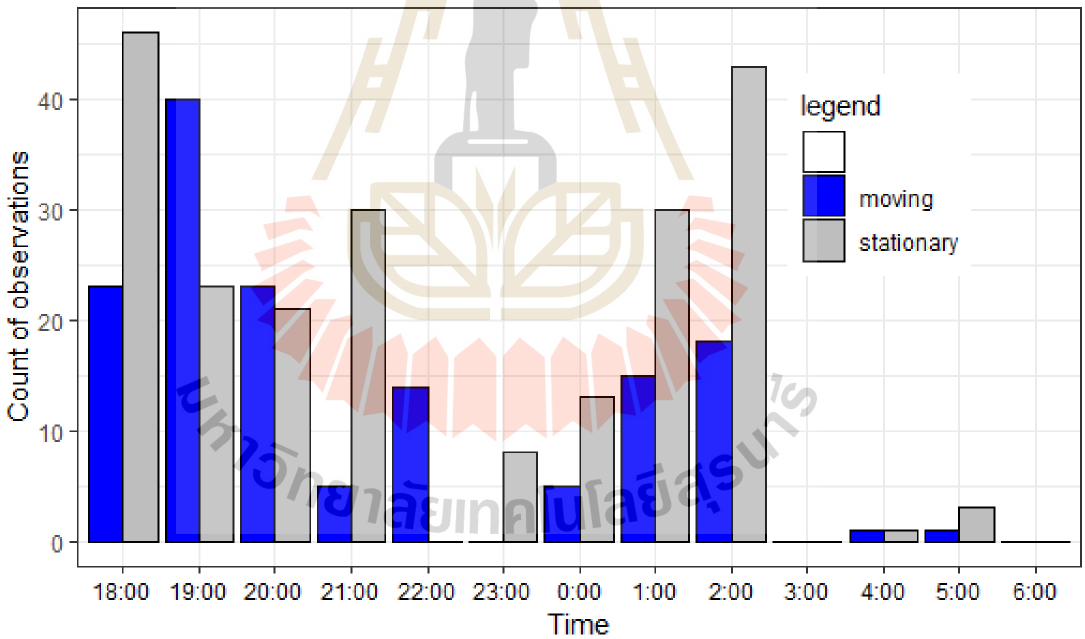


Figure 4.9 Summary of activity at BUFA003 and BUFA004 nest site.

4.1.7 Behavior

Through the deployment of field cameras, I captured several unique natural history observations. Herein, I summarize two major life history events, mating behavior between BUFA003 and BUFA001 and nest attendance at a shared nesting site by BUFA003 and BUFA004. Mating between the two individuals likely occured two years in a row, as both snakes shared a single shelter site for 3 days in (Dec. 9th – Dec. 11th) in 2016 and again met at a different location approximately 230 meters to the north along the same field margin for 5 days (Nov.3rd – Nov. 7th) and an additional day (Nov. 8th) at a nearby shelter site (46 meters) in 2017 (See Appendix 2-A, 2-B for visual summaries of movement and locations used during both mating events). However, the portion of margin used in 2016 had been demolished during the creation of a new irrigation canal prior to the second mating event in 2017. In both instances, BUFA003 arrived at the site nights before she was met by BUFA001. The mating behavior of the two snakes was briefly captured on camera outside the shelter site burrow on the night of Nov. 7, 2017 (Figure 4.9).

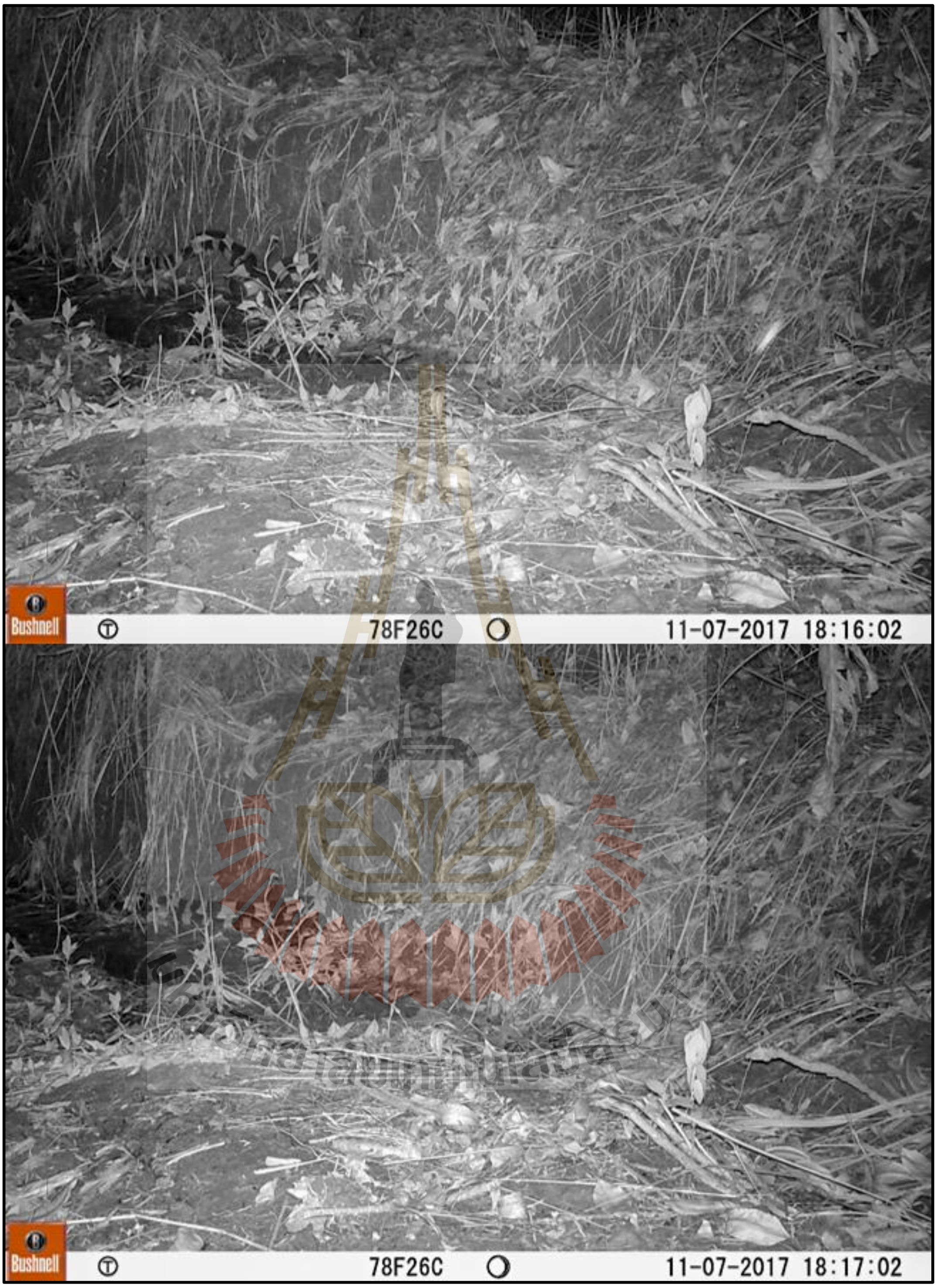


Figure 4.10 Second mating even between BUFA001 and BUFA003 outside of shared shelter site on November 07, 2017.

The two females, BUFA003 and BUFA004 nested between April to June 2017 in an elevated earthen margin, which divided two agricultural fields. Both females exhibited nest attendance and used multiple burrow entrances that were likely connected underground, forming a single burrow complex. During day tracks, both females were frequently pinpointed to below ground burrows approximately 2 meters apart. They partitioned the burrow complex, with BUFA004 primarily entering and exiting burrows on the west side of the complex, and BUFA003 on the east.

I stationed two Bushnell field cameras at the conjoined nesting site to monitor activity and behaviors. The cameras were set to capture photos on a 1-minute interval, providing glimpses of krait activity. We observed various nesting behaviors, including body rolling by BUFA003 shortly before neonates began emerging from the nest (Figure 4.12). This behavior was only captured on camera once, and may be further evidence of nest attendance, as she appeared to have been removing amniotic material from her body by through abrasive contact with soil and leaf-litter.

The two females became active outside their burrow entrances only after dusk, and occasionally seen leaving their burrows within minutes of on another during the nesting period. On two separate occasions, both females appeared to make physical contact with one another outside the burrow entrances. Our observations were not limited to the two kraits at the nest site. We also captured photos of a Siamese spitting cobra (*Naja siamensis*), using adjacent burrows, approximately 1 meter from burrows currently inhabited by the nesting kraits.

