

**FORAGING ECOLOGY OF THE GREEN CAT SNAKE
(*BOIGA CYANEA*): A MAJOR AVIAN NEST PREDATOR
IN THE DRY EVERGREEN FORESTS OF SAKAERAT
ENVIRONMENTAL RESEARCH STATION**

The watermark is a large, semi-transparent logo of Suranaree University of Technology. It features a central figure of a person standing on a pedestal, surrounded by a circular emblem with a book and a lamp. The entire logo is enclosed within a decorative, scalloped border. The Thai text 'มหาวิทยาลัยเทคโนโลยีสุรนารี' is written in a circular path around the bottom of the logo.

Natalia Anji D'souza

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

Suranaree University of Technology

Academic Year 2020

นิเวศวิทยาการหากินของงูเขียวบอน (*BOIGA CYANEA*): สัตว์ล่ารังนกที่
สำคัญในพื้นที่ป่าดิบแล้งของสถานีวิจัยสิ่งแวดล้อมสะแกราช



นางสาวนาตาเลีย แองจี ดีชูชา

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
สาขาวิชาชีววิทยาลิ่งแวดล้อม
มหาวิทยาลัยเทคโนโลยีสุรนารี
ปีการศึกษา 2563

**FORAGING ECOLOGY OF THE GREEN CAT SNAKE (*BOIGA
CYANEA*): A MAJOR AVIAN NEST PREDATOR IN THE DRY
EVERGREEN FORESTS OF SAKAERAT ENVIRONMENTAL
RESEARCH STATION**

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 Thomas Strine)

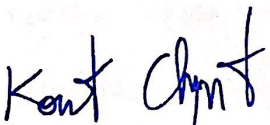
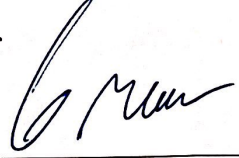
Member (Thesis Advisor)


(Asst. Prof. Dr. George Gale)

Member (Co-advisor)


(Director Surachit Waengsothorn)

Member


(Assoc. Prof. Flt. Lt. Dr. Kontorn Chamniprasart) 
(Asst. Prof. Dr. Worawat Meevasana)

Vice Rector for Academic Affairs
and Internationalization

Dean of Institute of Science

นาตาลี แองจี ดีซุซา : นิเวศวิทยาการหากินของงูเขียวบอน (*Boiga cyanea*): สัตว์ล่ารังนก
ในพื้นที่ป่าดิบแล้งของสถานีวิจัยสิ่งแวดล้อมสะแกราช (FORAGING ECOLOGY OF
THE GREEN CAT SNAKE (*BOIGA CYANEA*): A MAJOR AVIAN NEST PREDATOR
IN THE DRY EVERGREEN FORESTS OF SAKAERAT ENVIRONMENTAL
RESEARCH STATION). อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน โทมัส สไตร์น. 65 หน้า

BOIGA CYANEA /การล่ารังของสัตว์ปีก/ การใช้วิทยุติดตามตัว/ การใช้พื้นที่/ รูปแบบของกิจกรรม/
พฤติกรรม/ ฤดูกาล/ สัตว์หากินในเวลากลางวัน

การล่าเป็นสาเหตุสำคัญของความล้มเหลวในการทำรังและวางไข่ในนกสายพันธุ์ต่าง ๆ
เป็นส่วนใหญ่ ซึ่งงานวิจัยทางนิเวศวิทยาส่วนหนึ่งได้ระบุว่ากลุ่มของงูถือเป็นหนึ่งในผู้ล่ารังนกที่
สำคัญแต่มีรายงานเพียงไม่กี่ชิ้นเท่านั้นที่ได้ตรวจสอบรายละเอียดและพฤติกรรมที่เกี่ยวข้องกับการ
ปล้นสะดมของผู้ล่า ในการศึกษาที่เฝ้าติดตามรังนกภายในพื้นที่ป่าดิบแล้ง บริเวณแกนกลางของ
พื้นที่สงวนชีวมณฑลสะแกราชตั้งแต่ปี 2556 พบว่างูเขียวบอน (*Boiga cyanea*) เป็นผู้ล่าที่มีความ
โดดเด่นภายในพื้นที่ ที่มีส่วนต่อการสูญเสียไข่และลูกนกถึงร้อยละ 22 - 33

ในโครงการวิจัยนี้มุ่งเป้าไปที่ (1) การหาขอบเขตการใช้พื้นที่ของ *B. cyanea* ทั้งในและ
นอกช่วงฤดูการทำรังของนก (2) หาปริมาณในกิจกรรมของ *B. cyanea* ทั้งในและนอกช่วงฤดูการ
ทำรังของนก และ (3) สืบหารูปแบบกิจกรรมที่เกี่ยวข้องกับการปล้นสะดมรังนกภายในพื้นที่สงวน
ชีวมณฑลสะแกราช โดยเฝ้าติดตามกลุ่มเป้าหมายวัยผู้ใหญ่จำนวน 14 ตัว (เพศผู้ 5 ตัว และเพศเมีย
9 ตัว) ระหว่างวันที่ 21 ตุลาคม 2560 ถึง 8 มิถุนายน 2562 เป็นจำนวน 1317 ครั้ง (ช่วงเวลา
กลางวัน 907 ครั้ง และกลางคืน 410 ครั้ง) โดยใช้ dynamic Brownian bridge movement models
(dBBMM) ในการคำนวณค่าประมาณการใช้พื้นที่และกิจกรรมของงูเขียวบอน (*Boiga cyanea*)
พบว่ามีการใช้พื้นที่โดยเฉลี่ยในเพศผู้และเพศเมียคิดเป็น 18.17 ± 6.43 ha และ 3.11 ± 0.72 ha
ตามลำดับ และโดยภาพรวมมีการใช้พื้นที่ในช่วงฤดูทำรังและนอกฤดูทำรังของนกประมาณ 11.81
 ± 4.27 ha และ 1.96 ± 0.63 ha ตามลำดับ เพศผู้มีกิจกรรมการเคลื่อนที่สูงกว่าเพศเมียในด้าน
ความถี่และระยะทาง โดยมีความแปรปรวนของการเคลื่อนที่ในเพศผู้และเพศเมียคิดเป็น $5.08 \pm$
 $1.50 \sigma m^2$ และ $1.16 \pm 0.29 \sigma m^2$ ตามลำดับ และทั้งสองเพศมีการเคลื่อนที่เพิ่มขึ้นในช่วงฤดูการ
ทำรังของนกสูงกว่านอกฤดูการทำรัง โดยมีความแปรปรวนของการเคลื่อนที่ $3.73 \pm 1 \sigma m^2$ และ
 $0.5 \pm 0.15 \sigma m^2$ ตามลำดับ

การศึกษาของเราได้ให้ข้อมูลเชิงลึกเกี่ยวกับนิเวศวิทยาการหาอาหารของผู้ล่ารังนกอันดับต้นในระบบนิเวศเขตร้อน และงานวิจัยในอนาคตมุ่งเน้นในการปรับปรุงและขยายองค์ความรู้เกี่ยวกับอาหารของ *B. cyanea* ในด้านช่วงวัยและสายพันธุ์ของนกที่เป็นเหยื่อ เพื่อชี้ให้เห็นถึงความต้องการเพื่อการอนุรักษ์ *B. cyanea* และใช้ร่วมพัฒนากลยุทธ์การอนุรักษ์สายพันธุ์นกในพื้นที่ที่มีความหนาแน่นของ *B. cyanea* สูง



สาขาวิชาชีววิทยา
ปีการศึกษา 2563

ลายมือชื่อนักศึกษา Anji D'souza
ลายมือชื่ออาจารย์ที่ปรึกษา [Signature]

NATALIA ANJI D'SOUZA : FORAGING ECOLOGY OF THE GREEN
CAT SNAKE (*BOIGA CYANEA*): A MAJOR AVIAN NEST PREDATOR
IN THE DRY EVERGREEN FORESTS OF SAKAERAT
ENVIRONMENTAL RESEARCH STATION. THESIS ADVISOR :
COLIN THOMAS STRINE, Ph.D. 65 PP.

BOIGA CYANEA / AVIAN NEST PREDATION / RADIO-TELEMETRY / SPACE
USE / ACTIVITY PATTERN / SEASONAL / NOCTURNAL

Predation is the leading cause of egg and nestling mortality in most bird species. A number of ecological studies have identified snakes as important avian nest predators. However, only a few studies have attempted to examine the predators themselves and how their behaviour relates to nest predation. A nest monitoring study has been conducted within the dry evergreen forests of the core area of the Sakaerat Biosphere Reserve since 2013. This study revealed that *Boiga cyanea* is the most locally-dominant snake predator responsible for 22% – 33% of egg and fledgling mortalities.

In this research project we aimed to: (1) quantify *B. cyanea* space use across the avian nesting and non-nesting seasons; (2) quantify *B. cyanea* activity across the avian nesting and non-nesting seasons; and (3) explore *B. cyanea* activity patterns in relation to avian nest predation at SBR. We radio-tracked a total of 14 adult *B. cyanea* – 5 males and 9 females between 21 October 2017 and 8 June 2019. We recorded a total of 1317 fixes – 907 during daylight and 410 at night.

We used dynamic Brownian bridge movement models to derive estimates on *B. cyanea* space use and activity during the study. On average, males used areas of approximately 18.17 ± 6.43 ha, while females used 3.11 ± 0.72 ha. Our individuals used approximately 11.81 ± 4.27 ha during the avian nesting season, and 1.96 ± 0.63 ha during the non-nesting season. Males appeared to move more frequently and farther than females during our study. The motion variance for males was $5.08 \pm 1.50 \sigma_m^2$, while that for females was $1.16 \pm 0.29 \sigma_m^2$. Males and females appeared to move more during the nesting season than in the non-nesting season. The motion variance for the nesting season was $3.73 \pm 1 \sigma_m^2$, while that for the non-nesting season was $0.5 \pm 0.15 \sigma_m^2$.

Our study provides insight into the foraging ecology of a primary avian nest predator in a tropical ecosystem. Future research should focus on refining our understanding of *B. cyanea* diet. Understanding *B. cyanea* dietary preferences for specific avian life stages or species could elucidate conservation needs for *B. cyanea*, as well as assist in developing conservation strategies for targeted bird species in areas of high *B. cyanea* density.

School of Biology

Academic Year 2020

Student's Signature

Anji D'souza

Advisor's Signature



ACKNOWLEDGEMENTS

First and foremost, I sincerely thank the National Science and Technology Development Agency (NSTDA) for funding our project for its entire duration. I thank the National Research Council of Thailand (NRCT) for granting me permission to conduct research in Thailand. I thank Suranaree University of Technology, and in particular Aj. Duangkamol Maensiri, Pluemjit Boonpueng, Aj. Rapee Gosalawit and Sirinda Boonphum for facilitating paperwork with the NSTDA and the NRCT. I thank the Thailand Institute of Scientific and Technological Research (TISTR) for allowing me to conduct my research within the Sakaerat Biosphere Reserve, and for supporting me through a student scholarship. I sincerely thank Sakaerat Environmental Research Station, and in particular, Director Surachit, for all the logistic support I received whenever I needed it, throughout my time at Sakaerat – my home for the last four years. I thank Nithina Kaewtonghkum for all the help she promptly and selflessly gave me. I thank Nakhon Ratchasima Zoo, and in particular D.V.M. Wirongrong Changpet, for providing veterinary expertise.

I thank my thesis advisor and mentor since 2016 – Dr. Colin Strine, for giving me the opportunity to experience what it takes to conduct ecological research. I have learned a lot from him throughout the years, and I am extremely grateful for all the opportunities, resources and faith he bestowed on me since day one. I express my sincerest gratitude to my co-advisor, Dr. George Gale, not only for his academic assistance throughout the project, but also for his constant calming influence on me. I

thank Daphawan Khamcha for her assistance with several official Thai documents and for sharing her data with me. I thank Rongrong Angkaew for patiently responding to all my queries regarding nest predations at SERS. I also thank Kanoktip Somsiri and Marisa Pringproh for sharing bird team's data with me.

I express my most sincerest gratitude to my field team: Nathaniel Quarrell, Jizel Miles, Thomas Prewett, Rose Stroup and Harry Ward-Smith for their time, devotion, enthusiasm, work ethic and friendship. You played an integral role in this project, and without you, we would not be able to attain the results within this thesis.

I express my sincere thanks to Benjamin Marshall for guiding and assisting me with major analyses and coding. I also thank Russell Gray and Yan Ru for providing me with statistical assistance. I thank Inês Silva and Matthew Crane for their insight during the early stages of this project.

I thank all my fellow researchers at Sakaerat, whose help I deeply cherish, and with whom I have had memorable moments. Honorable mentions: Max Jones, Samantha Smith-Jones, Ysabella Montañó, Tyler Knierim, Curtis Radcliffe, Dawn Cook, Curt Barnes and Porramin Patungtaro.

A special thanks goes to Bartosz Nadolski, Cameron Hodges, Jack Christie, Jesse Goodyear, Jizel Miles and Matthew Ward for their friendships and for playing a role in my professional and personal development.

A final thanks goes to my mother, Thelma and my best friend, Gaia. Grazie di essere un sostegno presente e costante.

CONTENTS

	Page
ABSTRACT IN THAI.....	I
ABSTRACT IN ENGLISH.....	III
ACKNOWLEDGEMENTS.....	VI
CONTENTS.....	VII
LIST OF TABLES.....	X
LIST OF FIGURES.....	XI
CHAPTER	
I INTRODUCTION.....	1
1.1 Introduction.....	1
1.2 Research objectives.....	3
1.3 Research hypothesis.....	3
1.4 Scope and limitations of the study.....	3
II LITERATURE REVIEW.....	5
2.1 Predator – prey interactions.....	5
2.2 Snake predator ecology.....	6
2.3 Snake activity.....	7
2.4 Radio-telemetry.....	8
2.5 Study species.....	10
III MATERIALS AND METHODS.....	12
3.1 Study site.....	12

CONTENTS (Continued)

	Page
3.2 Study sample.....	13
3.3 Radio-telemetry.....	14
3.4 Nest monitoring.....	16
3.5 Data analyses.....	17
3.5.1 Space use.....	18
3.5.2 Activity patterns.....	19
3.5.2.1 Seasonal activity.....	19
3.5.2.2 Nocturnal activity.....	20
IV RESULTS AND DISCUSSION.....	22
4.1 Results.....	22
4.1.1 Biometric processing.....	22
4.1.2 Radio-telemetry.....	26
4.1.3 Space use.....	30
4.1.3.1 Horizontal movements.....	30
4.1.3.1.1 Seasonal horizontal movements.....	30
4.1.3.1.2 Nocturnal horizontal movements.....	33
4.1.3.2 Vertical movements.....	34
4.1.3.3 Occurrence distribution.....	36
4.1.4 Activity patterns.....	40
4.1.4.1 Seasonal patterns.....	40

CONTENTS (Continued)

	Page
4.1.4.2 Nocturnal patterns.....	45
4.1.4.2.1 Influence of abiotic variables.....	47
4.1.5 Refugia use.....	52
4.1.6 Natural history.....	54
4.1.6.1 <i>Boiga cyanea</i> as a predator.....	54
4.1.6.2 <i>Boiga cyanea</i> as prey.....	54
4.2 Discussion.....	54
4.2.1 Space use.....	54
4.2.2 Activity patterns.....	56
VI CONCLUSION AND RECOMMENDATION.....	60
5.1 Conclusion.....	60
REFERENCES.....	63
SUPPLEMENTARY MATERIALS.....	79
APPENDIX.....	89
CURRICULUM VITAE.....	90

LIST OF TABLES

Table		Page
4.1	Summary table of the biometric processing data collected for all the <i>Boiga cyanea</i> captured and processed between 1 June 2017 and 1 July 2019 at Sakaerat Biosphere Reserve.....	22
4.2	Tracking summaries of radio-tracked <i>Boiga cyanea</i> between 21 October 2017 and 8 June 2019.....	28
4.3	Movement summaries of radio-tracked <i>Boiga cyanea</i> between 21 October 2017 and 8 June 2019 at SBR.....	31
4.4	Night-time movement summaries of radio-tracked <i>B. cyanea</i> from their previous daytime refugia, and predations by <i>B. cyanea</i> recorded between 2013 and 2019 via the nest monitoring cameras at SBR.....	33
4.5	Utilization distributions of radio-tracked <i>Boiga cyanea</i> between 21 October 2017 and 8 June 2019.....	38
4.6	Motion variance summaries of radio-tracked <i>Boiga cyanea</i> between 21 October 2017 and 8 June 2019.....	42
4.7	Candidate models assessing predictors of nocturnal movement. Models are ranked by Akaike's Information Criterion corrected for small samples (AIC_c) with degrees of freedom (df), difference in AIC_c (ΔAIC_c), model likelihood, and Akaike's weights (ω_i).....	49
4.8	Diurnal arboreal and terrestrial refugia used by our radio-tracked individuals.....	52

LIST OF FIGURES

Figure		Page
3.1	Map of the core area of the Sakaerat Biosphere Reserve with its location within Thailand (blue) and Southeast Asia.....	13
4.1	Photographs taken during morphometric data collection of captured <i>Boiga cyanea</i> at Sakaerat Biosphere Reserve. A) Tail length; the snake was placed along a measuring tube, on which we accurately measured tail length from the tip of the anal scale to tip of the tail, and snout-to-vent length (SVL), from tip of the anal scale to tip of rostral scale. B) Girth at 75% SVL; we collected girths with a dial caliper at 25%, 50% and 75% of the snake's SVL. C) Head width; we collected head length from tip of the rostral scale to behind the jaw, and head width at the widest point of the head, using a dial caliper. D) Mass; we collected mass by placing the snake coiled up on a tray using a digital weighing scale. E) Snake brand; we used a heat brander to mark the processed snakes with a unique identifying number. Branding our snakes allowed us to readily identify them in the field with no / minimal disturbance, especially when we did not have our radio-receiver with us to confirm whether the snake was radio-tracked or not.....	25
4.2	Tracking durations for our radio-telemetered individuals between October 2017 and June 2019.....	27

LIST OF FIGURES (Continued)

Figure		Page
4.3	Euclidean distances between consecutive diurnal locations displayed for each month of male and female individuals radio-tracked between 21 October 2017 and 8 June 2019 at SBR.....	31
4.4	Density plot of nocturnal heights recorded for radio-telemetered <i>B. cyanea</i> during the avian nesting and non-nesting seasons at SBR.....	35
4.5	Comparison between heights of avian nests monitored and nests depredated by <i>B. cyanea</i> between 2013 and 2019, and <i>B. cyanea</i> at night during our study.....	36
4.6	95% dBBMM utilization distribution map for all individuals between 21 October 2017 and 8 June 2019.....	40
4.7	Motion variance for each radio-telemetered <i>B. cyanea</i> between 21 October 2017 and 8 June 2019 with the avian nesting seasons highlighted in grey.....	41
4.8	Overlaid monthly motion variance for male and female radio-Telemetered <i>B. cyanea</i> during the study with avian nesting season (4 Feb – 5 Aug) in grey.....	42
4.9	Seasonal differences in motion variance between sexes. A) Box and jittered scatter plots of seasonal motion variance values split between female and male. B) Model averaging results with point estimates and 95% Bayesian credible intervals.....	44

LIST OF FIGURES (Continued)

Figure	Page	
4.10	<p><i>B. cyanea</i> predation rate (monthly total of nests depredated over monthly total of camera exposure days) during the 2018 and 2019 avian nesting seasons superimposed on total monthly predations between 2013 and 2019.....</p>	45
4.11	<p>Density curves for nocturnal snake activity and avian nest predations by <i>B. cyanea</i>. The overlap coefficient of the two curves is equal to the shaded grey area intersecting the two curves.....</p>	46
4.12	<p>Euclidean distances between snake locations at specific nocturnal hours and their previous daytime refugia during the avian nesting season and the non-nesting season. The data illustrated are collected from individuals radio-tracked between 14 March 2018 and 3 September 2018, and between 15 January 2019 and 8 June 2019.....</p>	47
4.13	<p>Relationship between ambient relative humidity and ambient temperature with real (black dots) and predicted values (colored lines).....</p>	48
4.14	<p>Use of different diurnal, arboreal refugia by the each individual during the study.....</p>	53
4.15	<p>Use of different diurnal, terrestrial refugia by the each individual during the study.</p>	53

CHAPTER I

INTRODUCTION

1.1 Introduction

Tropical forests are being degraded and lost at an unprecedented rate due to habitat loss, fragmentation and conversion, climate change and anthropogenic exploitation (Turner, 1996; Robinson and Sherry, 2012). As a result, tropical forest birds have suffered widespread population declines. Research shows that elevated rates of avian nest predation is the leading cause for reduced avian reproductive success (Robinson and Sherry, 2012).

Nest predation affects avian ecology by influencing nest site selection, life history traits, and community structures (Weatherhead and Blouin-Demers, 2004; Thompson, 2007). Declining avian populations and species richness are likely to degrade vital ecological processes such as seed dispersal, pollination and invertebrate population control (Sekercioglu *et al.*, 2004). Research on avian reproductive ecology identifies snakes as significant avian nest predators among the nest predator community (Conry, 1988; Sperry *et al.*, 2008; Pierce and Pobprasert, 2013). Most research however, has focused primarily on birds and has typically inferred predator behaviour through indirect measures of predator activity (visual encounter surveys, capture rates etc.) and patterns of nest success (Weatherhead and Blouin-Demers, 2004a).

In order to fully understand these complex predator – prey interactions between snakes and nests, ecologists ought to directly study the predators in addition to their prey (Weatherhead and Blouin-Demers, 2004a). One approach towards attaining this goal is radio-telemetry (DeGregorio *et al.*, 2014). Radio-telemetry allows us to not only examine space use and activity patterns of individuals and populations, but also the cues likely eliciting these behaviours (Whitaker and Shine, 2003; DeGregorio *et al.*, 2014). Recent technological developments in radio-telemetry in fact, have allowed us to also study smaller species that often occur at low densities, and are highly cryptic and secretive (Whitaker and Shine, 2003).