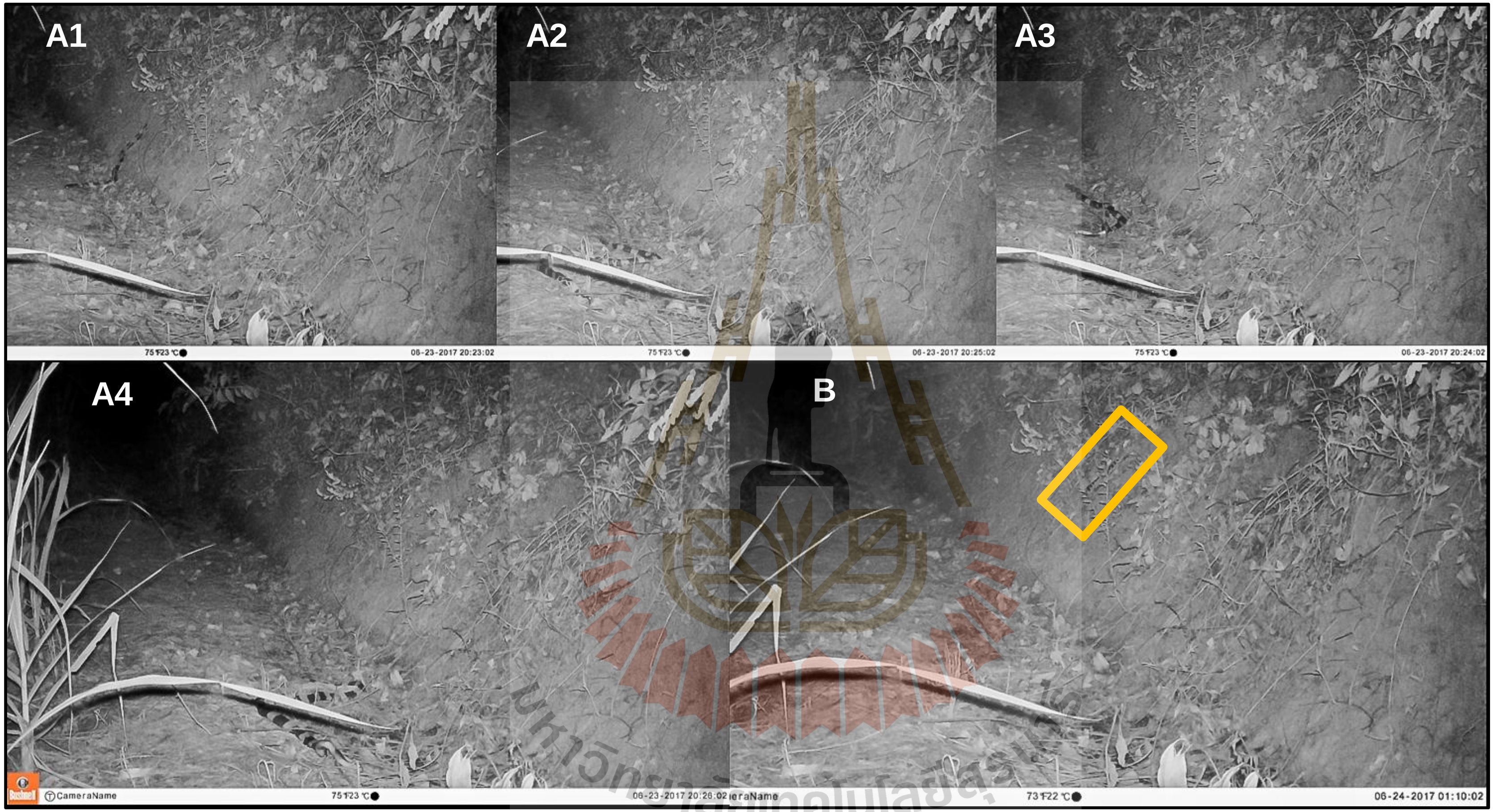


Figure 4.11 Nest attending behaviors: A) Body rolling behavior by female, BUFA004 as she emerges from nest in burrow, B) First hatchling emerges from burrow entrance hours later.

The two kraits spent most of their observable time with just their heads protruding from within their burrow entrances (55.28% of all observations), followed by periscoping from inside burrows (19.02%), moving entirely outside burrows but within close proximity (13.95%), entering or exiting burrow (07.33%), and remaining stationary immediately outside of burrow entrance (05.17%) (Table 4.10; Figure 4.11).

Table 4.10 Ethogram of female krait behaviors captured on camera at the shelter site including total counts of images separated by each dominant behavior.

Behaviour ID	Description	Total observations
Peak	Head and neck (heads apx. length of neck) protruding from or visible in burrow entrance	1517
Scope	Head to end of anterior half of body length protruding from burrow	390
Moving	Entirely out of burrow and moving between photo intervals	383
Stationary	Entirely out of burrow and stationary for at least 2 consecutive photos	142
Part_out	> first anterior half of body protruding from burrow (i.e. exiting burrow)	111
Exit frame	Image of exterior body crossing frame	90
Part_in	> last exterior half of body protruding from burrow (i.e. entering burrow)	62
Enter frame	Image of anterior body entering frame	49
	Total:	**2,744**

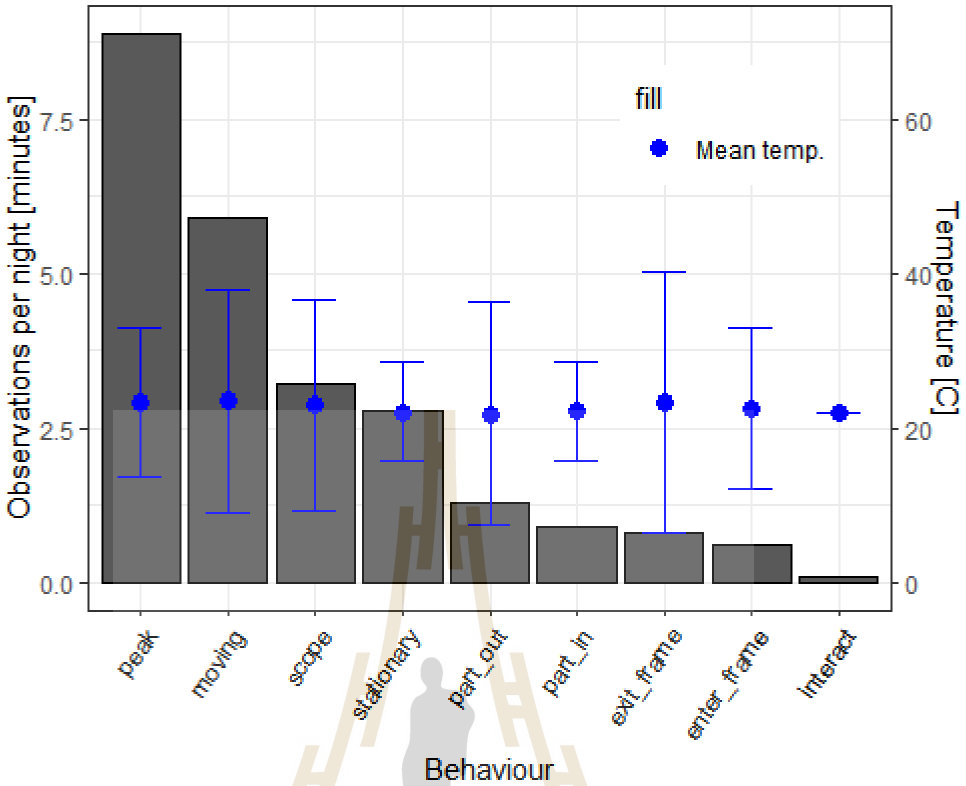


Figure 4.12 Mean behavioral observations per night for BUFA003 and BUFA004 during nesting period. Blue points illustrate mean ambient temperatures take from Bushnell images of each separate behavioral photo-observations with standard error bars.

4.2 Discussion

4.2.1 Spatial ecology and movement

My study provides the first research on the spatial ecology of *Bungarus fasciatus* and the most in-depth investigation for any species in the Bungarus genus. Previously, only two smaller studies had reported on the movements of kraits, both Malayan kraits (*Bungarus candidus*), also from within the SBR, Thailand (Knierim et al., 2018; Mohammadi et al., 2014). In the first study by Mohammadi et al. (2014), an adult male *B. candidus* was radio tracked daily for 21 days, during which time relocated 5 times and occupied a 100% MCP area of 12.30 ha. An individual juvenile male *B. candidus* was radio tracked for 68 days and acquired a 100% MCP area of 3.23 ha and 1.80 ha for 95% MCP (Knierim et al., 2018).