Boiga cyanea is a tropical, arboreal, nocturnal, colubrid snake that has been recognized as a significant avian nest predator through ongoing nest monitoring studies (Khamcha *et al.*, 2018a; Pierce and Pobprasert, 2013; Angkaew *et al.*, 2019; Pierce *et al.*, 2020). Until now, there has been little to no research attempting to understand this species' free-ranging ecology.

This research project aims to be the first radio-telemetry study to investigate the space use and activity patterns of *B. cyanea* in relation to nest success. It is the first attempt to explore snake-bird interactions simultaneously within the same study site in southeast Asia. Our findings will help broaden our understanding of snake-bird dynamics in tropical Asia, and might be applicable to other parts of Thailand, where the species' congeners are also important nest predators (Donald *et al.*, 2009). This project will focus within the dry evergreen forests of the core area of the Sakaerat Biosphere Reserve (SBR) in Northeast Thailand.

1.2 Research objectives

- 1.2.1 Quantify space use of *Boiga cyanea* during the study period via daylight and night-time locations across the avian nesting and non-nesting seasons.
- 1.2.2 Quantify activity of *Boiga cyanea* during the study period across the nesting and non-nesting seasons.
- 1.2.3 Explore activity patterns of *Boiga cyanea* in relation to avian nest predation at Sakaerat Biosphere Reserve.

1.3 Research hypotheses

- 1.3.1 Space use of *Boiga cyanea* during the study period will be reduced during the avian nesting compared to the non-nesting season.
- 1.3.2 Activity of *Boiga cyanea* during the study period will be higher during the nesting season compared to the non-nesting season.
- 1.3.3 *Boiga cyanea* activity will follow a similar trend to that of the nest predations during the avian nesting season.

1.4 Scope and limitations of the study

The study was conducted within the dry evergreen forests of the core area of the Sakaerat Biosphere Reserve (SBR), Northeast Thailand. Data were collected between 21 October 2017 and 8 June 2019. We radio-tracked a total of 14 adult *B. cyanea* – 5 males and 9 females.

This project gathers baseline information on the free-ranging ecology of a relatively unstudied, major avian nest predator within the dry evergreen forests of

SBR. We attempted to explore the movements of a known, primary avian nest predator in relation to avian nest predations of the local bird population, by simultaneously documenting predator and prey activity. Our study adds to the current knowledge on avian nest predation ecology within the tropics, in particular, in Southeast Asia. This study further provides scope for improving methodologies in data collection for similar future studies. The findings from this study could provide preliminary information for research exploring the effects of anthropogenic disturbance on primary nest predators inhabiting forest fragments.

This study suffered frequent losses of study individuals primarily due to premature radio-transmitter failures. Because of this, we were unable to get much long-term and overlapping data across individuals and across the avian nesting and non-nesting seasons. Furthermore, due to the relatively slender and vertically compressed body structure of *B. cyanea*, we had to bias our study sample towards individuals big enough to accommodate a 1.8g transmitter in their coelomic cavities. The avian nesting seasons 2018 and 2019 witnessed lower nest predations by *B. cyanea* compared to the previous years. For these reasons, we ought to be cautious in extrapolating inferences spatially and temporally.

CHAPTER II

LITERATURE REVIEW

2.1 Predator-prey interactions

Predation is a major biotic interaction that leads to the removal of individuals from ecological systems and influences population dynamics, species distributions and community structures (Stenseth *et al.*, 1997; Barbosa and Castellanos, 2005; Mullin and Seigel, 2009; Tyson *et al.*, 2010). Prey species avoid predation by adopting anti-predator strategies that maximize foraging success and minimize predation risk (Lima, 1998). Their anti-predator tactics include reducing activity or shifting foraging patterns spatially or temporally, depending on the types of predators and their respective foraging ecology (Kotler *et al.*, 1992).

Birds are one of the most extensively researched taxon because of their relative ease of being well-represented in studies of breeding biology (Weatherhead and Blouin-Demers, 2004a). Avian nest predation is reported to be the primary cause for egg and fledgling mortality in most bird species, accounting for approximately 80% of nest failures (Martin, 1993; Remeš *et al.*, 2012; DeGregorio *et al.*, 2016a). Nest predation influences nest site selection, life histories, and community structures in birds (Thompson, 2007). The majority of nest predation research has primarily inferred predator behaviour indirectly through capture rates, point counts, visual encounter surveys and evidence of past predator activities (Weatherhead and Blouin-Demers 2004a; Sperry *et al.*, 2008). Researchers understand that there is a need to

directly examine the predators alongside their prey to better explore these complex predator-prey dynamics (Menezes and Marini, 2017).

Evidence from nest monitoring studies using cameras and continuous recording video systems suggest that snakes are major, widespread nest predators (Robinson *et al.*, 2005; Pierce and Pobprasert, 2007; Ribeiro-Silva *et al.*, 2018). Significant research on snake-bird interactions is limited. Snakes' highly cryptic nature and occurrences at low densities have challenged researchers wanting to conduct meaningful predator research to explore dynamics between snakes and avian nests (DeGregorio *et al.*, 2014).

2.2 Snake predator ecology

There are over 3,400 extant snake species described today that occupy fossorial, arboreal, terrestrial and aquatic environments, and range from arid deserts to open oceans (Hsiang *et al.*, 2015). Snakes are unrivaled among predators in their ability to predate upon such a diverse array of prey items; their diets include gastropods, arthropods, cephalopods, amphibians and their eggs and larvae, reptiles and their eggs, birds and their eggs, and mammals. Diets of specialized predator species can still vary between life stages, sizes, sexes, individuals, seasons and geographic locations (Greene, 1997).

Snakes detect their prey by relying on a combination of sensory cues. Besides vision and the perception of vibrations through the lower jaw, they have a heightened sense of chemoreception thanks to the Jacobson's organ, located in the roof of the mouth (Berkovitz and Shellis, 2017). Some snake species initiate foraging as a response to available volatile chemosensory information, and initiate predation as a

response to visual stimuli of parental activity, confirming the presence of the nests (Mullin and Cooper, 1998). Nocturnal predators likely use diurnal nest activity as a visual cue to predate upon nests at night when parental defenses are lowered (Stake *et al.*, 2005; DeGregorio *et al.*, 2015). DeGregorio *et al.* (2016) reported that predation probability reflected predator habitat use and accessibility to nests, and varied in relation to the nesting characteristics of birds, such as body size, nesting habitat, and nest height. Understanding predator movements and habitat use will likely elucidate important links within natural predator-prey systems.

2.3 Snake activity

Activity patterns of snakes are generally either diurnal or nocturnal; some species however, can alter their activity cycles daily or seasonally depending on local climatic conditions or seasonal variations. Examples of strictly diurnal species are the Rough green snake *Opheodrys aestivus* and the Orange-bellied racer *Mastigodryas melanolomus*; examples of strictly nocturnal taxa instead, are Cat snakes (*Boiga* sp.) and Cat-eyed snakes (*Leptodeira* sp.). Snake activity varies in relation to prey availability, predator susceptibility, seasonal variation, temperature, humidity, lunar light levels, and habitat connectivity and complexity (Greene, 1997).

Christian *et al.* (2007) observed a decrease in activity between foraging sites during the dry season in comparison to the wet season in the Northern death adder *Acanthophis praelongus*. Sperry *et al.* (2013) reported a positive correlation between nocturnal activity and warmer nighttime temperatures in the Texas ratsnake *Pantherophis obsoleta*. Daltry *et al.* (1998) documented a strong, positive correlation between nocturnal activity and relative humidity in Malayan pit vipers *Calloselasma*

rhodostoma. Lillywhite and Brischoux (2012) found an increase in nocturnal foraging behaviour with higher lunar illumination in Cottonmouth snakes *Agkistrodon piscivores*. Koenig *et al.* (2007) suggested that predation probability by arboreal snakes might be enhanced by vines along tree trunks and tree canopy connectivity, as observed with the Puerto Rican boa *Epicrates inornatus* (Wunderle *et al.*, 2004) and the Jamaican boa *Epicrates subflavus*.

2.4 Radio-telemetry

The most conventional approach for studying the free-ranging ecology of cryptic taxa, such as snakes, is radio-telemetry (Weatherhead and Charland, 1985; Whitaker and Shine, 2003; Boback *et al.*, 2020). This technique involves the transmission of radio signals from a radio-transmitter attached to or implanted within a free-ranging individual, to a radio-receiver (Andrusiak *et al.*, 1998). Radio-telemetry is used to gain valuable insights into species' biology that would otherwise be difficult to study, namely – animal physiology and behaviour, activity and movement patterns, migrations and dispersals, home range sizes, habitat use, resource selection, population size estimates, relative densities, survival rates, and fecundity (Millspaugh and Marzluff, 2001). This technique has gained recognition thanks to its efficiency, precision, and low time and energy requirements (Ujvari and Korsos, 2000); however, its benefits should justify the potential negative effects on the radio-telemetered individuals' physiology and behaviour (Weatherhead and Blouin-Demers, 2004b).

Little was known about the biology, behaviour, life history, and thermal and spatial ecology of free-ranging snakes until the early 1970s, when the first radio-telemetric studies on snakes were carried out (Ujvari and Korsos, 2000). To our

knowledge, only the Texas ratsnake *Pantherophis obsoletus*, the Eastern ratsnake *P. alleghaniensis* and the Corn snake *P. guttatus* in North America (Weatherhead and Charland, 1985; Blouin-Demers and Weatherhead, 2001b; Sperry *et al.*, 2008; Sperry and Weatherhead, 2009; DeGregorio *et al.*, 2014; DeGregorio *et al.*, 2016a, DeGregorio *et al.*, 2016b) and the introduced Brown tree snake *Boiga irregularis* on Guam (Conry, 1988; Savidge, 1988; Rodda *et al.*, 1992) have been well-documented with regards to avian nest predation through radio-telemetry.

Ratsnakes have been identified as significant nest predators across much of the Southeastern and Central United States (DeGregorio *et al.*, 2016a), with avian prey becoming increasingly important to their diet, especially during the avian nesting season (Sperry and Weatherhead, 2009). Radio-telemetric studies on North American Ratsnakes have explored their habitat use and selection, daily and seasonal variations in their activity patterns, and factors enhancing predation probability. Blouin-Demers and Weatherhead (2001b) observed *P. obsoletus* exhibiting a stronger preference for edge habitats compared to closed forest habitats, possibly for their thermoregulatory properties. Sperry and Weatherhead (2009) reported a preference for refuge sites with high vegetation cover during colder, inactive seasons and a preference for refuges in open habitats during warmer, active seasons. Sperry *et al.* (2013) documented a shift from primarily diurnal, to crepuscular, to completely nocturnal activity, depending on the season and geographic location. DeGregorio *et al.* (2016b) found an increase in predation by *P. guttatus* over the bird nesting season, and an increase in Ratsnake-specific predation when the snakes moved the farthest.

The Brown tree snake, native to Indonesia, New Guinea, the Solomon Islands, and parts of Australia, was accidentally introduced to Guam after World War II,

where it became responsible for the extirpation and decline of over 10 native forest bird species (Conry, 1988; Rodda *et al.*, 1992). Radio-telemetric studies on the introduced Brown tree snake have explored their nightly and seasonal movements, their habitat use, and the thermal profile and selection of their shelter sites (Santana-Bendix, 1994; Tobin *et al.*, 1999; Hetherington *et al.*, 2006). The case study in Guam provides evidence for the detrimental ecological impacts uncontrolled snake predations can have on wild nesting bird populations (Fritts and Rodda, 1998).

2.5 Study species

Despite growing recognition implicating snakes as major avian nest predators in southeast Asia, particularly nocturnal, arboreal species (Donald *et al.*, 2009; Pierce and Pobprasert, 2013; Pierce *et al.*, 2020), there has been little to no research carried out on the predators' free-ranging ecology. Khamcha *et al.* (2018a) found that snakes depredated 34% of 287 nests monitored for over 20 forest bird species. The Green cat snake *Boiga cyanea* has been identified as the most locally-dominant snake predator in the evergreen forests of Northeast Thailand, and is responsible for approximately 22% to 33% of egg and fledgling mortalities (Khamcha *et al.*, 2018b; Angkaew *et al.*, 2019; Pierce *et al.*, 2020).

The Green cat snake belongs to the genus *Boiga*. Species of this genus are slender Colubrids ranging from medium-sized to large (1-2 meters) (Cox *et al.*, 2012). Currently, there are 34 *Boiga* species distributed across from tropical Africa through Southern Asia to Melanesia and Australia. *Boiga* species are commonly referred to as tree snakes or cat snakes, due to their vertical, elliptical pupils and large eyes. They are primarily nocturnal, arboreal or semi-arboreal, oviparous, opisthoglyphic, and

euryphagic (Rodda *et al.*, 1999). The Brown tree snake is the only *Boiga* species whose free-ranging ecology has been extensively researched, mainly because of its costly ecological and economic impacts as an introduced species.

B. cyanea is a medium to long bodied, vertically compressed colubrid. Hatchlings are approximately 35 cm in length, while adults can reach up to 186 cm (Chan-ard *et al.*, 2015; Cox *et al.*, 1998). Females are typically larger than males, which can reach up to 153 cm (Cox *et al.*, 2012). Adults are uniformly olive-green in color, displaying a bluish hue (Chan-ard *et al.*, 2015). Juveniles and sub-adults have a reddish-brown or greyish-olive dorsum respectively, a yellowish-green head, and yellow supralabials (Ziegler *et al.*, 2010). The ventral scales are greenish-yellow anteriorly and greenish-white posteriorly, and the chin shields and gular scales are white with a bluish tint (Cox *et al.*, 1998). *B. cyanea* occurs in Thailand, Bangladesh, Bhutan, Cambodia, China, India, Laos, Myanmar, Nepal and Vietnam, and ranges across a variety of habitats from lowlands to 2100m above sea level (Cox *et al.*, 2012).

There is little to no literature available on the free-ranging ecology of *B. cyanea*: our current knowledge on this species derives from occurrence records, natural history notes (Bulian and Bannasan, 1999), captive husbandry and venom studies (Mackessy, 2002). This study attempts to explore *B. cyanea* foraging ecology as a major avian nest predator with the dry evergreen forests of the Sakaerat Biosphere Reserve, Northeast Thailand.

CHAPTER III

MATERIALS AND METHODS

3.1 Study site

We conducted our study within the core area of the Sakaerat Biosphere Reserve (SBR; UNESCO-MAB Biosphere Reserve), Nakhon Ratchasima Province, Thailand (14.44 – 14.55°N, 101.88 – 101.95°E). The core area of the SBR occupies 5,700 ha of protected landscape that ranges between elevations of 280 m and 762 m. The core area comprises a matrix of dense dry evergreen forest, open dry dipterocarp forest, transitional mixed deciduous vegetation, and a field research station that occupies less than 2% of the core area. The dominant vegetation within the dry evergreen forest includes *Hopea ferrea*, *H. odorata* and *Hydnocarpus ilicifolia*, while that within the dry dipterocarp forest includes *Shorea obtusa*, *S. siamensis*, *Dipterocarpus intricatus* and *Gardenia sootepensis*. Marshall *et al.* (2020) summarized the annual seasonal weather patterns within the core area of SBR between 2012 and 2018 as follows: the hot season (33.8 ± 2.8 °C and 2.5 ± 7.9 mm rainfall) , the wet season (29.9 ± 2.2 °C and 5.9 ± 11.1 mm rainfall), and the dry season (29.0 ± 3.5 °C and 0.2 ± 0.8 mm rainfall).

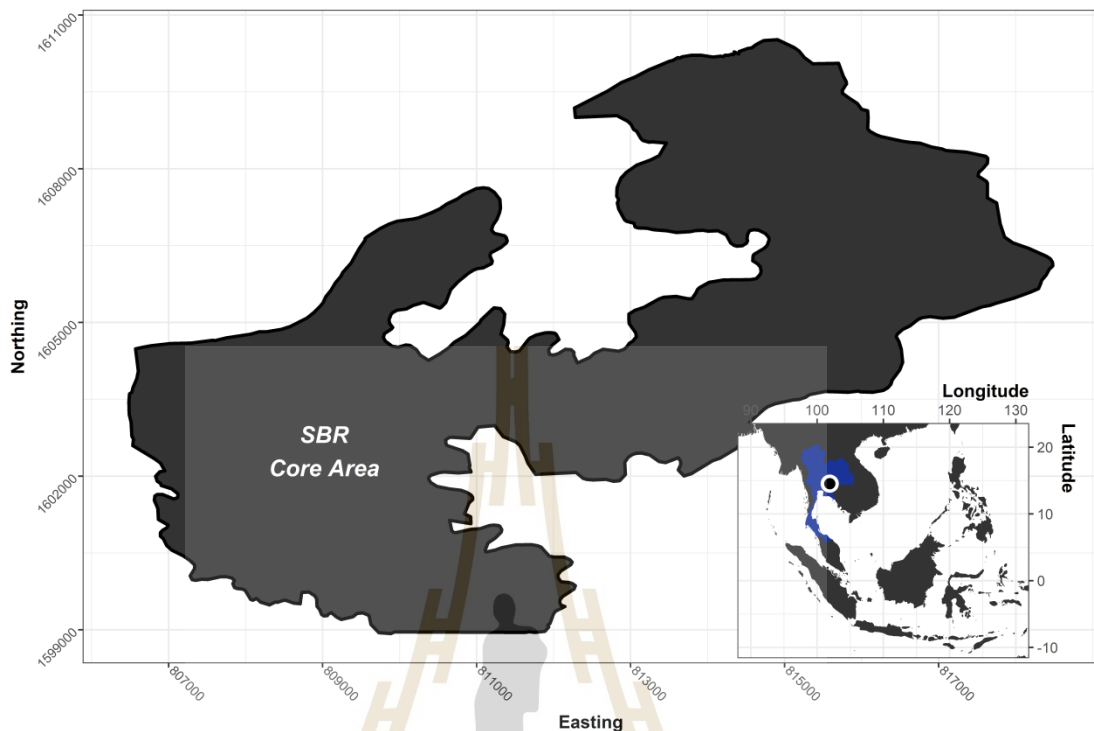


Figure 3.1 Map of the core area of the Sakaerat Biosphere Reserve with its location within Thailand (blue) and Southeast Asia.

3.2 Study sample

We obtained *Boiga cyanea* through opportunistic captures, notifications or targeted nocturnal surveys in the dry evergreen forests of the SBR. Once captured, all individuals were safely transported to the field station, where they were housed in sterile plastic boxes until their biometric processing. During processing, we determined individuals' age class, body score, sex, tail lengths (TL), snout-to-vent lengths (SVL), girths, head measurements, and mass. Upon collecting the snakes' biometrics, we assessed their suitability for radio-telemetry. Our selection criteria for including individuals into the sample required them to be adults with a high body

score that were able to undergo an implantation surgery and accommodate a 1.8g VHF radio-transmitter (Model BD-2T or BD-2, Holohil Systems Incorporated, Ontario, Canada) in their coelomic cavity. We ensured that the radio-transmitters weighed less than 3% of the snakes' body mass. We further excluded injured and heavily gravid individuals from the sample.

Implantation surgeries on suitable individuals were strictly performed by Dr. Wirongrong Changphet – a qualified wildlife veterinarian from Nakhon Ratchasima Zoo, in accordance with the Veterinary Practices Act B.E. 2545. We anesthetized our snakes via inhalation using Isoflurane, and followed a modified surgical technique described by Reinert and Cundall (1982). The BD-2T and BD-2 radio-transmitters had a standard battery life of 14 weeks at approximately 30 °C. The BD-2T model was temperature sensitive, unlike the BD-2 model. The BD-2T's pulse rate varied with changes in the snakes' internal body temperature: faster pulse rates indicated higher body temperatures. The BD-2T and BD-2 model Holohil radio-transmitters should provide a 500 – 1000 m signal range (Holohil Systems Incorporated, Ontario, Canada). The topography at SBR however, typically reduced signal range to 150 – 250 m. We released all implanted individuals within 30m of their capture location, within 12 hours post-surgery to allow for recovery and thermoregulation.

3.3 Radio-telemetry

We investigated the movement patterns of adult *Boiga cyanea* using manual radio-telemetry. We located all individuals once, every day to identify snake refugia. We also located individuals at night to assess snake activity. At night, we located each individual between one to three times at approximately four hour intervals, every

alternate night. Exceptional circumstances in which we did not locate the snakes included equipment failures, staff unavailability, adverse weather conditions, individuals awaiting transmitter replacement at the research station and inability to detect radio-signal for extended periods of time despite intensive search effort. We estimated snake locations via the homing method (Amelon *et al.*, 2009) and pushed for visual observations whenever possible at night to confirm the accuracy of the telemetered locations. We moved discreetly around our snakes and limited the amount of time spent in their vicinity once located, to minimize disturbance.