The three *B. fasciatus* whose home ranges reached asymptote in this study utilized 149.55 ha 95% MCP home range (BUFA001), while the two females used 21.75 ± 08.08 ha 95% MCP ranges, much larger than the mean 100% MCP of 07.77 ha from the two *B. candidus* studies. The authors of these two studies indicate their *B. candidus* were not radio tracked long enough to acquire maximum home range sizes during the relatively short study periods. Caution should be taken when comparing *B. fasciatus* and *B. candidus* as they are of course different species, with *B. fasciatus* reaching larger body sizes (Chanhome et al., 2011). Body size varied between the adult *B. candidus* from Mohammadi et al. (2014), who had an SVL = 87.4 cm, and mass = 138.1 g, and the females *B. fasciatus* in this report: 16.01 ± 25 mm SVL; 1439.5 ± 9.5 g body mass.

Although data was normal across all kraits during the simultaneous tracking period of BUFA001, BUFA003, and BUFA004 for 95% MCP estimates (Shapiro-

Wilks Test: $W = 0.2923$, $p > .05$), 100% MCP ($W = 0.8613$, $p > .05$), 50% kernels ($W = 0.9524$, $p > .05$), and 95% kernels ($W = 0.9856$, $p > .05$ and all estimates had homogenous in variance (Levene's Test: $F = 0.4157$, $p > .05$) I refrained from reporting statistics test results for differences between home range estimates as they are not reasonable for my small sample of study animals. However, if sample of kraits were to have been larger, I would ideally use ANCOVA following (Strine et al., 2018), assuming the assumptions of normality and homogeny of variance held true. In the case that ANCOVA's assumptions were not met, I would have used nonparametric tests such as the Kruskal-Wallace Test if data was not normal but remained homoscedastic between groups (Sabo and Boone, 2016) or Mann-Whitney *U* Test. Mann-Whitney *U* Test with Spearman's Rank Correlation could be used to test whether krait biometric characteristics correlate with home range sizes, distances moved, and frequency of relocation.

4.2.2 Habitat preference

Despite only accounting for 16.15% across the 4 snake's study areas, the 4 habitat features (ponds, margins, canals, dikes) had the highest preference scores (Figure 4.5). An individual Malayan krait (*Bungarus candidus*) in an upland agricultural area in the SBR also showed strong preference for a heavily vegetated field margin (Knierim et al., 2018). Similarly, king cobras (*Ophiophagus hannah*) in the SBR also demonstrated strong preference for irrigational canals and field margins in agricultural habitats (Marshall et al., 2018), as canals facilitate routes of travel for snakes through unfavorable landscapes (Whitaker and Shine, 2000). Rice paddy dikes and termite mounds in Northeast Thailand have been shown to serve as biodiversity reservoirs for microfauna (Choosai et al., 2009) and agronomically beneficial arthropods (Ichihara et al., 2014), compared to the surrounding monocultured paddies. Vegetated paddy dikes are also thought to be important microhabitat features for some vertebrates and host higher abundances of field paddy rats, (*Rattus argentiventer)* in Indonesia (Brown et al., 2001), and tree frogs (*Dryophytes japonicus* and *D. suweonensis*) in South Korea (Groffen et al., 2018). Surveys of rice fields for *R. argentiventer* burrow entrances by Brown et al. (2001), identified field dikes and canals as the two microhabitats having the highest densities of rat burrows. Both rodents and amphibians may be potential prey items for banded kraits (Chan-ard et al., 2015). While burrows excavated by rodents may additionally provide kraits structural refuge in an otherwise exposed landscape. Ultimately, kraits use of field margins and water features in agricultural habitats is likely related to the disturbance levels or availability of prey, and shelter sites. Snake’s habitat use is often explained by multiple factors (Heard et al., 2004). Therefore, assessments of micro habitat characteristics at known krait shelter sites is required to further our inquiry.

Human settlement only comprised 1.83% of krait MCP-combined study area (Table 3.1) and the kraits avoided these human-occupied habitats along the habitat preference index (Figure 4.6). I caution the interpretation of settlement avoidance because there are reports of banded kraits inhabiting urban areas in India (Purkayastha et al., 2011). Pandey et al. (2018) even document 4 individual *B. fasciatus* collected within human settlements in Nepal, 3 from the floor inside households, and 1 from the confines of a yard.

4.2.3 Shelter site selection

Shelter sites (particularly burrow densities) are an important habitat feature for banded kraits in the highly disturbed agricultural habitats of the Sakaerat Biosphere Reserve. Adequate refuge sites characterized by high burrow densities, likely represent burrow complexes having multiple entrances and may be a limiting factor for banded kraits and other vertebrates living in the otherwise productive rice dominant system. Embankment slope and aspect in which burrows were found along did not appear in my top models. However, aspect was a significant predictor for brown snake (*Pseudonaja textilis*) burrow selection along embankments in Australia's subtropical Murrumbidgee Irrigation Area (Whitaker and Shine, 2003). Brown snakes of both sexes selected burrows on north facing slopes during cooler periods of the year as did females while nesting. North facing aspects in the Southern Hemisphere receive more direct sunlight and are thought to provide optimal conditions for brown snakes, as many females showed fidelity for specific overwintering burrows (Whitaker and Shine, 2003). The height of elevated field dikes and margins may also be important for non-aquatic vertebrates, especially burrowing mammals during the growing season, when rice paddies become inundated. Although we did not see a significant relationship between burrow density and height (r (77) = .49, p > .05).

Eucalyptus species including *Eucalyptus camaldulensis, E. tereticornis, E. urophylla* are commonly grown on rice paddy dikes in Northeast Thailand due to the species water requirements, increasing unused areas economical production, and to mitigate erosion (Valo, 2014). There was not a significant relationship between density of mammal burrows (p > 0.01, *Fisher's exact test*) and the presence of *E. camaldulensis*. However, tree roots may preserve the integrity of complex burrow tunnels (Clark, 1951). The presence of economically valuable eucalyptus trees and unmanicured herbaceous vegetation may be an indication of the length of time since major disturbance.

In Thailand eucalyptus trees are usually harvested on 3-5-year intervals in perennial successions and undergo yearly understory residue burning (Manavakun, 2014). Adjacent, rice fields are usually harvested twice per year at my study site (personal observation) and throughout much of Thailand (Kanokkanjana and Garivait, 2013). Davis and Doherty (2015), found the abundance and richness of a herpetological community in a forest fragment took two years to return to pre-fire levels. Abundance of reptiles is also thought to increase with understory vegetation cover in tree plantations Understory vegetation cover in tree plantations and decrease with ground exposure (Carpio et al., 2016). During the study period I observed the mechanical rearrangement of dikes, margins, and canal banks by heavy machinery within 100 m of krait locations during 3.65% of tracks, as well as regular vegetation management including: burning, herbicide application, grazing, harvesting and mowing during 4.31% of tracks.

4.2.4 Nocturnal activity

My study is the first in-depth attempt to confirm periods of banded krait temporal activity. Previous literature suggests *B. fasciatus* and other Thai kraits are nocturnally active (Chanard et al., 2015; Stuart et al., 2013). However, these reports are presented without quantifiable observation data. Although, my sample size limits the applicability of models to estimate potential drivers of banded krait activity, I can confirm that the *B. fasciatus* in this study were highly nocturnal. There were 0 instances of active movement out of 902 total diurnal tracks occurring between 08:00 - 18:00 h, throughout the entire study period. Additionally, only 1 of 2,744 images that were captured once per minute by field cameras stationed at BUFA003 and BUFA004 nesting site showed activity before or after sunset. The single photo was of one of the kraits entering their burrow between 05:00 – 06:00 h.

4.2.5 Behavior and natural history

Nest attendance and other parental behaviors are not well documented in snakes. Nest attendance along with varying degrees of parental care have been substantially documented among viviparous viper species and appears a common trait in temperate regions (Butler et al., 1995; Clark et al., 2012; Halliwell et al., 2018; Hill III et al., 2006; Muellman et al., 2018) as well as in some Pythonidae species (Alexander, 2018; Brashears and Denardo, 2012). Descriptive literature on nest attendance is particularly scare for the family Elapidae. King cobras (*Ophiophagus hannah*) are large elapid snakes and are females are known to attend their nests which they build from vegetation on the forest floor (Dolia, 2018; Whitaker et al., 2013). Similarly, radio tracked Indochinese spitting cobras (*Naja siamensis*) are thought to attend egg clutches for the extent of the incubation periods in Thailand (B. Nodolski personal communication, 2018).