Each time we located a snake, we recorded the date and the pinpoint time. We marked the snake's location – most times a tree or a plant – with flagging tape with the snake's unique identification, the date and the time. We reported whether we attained a visual observation on the snake and if so, we described the behaviour it was exhibiting. We assessed whether the snake was stationary or moving through radio-signal patterns and/or visual observations. We estimated the snake's location along with its accuracy with a hand-held global positioning system (GPS) unit (Garmin GPSMAP 64s, Garmin Ltd., United States) using the Universal Transverse Mercator (UTM; 47N World Geodetic System 84) coordinate system. We determined whether the snake's position was arboreal (>0 m) or terrestrial (≤ 0 m), and measured its height off the ground for each visual observation. We noted the ambient temperature ($^{\circ}\text{C}$) and relative humidity (%) at approximately 1.5 m above ground at the snake's location. We obtained daily minimum and maximum recorded temperatures ($^{\circ}\text{C}$), daily average humidity (%), and daily rainfall (mm) from five meteorological stations at SBR. Approximately 10% of our dataset contained missing ambient temperatures and relative humidity. To avoid losing the whole data point during which climatic

variables were not recorded, we decided to impute missing values. To do this, we had to ascertain that our data were missing completely at random. We ran Little's test (Little, 1988) to assess whether the probability of our missing data was unrelated to other measured variables (Baraldi and Enders, 2010). We compared relative humidity to the daily average humidity recorded by the meteorological stations and obtained a p-value of 0.95 ($\alpha = 0.05$), suggesting that our data are likely missing completely at random. We used the *mice* package (van Buuren and Groothuis-Oudshoorn, 2011) to impute missing ambient temperature and ambient relative humidity based on the daily minimum and maximum temperatures, the daily average humidity and the daily rainfall recorded at the meteorological stations closest to each individual's locations. We used the *suncalc* package (Thieurmel and Elmarhraoui, 2019) for daily lunar illumination data specific to the snake's geographic coordinates. We calculated the snake's internal body temperature by measuring its transmitter's pulse interval and inputting it into the unique 3rd degree polynomial equations for each BD-2T model transmitter provided by Holohil Systems Incorporated, Ontario, Canada.

3.4 Nest monitoring

Researchers from King Mongkut's University of Technology Thonburi (KMUTT), Thailand have been monitoring avian nests every year since 2013, in the dry evergreen forests of the Sakaerat Biosphere Reserve (SBR). They identified the nest predators of 12 species of forest bird species during their nesting seasons – typically from February to August, using continuous recording video systems following Pierce and Pobprasert (2007). They have granted us access to the dataset of nest predations caused by *B. cyanea* between 2013 and 2019. The dataset includes

information on the bird species predated upon, the nest heights, the dates the nests were found and filmed, and the date, time and geographic coordinates (UTM projection) of the predation events. We defined the start of the avian nesting season as the date of discovery of the first forest bird nest, and the end of the avian nesting season as the date of last nest predation or nest abandonment. The 2018 nesting season began on 4 February and ended on 31 July, and the 2019 nesting season began on 4 March and ended on 5 August. We report the nesting season as between 4 February to 5 August for the duration of our study.

3.5 Data analyses

We used *R v.4.0.3* (R Core Team, 2020) and *R Studio v.1.3.1093* (R Studio Team, 2019) for data manipulation, analyses and visualization. For data manipulation, we used packages: *dplyr v.0.8.5* (Wickham *et al.*, 2020), *lubridate v.1.7.8* (Grolemund and Wickham, 2011), *tidybayes v.2.1.1* (Kay, 2020), *reshape2 v.1.4.4* (Wickham, 2007), *raster v.3.1.5* (Hijmans, 2020). For data analyses, we used packages: *mice v.3.11.0* (van Buuren and Groothuis-Oudshoorn, 2011), *suncalc v.0.5.0* (Thieurmel and Elmarhraoui, 2019), *move v.4.0.0* (Kranstauber *et al.*, 2020), *brms v.2.14.0* (Bürkner, 2018), *performance v.0.4.7* (Lüdtke *et al.*, 2020), *lme4 v.1.1.23* (Bates *et al.*, 2015), *bestNormalize v.1.5.0* (Peterson, 2019), *overlap v.0.3.3* (Ridout and Linkie, 2009), *arm v.1.11.1* (Gelman and Su, 2020), *wiqid v.0.3.0* (Meredith, 2020), *adehabitatsHR v.0.4.18* (Calenge, 2006), *rgeos v.0.5.3* (Bivand and Rundel, 2020), *recurse v.1.1.2* (Bracis *et al.*, 2018), *cluster v.2.1.0* (Maechler *et al.*, 2019), *MASS v.7.3.53* (Venables and Ripley, 2002), *astroFns v.4.1.0* (Harris, 2012). For data visualization, we used packages: *ggplot2 v.3.3.0* (Wickham, 2016), *ggpubr v.0.4.0*

(Kassambara, 2020), *scales v.1.1.1* (Wickham and Seidel, 2020), *scico v.1.2.0* (Pedersen and Cramer, 2020), *ggspatial v.1.1.3* (Dunnington, 2020), *gtable v.0.3.0* (Wickham and Pedersen, 2019), *cowplot v.1.0.0* (Wilke, 2019), *bayesplot v.1.7.2* (Gabry and Mahr, 2020), *ggridges v.0.5.2* (Wilke, 2020b), *ggtext v.0.1.0* (Wilke, 2020a), *viridis v.0.5.1* (Garnier, 2018), *plotrix v.3.7.8* (Lemon, 2006).

3.5.1 Space use

We conducted descriptive tests using the *dplyr* package (Wickham *et al.*, 2020) to report means \pm standard errors, or medians and their interquartile range (IQR) when our data presented outliers. We used Markov chain Monte Carlo (MCMC) simulations for Bayesian inference on posterior distributions between groups. We report their 95% Bayesian credible intervals (BCrI) using the Highest Density Interval (HDI) method, and their point estimates as the true difference between group means. We checked for MCMC convergence by graphically assessing their trace plots. We report Pearson's Chi-squared test to assess significance ($p = 0.05$) between moving and stationary behaviours during the avian nesting and non-nesting seasons.

We quantified space use by estimating utilization distributions and movement pathways using dynamic Brownian bridge movement models (dBBMM). We produced dBBMM estimates using the *move* package (Kranstauber *et al.*, 2020). This method was originally developed to analyze GPS telemetry data for mammals and birds (Kranstauber *et al.*, 2012); however, it has been recently applied to VHF telemetry data on reptiles as well (Silva *et al.*, 2018, Knierim *et al.*, 2019, Smith *et al.*, 2020). Unlike traditional space use estimation methods like minimum convex

polygons (MCP) and kernel density utilization distributions (KDUD), dBBMMs account for spatial and temporal autocorrelation, accuracy of the GPS locations, and irregular sampling intervals. We finalized on a moving window size of 9 data points to detect variations in behavioural states between three day periods – the average time our individuals would remain stationary. We finalized on a margin size of 3 data points to detect variations between active and inactive behaviours. We had run dBBMMs with larger window and margin sizes ($w = 11, m = 5$, Table S1; $w = 15, m = 7$, Table S2; $w = 21, m = 9$, Table S3) to assess how utilization distributions varied for individuals. However, we settled on using a window size of 9 and margin size of 3, as we did not want to lose finer-scale variations given the very short tracking durations of some individuals. We used the mean GPS accuracy of all telemetered locations as the error associated with each data point. We selected 90%, 95% and 99% dBBMM isopleth contours to delineate estimated utilization distributions during the study period.

3.5.2 Activity patterns

3.5.2.1 Seasonal activity

The dBBMM output includes estimates for an animal's mobility – referred to as the Brownian motion variance (σ_m^2). These estimates describe behavioural changes along an individual's movement pathways (Kranstauber *et al.*, 2012), based on user-defined, biologically relevant, window and margin sizes. Throughout this report, we interpret motion variance as a proxy for *B. cyanea* foraging activity.

We used a Bayesian regressive model using the *brms* package (Bürkner, 2018) to assess how motion variance varied between the nesting and non-nesting seasons,

and males and females. We used the *bestNormalize* package (Peterson, 2019) to render our motion variance Gaussian. We opted for a Bayesian approach because the assumptions for the normality of residuals are relaxed and the estimates are more conservative. We incorporated the default priors into our model as we did not have any reliable prior information to base our motion variance on. Our model parameters included motion variance as the response variable, season and sex as the predictor variables, and individual identification as the random effect [$\sigma_m^2 \sim \text{Season} + \text{Sex} + (1|\text{ID})$]. We ran 5 chains with 5000 iterations to achieve model convergence. We determined model convergence when Gelman and Rubin (1992) potential scale reduction statistic, Rhat, equated to one. We created 3 models, and coded female *B. cyanea* during the nesting season as the intercept, and the non-nesting season and males as the two coefficients. We used the *bayesplot* package (Gabry and Mahr, 2020) as a visual diagnosis for autocorrelation of all model variables, and for posterior predictive checking of observed data compared to simulated data. We used the *performance* package (Lüdtke *et al.*, 2020) to derive the R-squared (R^2) regression metric to estimate the proportion of variation explained by the predictor variables. We averaged our model and estimated the effects of season and sex on motion variance.

3.5.2.2 Nocturnal activity

We ran a generalized linear mixed-effects models (GLMM) with a binomial distribution using the *lme4* package (Bates *et al.*, 2015) to assess whether abiotic variables were good predictors of whether a snake was detected moving or not during our night-time fixes. Our model parameters included whether a snake was observed moving or not during the fix, the imputed ambient temperature (°C) and imputed

ambient humidity (%), daily rainfall (mm), or lunar illumination (%), and individual identifications as the random effect [Nocturnal movement ~ Abiotic variable + (1|ID)]. We used the *performance* package (Lüdecke *et al.*, 2020) to check model assumptions, such as residual autocorrelation, multicollinearity, normality of residuals and outliers, and error variance heteroscedasticity. We derived R-squared measures (R^2) to indicate the variation explained by the fixed and random effects. We ranked our models using Akaike's Information Criterion (AIC; Akaike, 1973) corrected for small sample sizes (AIC_c; Hurvich and Tsai, 1989). We also used the *performance* package (Lüdecke *et al.*, 2020) to compute indices of our regression models' performance, and to compare their quality against each other.

We further explored nocturnal activity of our snakes in relation to nest predation activity recorded by the nest monitoring cameras at SBR between 2013 and 2019 using the *overlap* package (Ridout and Linkie, 2009). This function helped produce kernel densities of temporal activity patterns and estimate coefficients of overlapping densities.

CHAPTER IV

RESULTS AND DISUSSION

4.1 Results

4.1.1 Biometric processing

We captured a total of 44 *Boiga cyanea* within the core area of the Sakaerat Biosphere Reserve (SBR) between 1 June 2017 and 1 July 2019. Of the 44 individuals captured, 18 were caught during 904 man hours of active surveys, 4 through notifications from collaborating research teams, and 22 through opportunistic encounters. The biometric processing data for the 44 individuals captured are as presented in Table 4.1.

Table 4.1 Summary table of the biometric processing data collected for all the *Boiga cyanea* captured and processed between 1 June 2017 and 1 July 2019 at Sakaerat Biosphere Reserve.

Snake ID	Sex	Age Class	Snout to Vent Length (cm)	Tail Length (cm)	Total Body Length (cm)	Mass (g)
BOCY057	M	Adult	112	32	144	104.8
BOCY058	M	Adult	93	29	122	98.2
BOCY059 ^t	F	Adult	91.4	26.1	117.5	109.6

Table 4.1 (Continued).

Snake ID	Sex	Age Class	Snout to Vent Length (cm)	Tail Length (cm)	Total Body Length (cm)	Mass (g)
BOCY060 ^t	M	Adult	104.0	33.9	137.9	131.9
BOCY061 ^t	F	Adult	95.2	26.6	121.8	107
BOCY062	M	Neonate	50.7	14.1	64.8	13.1
BOCY063 ^t	M	Adult	110	34.6	144.6	143.8
BOCY064	F	Adult	117.4	33.5	150.9	266.6
BOCY065	M	Adult	91	21.4	112.4	92.2
BOCY066 ^t	F	Adult	97.3	28.4	125.7	113.4
BOCY067	M	Adult	104	33	137	129.4
BOCY068	M	Adult	116.4	34.4	150.8	139.6
BOCY069 ^t	F	Adult	108.6	22.7	131.3	121.3
BOCY070 ^t	M	Adult	104.6	32.1	136.7	135.9
BOCY071 ^t	M	Adult	120	31	151	108
BOCY072	M	Adult	102.4	34.6	137	148.4
BOCY073	F	Neonate	46.2	14.1	60.3	12.5
BOCY074	M	Adult	115.4	35.4	150.8	141
BOCY075	M	Juvenile	80	24.9	104.9	53.4
BOCY076 ^t	M	Adult	115	36	151	123
BOCY077	M	Adult	109.4	26.7	136.1	145.7
BOCY078	F	Adult	93.4	27.7	121.1	98.5
BOCY079	F	Adult	90.8	27	117.8	111.4
BOCY080	F	Juvenile	79.6	22.3	101.9	49.8

Table 4.1 (Continued).

Snake ID	Sex	Age Class	Snout to Vent Length (cm)	Tail Length (cm)	Total Body Length (cm)	Mass (g)
BOCY081	M	Juvenile	71.9	22.2	94.1	43.8
BOCY082 ^t	F	Adult	120.4	30.2	150.6	98
BOCY083	M	Juvenile	64.5	19	83.5	27.8
BOCY084	M	Adult	116.3	37.6	153.9	175.8
BOCY085	M	Adult	74	27	101	67.8
BOCY086 ^t	M	Adult	96	30.2	126.2	107.4
BOCY087 ^t	F	Adult	120.5	33.5	154	150.3
BOCY088 ^t	F	Adult	111.4	30.8	142.2	155.1
BOCY089	M	Adult	91.1	27.2	118.3	77.4
BOCY090 ^t	F	Adult	102.8	23.7	126.5	122.6
BOCY091	M	Adult	85.2	26.4	111.6	49.4
BOCY092 ^t	F	Adult	105	32.6	137.6	150.6
BOCY093	M	Neonate	42.8	11.8	54.6	10.8
BOCY094 ^t	M	Adult	117.4	34.3	151.7	170.4
BOCY095	F	Adult	78.7	23.3	102	40.5
BOCY096	F	Adult	116.8	32.5	149.3	213.7
BOCY097	F	Adult	110.2	20.8	131	140.1
BOCY098	M	Adult	94.6	30.6	125.2	63.3
BOCY099	M	Neonate	44	21	65	9.5
BOCY100	F	Adult	90.6	25.4	116	97.9



Figure 4.1 Photographs taken during morphometric data collection of captured *Boiga cyanea* at Sakaerat Biosphere Reserve. A) Tail length; the snake was placed along a measuring tube, on which we accurately measured tail length from the tip of the anal scale to tip of the tail, and snout-to-vent length (SVL), from tip of the anal scale to tip of rostral scale. B) Girth at 75% SVL; we collected girths with a dial caliper at 25%, 50% and 75% of the snake's SVL. C) Head width; we collected head length from tip of the rostral scale to behind the jaw, and head width at the widest point of the head, using a dial caliper. D) Mass; we collected mass by placing the snake coiled up on a

tray using a digital weighing scale. E) Snake brand; we used a heat brander to mark the processed snakes with a unique identifying number. Branding our snakes allowed us to readily identify them in the field with no / minimal disturbance, especially when we did not have our radio-receiver with us to confirm whether the snake was radio-tracked or not.

4.1.2 Radio-telemetry

We report the data collected from 14 radio-tacked adult *B. cyanea* – 5 males and 9 females in the core area of SBR, and present their tracking summaries in Table 4.2. We recorded daylight locations between 21 October 2017 and 8 June 2019, and night-time locations from 14 March 2018 to 3 September 2018, and from 15 January 2019 to 8 June 2019.

Tracking durations within the study sample varied considerably (Figure 4.2). We lost individuals for different reasons: premature transmitter failures ($n = 8$), inexplicable deaths ($n = 3$), predations ($n = 2$), and inaccessible capture locations ($n = 1$). Of the 14 radio-tracked *B. cyanea*, we were able to successfully recapture and re-implant only 2 individuals – F01 and M04.

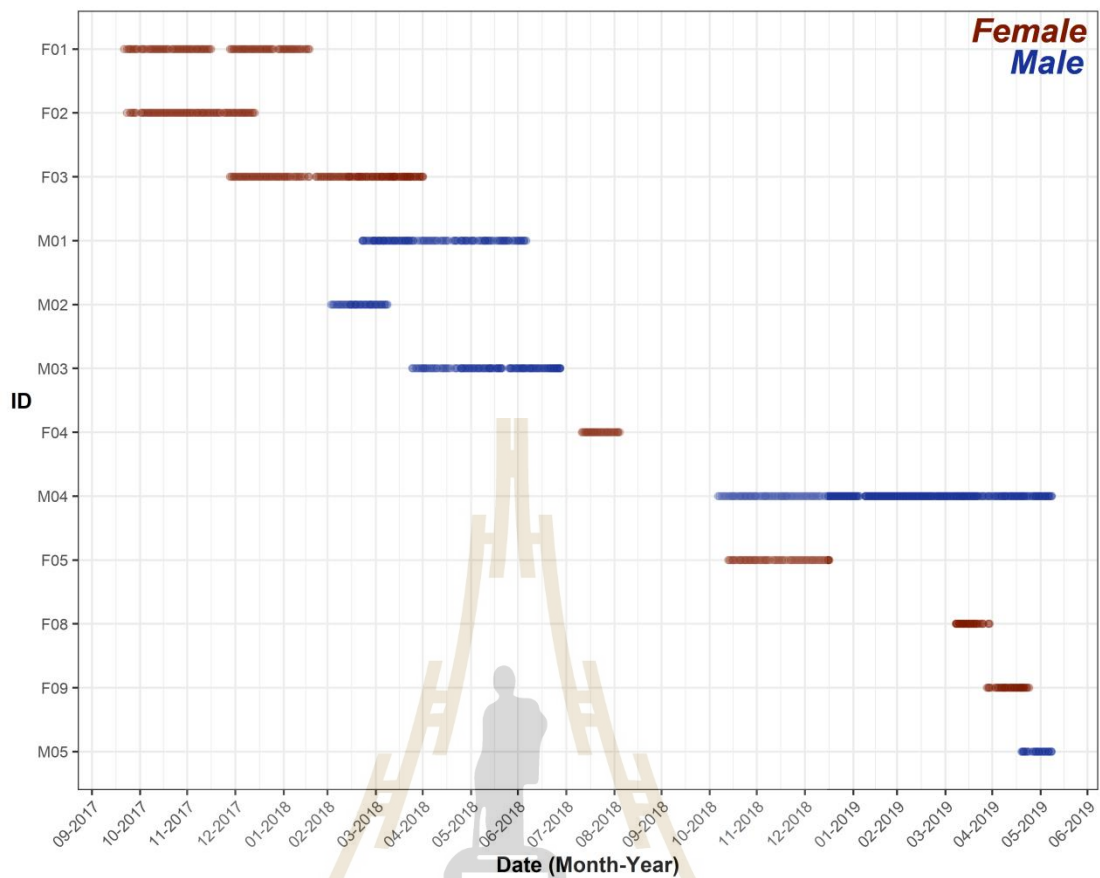


Figure 4.2 Tracking durations for our radio-telemetered individuals between October 2017 and June 2019.

We defined fixes as the number of times an individual was located, regardless of whether it had moved or not. We defined relocations as the number of times an individual had moved to a different location from its previous one. We recorded a total of 1317 fixes and 640 relocations. We recorded 907 daylight fixes and 410 night-time fixes. We recorded 780 fixes during the avian nesting season, of which 480 in daylight and 300 at night. We recorded 537 fixes during the non-nesting season, of which 427 in daylight and 110 at night.

Table 4.2 Tracking summaries of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019.

Snake ID	SVL (mm)	Tracking Period	Days Tracked	Fixes	Relocations	Time Lag (hr)	Revisit frequency	Time stationary
F01	914	21/10/2017 - 17/02/2018	119	102	72	28.22 ± 2.7	18.80 ± 3.05	2.18 ± 0.30
F02	973	23/10/2017 - 13/01/2018	82	79	40	25.18 ± 0.92	11.10 ± 0.87	5.75 ± 0.65
F03	1086	28/12/2017 - 01/05/2018	124	146	69	20.51 ± 0.9	16.60 ± 1.21	3.04 ± 0.23
M01	1046	23/03/2018 - 06/07/2018	105	134	59	18.96 ± 1.03	22.60 ± 1.62	9.59 ± 1.27
M02	1200	03/03/2018 - 08/04/2018	36	48	25	18.36 ± 1.13	2.28 ± 0.23	1.60 ± 0.18
M03	1150	24/04/2018 - 28/07/2018	95	129	83	17.81 ± 1.17	12.30 ± 2.46	1.69 ± 0.23
F04	1204	11/08/2018 - 04/09/2018	24	44	28	13.53 ± 1.02	2.21 ± 1.06	1.60 ± 0.30
M04	960	06/11/2018 - 08/06/2019	214	395	168	13.03 ± 0.5	28.10 ± 1.35	2.25 ± 0.13
F05	1205	12/11/2018 - 16/01/2019	65	73	33	21.6 ± 0.98	11.80 ± 1.15	5.73 ± 0.71

Table 4.2 (Continued).

Snake ID	SVL (mm)	Tracking Period	Days Tracked	Fixes	Relocations	Time Lag (hr)	Revisit frequency	Time stationary
F06	1114	12/11/2018 - 01/12/2018	18	25	2	18.45 ± 1.31	0.61 ± 0.08	5.49 ± 0.62
F07	1028	23/03/2019 - 30/03/2019	7	15	4	11.83 ± 2.29	1.15 ± 0.15	1.49 ± 0.09
F08	952	07/04/2019 - 29/04/2019	22	46	18	11.55 ± 1.91	2.70 ± 0.00	2.22 ± 0.34
F09	1050	27/04/2019 - 24/05/2019	27	48	16	13.9 ± 1.51	6.79 ± 1.14	3.00 ± 0.39
M05	1174	19/05/2019 - 08/06/2019	19	33	23	14.59 ± 2.19	-	0.54 ± 0.15
Female	1058 ± 35	21/10/2017 – 24/05/2019	54 ± 15	64 ± 14	31 ± 8	20.57 ± 0.64	7.97 ± 2.29	3.39 ± 0.59
Male	1106 ± 45	23/03/2018 – 08/06/2019	94 ± 34	148 ± 65	72 ± 27	15.35 ± 0.41	16.32 ± 5.71	3.13 ± 1.64
Total	1075 ± 27	21/10/2017 – 08/06/2019	68 ± 16	94 ± 26	46 ± 12	17.63 ± 0.37	10.54 ± 2.49	3.29 ± 0.66

***SVL:** Snout-to-Vent Length; **Revisit frequency:** mean number of days between revisits to a previously used location; **Time**

stationary: mean number of days spent sheltering.