Reports of krait nesting in captivity have been published in Chanhome et al., 2013; Chanhome et al., 2001) from the Queen Saovabha Memorial Institute in Bangkok. An unknown number of wild-caught female *B. facsiatus* laid three clutches totaling 29 eggs of which 21 hatched after 57 – 63 days (Chanhome et al., 2001). The two females in my study spent longer periods at their nest site. BUFA004 entered the nest site on April 5, 2017 and remained there for 75 days, except for 8 separate days at nearby shelter sites. The other female, BUFA003 initially entered the nesting site on April 14, 2017 and remained in the nesting chamber for 77 days, during which time only spending 2 days at different shelter sites away from the nest. The first neonate hatchlings began emerging on the night of June 23, 2017, when three individuals were captured on camera,79 days after BUFA004 initially arrived at the site. Three more hatchlings were physically captured in the field the following night to be processed (Table 4.2), as they emerged from two different burrow entrances. A second group of neonates were captured on camera exiting the burrows four days later April 28, 2017 and the following night of April 29, 2017.

CHAPTER V

CONCLUSION

Conclusions drawn from my study are limited due to our difficulty in locating representative sample sizes of banded kraits in the SBR. The low capture rates during active night surveys (1 krait per 118 surveys; Table 4.1) and staggered acquisition of study animals resulted in long periods without simultaneously tracked kraits, further reducing my ability to make statistical comparisons between conspecific sex, age class, and temporal groups. Banded kraits appear to utilize relatively large home ranges and are able to tolerate heavily disturbed habitats if adequate microhabitats facilitating important life history events (sheltering, foraging, mating, and nesting) persist.

Future studies on banded krait ecology should attempt to acquire larger samples of tracked kraits and quantitively assessing spatial and habitat requirements throughout their wide geographic distribution. Studies assessing banded krait abundance in a variety of habitats throughout their range may also provide insight into the species tolerance of varying degrees of human disturbance and habitat alteration. Although kraits in my study inhabited a rice dominated agricultural, banded kraits have been reported from a wide variety of habitats including: urban green spaces (Purkayastha et al., 2011), rural villages (Pandey et al., 2018; and estuarine wetlands (Kurniawan et al., 2018). Additional surveys targeting banded krait populations at other sites may elucidate commonly preferred habitat characteristics Traditionally irrigated rice systems share ecological similarities with natural wetlands (Luo et al., 2014; Schoenly et al., 1998; Wood et al., 2010), therefore the presence of banded kraits may have a strong association with proximity to water.

My study found that kraits used rodent burrows for mating, nesting, and sheltered in along waterways and field margins, and preferred shelter sites having higher burrow densities. Future work should also assess microhabitat features used by banded kraits as diurnal retreats and as mating and nesting sites. Animal burrows can be limited resource, providing shared refuge for an array of species in otherwise harsh environments (Hofstede and Dziminski, 2017; Pike and Mitchell, 2013). There are well documented cases of commensal burrow use between the burrow's creators and its inhabitants, such as the case of gopher tortoises (Gopherus Polyphemus) and the many known mammals and reptiles, including the federally protected indigo snake (Drymarchon couperi) and Eastern diamondback rattlesnake (Crotalus adamanteus) in the United States (Dziadzio and Smith, 2016; Lips, 2009).

Banded kraits possess potent neurotoxins and if bitten, cause life threatening envenomation's in humans, though incidents in Thailand are scarce (Tongpoo et al., 2018). Therefore, study of venomous species living in habitat co-inhabited with humans will provide information that can be applied towards snake-bite avoidance education and behavioral changes for people in snake-bite prone areas. On the other hand, humans and their activities pose significant threats to snakes (Dutta et al., 2016; Shine et al., 1998; Strine et al., 2014; Whitaker and Shine, 2000). Kraits are not exempt from this trend, with Pandey et al. (2018) documenting eleven instances in which *B. fasciatus* were killed by humans in rural Nepal, and the mortality of a Malayan krait (*Bungarus candidus*) killed as unintended bycatch in a farmer's aquatic funnel trap (Crane et al., 2016).

In my study of banded kraits, two of the four radio tracked animals died as the unintendedly consequence of farm management activities. The impact to snake and other vertebrate communities by “everyday” unintended consequences of human activities should by investigated as well as the obvious direct killing of snakes by humans. Negative perception and subsequent persecution of snakes, including kraits, is often the result of misidentification and indiscriminate killing of snakes (Pandey et al., 2016) resulting in an increased risk of being bitten (Morandi et al., 1997). For a sustainable future allowing cohabitation of space between humans and snakes, researcher must direct their efforts towards understanding specie’s ecology across multiple scales, especially in the human-dominated ecosystems of today. Findings must then be applied in creation and implementation of educational programs geared towards reducing negative perceptions of snakes and the overuse of harmful human activities.

REFERENCES

REFERENCES

Alexander, G.J. (2018). Reproductive biology and maternal care of neonates in Southern African Python (*Python natalensis*). **Journal of Zoology** (305): 141-148.

Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. **Journal of Wildlife Management** 74(6): 1175-1178.

Blouin-Demers, G., and Fox, S.F. (2006): Kernels are not accurate estimators of home-range size for herpetofauna. **Copeia**. 2006(4): 797-802.

Brashears, J., and Denardo, D.F. (2012). Do brooding pythons recognize their clutches? Investigating external cues for offspring recognition in the Children's Python, *Antaresia childreni*. **Ethology** 118(8): 793-798.

Brown, P.R., Douangboupha, B., Htwe, N.W., Jacob, J., Mulungu, L., Nguyen Thi My Phung, Stuart, A.M., Sudarmaji. (2017). Control of rodent pests in rice cultivation. **Burleigh Dodds Science Publishing Limited**, pp. 343-376.

Brown, P.R., Singleton, G.R., and Sudarmaji (2001). Habitat use and movements of the Rice-Field Rat, *Rattus argentiventer*, in West Java, Indonesia. **Mammalia** 65(2):151-166

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., and Humle, T. (2017). Activity and habitat use of chimpanzees (*Pantroglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. **International Journal of Primatology** 38(2): 282-302.

Burnham, K.P., and Anderson, D.R. (2003). Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, US.

Butler, H., Malone, B.A., and Clemann, N.B. (2005a). Activity patterns and habitat preferences of translocated and resident Tiger Snakes (*Notechis scutatus*) in a suburban landscape. **Wildlife Research** 32(2): 157.

Butler, H., Malone, B.A., and Clemann, N.B. (2005b). The effects of translocation on the spatial ecology of Tiger Snakes (*Notechis scutatus*) in a suburban landscape. **Wildlife Research** 32(1): 165-171.

Butler, J.A., Hull, T.W., and Franz, R. (1995). Neonate aggregations and maternal attendance of young in the Eastern Diamondback Rattlesnake, *Crotalus adamanteus*. **Copeia** 1995(1): 196-198.

Carpio, A.J., Oteros, O., and Tortosa, F.S., Guerrero-Casado, J. (2016). Land use and biodiversity patterns of the herpetofauna: The role of olive groves. **Acta Oecologica** 70: 103-111.

Castoe, T.A., Smith, E.N., Brown, R.M., and Parkinson, C.L. (2007). Higher-level phylogeny of Asian and American coralsnakes, their placement within the Elapidae (Squamata), and the systematic affinities of the enigmatic Asian Coralsnake *Hemibungarus calligaster*. **Zoological Journal of the Linnean Society**. 151(4): 809-831.

Chan-Ard, T., Nabhitabhata, J., and Parr., J.W. (2015). A Field Guide to The Reptiles of Thailand. Oxford University Press.

Chanhome, L., Jintakune, P., Wilde, H., and Cox, M.J. (2001). Venomous Snake Husbandry in Thailand. **Wilderness and Environmental Medicine** 12(1): 17-23.

Chanhome, L., Cox, M.J., Vasaruchapong, T., Chaiyabutr, N., and Sitprija, V. (2011). Characterization of venomous snakes of Thailand. **Asian Biomedicine** 5(3): 311-328.

Choosai, C., Mathieu, J., Hanboonsong, J., and Jouquet, P. (2009). Termite mounds and dykes are biodiversity refuges in paddy fields in north-eastern Thailand. **Environmental Conservation** 36(1): 71.

Clark, R.W., Brown, W.S., Stechert, R., and Greene, H.W. (2012). Cryptic sociality in rattlesnakes (*Crotalus horridus*) detected by kinship analysis. **Biology Letters** 8(4): 523-525.

Clark, W.K. (1951). Ecological life history of the armadillo in the Eastern Edwards Plateau region. **The American Midland Naturalist** 46(2): 337-358.

Crane, M., Oliver, K., Silva, I., Aksornneam, A., Artchawakom, T., and Strine, C.T. (2016). A report of a Malayan Krait snake *Bungarus candidus* mortality as by-catch in a local fish trap from Nakhon Ratchasima, Thailand. **Tropical Conservation Science** 9(91): 313-320.