4.1.3 Space Use

4.1.3.1 Horizontal movements

4.1.3.1.1 Seasonal horizontal movements

We report the movement summaries of only 12 radio-tracked individuals in Table 4.3. We chose to omit F06 and F07 because they were radio-tracked for only 18 and 7 days respectively, during which they did not move much, therefore limiting our inferences on their movements.

We define mean daily displacement (MDD) as the average Euclidean distance recorded between successive diurnal fixes (Figure 4.3). Males and females in general moved about 50 m daily. Males moved approximately two and a half times more between consecutive daylight fixes, than females (point estimate: 50.34; 95% BCrI: 8.19 – 95.8). On average, our snakes also moved over two and a half times more during the avian nesting season compared to the non-nesting season (point estimate: 39.39; 95% BCrI: 7.04 – 71.11). The MDD during the avian nesting season ($n = 9$) was 60.89 ± 12.4 m, and that for the non-nesting season ($n = 6$) was 21.5 ± 5.96 m.

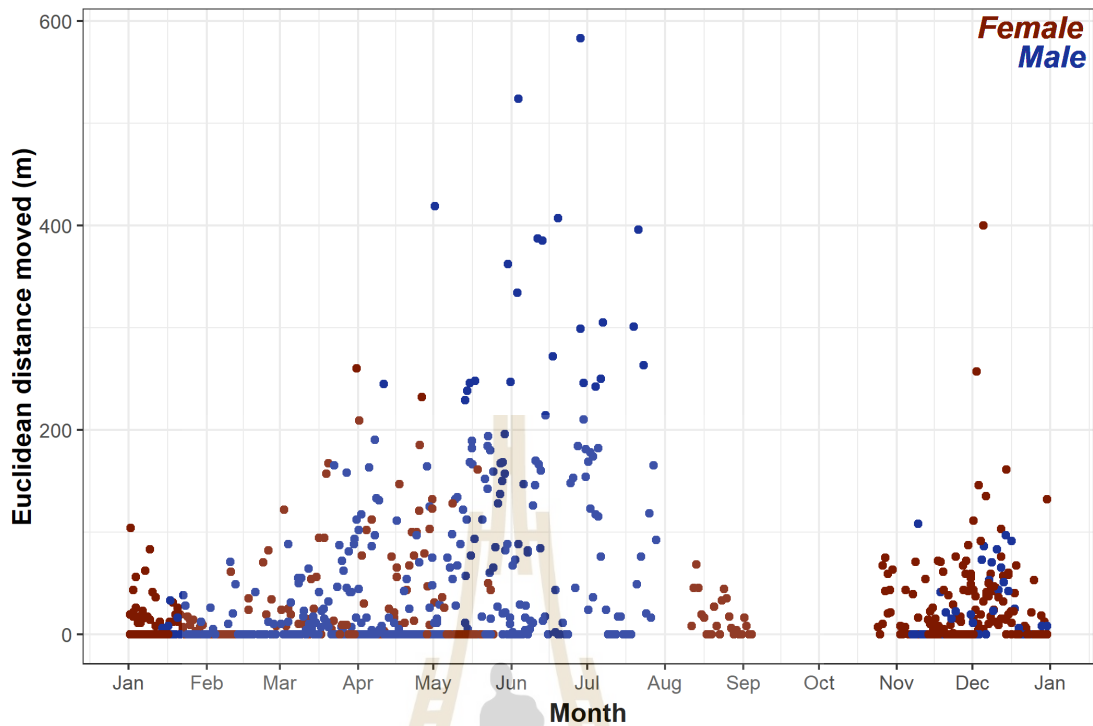


Figure 4.3 Euclidean distances between consecutive diurnal locations displayed for each month of male and female individuals radio-tracked between 21 October 2017 and 8 June 2019 at SBR.

Table 4.3 Movement summaries of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019.

ID	SVL (mm)	MDD (m)		MDD (m)	Max. Distance moved (m)	Max. Days Sta.
		Nesting	Non-nesting			
F01	914	9	25	14	161	11
F02	973	-	9	9	132	24
F03	1086	37	8	38	260	13
M01	1046	88	-	88	385	33

Table 4.3 (Continued).

ID	SVL (mm)	MDD (m) Nesting	MDD (m) Non- nesting	MDD (m)	Max. Distance moved (m)	Max. Days Sta.
F01	914	9	25	14	161	11
F02	973	-	9	9	132	24
F03	1086	37	8	38	260	13
M01	1046	88	-	88	385	33
M02	1200	46	-	46	190	4
M03	1150	115	-	115	583	4
F04	1204	-	28	28	68	3
M04	960	41	13	50	245	11
F05	1205	-	46	46	400	23
F08	952	45	-	45	402	4
F09	1050	50	-	50	167	9
M05	1174	117	-	117	524	1
F	1055 ± 44	35.3 ± 9.2	23.2 ± 7	32.9 ± 6.2	227.1 ± 49.7	12 ± 3
M	1106 ± 45	81.4 ± 16.3	13	83.2 ± 15.3	385.4 ± 76.2	11 ± 6
Total	1076 ± 31	60.9 ± 12.4	21.5 ± 6	53.8 ± 10.2	293.1 ± 47.1	12 ± 3

***SVL**: Snout-to-Vent Length; **MDD**: Mean Daily displacement.

4.1.3.1.2 Nocturnal horizontal movements

On average, our snakes seemed to move the furthest Euclidean distances from their daytime refugia by about 2000 hrs (Table 4.4), after which, they seemed to decrease their straight-line distances from their refugia, foraging around an area for the remainder of the night.

Table 4.4 Night-time movement summaries of radio-tracked *B. cyanea* from their previous daytime refugia, and predations by *B. cyanea* recorded between 2013 and 2019 via the nest monitoring cameras at SBR.

Hour	Mean Euclidean distance (m)	Max. distance moved (m)	Total Fixes	Predation events
1800	24	24	3	3
1900	26.2 ± 4.93	53	33	18
2000	49.1 ± 5.08	157	81	7
2100	54.4 ± 8.16	212	56	8
2200	68.4 ± 14.2	187	21	4
2300	43.5 ± 11.2	158	20	4
0000	48.6 ± 7.81	178	46	4
0100	73.4 ± 10.9	250	38	3
0200	109 ± 22.3	228	15	3

Table 4.4 (Continued).

Hour	Mean Euclidean distance (m)	Max. distance moved (m)	Total Fixes	Predation events
0300	70.6 ± 19.2	179	14	4
0400	60.8 ± 9.95	233	52	3
0500	72 ± 10.5	176	30	0

4.1.3.2 Vertical movements

We recorded a total of 158 confirmed height observations, of which 48 in daylight and 110 at night. All daylight observations were below 10 m (range: 0 – 10 m). For the 48 out of 907 daylight fixes, our snakes sheltered in the understory (> 0 m) at a mean height of 3.26 ± 0.48 m ($n = 31$). Our proximity and detection ability heavily biased our daytime visual confirmations, so we cannot provide any meaningful statistics on their diurnal sheltering heights. During the 862 diurnal fixes for which we could not confirm their sheltering heights, our snakes were likely located over 2 m above the ground.

At night, we observed our snakes to move between 0 and 17 m. Our snakes in general, moved closer to the ground at night (median height: 1.5 m; IQR: 3.5). Of the 110 night-time locations during the study, we confirmed 102 visual observations during the avian nesting season (Figure 4.4). During the nesting season, our snakes moved closer to the ground (median height: 1.5 m; IQR: 3) compared to the non-nesting season (median height: 3.25 m; IQR: 5.42).

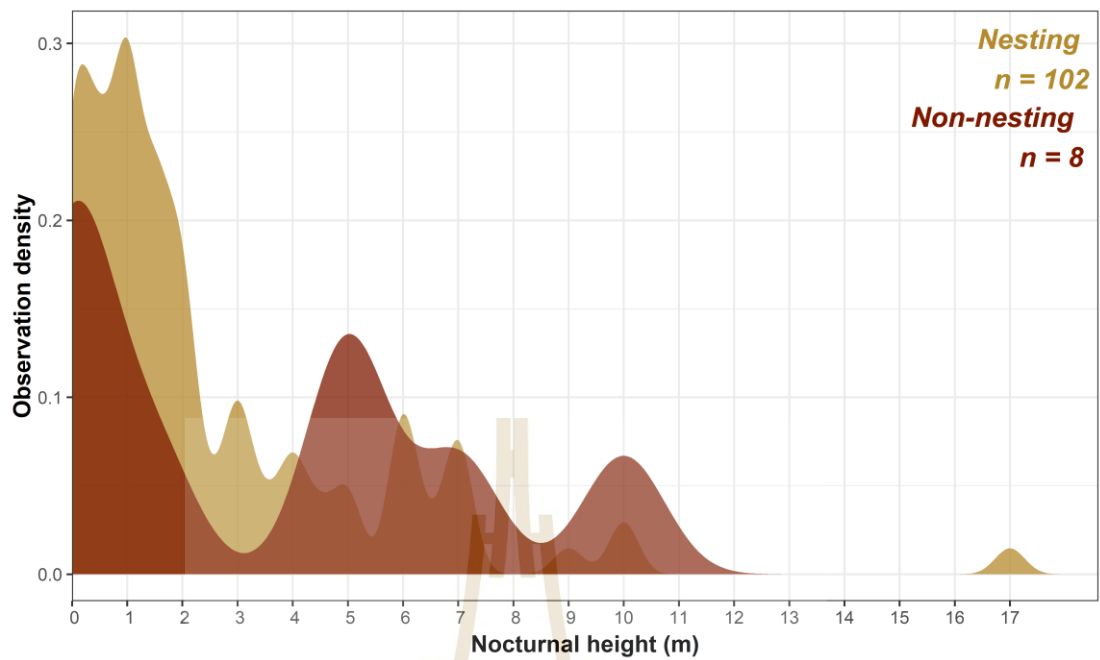


Figure 4.4 Density plot of nocturnal heights recorded for radio-telemetered *B. cyanea* during the avian nesting and non-nesting seasons at SBR.

At SBR, the researchers from KMUTT monitored 856 avian nests between 2013 and 2019. The nests monitored were located between 0 and 25 m (median height: 1.5 m; IQR: 4.51; Figure 4.5). The cameras recorded 53 nest predations by *B. cyanea* between 2013 and 2019. The nests depredated were located between 0 and 6 m (median height: 1 m; IQR: 1).

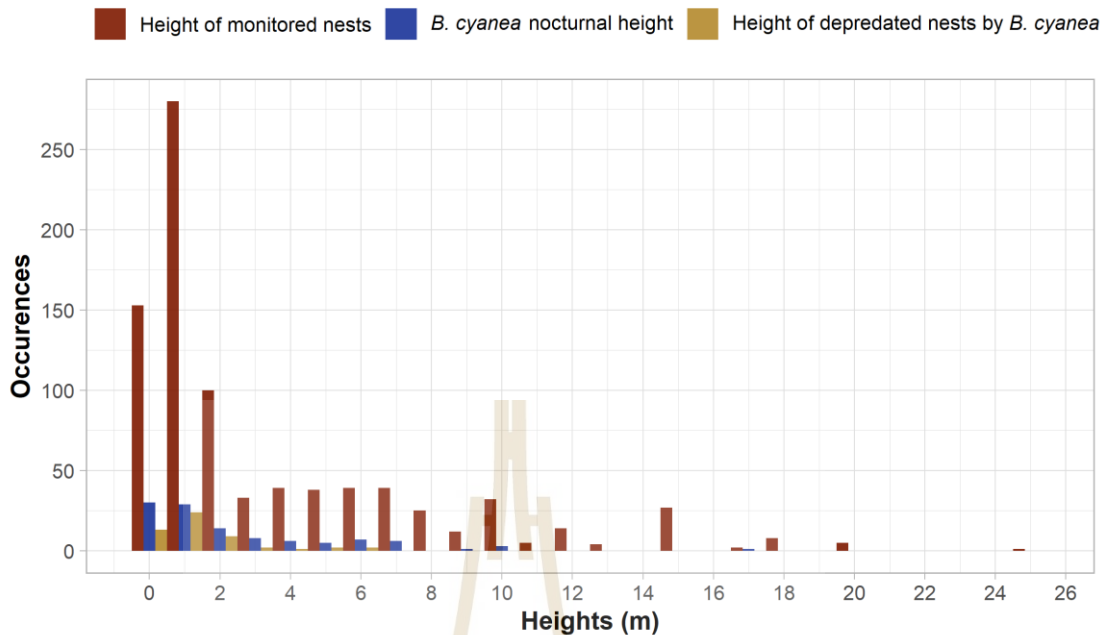


Figure 4.5 Comparison between heights of avian nests monitored and nests depredated by *B. cyanea* between 2013 and 2019, and *B. cyanea* at night during our study.

4.1.3.3 Occurrence distribution

We were unable to derive any dBBMM outputs for F06 (tracking days: 18) and F07 (tracking days: 7), given the window (9) and margin sizes (3). We made inferences based on the 95% contours to exclude exploratory movements (Table 4.5).

Our males used areas six times larger than females (point estimate: 15.09; 95% BCrI: -3.34 – 33). Because we only radio-tracked one male during the non-nesting season, we cannot make any inferences on male space use across the nesting and non-nesting seasons. Our females used areas twice as large during the nesting season compared to the non-nesting season (point estimate: 1.80; 95% BCrI: -3.43 –

7.02). In general, our snakes used areas six times larger in the nesting season than in the non-nesting season (point estimate: 9.84; 95% BCrI: -0.02 – 20).



Table 4.5 Utilization distributions of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019.

Snake ID	Days Tracked	90% dBBMM (ha)	95% dBBMM (ha)	99% dBBMM (ha)	Days Tracked Nesting	95% dBBMM Nesting (ha)	Days Tracked Non-nesting	95% dBBMM Non-nesting (ha)
F01	119	1.66	2.13	3.17	13	0.32	105	2.19
F02	82	0.89	1.48	2.70	-	-	82	1.48
F03	124	4.09	6.31	11.40	86	7.55	37	0.09
M01	105	27.48	37.57	59.78	105	37.57	-	-
M02	36	1.99	2.85	4.21	36	2.85	-	-
M03	95	18.35	24.81	39.55	95	24.81	-	-
F04	24	0.56	0.84	1.45	-	-	24	0.84
M04	214	3.97	5.29	8.74	96	6.3	117	2.73

Table 4.5 (Continued).

Snake ID	Days Tracked	90% dBBMM (ha)	95% dBBMM (ha)	99% dBBMM (ha)	Days Tracked Nesting	95% dBBMM Nesting (ha)	Days Tracked Non-nesting	95% dBBMM Non-nesting (ha)
F05	65	1.21	4.45	12.34	-	-	65	4.45
F08	22	2.52	3.84	7.20	22	3.84	-	-
F09	27	1.85	2.70	4.80	27	2.70	-	-
M05	19	15.84	20.32	29.80	19	20.32	-	-
Female	66 ± 17	1.82 ± 0.44	3.11 ± 0.72	6.15 ± 1.63	37 ± 17	3.60 ± 1.51	63 ± 15	1.81 ± 0.75
Male	94 ± 34	13.53 ± 4.73	18.17 ± 6.43	28.42 ± 10.2	70 ± 18	18.37 ± 6.33	117	2.73
Total	78 ± 17	6.7 ± 2.55	9.38 ± 3.38	15.43 ± 5.25	55 ± 13	11.81 ± 4.27	72 ± 15	1.96 ± 0.63

***dBBMM:** Dynamic Brownian bridge movement model estimate; **Nesting:** avian nesting season; **Non-nesting:** avian non-nesting season.

We illustrate the utilization distributions of our snakes during the study period within 99% dBBMM isopleth contours in Figure 4.6.

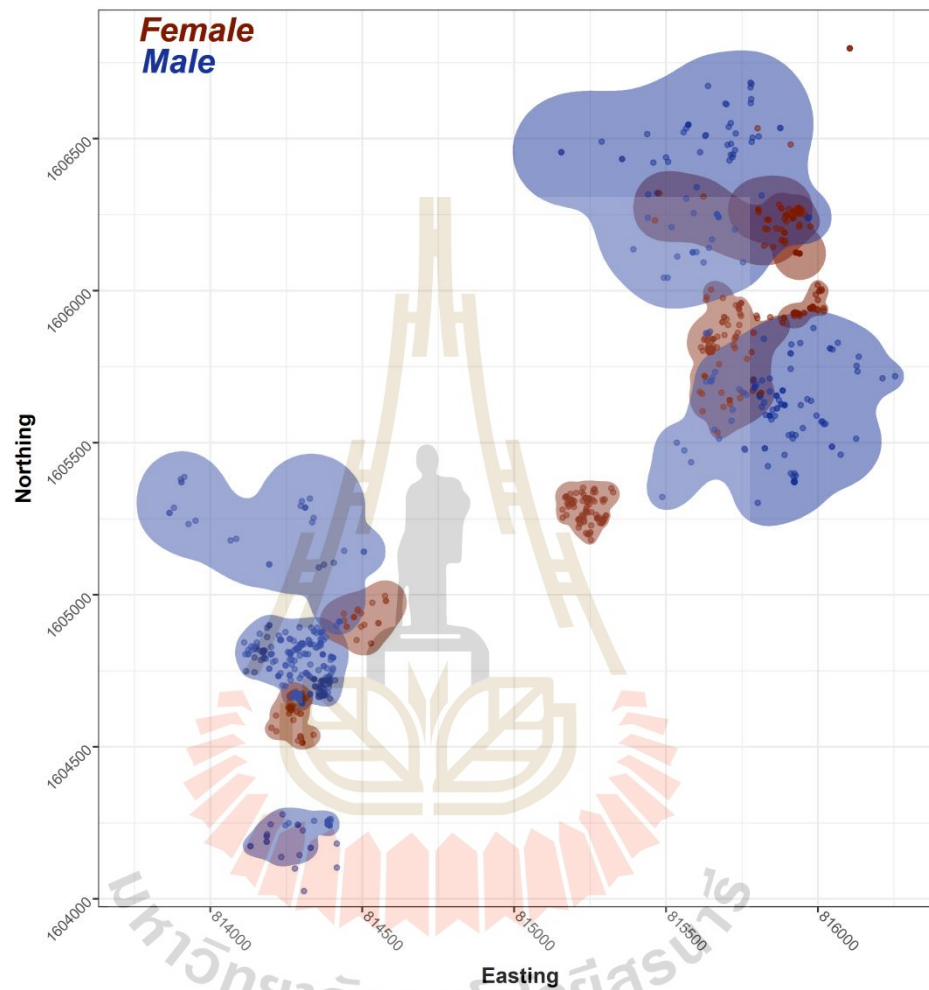


Figure 4.6 dBBMM utilization distribution map for all individuals between 21 October 2017 and 8 June 2019.

4.1.4 Activity patterns

4.1.4.1 Seasonal patterns

As a by-product of the dBBMM analyses, we interpreted the motion variance (σ_m^2) as a proxy for our snakes' foraging activity during our study period (Figure 4.7;

Table 4.6). Our males were approximately four times more active than our females (point estimate: 3.91; 95% BCrI: -0.12 – 8.16; Figure 4.8) during the study. We cannot make inferences on male activity across the nesting and non-nesting seasons, because we only radio-tracked one male during the nesting season. Our females however, were approximately 3 times more active during the nesting season compared to the non-nesting season (point estimate: 1.08; 95% BCrI: -0.52 – 2.73). In general, our snakes were over seven and a half times more active during the nesting season compared to the non-nesting season (point estimate: 3.24; 95% BCrI: 0.874 – 5.56).

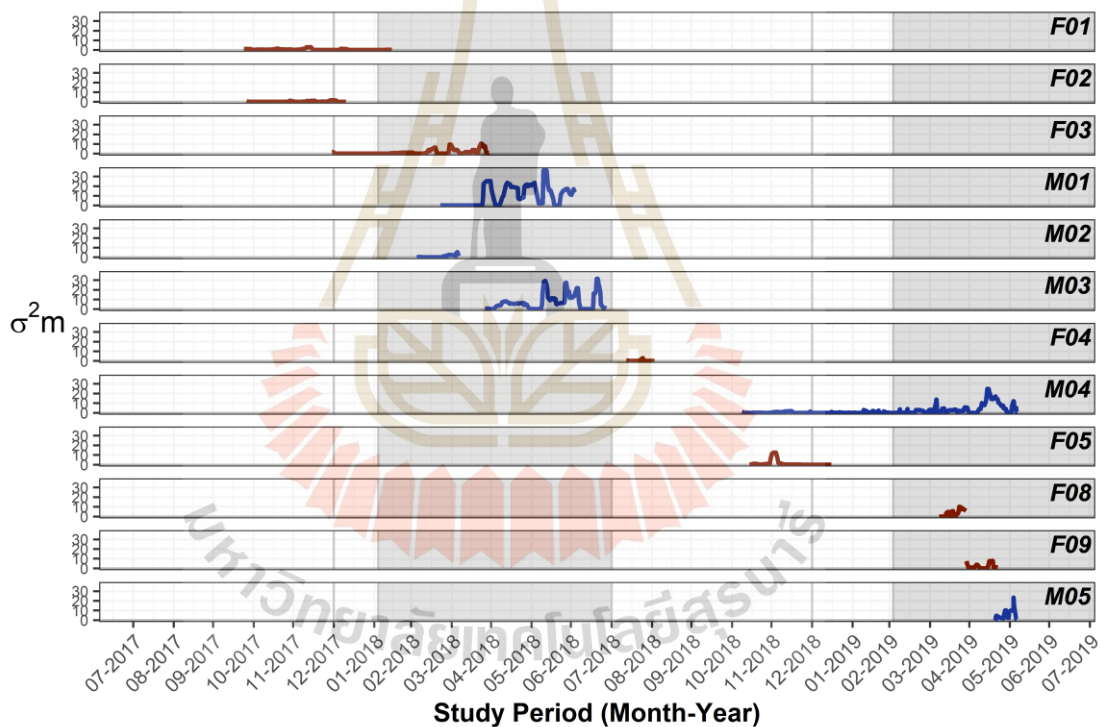


Figure 4.7 Motion variance for each radio-telemetered *B. cyanea* between 21 October 2017 and 8 June 2019 with the avian nesting seasons highlighted in grey.