Croak, B.M., Crowther, M.S., Webb, J.K., and Shine, R. (2013). Movements and habitat use of an endangered snake, *Hoplocephalus bungaroides* (Elapidae): Implications for conservation. **PloS ONE** 8(4): p.e61711.

Davis, R.A., and Doherty, T.S. (2015). Rapid recovery of an urban remnant reptile community following summer wildfire. **PLoS ONE** 10(5): p.e0127925.

DeGregorio, B.A., Manning, J.V., Bieser, N., and Kingsbury, B.A. (2011). The spatial ecology of the Eastern Massasauga (*Sistrurus catenatus*) in northern Michigan. **Herpetologica** 67(1): 71-79.

Dziadzio, M.C., Smith, L.L. (2016). Vertebrate Use of Gopher Tortoise Burrows and Aprons. **Southeastern Naturalist** 15(4): 586-594.

Dolia, J. (2018). Notes on the distribution and natural history of the King Cobra (*Ophiophagus hannah* Cantor, 1836) from the Kumaon Hills of Uttarakhand, India. **Herpetology Notes** 11: 217-222.

Duncan, P. (1983). Determinants of the use of habitat by horses in a Mediterranean wetland. **The Journal of Animal Ecology** 52: 93-109.

Dutta, S., Jana, H.P., Saha, S., and Mukhopadhyay, S.K. (2016). The cause and consequences of road mortality of herpetofauna in Durgapur, West Bengal, India. **Russian Journal of Ecology** 47(1): 88-95.

Figueroa, A., McKelvy, A.D., Grismer, L.L., Bell, C.D., and Lailvaux, S.P. (2016). A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. **PLoS ONE** 11(9): p.e0161070.

Fitzgerald, M., Lazell, B., and Shine, R. (2010). Ecology and conservation of the Pale-Headed Snake (*Hoplocephalus bitorquatus*, Elapidae). **Australian Zoologist** 35(2): 283-290.

Fitzgerald, M., Shine, R., and Lemckert, F. (2003). A reluctant heliotherm: thermal ecology of the arboreal snake *Hoplocephalus stephensii* (Elapidae) in dense forest. **Journal of Thermal Biology** 28(67): 515-524.

Fitzgerald, M., Shine, R., and Lemckert, F. (2002). Radiotelemetric study of habitat use by the arboreal snake *Hoplocephalus stephensii* (Elapidae) in eastern Australia. **Copeia** 2002(2): 321-332.

Lips, K. (2009). Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats. **Journal of Herpetology** 25(4): 477-481.

Fry, B.G., Vidal, N., Van-der Weerd, N., Kochua, E., and Renjifo, C. (2009). Evolution and diversification of the toxicofera reptile venom system. **Journal of Proteomics** 72(2009): 127-136.

Gionfriddo, J., Paul, P., Krausman, R., and Press, A. (1986). Summer habitat use by mountain sheep. **Habitat** 50(2): 331–336.

Gomes, A., Pratim-Saha, P., Bhattacharya, S., Ghosh, S., and Gomes, A. (2017). Therapeutic potential of krait venom. **Toxicon** 131: 48–53.

Groffen, J., Borzée, A., and Jang, Y. (2018). Preference for natural borders in rice paddies by two treefrog species. **Animal Cells and Systems** 22(3): 205-211.

Halliwell, B., Uller, T., Holland, B.R., and While, G.M. (2018). Live bearing promotes the evolution of sociality in reptiles. **Nature Communications** 8(1): 2030.

Hart, K.M., Cherkiss, M.S., Smith, B.J., Mazzotti, F.J., Fujisaki, I., Snow, R.W., and Dorcus, M.R. (2015). Home range, habitat use, and movement patterns of non-native Burmese Pythons in Everglades National Park, Florida, USA. **Animal Biotelemetry** 3(1): 8.

Heard, G.W., Black, D., and Robertson, P. (2004). Habitat use by the Inland Carpet Python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. **Austral Ecology** 29(4): 446-460.

Hill III, J.G., Chanhome, L., Artchawakom, T., Thirakhupt, K., and VORIS, H.K. (2006). Nest attendance by a female Malayan Pit Viper (*Calloselasma rhodostoma*) in Northeast Thailand. **The Natural History Journal of Chulalongkorn University** 6(2): 57-66.

Hofstede, L., and Dziminski, M.A. (2017). Greater Bilby burrows: important structures for a range of species in an arid environment. **Australian Mammalogy** 39(2): 227-237.

Ichihara, M., Matsuno, K., Inagaki, H., Saiki, C., Mizumoto, S., Yamaguchi, S., Yamashita, M., and Sawada, H. (2014). Creation of paddy levees to enhance the ecosystem service of weed seed predation by crickets. **Landscape and Ecological Engineering** 11(1): 227-233.

International Union for Conservation of Nature. (2013). The IUCN Red List of Threatened Species. Retrieved September 17, 2017, [Online]. Available: www.iucnredlist.org.

Ismail, K.A. (2013). Snakebite and envenomation management in Malaysia. **Clinical Toxicology** pp. 1-27.

Kanokkanjana, K., and Garivait, S. (2013). Alternative rice straw management practices to reduce field open burning in Thailand. **International Journal of Environmental Science and Development** 4(2): 119-123.

Karraker, N.E., Strine, C.T., Crane, M., and Devan-Song A., *Dryocalamus subannulatus* (Malayan Bridle Snake) Behavior. **Herpetological Review**. (Accepted, Dec. 2014)

Kelly, C.M., Barker, N.P., Villet, M.H., and Broadley, D.G. (2009). Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. **Cladistics** 25(1): 38-63.

Karraker, N.E., Strine C.T., Crane M., and Devan-Song, A. *Dryocalamus subannulatus* (Malayan Bridle Snake) Behavior. **Herpetological Review**. (Accepted, Dec. 2014)

Kerkkamp, H.M., Casewell, N.R., and Vonk, F.J. (2017). Evolution of the snake venom delivery system. **Evolution of Venomous Animals and Their Toxins** Springer, Dordrecht, pp. 303-316.

Knierim, T.K, Marshall, B.M., Hayes, L., Waengsothorn, S., Suwanwaree, P., and Strine, C.T. (2018). The movements and habitat preferences of a Malayan Krait (*Bungarus candidus*) in an agricultural landscape. **Herpetological Bulletin** 143: 30–33.

Knierim, T., Barnes, C., and Hodges, C. (2017). *Bungarus fasciatus* (Banded Krait) Diet/Scavenging. **Herpetological Review** 48: 204-205.

Knutson, M.G., Herner-Thongmartin, J.H., Thongmartin, W.E., Kapfer, J.M., Nelson, J.C. (2018). Habitat selection, movement patterns, and hazards encountered by Northern Leopard Frogs (*Lithobates pipiens*) in an agricultural landscape. **Herpetological Conservation and Biology** 13(1): 113-130.

Kurniawan, N., Firdaus, A.S., Nugraha, F.A.D., Maulidi, A., and Kurnianto, A.S. (2018). Fishermen's perspective on herpetofauna: a case study from Kuala Tungkal, Tanjung Jabung Barat, Jambi. **Journal of Tropical Life Science** 8(1): 1-5.

Laszlo, J. (1975). Probing as a practical method of sex recognition in snakes. **International Zoo Yearbook** 15(1): 178-179.

Laver, P.N., Kelly, M.J. (2008). A critical review of home range studies. **Journal of Wildlife Management** 72(1): 290-298.

Llewelyn, J., Phillips, B.L., Brown, G.P., Schwarzkopf, L. Alford, R.A., Shine, R. (2011). Adaptation or Preadaptation: why are keelback snakes (*Tropidonophis mairii*) less vulnerable to invasive Cane Toads (*Bufo marinus*) than are other Australian snakes? **Evolutionary Ecology** 25(1): 13-24.

Llewelyn, J.S., Phillips, B.L., and Shine, R. (2009). Sublethal costs associated with the consumption of toxic prey by snakes. **Austral Ecology** 34: 179-184.

Luo, Y., Fu, H., and Traore, S. (2014). Biodiversity conservation in rice paddies in China: toward ecological sustainability. **Sustainability** 6(9): 6107-6124.

Manly, B.F., McDonald, L., Thomas, D., McDonald, T.L., and Erickson, W.P. (2002). Resource selection by animals. Second. New York, Boston, Dordrecht, London, Moscow.

Manavakun, N. (2014). Harvesting operations in eucalyptus plantations in Thailand. Master Thesis, University of Helsinki, Finland.