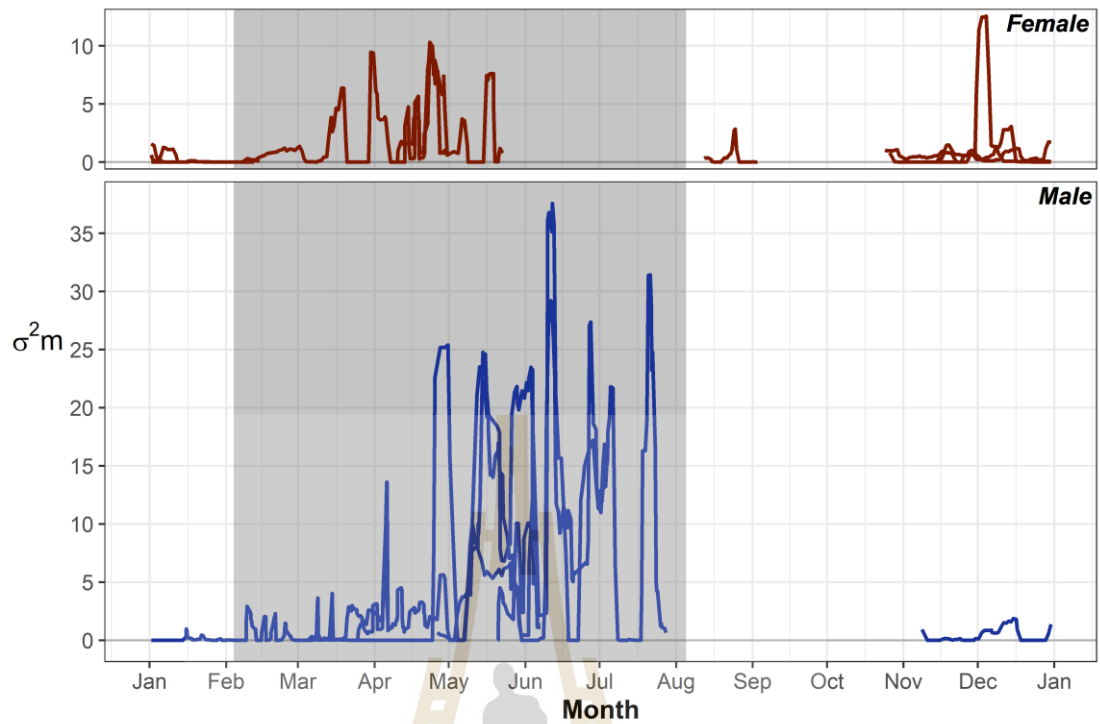


Figure 4.8 Overlaid monthly motion variance for male and female radio-telemetered *B. cyanea* during the study with avian nesting season (4 Feb – 5 Aug) in grey.

Table 4.6 Motion variance summaries of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019.

Snake ID	Days	$\sigma_m^2 \pm SE$	Days Nesting	$\sigma_m^2 \pm SE$ Nesting	Days Non-nesting	$\sigma_m^2 \pm SE$ Non-nesting
F01	119	0.55 ± 0.07	13	0.15 ± 0.04	105	0.63 ± 0.07
F02	82	0.35 ± 0.06	-	-	82	0.35 ± 0.06
F03	124	1.62 ± 0.21	86	2.17 ± 0.27	37	0.14 ± 0.07
M01	105	8.34 ± 0.91	105	8.49 ± 0.91	-	-

Table 4.6 (Continued).

Snake ID	Days	$\sigma_m^2 \pm SE$	Days Nesting	$\sigma_m^2 \pm SE$ Nesting	Days Non-nesting	$\sigma_m^2 \pm SE$ Non-nesting
M02	36	0.90 ± 0.19	36	0.90 ± 0.19	-	-
M03	95	7.77 ± 0.77	95	7.76 ± 0.77	-	-
F04	24	0.34 ± 0.10	-	-	24	0.34 ± 0.10
M04	214	2.21 ± 0.22	96	3.94 ± 0.38	117	0.36 ± 0.04
F05	65	1.16 ± 0.37	-	-	65	1.16 ± 0.37
F08	22	1.87 ± 0.50	22	1.88 ± 0.50	-	-
F09	27	2.24 ± 0.44	27	2.24 ± 0.44	-	-
M05	19	6.16 ± 0.92	19	5.89 ± 1.02	-	-
Female	66 ± 17	1.16 ± 0.29	37 ± 17	1.61 ± 0.49	63 ± 15	0.52 ± 0.18
Male	94 ± 34	5.08 ± 1.50	70 ± 18	5.42 ± 1.36	117	0.36
Total	78 ± 17	2.79 ± 0.84	55 ± 13	3.73 ± 1	72 ± 15	0.5 ± 0.15

* $\sigma_m^2 \pm SE$: Motion variance and standard error; **Nesting**: avian nesting season; **Non-nesting**: avian non-nesting season.

Our Bayesian regression model shows no evidence of autocorrelation between the model variables; the autocorrelation parameters diminish to around zero by about

25 lags. The posterior predictive check plot (Figure S4) suggests that our simulated data does not perfectly replicate our observed data, thus reducing model fit. Our Bayesian regression model results (Figure 4.9B) add support to the dispersion of motion variances during the nesting and non-nesting seasons, across males and females (conditional $R^2 = 0.327$; Figure 4.9A). In general, males and females displayed higher activity during the nesting season compared to the non-nesting season. The coefficients for activity during the non-nesting season (-0.5 ± 0.15 , 95% BCrI: $-0.35 - 0.25$), and for males (-0.11 ± 0.33 , 95% BCrI: $-0.79 - 0.54$) were both negative, suggesting lower activity. Males exhibited more individual variation in activity, compared to females – most likely because we only radio-tracked one male during the non-nesting season. The overlap between coefficients suggest that seasons and sex are not the only two factors affecting snake activity.

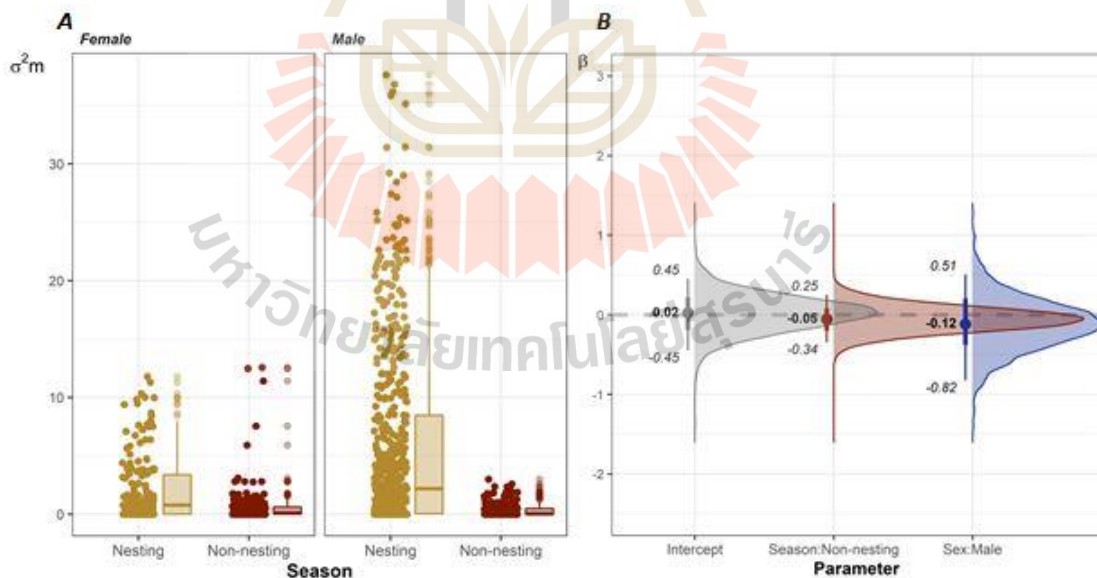


Figure 4.9 Seasonal differences in motion variance between sexes. A) Box and jittered scatter plots of seasonal motion variance values split between female and male. B) Model averaging results with point estimates and 95% Bayesian credible intervals.

The nest monitoring cameras running between 2013 and 2019 recorded most predations by *B. cyanea* between April and May (Figure 4.10). Unfortunately in 2018 and 2019, only 3 and 5 avian nests respectively had been depredated by *B. cyanea* (Figure S5). We accounted for monthly trap effort by dividing the total number of nest predations each month by the total number of exposure days each month of the nest cameras.

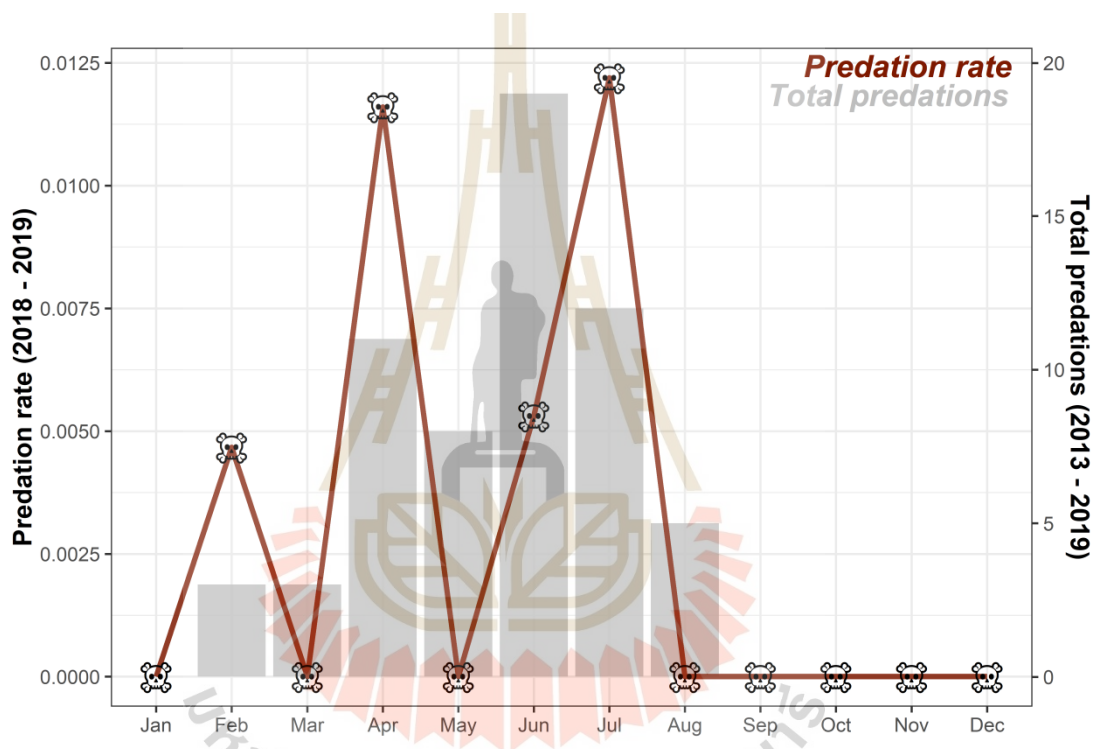


Figure 4.10 *B. cyanea* predation rate (monthly total of nests depredated over monthly total of camera exposure days) during the 2018 and 2019 avian nesting seasons superimposed on total monthly predations between 2013 and 2019.

4.1.4.2 Nocturnal patterns

Our snakes were typically observed moving throughout the night, if they had moved from their diurnal refugia by approximately four hours after sunset (Table S4).

There is considerable temporal overlap ($D_{hat} = 0.68$) between *B. cyanea* predation activity recorded by the nest monitoring cameras, and radio-tracked *B. cyanea* foraging activity (Figure 4.11). Most nest predations occurred just after dark, around 2000 hours, while foraging activity appears consistent throughout the night. We observe three peaks in snake foraging activity because we located our snakes between two to three times a night, at approximately four hour intervals.

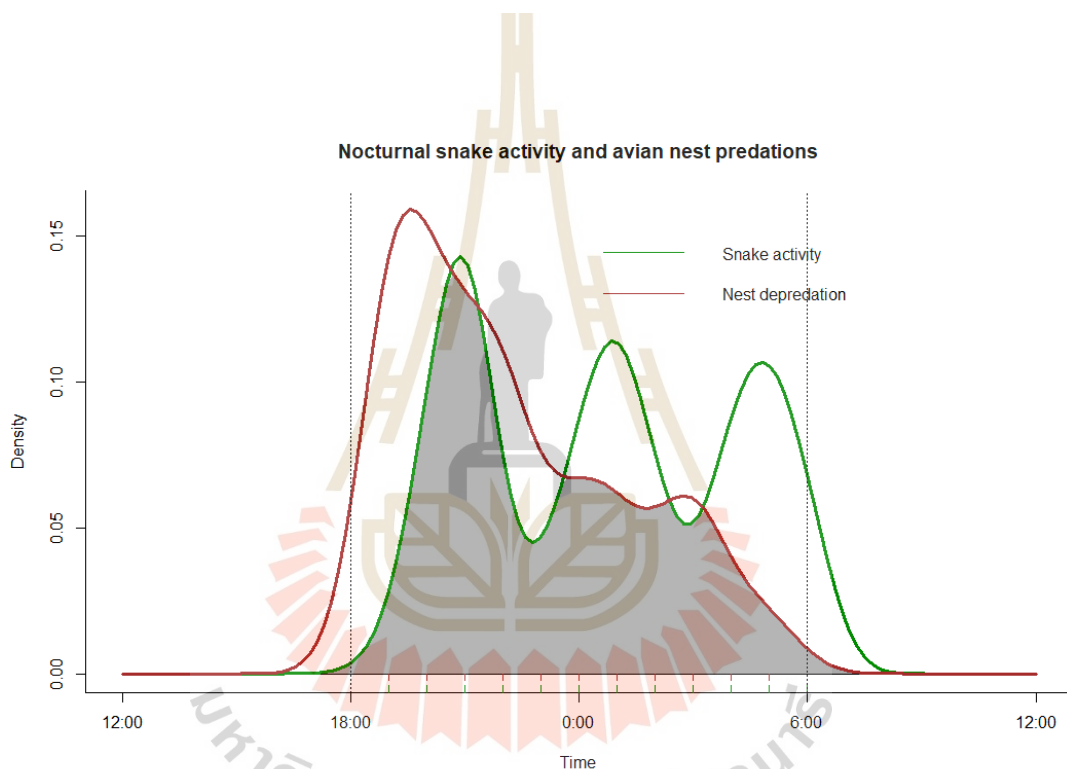


Figure 4.11 Density curves for nocturnal snake activity and avian nest predations by *B. cyanea*. The overlap coefficient of the two curves is equal to the shaded grey area intersecting the two curves.

Our snakes travelled longer distances on average at night during the avian nesting season ($n = 300$) compared to the non-nesting season ($n = 110$; Figure 4.11). Movement and stationary behaviors were significantly different during the avian

nesting and non-nesting seasons (Pearson's Chi-squared Test, p -value = 0.003). We detected our snakes moving 58% of the time ($n = 174$) during the nesting season, and 41% of the time ($n = 45$) during the non-nesting season.

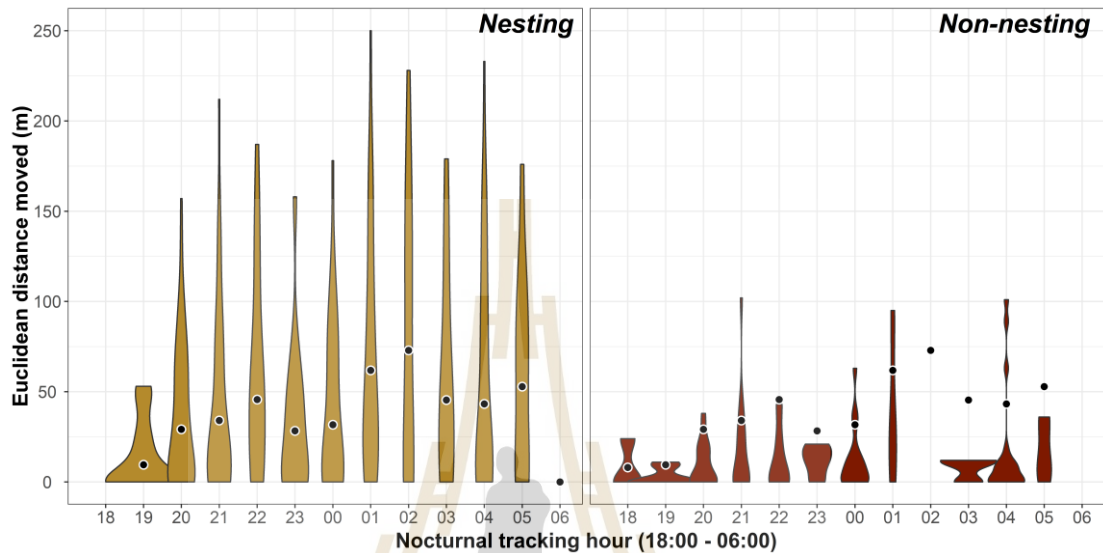


Figure 4.12 Euclidean distances between snake locations at specific nocturnal hours and their previous daytime refugia during the avian nesting season and the non-nesting season. The data illustrated are collected from individuals radio-tracked between 14 March 2018 and 3 September 2018, and between 15 January 2019 and 8 June 2019.

4.1.4.2.1 Influence of abiotic variables

In general, abiotic variables (ambient temperature, relative humidity, rainfall and moon illumination) seemed to be poor predictors of whether a snake was detected moving or not moving. We added season – nesting and non-nesting, and sex as additional variables to the single abiotic variable models to assess whether they explained the variation in our data better (Table 4.7). All models presented low correlation between predictor variables. There is a reoccurring oddness in the

normality of residuals and the homogeneity of variance plots indicating that the models are not fitting that well to our data. This is reflected in their low R^2 scores, which suggest that models do not explain much of the variation in the data. The variation might be due to other predictors we have not included in the models, or just due to random variation. We also include model performance in Table to describe how well the models fit our data based on model parsimony.

The best model for predicting nocturnal movement were the humidity and temperature model, supported by the lowest AIC_c value ($AIC_c = 505.68$). However, the relationship is weak (Figure 4.13), with low R^2 scores: 28.7% of the variation is explained by the model, of which 19.5% by the fixed effects.

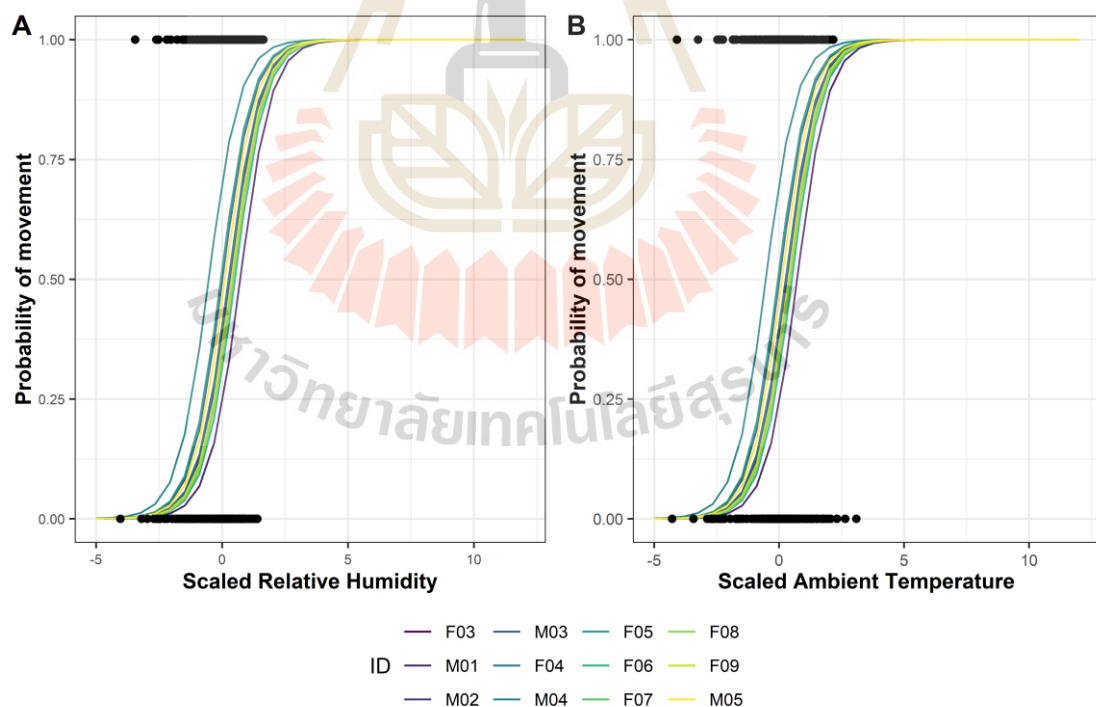


Figure 4.13 Relationship between ambient relative humidity and ambient temperature with real (black dots) and predicted values (colored lines).