Marshall, B.M., Strine, C.T., Jones, M.D., Artchawakom, T., Silva, I., Suwanwaree, P., and Goode, M. (2018). Space fit for a king: spatial ecology of King Cobras (*Ophiophagus hannah*) in Sakaerat Biosphere Reserve, Northeastern Thailand. **Amphibia-Reptilia. (**Accepted, Sep. 2018)

Martin, L.J., Blossey, B., and Ellis, E. (2012). Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. **Frontiers in Ecology and the Environment** 10(4): 195-201.

Mohammadi, S., Kluever, B.M., Tamashiro, T., Amano, Y., and Hill III, J.G. (2014). Spatial and thermal observations of a Malayan Krait (*Bungarus candidus*) from Thailand. **The Natural History Journal of Chulalongkorn University** 14(1): 21-26.

Morandi, N., Williams, J., and Facep, M.D. (1997). Snakebite injuries: contributing factors and intentionality of exposure. **Wilderness and Environmental Medicine** 8(3): 152-155.

Muellman, P.J., Da-Cunha, O., and Montgomery, C.E. (2018). *Crotalus horridus* (Timber Rattlesnake) maternal scent trailing by neonates. **Northeastern Naturalist** 25(1): 50-55.

Nakagawa, S., and Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. **Methods in Ecology and Evolution** 4(2): 133-142.

Ongsomwang, S., and Sutthivanich, I. (2014). Integration of Remotely Sensed Data and Forest Landscape Pattern Analysis in Sakaerat Biosphere Reserve. **Suranaree Journal of Science and Technology** 21: 233-248.

Panagides, N., Jackson, T.N.W., Ikonomopoulou, M.P., Arbuckle, K., Pretzler, R., Yang, D.C., Ali, S.A., Koludarov, J.D., Dobson, J., Sanker, B., Asselin, A., Santana, R.C., Hendrikx, I., Vander Ploeg, H., Tai-A-Pin, J., et al. (2017). How the cobra got its flesh-eating venom: cytotoxicity as a defensive innovation and its co-evolution with hooding, aposematic marking, and spitting. **Toxins** 9(3): 103.

Pandey, D.P., Pandey, G.S., Devkota, K., and Goode, M. (2016). Public perceptions of snakes and snakebite management : implications for conservation and human health in southern Nepal. **Journal of Ethnobiology and Ethnomedicine** 12(1): 12-22.

Pandey, D.P., Dusan, J., Sapkota, S., Lama, H.R., Lama, B., Pokharel, K., Goode, M., and Kuch, U. (2018). New records of snakes from Chitwan National Park and vicinity , Central Nepal. **Herpetology Notes** 11: 679–696.

Pike, D.A., and Mitchell, J.C. (2013). Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. **Animal Conservation** 16(6): 694-703.

Tongpoo, A., Sriapha, C., Pradoo, A., Udomsubpayakul, U., Srisuma, S., Wananukul, W., and Trakulsrichai, S. (2018). Krait Envenomation in Thailand. **Therapeutics and Clinical Risk Management** 14: 1711.

Purkayastha, J., Das, M., and Sengupta, S. (2011). Urban herpetofauna: a case study in Guwahati City of Assam, India. **Herpetology Notes** 4: 195-202.

Ratanabanangkoon, K., Tan, K.Y., Eursakun, S., Tan, C.H., Simsiriwong, P., Pamornsakda, T., Wiriyarat, W., Klinpayom, C., and Tan, N.H. (2016). A simple and novel strategy for the production of a pan-specific antiserum against elapid snakes of Asia. **PLOS Neglected Tropical Diseases** 10(4): p.e0004565.

Rusmili, M.R.A., Yee, T.T., Mustafa, M.R., Hodgson, W.C., and Othman, I. (2014). Isolation and characterization of a presynaptic neurotoxin, P-elapitoxin-Bf1a from Malaysian *Bungarus fasciatus* venom. **Biochemical Pharmacology** 91(3): 409-416.

Sabo, R., and Boone, E. (2016). Statistical Research Methods. **Springer-Verlag New York.**

Sakaerat Environmental Research Station. (2017). [Online] Retrieved January 15, 2017, Available: http://www.tistr.or.th/sakaerat/SakaeratE/index.php.

Sanders, K.L., Lee, M.S., Leys, R., Foster, R., and Scott-Keogh, J. (2008). Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. **Journal of Evolutionary Biology** 21(3): 682-695.

Sanders, K.L., Lee, M.S., Bertozzi, T., and Rasmussen, A.R. (2013). Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). **Molecular Phylogenetics and Evolution** 66(3): 575-591.

Savage, J.M., and Slowinski, J.B. (1992). The Colouration of the venomous coral snakes (Family Elapidae) and their mimics (Families Aniliidae and Colubridae). **Biological Journal of the Linnean Society** 45(3): 235-254.

Seaman, D.E., and Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. **Ecology** 77: 2075-2085.

Schoenly, K.G., Justo Jr, H.D., Barrion, A.T., Harris, M.K., and Bottrell, D.G. (1998). Analysis of invertebrate biodiversity in a Philippine farmer's irrigated rice field. **Environmental Entomology** 27(5): 1125-1136.

Shine, R. (1979). Activity patterns in Australian Elapid snakes (Squamata: Serpentes: Elapidae). **Herpetologica** 35: 1-11.

Shine, R. (1987). Intraspecific variation in thermoregulation,movements and habitat use by australian Blacksnakes *Pseudechis porphyriacus*. **Journal of Herpetology** pp. 165-177.

Shine, R., Webb, J.K., Fitzgerald, M, and Sumner, J. (1998). The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes : Elapidae). **Wildlife Research** 25(3): 285.

Silva, I., Crane, M., Suwanwaree, P., Strine, C., and Goode, M. (2018). Using Dynamic Brownian Bridge Movement Models to identify home range size and movement patterns in King Cobras. **PloS ONE** 13(9): e0203449.

Slowinski, J.B., and Keogh, S.J. (2000). Phylogenetic relationships of elapid snakes based on cytochrome b MtDNA sequences. **Molecular Phylogenetics and Evolution** 15(1): 157-164.

Reinert, H.K., and Cundall, D. (1982). An improved surgical implantation method for radio-tracking snakes. **Copeia** 1982(3): 702-705.

Somaweera, R., and Somaweera, N. (2010). Serpents in jars: the snake wine industry in Vietnam. **Journal of Threatened Taxa** 2(11): 1251-1260.

Strine, C., Silva, I., Barnes, C.H., Marshall, B.M., Artchawakom, T., Hill, J., and Suwanwaree, P. (2018). Spatial ecology of a small arboreal ambush predator, *Trimeresurus macrops* Kramer, 1977, in Northeast Thailand. **Amphibia-Reptilia** 39(3): 335-345.

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

Stiles, R.M., Halliday, T.R., Engbrecht, N.J., Swan, J.W., and Lannoo, M.J. (2017). Wildlife cameras reveal high resolution activity patterns in threatened Crawfish Frogs (*Lithobates areolatus*). **Herpetological Conservation and Biology** 12(1): 160-170.

The Reptile Database. (2017). *Bungarus facsiatus.* Retrieved December 15, 2017, [Online]. Available: http://www.reptile-database.org.

TISTR. (2018). Sakaerat Environmental Research Station: Geography/Climate. [Online]. Available: http://www.tistr.or.th/sakaerat.htm.

Tongyai, P. (1983). Sakaerat Environmental Research Station. It’s role as knowledge base for the determination of forest lands conservation policies for establishing maximum sustainable yields on forest resources.*in* NRC/KU/TISTR, editor. Thailand Institute of Research and Technology, Bankgok Thailand.

UNESCO. (2017). Ecological Sciences for Sustainable Development. Retrieved October 23, 2017, [Online]. Available: http://www.unesco.org/new/en/natural sciences/environment/ecological-sciences/biosphere-reserves/.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D.W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. **Ecology** 90(1): 23-30.

Valo, M. (2014). Why farmers choose agroforestry ? A case study from the Province of Sa Kaeo, Thailand. Master Thesis, University of Helsinki, Finland.

Vanek, J.P., and Wasko, D.K. (2017). Spatial ecology of the Eastern Hog-Nosed Snake (*Heterodon platirhinos*) at the northeastern limit of its range. **Herpetological Conservation and Biology** 12(1): 109-118.

Vongphoumy, I., Chanthilat, P., Vilayvong, P., and Blessmann, J. (2016). Prospective, consecutive case series of 158 snakebite patients treated at Savannakhet provincial hospital, Lao People's Democratic Republic with high incidence of anaphylactic shock to horse derived F (ab') 2 antivenom. **Toxicon** 117: 13-21.