Table 4.7 Candidate models assessing predictors of nocturnal movement. Models are ranked by Akaike's Information Criterion corrected for small samples (AIC_c) with degrees of freedom (df), difference in AIC_c (ΔAIC_c), model likelihood, and Akaike's weights (ω_i).

Model	R^2	AIC_c	ΔAIC_c	Model likelihood	ω_i	df	Performance score (%)
Nocturnal movement ~ Humidity + Temperature	0.287	505.68	0.000	1.000	0.916	4	63.86
Nocturnal movement ~ Humidity + Season	0.292	511.075	5.395	0.067	0.062	4	54.45
Nocturnal movement ~ Humidity + Sex + Season	0.291	513.097	7.417	0.025	0.022	5	51.84
Nocturnal movement ~ Humidity + Moon	0.198	524.609	18.929	0.000	0.000	4	39.36
Nocturnal movement ~ Humidity	0.188	524.802	19.122	0.000	0.000	3	39.14
Nocturnal movement ~ Humidity + Sex	0.186	526.079	20.398	0.000	0.000	4	37.49
Nocturnal movement ~ Moon + Season	0.268	532.773	27.092	0.000	0.000	4	47.89

Table 4.7 (Continued).

Model	R^2	AIC_c	ΔAIC_c	Model likelihood	ω_i	df	Performance score (%)
Nocturnal movement ~ Moon + Sex + Season	0.264	534.565	28.884	0.000	0.000	5	45.91
Nocturnal movement ~ Rain + Season	0.221	538.710	33.029	0.000	0.000	4	48.60
Nocturnal movement ~ Temperature + Season	0.226	539.679	33.998	0.000	0.000	4	45.48
Nocturnal movement ~ Rain + Sex + Season	0.216	540.440	34.760	0.000	0.000	5	46.44
Nocturnal movement ~ Temperature + Sex + Season	0.223	541.519	35.839	0.000	0.000	5	44.17
Nocturnal movement ~ Rain + Moon	0.123	554.747	49.067	0.000	0.000	4	26.11
Nocturnal movement ~ Moon	0.112	555.696	50.016	0.000	0.000	3	29.33
Nocturnal movement ~ Moon + Sex	0.110	555.722	50.041	0.000	0.000	4	22.99

Table 4.7 (Continued).

Model	R^2	AIC_c	ΔAIC_c	Model likelihood	ω_i	df	Performance score (%)
Nocturnal movement ~ Temperature + Moon	0.127	555.773	50.093	0.000	0.000	4	25.55
Nocturnal movement ~ Rain	0.104	556.512	50.831	0.000	0.000	3	33.41
Nocturnal movement ~ Rain + Sex	0.100	556.551	50.871	0.000	0.000	4	29.40
Nocturnal movement ~ Temperature + Rain	0.115	556.897	51.216	0.000	0.000	4	23.58
Nocturnal movement ~ Temperature + Sex	0.100	557.464	51.784	0.000	0.000	4	24.06
Nocturnal movement ~ Temperature	0.105	557.498	51.818	0.000	0.000	3	26.19

***Humidity**: Ambient relative humidity; **Temperature**: Ambient temperature; **Rain**: Daily average rainfall; **Moon**: Lunar illumination; **Season**: Avian nesting or non-nesting season; **Sex**: Male or female.

4.1.5 Refugia use

Out of the 907 diurnal locations, we determined 892 locations to be arboreal and 15 terrestrial. Unfortunately, we were only able to accurately determine refugia for 37 arboreal locations (Figure 4.14) and 11 terrestrial refugia (Figure 4.15).

Our snakes primarily sheltered above ground (> 0 m) within tree cavities and broken branches (Table 4.8). Our snakes were observed to return to previously used shelters multiple times. On the few occasions our snakes were observed on the ground, they primarily sheltered among forest litter (Table 4.8).

Table 4.8 Diurnal arboreal and terrestrial refugia used by our radio-tracked individuals.

Arboreal refugium	Total	Unique refugia	Terrestrial refugium	Total	Unique refugia
Broken trunk/branch	15	10	Forest litter	5	5
Tree cavity	12	12	Open / low vegetation	3	3
Liana	5	3	Fallen log	1	1
Foliage	3	3	Termitarium	1	1
Under bark	2	2	Manmade	1	1

***Total:** Total number of times a refugium type was used.

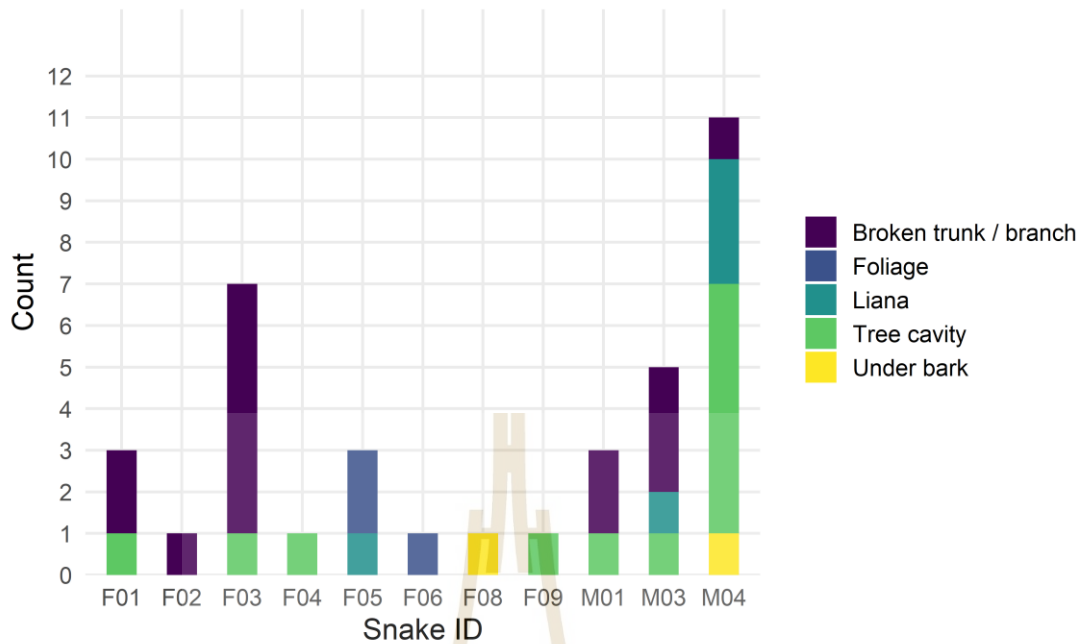


Figure 4.14 Use of different diurnal, arboreal refugia by the each individual during the study.

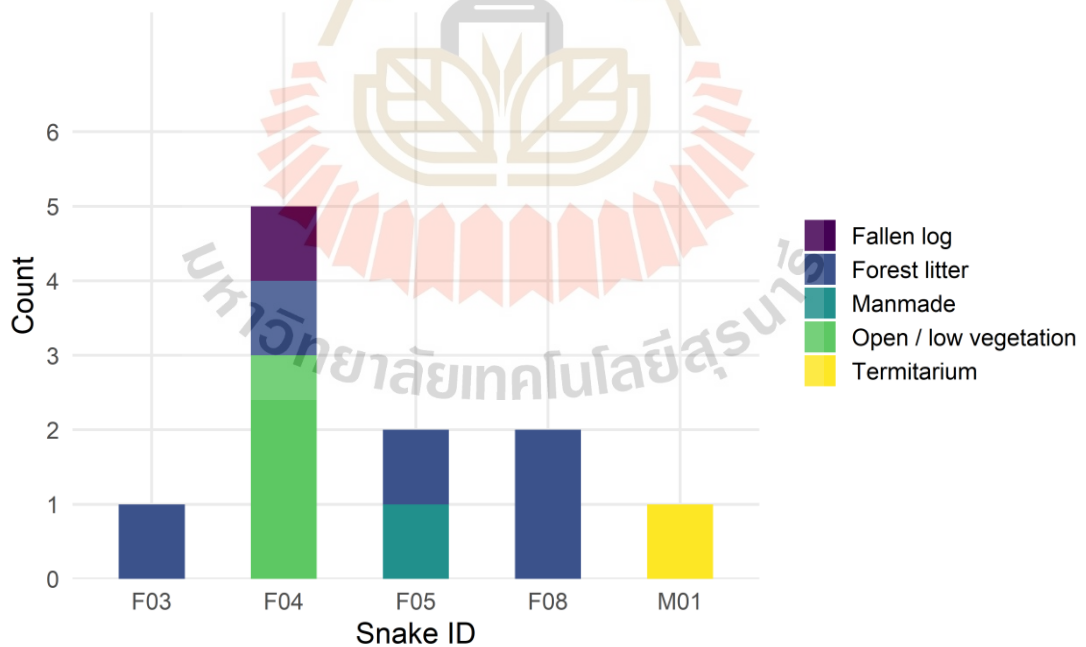


Figure 4.15 Use of different diurnal, terrestrial refugia by the each individual during the study.

4.1.6 Natural history

4.1.6.1 *Boiga cyanea* as a predator

We have recorded two visual confirmations of M04 preying upon two lizard species: *Calotes sp.* and *Acanthosaura sp.* The *Calotes sp.* predation was observed on 13 February 2019 at 00:39 during which the snake was about 5 m off the ground. The *Acanthosaura sp.* predation was observed on 21 April 2019 at 05:02 during which the snake was 2 m off the ground.

4.1.6.2 *Boiga cyanea* as prey

We had two of our radio-tracked individuals preyed upon – F08 by a King cobra *Ophiophagus hannah* on 30 April 2019 and M02 by an unidentified mammal on 8 April 2018.

4.2 Discussion

4.2.1 Space use

Our male and female radio-tracked snakes moved and used spaces differently during the study. Our males moved two and a half times farther daily, and used spaces five and a half times larger than our females. Daily movements of our snakes (53.83 ± 10.17 m) appear comparable to those reported on the congeneric *B. irregularis* by Santana-Bendix (1994; 54.5 ± 7.7 m, $n = 11$) and by Tobin *et al.* (1999; 64.4 ± 4.7 m, $n = 60$) on Guam. While the straight-line distances are comparable, we only know about *B. irregularis* movements and space use from its invasive range. These movements therefore, are likely influenced by the lack of predators, abundance of prey species, and the lack of predator-specific defenses of prey species in Guam, at the time of these studies (Fritts and Rodda, 1998). Because our native *B. cyanea*

moved similarly, it may likewise indicate fairly abundant prey within SBR. The habitat in Guam where telemetry studies were conducted – edge habitats (Santana-Bendix, 1994) and primary and secondary-growth forests with dense sub-canopy and understory vegetation (Tobin *et al.*, 1999), is broadly comparable to the vegetation in the dry evergreen forests of SBR. This might further strengthen our comparisons of the movements across the two congeneric species.

Most studies on snakes report males typically using larger spaces than females (Weatherhead *et al.*, 2002; Whitaker and Shine, 2003; Hyslop *et al.*, 2014). Previous studies on *B. irregularis* have quantified space use using Minimum Convex Polygons. These estimators are not comparable with the estimates derived from dynamic Brownian bridge movement models. The inferences we can make are therefore limited to the variations in the predictions of distribution occurrences during the study period between the 90%, 95% and 99% isopleth contours. On average, the 90% and 99% contours are one and a half times smaller and bigger respectively of the 95% contour. Had we located our snakes at regular intervals every night, rather than every alternate night, we might have estimated more fine scale locations and distribution occurrences during the study period. We chose to limit the number of night-time fixes as we did not want the constant presence and necessary light use by observers to affect snake movement behaviour. We felt that alternate night fixes maintained a good balance of regular locations and movement data, whilst allowing for natural observations and unbiased behavior. This is supported by simulations run on several reptile species, indicating reduced tracking intensity from every night to alternate nights, can still provide accurate space use estimates (Silva *et al.*, 2020).

Our snakes typically ($\approx 95\%$ daylight fixes) sheltered higher up in the canopy during the day and descended closer to the ground at night to forage. Our observations are similar to those reported on *B. irregularis* (Rodda *et al.*, 1992) and *B. nigriceps* (Fujishima *et al.*, 2020; In press). Rodda (1992) observed most *B. irregularis* ($\approx 77\%$) foraging within 3 m off the ground, suggesting that this might reflect active foraging of quiescent prey species in the understory. At SBR, the nest predation records reveal that *B. cyanea* primarily depredated White-rumped Shama *Copsychus malabaricus* and Scaly-crowned Babbler *Malacopteron cinereum* nests. White-rumped Shammas typically nest at around 2.32 m and Scaly-crowned Babblers at 0.98 m (Somsiri *et al.*, 2020). Our snakes also primarily moved within 3 m off the ground (median: 1.5 m; IQR: 3) during the avian nesting season. Similar to *B. irregularis*, this might reflect active foraging of understory nesting birds. Additionally, since White-rumped Shammas are open-cavity nesters (Khamcha *et al.*, 2018a), the head morphology and gape size (Shine, 1991) of *B. cyanea* might be particularly adapted to depredating these cavity nesters.

4.2.2 Activity patterns

Our snakes moved approximately seven times farther and more frequently during the avian nesting season compared to the non-nesting season. The nesting season spans from February to August and overlaps with the wet season, which spans from May to October. Khamcha *et al.* (2018a) suggested that the correlation between nest predations by *B. cyanea* and rainfall might be due to increased *B. cyanea* activity – which our data seem to also support. The rains might trigger increases in invertebrate and herpetofauna activity, which in turn might trigger activity increases

in higher trophic levels (Saenz *et al.*, 2006; Illera and Diaz, 2008). Higher activity of prey species might increase their detectability by predators. Multiple biotic (Kotler *et al.*, 1992; Horesh *et al.*, 2017) and abiotic factors might be simultaneously driving increases in *B. cyanea* activity during the avian nesting season at SBR. Tobin *et al.* (1999) however observed no difference in the congeneric *B. irregularis*' activity between the rainy and dry seasons on Guam.

Differences in activity between the nesting and non-nesting seasons, were more pronounced in males than in females. This might be because we only radio-tracked one male during the non-nesting season and we do not know whether its activity reflects that of the general male population at SBR. Higher male activity during the avian nesting season at SBR, might also be associated with *B. cyanea* mating season (Bulian and Bannasan, 1999). Typically, during the snake mating seasons, males are known to display higher activity.

We did not detect any movement behaviour from our snakes during daylight hours throughout our study, suggesting that *B. cyanea* are primarily nocturnal. Bulian and Bannasan (1999) report similar observations with regards to movement behaviour, but has observed individuals copulating during the early hours of daylight, around 0700 hours. Only on one occasion – 20 May 2019, we located our male M05 and female F09 within the same shelter during our daylight fix. *B. cyanea* might copulating during daylight hours, but restricts movements to the night. *B. cyanea* appear to start their foraging activity at dusk, just after sunset, and end it at dawn, just before sunrise. *B. irregularis* on Guam appear to display similar nocturnal foraging patterns (Fritts and Chiszar, 1999; Lardner *et al.*, 2014).

Our data suggest that our snakes were likely to move throughout the night if they were detected moving within 4 hours after sunset. This activity pattern might indirectly imply that *B. cyanea* are primarily active foragers rather than ambush predators. If they are hunting for relatively stationary prey, such as eggs and nestlings, an active foraging strategy might be more efficient. *B. irregularis* exhibit a combination of the two hunting modes (Rodda *et al.*, 1992); *B. cyanea* might also display both modes, but our tracking regime might have failed to infer them.

We did not observe any avian nest predations by our study individuals during their radio-telemetry. This could suggest that our individuals might have depredated avian nests when we were not locating them, or they had not depredated avian nests at all. The nest monitoring cameras recorded only 3 and 5 nest predations by *B. cyanea* during the nesting seasons in 2018 and 2019 respectively. The low number of predations might be a result of changes in avian nesting ecology or changes in *B. cyanea* populations or foraging – for example, low encounter rates of active avian nests, active selection of prey sizes or gape limitations (Shine, 1991). Additional reasons might include lower nest detection rates or lower field effort.

Active foraging increases the probability of encountering a high diversity of sedentary and active prey species (Beaupre and Montgomery, 2007); this suggests that our *B. cyanea* might have still fed frequently on smaller, sparse and more abundant prey items like forest lizards (*Calotes sp.*), geckos or frogs (Bulian and Bannasan, 1999).

The nest monitoring cameras recorded most predations by *B. cyanea* during the early hours after sunset, at around 1900 hours. The ornithologists observed individual *B. cyanea* depredating single nest contents from the same nest on consecutive nights, until depredating all of the eggs and fledglings (Personal

communication, Angkaew). This suggests that the predators were likely to select refugia close to the birds' nests to maximize foraging success and minimize predation risk. Our data suggest that *B. cyanea* can travel an average of 26.2 ± 4.93 m, and a maximum of 53 m by 1900 hours. Fledglings and avian eggs might be effective prey items for *B. cyanea* (Pleguezuelos *et al.*, 2007): the faster *B. cyanea* are able to subdue and ingest prey, the faster they are able to return to their refugia, thus reducing their exposure to potential predators (Mullin and Cooper, 1998).



CHAPTER V

CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

This study is the first to explore space use and activity patterns of a regionally important snake predator, in relation to its prey. We quantified *B. cyanea* foraging activity during our study period assuming their movements, particularly during the avian nesting season, were related to foraging rather than other biological functions. For this reason, our findings regarding *B. cyanea* foraging behaviour must not be overstated. We must also be cautious in drawing inferences regarding space use and activity across sexes and across the avian nesting and non-nesting seasons, because of possible sources of sampling biases, as detailed in the STRANGE framework (Webster and Rutz, 2020).

Most study individuals were caught opportunistically during the study period, making our sample non-random and possibly not representative of the population at SBR. We chose to locate our snakes at night on alternate nights to compensate for our push for nocturnal, visual observations. Our presence undoubtedly caused behavioural changes in our snakes despite our efforts to minimize disturbance. Additionally, the avian nesting seasons in 2018 and 2019 witnessed lower nest predations by *B. cyanea* compared to previous years. Reasons for these natural changes in responsiveness are unknown. Therefore, the association between *B. cyanea* activity and avian nest

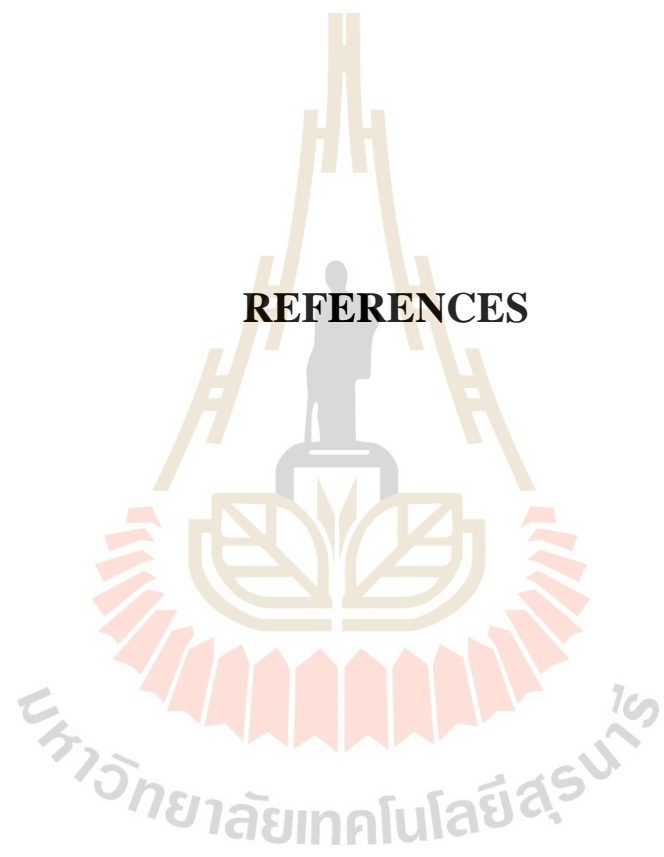
predations by *B. cyanea* during our study period might not reflect those of previous years.

In order to account for these limitations, we tried to use analyses appropriate for the data collected. Our findings suggest that our individuals used space and moved differently across sexes and across seasons.

Future research exploring the foraging ecology of *B. cyanea* should attempt to expand the sample size in order to reduce bias and increase local population representation. Khamcha *et al.* (2018a) reported higher rates of nest predation by *B. cyanea* towards forest interiors compared to forest edges. Future studies should attempt to sample individuals across a gradient of distances from forest edges, to explore edge effects on *B. cyanea* foraging. Being nocturnal, generalists, and exceptionally good climbers, *B. cyanea* can exploit multiple levels within the forest canopy, giving them a predatory advantage over other sympatric snakes. This highlights the need to explore the diet of *B. cyanea* to quantify what proportion avian eggs and nestlings constitute at SBR. Furthermore, studying *B. cyanea* patterns of prey selection – whether active or opportunistic, and how they locate avian nests could help refine our understanding of these predator – prey interactions.

Bird populations at SBR face significant predation pressure not only from nocturnal snakes, but also from the Northern Pig-tailed Macaque *Macaca leonina* (Kaisin *et al.*, 2018; Khamcha *et al.*, 2018a). Understanding the combined effect of these two major sympatric predators on nest survival could help develop management strategies to increase nest success. Lastly, our findings might be applicable to other parts of Thailand, where *B. cyanea* or its congeners might be important nest predators, especially of bird species of conservation concern (Donald *et al.*, 2009).

REFERENCES



REFERENCES

- Akaike, H. (1973). Information Theory and an Extension of the Maximum Likelihood Principle. In: Petrov, B. N., and Csaki, F., Eds., **International Symposium on Information Theory**. Pages: 267-281.
- Amelon, S. K., Dalton, D. C., Millspaugh, J. J., and Wolf, S. A. (2009). Radiotelemetry: techniques and analysis. In: Kunz, T. H.; Parsons, S. Eds., *Ecological and behavioral methods for the study of bats*. Pages: 57-77. Johns Hopkins University Press, Baltimore.
- Andrusiak, L., Walters, E. L., Eliot, T., and Simpsons, K. (1998). Wildlife Radiotelemetry. Standards for Components of British Columbia's Biodiversity No. 5. The Province of British Columbia. Published by the Resources Inventory Committee.
- Angkaew, R., Sankamethawee, W., Pierce, A. J., Savini, T., and Gale, G. A. (2019). Nesting near road edges improves nest success and post-fledging survival of White-rumped Shamas (*Copsychus malabaricus*) in northeastern Thailand. **The Condor**. 121: 1-15.
- Baraldi, A. N., and Enders, C. K. (2010). An introduction to modern missing data analyses. **Journal of School Psychology**. 48: 5-37.
- Barbosa, P., and Castellanos, I. (2005). *Ecology of Predator-Prey Interactions*. Oxford University Press, Oxford and New York.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. **Journal of Statistical Software**. 67(1): 1-48.

- Beaupre, S., and Montgomery, C. E. (2007). The meaning and consequences of foraging mode in snakes. In: *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge University Press.
- Berkovitz, B., and Shellis, P. (2017). Reptiles 2: Snakes. In: *The Teeth of Non-Mammalian Vertebrates*. Pages: 201–224. Elsevier.
- Bivand, R., and Rundel, C. (2020). rgeos: Interface to Geometry Engine - Open Source ('GEOS'). [On-line]. Available: <https://CRAN.R-project.org/package=rgeos>.
- Blouin-Demers, G., and Weatherhead, P. J. (2001a). An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes (*Elaphe obsoleta obsoleta*). **Journal of Animal Ecology**. 70: 1006-1013.
- Blouin-Demers, G., and Weatherhead, P. J. (2001b). Habitat Use by Black Rat Snakes (*Elaphe obsoleta obsoleta*) in Fragmented Forests. **Ecology**. 82: 2882-2896.
- Boback, S. M., Nafus, M. G., Yackel Adams, A. A., and Reed, R. N. (2020). Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. **Ecosphere**. 11.
- Bracis, C., Bildstein, K., and Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. **Ecography**. 41(11) : 1801-1811.
- Bulian, J., and Bannasan, T. T. A. (1999). Observations on *Boiga cyanea*. **Litteratura Serpenti**. 19: 175-183.
- Bürkner, P. C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. **The R Journal**. 10(1): 395-411.

- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. **Ecological Modelling**. 197: 516-519.
- Chan-ard, T., Parr, J. W. K., and Nabhitabhata, J. (2015). A Field Guide to the Reptiles of Thailand. Pages: 208-211.
- Cox, M. J., Hoover, M. F., Chanhom, L., and Thirakhupt, K. (2012). The Snakes of Thailand. Pages: 74, 101-106.
- Cox, M. J., van Dijk, P. P., Nabhitabhata, J., and Thirakhupt, K. (1998). A Photographic Guide to Snakes and Other Reptiles of Thailand and Southeast Asia. Pages: 74.
- Christian, K., Webb, J. K., Schultz, T., and Green, B. (2007). Effects of Seasonal Variation in Prey Abundance on Field Metabolism, Water Flux, and Activity of a Tropical Ambush Foraging Snake. **Physiological and Biochemical Zoology**. 80: 522-533.
- Conry, P. J. (1988). High Nest Predation by Brown Tree Snakes on Guam. **The Condor**. 90: 478-482.
- Daltry, J. C., Ross, T., Thorpe, R. S., and Wüster, W. (1998). Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. **Ecography**. 21: 25-34.
- DeGregorio, B. A., Chiavacci, S. J., Weatherhead, P. J., Willson, J. D., Benson, T. J., and Sperry, J. H. (2014). Snake predation on North American bird nests: culprits, patterns and future directions. **Journal of Avian Biology**. 45: 325-333.

- DeGregorio, B. A., Sperry, J. H., Ward, M. P., and Weatherhead, P. J. (2015). Wait Until Dark? Daily Activity Patterns and Nest Predation by Snakes. **Ethology**. 121: 1225-1234.
- DeGregorio, B. A., Weatherhead, P. J., and Sperry, J. H. (2016b). Ecology and predation behaviour of Corn snakes (*Pantherophis guttatus*) on avian nests. **Herpetological Conservation and Biology**. 11: 150-159.
- DeGregorio, B. A., Weatherhead, P. J., Ward, M. P., and Sperry, J. H. (2016a). Do seasonal patterns of rat snake (*Pantherophis obsoletus*) and black racer (*Coluber constrictor*) activity predict avian nest predation?. **Ecology and Evolution**. 6: 2034-2043.
- Donald, P. F., Aratrakorn, S., Win Htun, T., Eames, J. C., Hla, H., Thunhikorn, S., Sribua-Rod, K., Tinun, P., Aung, S. M., Zaw, S. M., and Buchanan, G. M. (2009). Population, distribution, habitat use and breeding of Gurney's Pitta *Pitta gurneyi* in Myanmar and Thailand. **Bird Conservation International**. 19: 353-366.
- Dunnington, D. (2020). ggspatial: Spatial Data Framework for ggplot2. [On-line]. Available: <https://CRAN.R-project.org/package=ggspatial>.
- Fritts, T. H., and Chiszar, D. (1999). Snakes on electrical transmission lines: patterns, causes, and strategies for reducing electrical outages due to snakes. In: Rodda, G. H., Sawai, Y., Chiszar, D., and Tanaka, H., Eds., Problem snake management: the Habu and the Brown Treesnake. Pages 89-103. Cornell University Press, Ithaca, New York.

- Fritts, T. H., and Rodda, G. H. (1998). The role of introduced species in the degradation of island ecosystems: A Case History of Guam. **Annual Review of Ecology and Systematics**. 29: 113-140.
- Gabry, J., Mahr, T. (2020). bayesplot: Plotting for Bayesian Models. [On-line]. Available: <https://mc-stan.org/bayesplot>.
- Garnier, S. (2018). viridis: Default Color Maps from 'matplotlib'. [On-line]. Available: <https://CRAN.R-project.org/package=viridis>.
- Gelman, A., and Rubin, D. B. (1992). Inference from Iterative Simulation Using Multiple Sequences. **Statistical Science**. 7: 457-472.
- Gelman A., and Su, Y. S. (2020). arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. [On-line]. Available: <https://CRAN.R-project.org/package=arm>.
- Greene, H. W. (1997). Snakes: The evolution of mystery in nature. University of California Press, London.
- Grolemund G., Wickham, H. (2011). Dates and Times Made Easy with lubridate. **Journal of Statistical Software**. 40(3): 1-25.
- Harris, A. (2012). astroFns: Astronomy: time and position functions, misc. utilities. [On-line]. Available: <https://CRAN.R-project.org/package=astroFns>.
- Hetherington, T. E., Coupe, B., Perry, G., Anderson, N. L., and Williams, J. B. (2006). Diurnal refuge-site selection by Brown Treesnakes (*Boiga irregularis*) on Guam. **Amphibia-Reptilia**. 0: 1-4.
- Horesh, S. J. A., Sivan, J., Rosenstrauch, A., Tesler, I., Degen, A. A., and Kam, M. (2017). Seasonal biotic and abiotic factors affecting hunting strategy in free-

- living Saharan sand vipers, *Cerastes vipera*. **Behavioural Processes**. 135: 40-44.
- Hsiang, A. Y., Field, D. J., Webster, T. H., Behlke, A. D., Davis, M. B., Racicot, R. A., and Gauthier, J. A. (2015). The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. **BMC Evolutionary Biology**. 15: 87-109.
- Hurvich, C. M., and Tsai, C. I. (1989). Regression and time series model selection in small samples. **Biometrika**. 76: 297-307.
- Hyslop, N. L., Meyers, J. M., Cooper, R. J., and Stevenson, D. J. (2014). Effects of Body Size and Sex of *Drymarchon couperi* (Eastern Indigo Snake) on Habitat Use, Movements, and Home Range Size in Georgia. **The Journal of Wildlife Management**. 78: 101-111.
- Illera, J. C., and Diaz, M. (2006). Reproduction in an endemic bird of a semiarid island: a food-mediated process. **Journal of Avian Biology**. 37: 447-456.
- Kaisin, O., Gazagne, E., Savini, T., Huynen, M. C., and Brotcorne, F. (2018). Foraging strategies underlying bird egg predation by macaques: A study using artificial nests. **American Journal of Primatology**. 80(11): e22916.
- Kassambara, A. (2020). ggpubr: 'ggplot2' Based Publication Ready Plots. [On-line]. Available: <https://CRAN.R-project.org/package=ggpubr>.
- Kay, M. (2020). tidybayes: Tidy Data and Geoms for Bayesian Models. [On-line]. Available: <https://doi.org/10.5281/zenodo.1308151>.
- Khamcha, D., Corlett, R. T., Powell, L. A., Savini, T., Lynam, A. J., and Gale, G. A. (2018b). Road induced edge effects on a forest bird community in tropical Asia. **Avian Research**. 9: 20-33.

- Khamcha, D., Powell, L. A., and Gale, G. A. (2018a). Effects of roadside edge on nest predators and nest survival of Asian tropical forest birds. **Global Ecology and Conservation**. 16: e00450.
- Knierim, T. K., Marshall, B. M., Hayes, L., Suwanwaree, P., and Strine, C. T. (2019). The movements and habitat preferences of a Malayan krait (*Bungarus candidus*) in an agrarian landscape. **Herpetological Bulletin**. 143: 30-33.
- Koenig, S. E., Wunderle Jr, J. M., and Enkerlin-Hoeflich, E. C. (2007). Vines and canopy contact: a route for snake predation on parrot nests. **Bird Conservation International**. 17: 79-91.
- Kotler, B. P., Blaustein, L., and Brown, J. S. (1992). Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. **Annales Zoologici Fennici**. 29: 199-206.
- Kranstauber B., Smolla, M., and Scharf, A. K. (2020). move: Visualizing and Analyzing Animal Track Data. [On-line]. Available: <https://CRAN.R-project.org/package=move>.
- Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M., and Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement: The dynamic Brownian bridge movement model. **Journal of Animal Ecology**. 81: 738-746.
- Lardner, B., Savidge, J. A., Reed, R. N., and Rodda, G. H. (2014). Movements and Activity of Juvenile Brown Treesnakes (*Boiga irregularis*). **Copeia**. 2014: 428-436.
- Lemon, J. (2006). Plotrix: a package in the red light district of R. **R-News**. 6(4): 8-12.

- Lillywhite, H. B., and Brischoux, F. (2012). Is it better in the moonlight? Nocturnal activity of insular cottonmouth snakes increases with lunar light levels: Cottonmouth activity and moonlight. **Journal of Zoology**. 286: 194-199.
- Lima, S. L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. **BioScience**. 48: 25-34.
- Little, R. J. A. (1988). A Test of Missing Completely at Random for Multivariate Data with Missing Values. **Journal of the American Statistical Association**. 83: 1198-1202.
- Lüdecke, D., Makowski, D., Waggoner, P., and Patil, I. (2020). Performance: Assessment of Regression Models Performance. [On-line]. Available: <https://CRAN.R-project.org/package=performance>.
- Mackessy, S. P. (2002). Biochemistry and pharmacology of Colubrid snake venoms. **Journal of Toxicology: Toxin Reviews**. 21: 43-83.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. (2019). cluster: Cluster Analysis Basics and Extensions. [On-line]. Available: <https://svn.r-project.org/R-packages/trunk/cluster>.
- Marshall, B. M., Crane, M., Silva, I., Strine, C. T., Jones, M. D., Hodges, C. W., Suwanwaree, P., Artchawakom, T., Waengsothorn, S., and Goode, M. (2020). No room to roam: King Cobras reduce movement in agriculture. **Movement Ecology**. 8: 33-47.
- Martin, T. E. (1993). Nest Predation and Nest Sites. **BioScience**. 43: 523-532.
- Menezes, J. C. T., and Marini, M. Â. (2017). Predators of bird nests in the Neotropics: a review. **Journal of Field Ornithology**. 88: 99-114.

- Meredith, M. (2020). wqid: Quick and Dirty Estimates for Wildlife Populations. [Online]. Available: <https://CRAN.R-project.org/package=wqid>.
- Millsbaugh, J. J., and Marzluff, J. M. (2001). Radio Tracking and Animal Populations. Academic Press, London.
- Mullin, S. J., and Cooper, R. J. (1998). The Foraging Ecology of the Gray Rat Snake (*Elaphe obsoleta spiloides*) - Visual Stimuli Facilitate Location of Arboreal Prey. **The American Midland Naturalist**. 140: 397-401.
- Mullin, S. J., and Seigel, R. A., editors. (2009). Snakes: ecology and conservation. Cornell University Press, Ithaca.
- Pedersen, T. L., and Cramer, F. (2020). scico: Colour Palettes Based on the Scientific Colour-Maps. [Online]. Available: <https://CRAN.R-project.org/package=scico>.
- Peterson R. A. (2019). Ordered quantile normalization: a semiparametric transformation built for the cross-validation era. **Journal of Applied Statistics**. 1-16.
- Pierce, A. J., and Pobprasert, K. (2007). A portable system for continuous monitoring of bird nests using digital video recorders. **Journal of Field Ornithology**. 78: 322-328.
- Pierce, A. J., and Pobprasert, K. (2013). Nest predators of southeast Asian evergreen forest birds identified through continuous video recording. **Ibis**. 155: 419-423.
- Pierce, A. J., Sankamethawee, W., Powell, L. A., and Gale, G. A. (2020). Patterns of nesting and nest success in an evergreen forest in Southeast Asia. **Emu - Austral Ornithology**. 120: 46-55.

- Pleguezuelos, J. M., Fernández-Cardenete, J. R., Honrubia, S., Feriche, M., and Villafranca, C. (2007). Correlates between morphology, diet and foraging mode in the Ladder Snake *Rhinechis scalaris* (Schinz, 1822). **Contributions to Zoology**. 76: 179-186.
- R Core Team. (2020). R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. [On-line]. Available: <https://www.r-project.org>.
- R Studio Team. (2020). RStudio: integrated development environment for R. Boston: RStudio, Inc. [On-line]. Available: <http://www.rstudio.com/>.
- Reinert, H. K., and Cundall, D. (1982). An Improved Surgical Implantation Method for Radio-Tracking Snakes. **Copeia**. 1982: 702-705.
- Remeš, V., Matysioková, B., and Cockburn, A. (2012). Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. **Journal of Avian Biology**. 43: 435-444.
- Ribeiro-Silva, L., Perrella, D. F., Biagolini-Jr, C., Zima, P., Piratelli, A. J., Schlindwein, M., Galetti-Jr, P., and Francisco, M. (2018). Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment. **Zoologia**. 35: 1-8.
- Ridout M., and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. **Journal of Agricultural, Biological, and Environmental Statistics**. 14(3): 322-337.
- Robert J. H. (2020). raster: Geographic Data Analysis and Modeling. [On-line]. Available: <https://CRAN.R-project.org/package=raster>.

- Robinson, W. D., Rompré, G., and Robinson, T. R. (2005). Videography of Panama bird nests shows snakes are principal predators. **Ornitologia Neotropical**. 16: 187-195.
- Robinson, W. D., and Sherry, T. W. (2012). Mechanisms of avian population decline and species loss in tropical forest fragments. **Journal of Ornithology**. 153: 141-152.
- Rodda, G. H., Fritts, T. H., and Conry, P. J. (1992). Origin and Population Growth of the Brown Tree Snake, *Boiga irregularis*, on Guam. **Pacific Science**. 46: 46-57.
- Rodda, G. H., Fritts, T. H., McCoid, M. J., and Campbell III, E. W. (1999). An Overview of the Biology of the Brown Treesnake (*Boiga irregularis*), a Costly Introduced Pest on Pacific Islands. In: Problem snake management: the habu and the brown treesnake. Pages: 44-80.
- Saenz, D., Fitzgerald, A., Baum, K. A., Conner, R. N., and Adams, D. (2006). Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. **Herpetological Monographs**. 20: 64-82.
- Santana-Bendix, M. A. (1994). Movements, activity patterns and habitat use of *Boiga irregularis* (Colubridae), an introduced predator in the island of Guam. Unpublished master's thesis. University of Arizona, Arizona.
- Savidge, J. A. (1988). Food Habits of *Boiga irregularis*, an Introduced Predator on Guam. **Journal of Herpetology**. 22: 275-282.
- Sekercioglu, C. H., Daily, G. C., and Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. **Proceedings of the National Academy of Sciences**. 101: 18042-18047.

- Shine, R. (1991). Why do larger snakes eat larger prey items?. **Functional Ecology**. 5(4): 493-502.
- Silva, I., Crane, M., Marshall, B. M., and Strine, C. T. (2020). Reptiles on the wrong track? Moving beyond traditional estimators with dynamic Brownian Bridge Movement Models. **Movement Ecology**. 8: 43.
- 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: e0203449.
- Smith, S. N., Jones, M. D., Marshall, B. M., Waengsothorn S., Gale, G. A., and Strine, C. T. (2020). Restricted constrictors: Space use and habitat selection of native Burmese pythons in Northeast Thailand. **Preprint, Ecology**.
- Somsiri, K., Gale, G. A., Pierce, A. J., Khamcha, D., and Sankamethawee, W. (2020). Habitat structure affects nest predation of the Scaly-crowned Babbler (*Malacopteron cinereum*) by macaques and snakes in a Thai-seasonal evergreen forest. **Journal of Ornithology**. 161: 389-398.
- Sperry, J. H., Peak, R. G., Cimprich, D. A., and Weatherhead, P. J. (2008). Snake Activity Affects Seasonal Variation in Nest Predation Risk for Birds. **Journal of Avian Biology**. 39: 379-383.
- Sperry, J. H., Ward, M. P., and Weatherhead, P. J. (2013). Effects of Temperature, Moon Phase, and Prey on Nocturnal Activity in Ratsnakes: An Automated Telemetry Study. **Journal of Herpetology**. 47: 105-111.
- Sperry, J. H., and Weatherhead, P. J. (2009). Does Prey Availability Determine Seasonal Patterns of Habitat Selection in Texas Ratsnakes. **Journal of Herpetology**. 43: 55-64.

- Stake, M. M., Thompson, F. R., Faaborg, J., and Burhans, D. E. (2005). Patterns of Snake Predation at Songbird Nests in Missouri and Texas. **Journal of Herpetology**. 39: 215-222.
- Stenseth, N. C., Falck, W., Bjørnstad, O. N., and Krebs, C. J. (1997). Population regulation in snowshoe hare and Canadian lynx: Asymmetric food web configurations between hare and lynx. **Proceedings of the National Academy of Sciences**. 94: 5147-5152.
- Thieurmel, B., and Elmarhraoui, A. (2019). suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. [On-line]. Available: <https://CRAN.R-project.org/package=suncalc>.
- Thompson, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. **Ibis**. 149: 98-109.
- Tobin, M. E., Sugihara, R. T., Pochop, P. A., and Linnell, M. A. (1999). Nightly and Seasonal Movements of *Boiga irregularis* on Guam. **Journal of Herpetology**. 33: 281-291.
- Turner, I. M. (1996). Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. **The Journal of Applied Ecology**. 33: 200.
- Tyson, R., Haines, S., and Hodges, K. (2010). Modelling the Canada lynx and snowshoe hare population cycle: The role of specialist predators. **Theoretical Ecology**. 3: 97-111.
- Ujvari, B., and Korsos, Z. (2000). Use of radiotelemetry in snakes: a review. **Acta Zoologica Academiae Scientiarum Hungaricae**. 46: 115-146.
- Van Buuren, S., and Groothuis-Oudshoorn, K. (2011). mice: Multivariate Imputation by Chained Equations in R. **Journal of Statistical Software**. 45(3): 1-67.

- Venables, W. N., and Ripley, B. D. (2002) *Modern Applied Statistics with S*. Fourth Edition. Springer: New York. ISBN 0-387-95457-0.
- Weatherhead, P. J., and Blouin-Demers, G. (2004a). Understanding avian nest predation: why ornithologists should study snakes. **Journal of Avian Biology**. 35: 185-190.
- Weatherhead, P. J., and Blouin-Demers, G. (2004b). Long-term effects of radiotelemetry on black ratsnakes. **Wildlife Society Bulletin**. 32: 900-906.
- Weatherhead, P. J., and Charland, M. B. (1985). Habitat Selection in an Ontario Population of the Snake, *Elaphe obsoleta*. **Journal of Herpetology**. 19: 12-19.
- Weatherhead, P., Prosser M., Gibbs, H., and Brown, G. (2002). Male reproductive success and sexual selection in northern water snakes determined by microsatellite DNA analysis. **Behavioral Ecology**. 13: 808-815.
- Webster, M. M., and Rutz, C. (2020). How STRANGE are your study animals? **Nature**. 582: 337-340.
- 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: 130-144.
- Wickham H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wickham, H., and Seidel, D. (2020). scales: Scale Functions for Visualization. [Online]. Available: <https://CRAN.R-project.org/package=scales>.
- Wickham, H., and Pedersen, T. L. (2019). gtable: Arrange 'Grobs' in Tables. [Online]. Available: <https://CRAN.R-project.org/package=gtable>.