Wasko, D.K., and Sasa, M. (2009). Activity patterns of a neotropical ambush predator: spatial ecology of the Fer-de-Lance (*Bothrops asper*, Serpentes: Viperidae) in Costa Rica. **Biotropica** 41(2): 241-249.

Webb, J.K., and Shine, R. (1997). A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. **Biological Conservation** 82(2): 203-217.

Webb, J.K. and Shine, R. (1997). Out on a limb: conservation implications of tree-hollow use by a threatened snake species (*Hoplocephalus bungaroides*: Serpentes, Elapidae). **Biological Conservation**. 81(1): 21-33.

Whitaker, N., Shankar, P.G., and Whitaker, R. (2013). Nesting ecology of the King Cobra (*Ophiophagus hannah*) in India. **Hamadryad** 36(2): 101-107.

Whitaker, P.B., and R. Shine. (2002). Thermal biology and activity patterns of the Eastern Brownsnake (*Pseudonaja textilis*): a radiotelemetric study. **Herpetologica** 58(4): 436-452.

Whitaker, P.B., and Shine, R. (2000). Sources of mortality of large elapid snakes in an agricultural landscape. **Journal of Herpetology** 34(1): 121-128.

Whitaker, P.B., and Shine, R. (2003). A radiotelemetric study of movements and shelter-site selection by free-ranging Brownsnakes (*Pseudonaja textilis*, Elapidae). **Herpetological Monographs** 17(1): 130-144.

Wilkinson, and Leonatti, S. (2014). Guide to venomous reptiles in veterinary practice. **Journal of Exotic Pet Medicine** 23(3): 337-346.

Wood, C., Qiao, Y., Li, P., Ding, P., Lu, B., and Xi, Y. (2010). Implications of rice agriculture for wild birds in China. **Waterbirds** 33(1): 30-43.

Worton, B.J. (1989). Kernel methods for estimating the utilization in home-range studies. **Ecology** 70(1): 164-168.

APPENDICES

APPENDIX A

HOME RANGE SPATIAL OVERLAP

Figure A-1. Percent overlap for 50% and 95% fixed kernel density home range estimates. Three simultaneously tracked kraits (BUFA001, BUFA003, BUFA004) from April 1, 2017 to September 30, 2017).

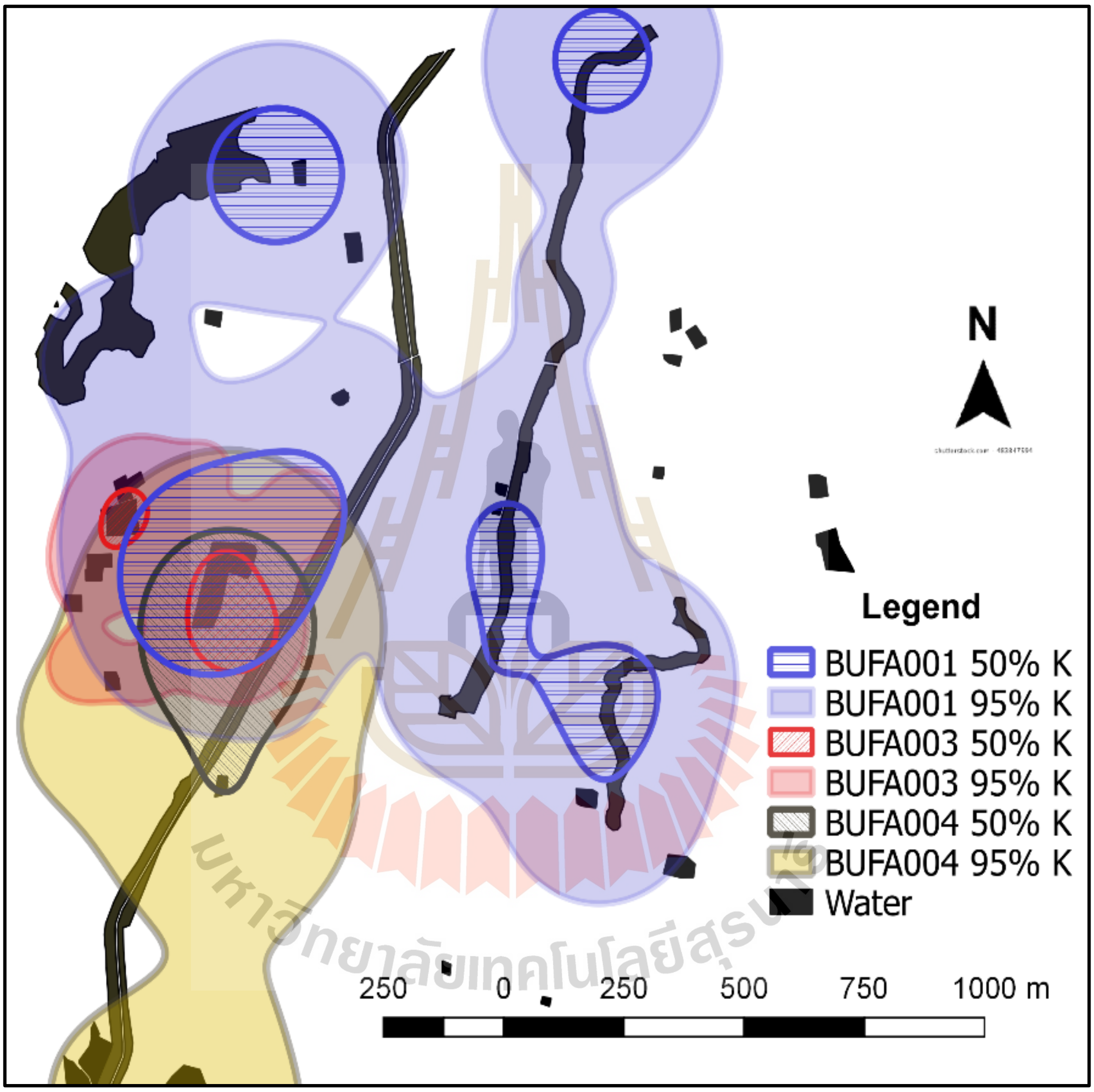
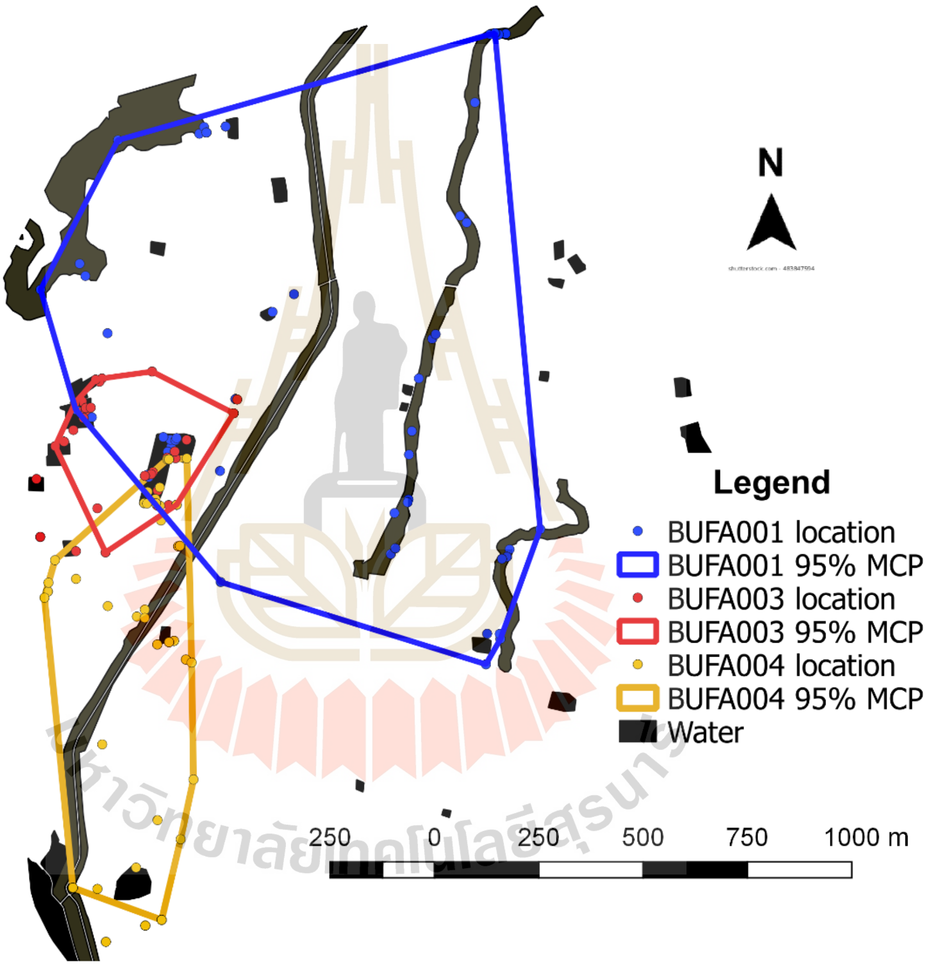


Figure A-2. Percent overlap for 95% MCP home range estimates. Three simultaneously tracked kraits (BUFA001, BUFA003, BUFA004) from April 1, 2017 to September 30, 2017).



APPENDIX B

MATING SPATIAL OVERLAP & MOVEMENT

Figure B-1 A) The distance of BUFA001 (dark blue) and BUFA003 (pink) diurnal pin-point locations from their mating site. Two-month period roughly centered around the 5 day**s** they share a shelter site. BUFA001 was temporarily removed from the field on November 14th for a regular health check-up. B) Distance to mating site from previous years (2016) mating event. BUFA003 was initially captured and released only days before being joined by BUFA001 in 2016.

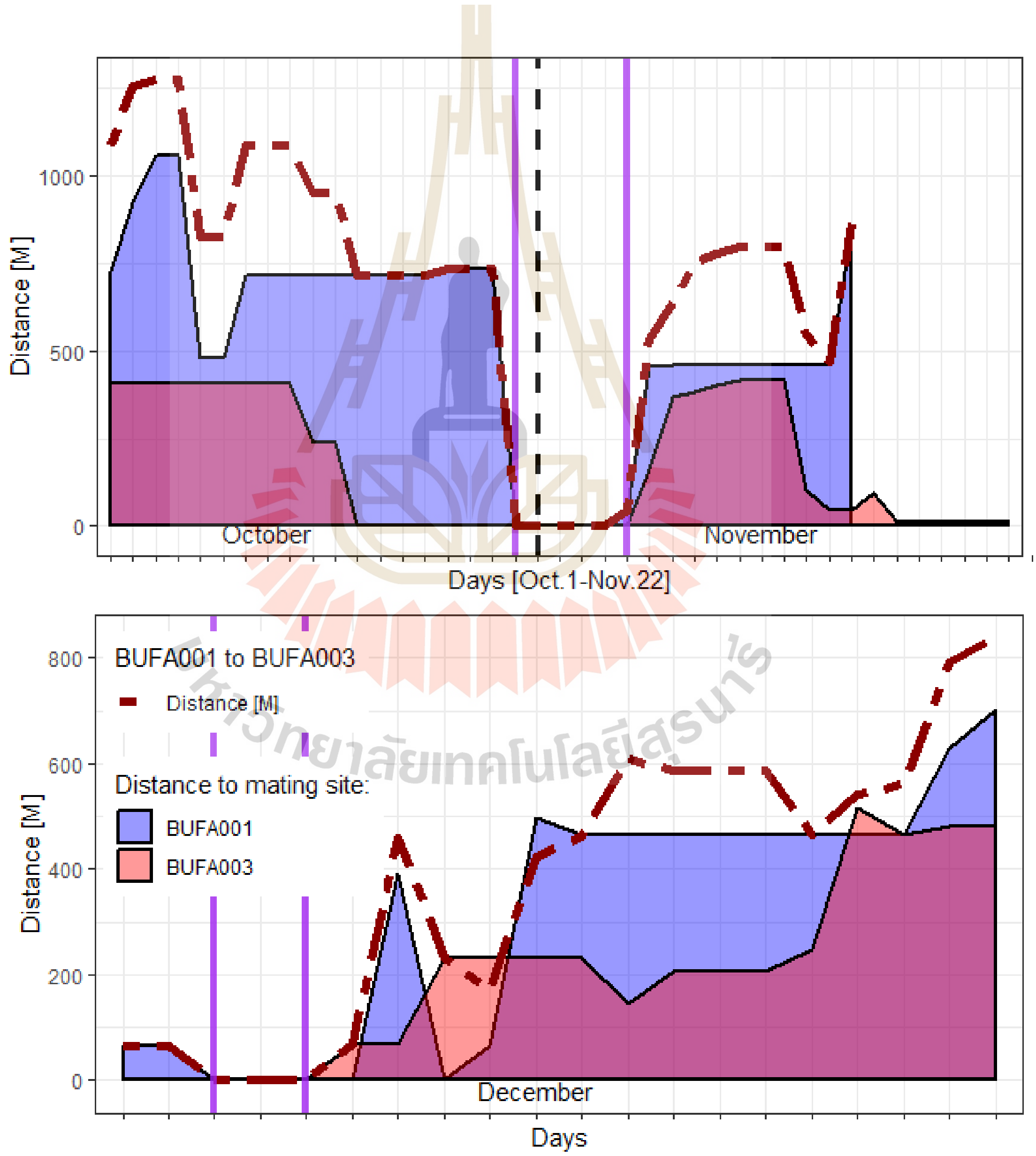
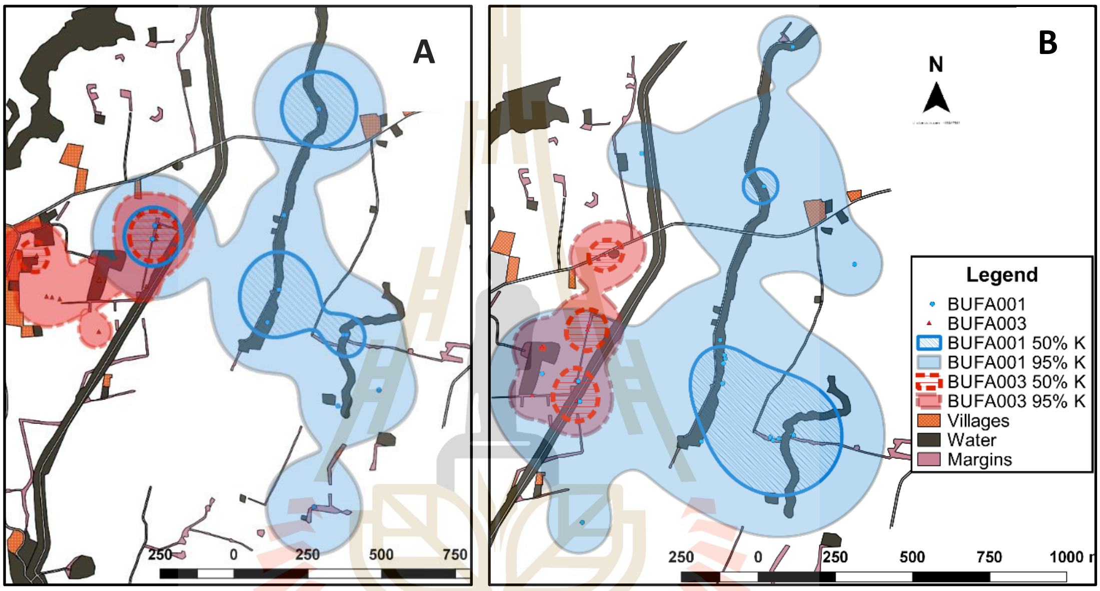


Figure B-2 A) Home ranges (95% kernel) estimates of two snakes during the same time period, October 1 – November 31, 2017. Pink = BUFA003, Blue = BUFA001. B) Home ranges during one-month period before and after mating event in 2016.



CURRICULUM VITAE

Name	Tyler K. Knierim
Date of birth	January 9th, 1992
Place of birth	Cedar Rapids, Iowa
Education	2014 B.A., Animal Ecology, Iowa State University, Ames, Iowa

Publications

Barnes, C.H., **Knierim**, **T.K.** (2018). A novel cave habitat use and range extension for the cryptic snake *Stegonotus muelleri* (Serpentes: Colubridae). **Phyllomedusa.** 17(2).

Ward, M., Ihlow, F., Nadolski, B., Crane, M., **Knierim, T.**, Artchawakom, T., Strine, C. (2018). First Record of male to male combat in the *Indotestudo elongata* (Blyth, 1853) in north-eastern Thailand. **Herpetology Notes**. 11: 585–587.

Knierim, T., Marshall., Hayes, L., Waengsothorn, S., Suwanwaree, P., Strine, C. (2018). The movements and habitat preferences of a Malayan krait (*Bungarus candidus*) in an agrarian landscape. **Herpetological Bulletin**. 30(143): 30–33.

Knierim, T., Barnes, C.H., and Hodges, C. (2017). *Bungarus fasciatus*: diet/scavenging. **Herpetological Review**. 48(1): 204-205.

Knierim, **T.**, Barnes, C.H., Strine, C.T., Suwanwaree, P., and Farren, W. (2017). *Enhydris subtaeniata*: diet. **Herpetological Review**. 48(2): 448-449.