- Wickham, H. (2007). Reshaping Data with the reshape Package. **Journal of Statistical Software**. 21(12): 1-20.
- Wickham, H., François, R., Henry, L., and Müller, K. (2020). dplyr: A Grammar of Data Manipulation. [On-line]. Available: <https://CRAN.R-project.org/package=dplyr>.
- Wilke, C. O. (2019). cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. [On-line]. Available: <https://CRAN.R-project.org/package=cowplot>.
- Wilke, C. O. (2020a). ggtext: Improved Text Rendering Support for 'ggplot2'. [On-line]. Available: <https://CRAN.R-project.org/package=ggtext>.
- Wilke, C. O. (2020b). ggribes: Ridgeline Plots in 'ggplot2'. [On-line]. Available: <https://CRAN.R-project.org/package=ggribes>.
- Wunderle, J. M., Mercado, J. E., Parresol, B., and Terranova, E. (2004). Spatial Ecology of Puerto Rican Boas (*Epicrates inornatus*) in a Hurricane Impacted Forest. **Biotropica**. 36: 555-571.
- Ziegler, T., Orlov, N. L., Giang, T. T., Truong, N. Q., Tao, N. T., Quyet, L. K., Khoi, N. V., and Thanh, V. N. (2010). New records of cat snakes, *Boiga* Fitzinger, 1826 (Squamata, Serpentes, Colubridae), from Vietnam, inclusive of an extended diagnosis of *Boiga bourreti* Tillack, Le & Ziegler, 2004. **Zoosystematics and Evolution**. 86: 263-274.

SUPPLEMENTARY MATERIALS



SUPPLEMENTARY MATERIALS

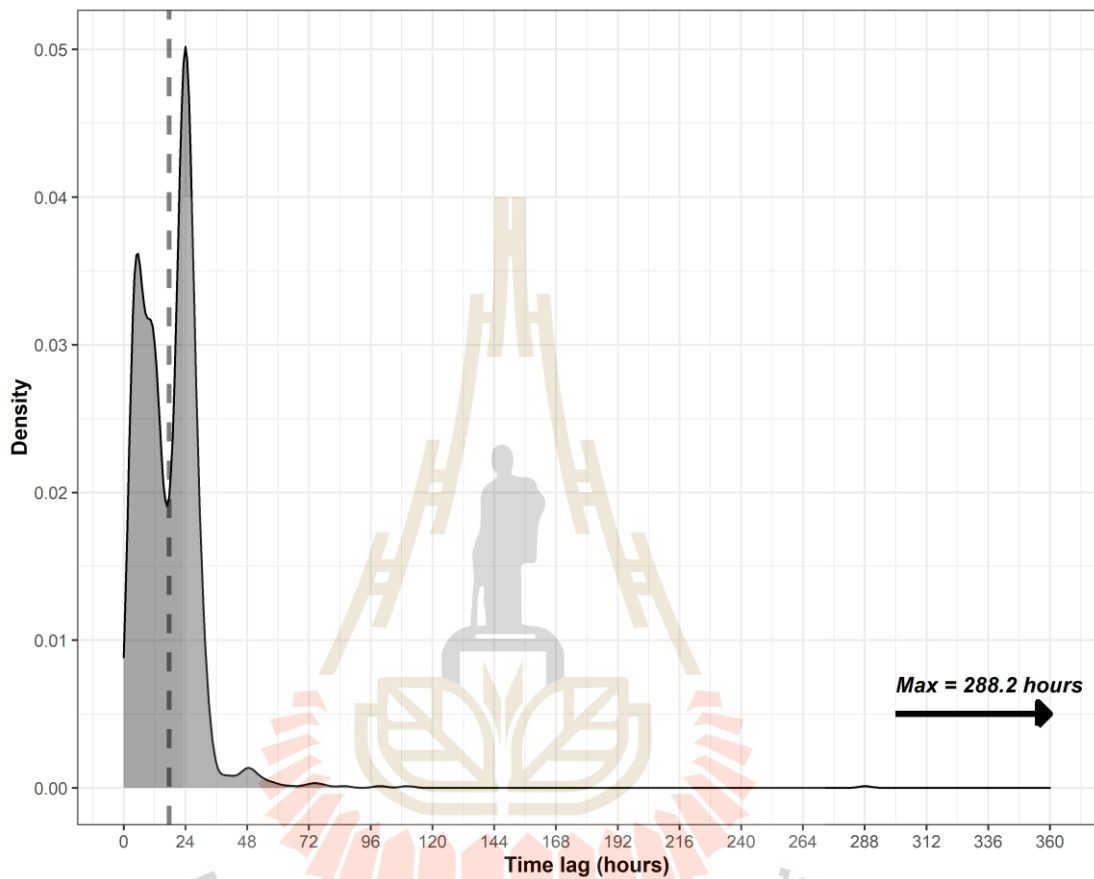


Figure S1 Density plot of the average time lag (≈ 18 hours) between fixes of our radio-tracked individuals. The peak around 48 hours most likely represents the intervals during which our snakes were missing because we were unable to detect their radio-signal despite intensive search effort. The peaks between 72 hours and 288 hours represent the intervals during which our snakes were likely awaiting transmitter replacement surgery at the research station.

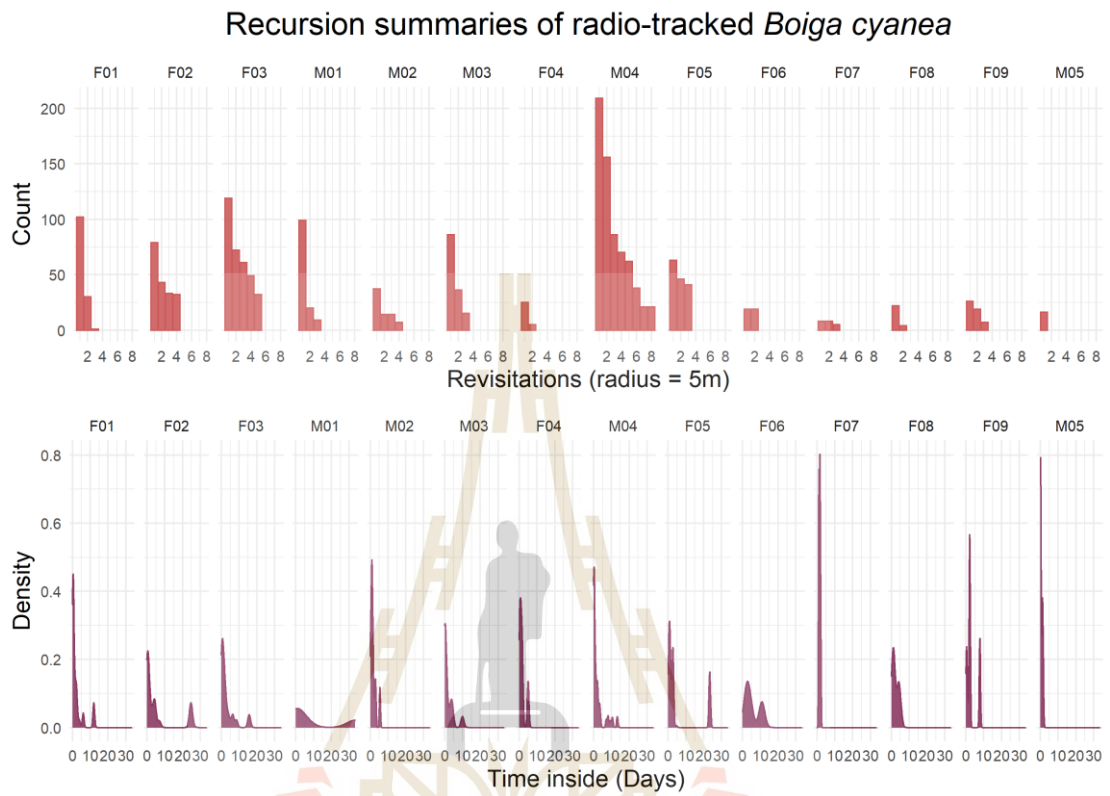


Figure S2 Recursion summaries for each of our radio-tracked *B. cyanea* within a 5 m radius around telemetered locations.

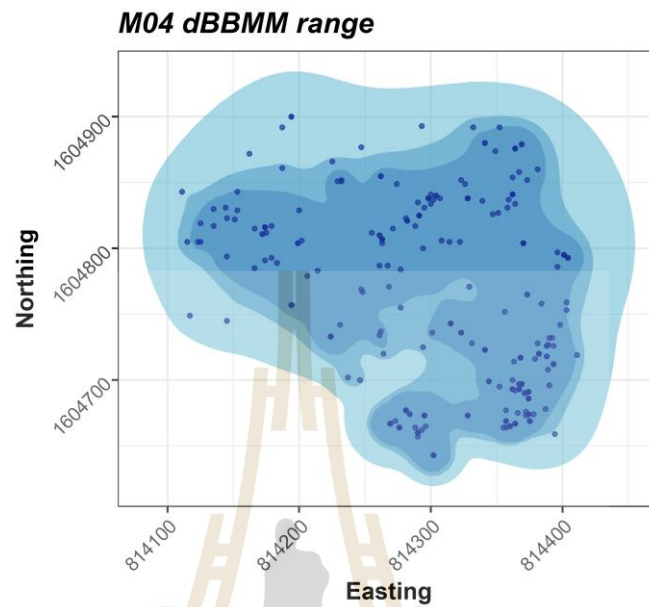


Figure S3 dBMM utilization distribution (window size = 9, margin size = 3) depicting 90%, 95% and 99% contours for our longest radio-tracked male, M04 between 6 November 2018 and 8 June 2019.

Table S1 Utilization distributions and motion variances of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019 using window size 11 and margin size 5.

Snake ID	Days Tracked	90% dBBMM (ha)	95% dBBMM (ha)	99% dBBMM (ha)	$\sigma_m^2 \pm SE$
F01	119	1.63	2.10	3.11	0.53 ± 0.06
F02	82	0.98	1.53	2.64	0.37 ± 0.05
F03	124	4.17	6.40	11.25	1.52 ± 0.19
M01	105	28.13	37.54	57.78	8.59 ± 0.91
M02	36	1.90	2.73	4.06	0.66 ± 0.14
M03	95	18.43	24.88	39.89	8.02 ± 0.78
F04	24	0.56	0.82	1.38	0.34 ± 0.1
M04	214	3.93	5.21	8.58	2.17 ± 0.21
F05	65	1.58	4.88	12.53	1.27 ± 0.35
F08	22	2.24	3.26	5.72	1.33 ± 0.37
F09	27	1.88	2.70	4.72	2.23 ± 0.45
M05	19	16.70	21.08	30.61	7.44 ± 1

***dBMM**: Dynamic Brownian bridge movement model estimate; * $\sigma_m^2 \pm SE$: Motion variance and standard error.

Table S2 Utilization distributions and motion variances of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019 using window size 15 and margin size 7.

Snake ID	Days Tracked	90% dBMM (ha)	95% dBMM (ha)	99% dBMM (ha)	$\sigma_m^2 \pm SE$
F01	119	1.70	2.17	3.15	0.5 ± 0.05
F02	82	0.99	1.48	2.45	0.35 ± 0.05
F03	124	3.86	5.89	10.27	1.64 ± 0.21
M01	105	27.68	36.31	54.35	8.37 ± 0.81
M02	36	1.80	2.67	4.16	0.69 ± 0.16
M03	95	18.70	25.06	39.66	8.11 ± 0.67
F04	24	0.53	0.77	1.29	0.32 ± 0.09
M04	214	4.01	5.27	8.57	2.08 ± 0.19
F05	65	2.19	5.53	12.68	1.33 ± 0.33
F08	22	1.88	2.60	4.26	1.31 ± 0.23
F09	27	1.81	2.52	4.19	2.11 ± 0.41
M05	19	11.86	15.34	22.92	7.85 ± 0.88

***dBMM**: Dynamic Brownian bridge movement model estimate; * $\sigma_m^2 \pm SE$: Motion variance and standard error.

Table S3 Utilization distributions and motion variances of radio-tracked *Boiga cyanea* between 21 October 2017 and 8 June 2019 using window size 21 and margin size 9.

Snake ID	Days Tracked	90% dBMM (ha)	95% dBMM (ha)	99% dBMM (ha)	$\sigma_m^2 \pm SE$
F01	119	1.79	2.26	3.25	0.5 ± 0.04
F02	82	0.86	1.34	2.32	0.36 ± 0.04
F03	124	3.77	5.56	9.24	1.51 ± 0.15
M01	105	27.23	35.39	51.96	8.02 ± 0.7
M02	36	1.63	2.53	4.03	0.97 ± 0.29
M03	95	18.67	25.08	39.34	7.62 ± 0.61
F04	24	0.65	0.87	1.35	0.42 ± 0.09
M04	214	4.12	5.39	8.60	2.17 ± 0.19
F05	65	2.82	6.24	12.76	1.57 ± 0.33
F08	22	2.12	2.90	4.70	1.77 ± 0.26
F09	27	1.76	2.41	3.88	1.88 ± 0.36
M05	19	5.67	7.37	11.38	6.47 ± 0.59

***dBMM**: Dynamic Brownian bridge movement model estimate; * $\sigma_m^2 \pm \text{SE}$:
Motion variance and standard error.

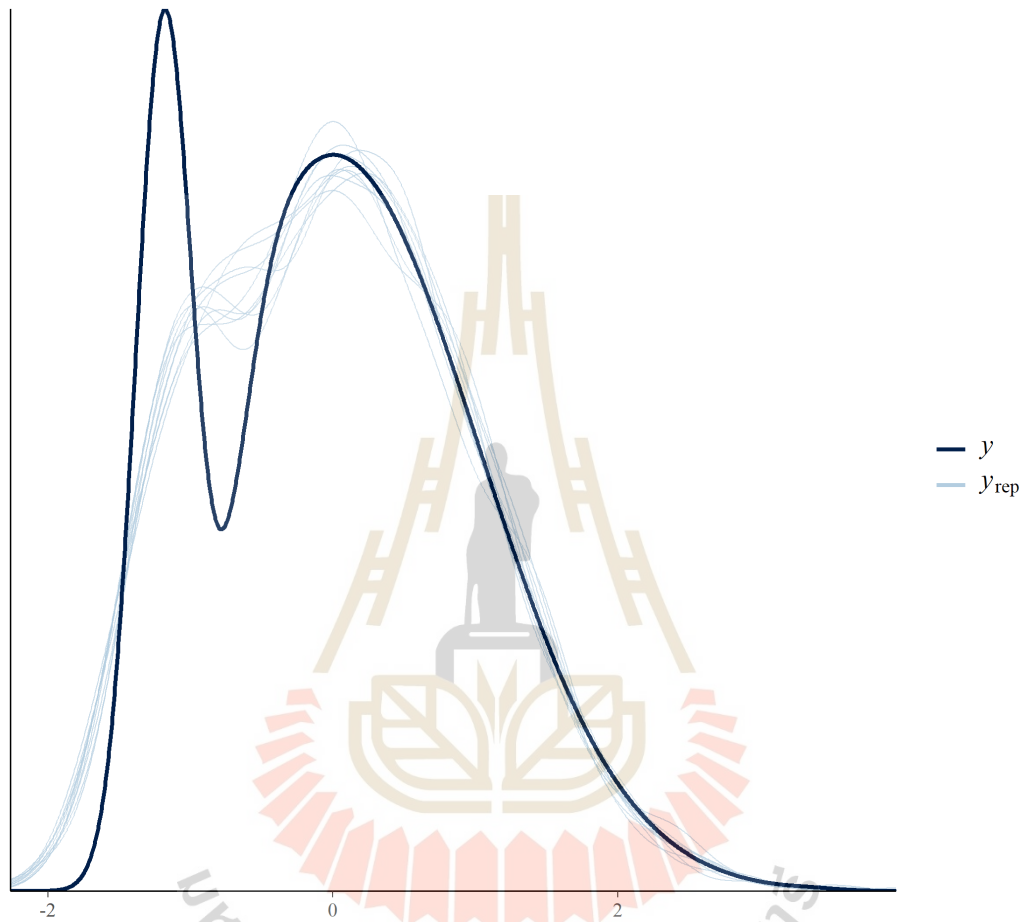


Figure S4 Posterior predictive check for Bayesian regression model plotting observed data (y) and simulated data (y_{rep}).

Table S4 Tracking interval summaries of nights with ≥ 2 nocturnal fixes, during which the snakes had moved from previous fix, or were observed moving.

Nocturnal fix	Fixes	Moved	Moving
1 st interval (18:00-21:59)	110 (35%)	66 (34%)	62 (37%)
2 nd interval (22:00-01:59)	97 (31%)	64 (33%)	58 (35%)
3 rd interval (02:00-07:00)	105 (34%)	66 (34%)	47 (28%)
Total	312	196 (63%)	197 (54%)



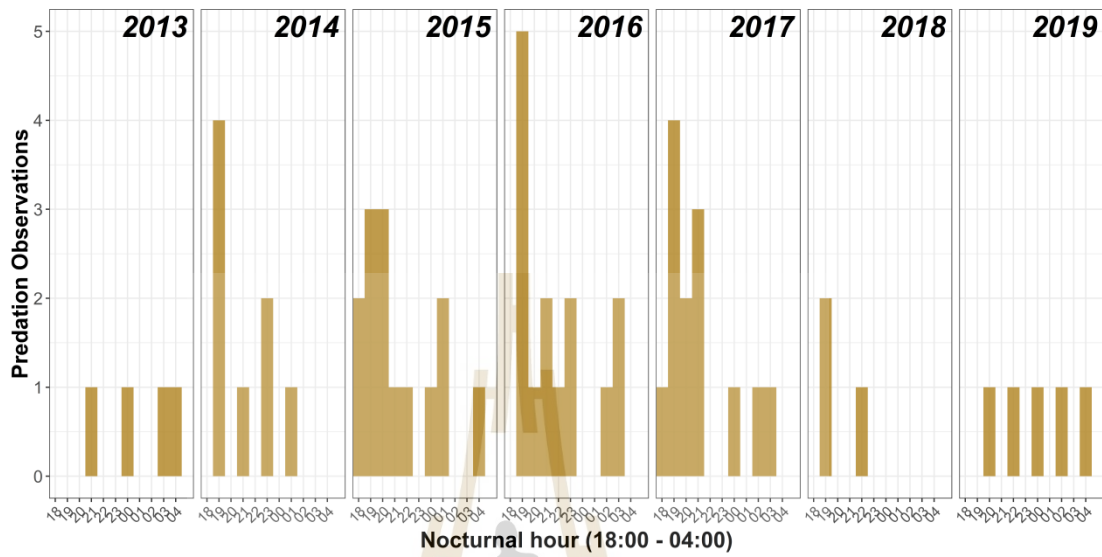
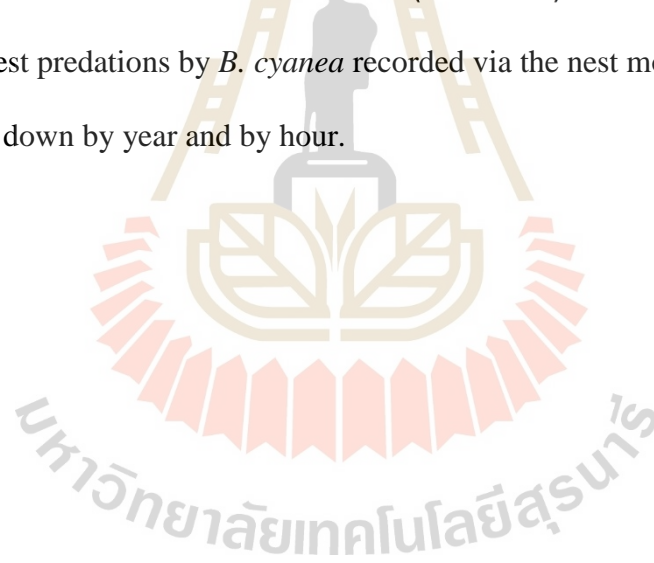
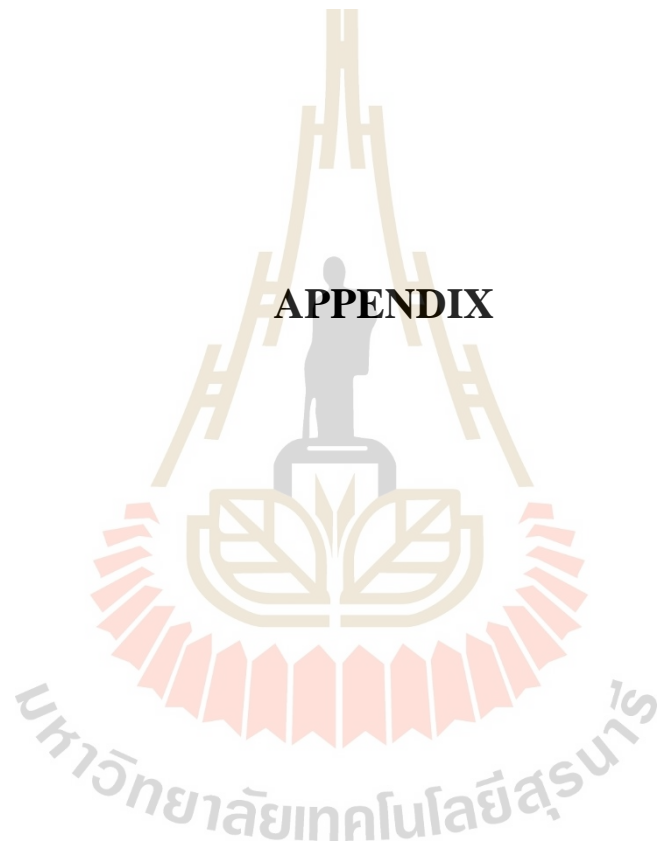


Figure S5 Nest predations by *B. cyanea* recorded via the nest monitoring cameras at SBR, broken down by year and by hour.



APPENDIX



APPENDIX

Table A1 Descriptions of refugia used by our radio-tracked *B. cyanea*.

Refugium	Description
Broken trunk/branch	A tree hollow formed as a result of a ruptured tree trunk or branch, big enough to shelter an adult <i>B. cyanea</i> .
Tree cavity	A semi-enclosed cavity which has naturally formed in the trunk or branch of a tree, big enough to allow an adult <i>B. cyanea</i> to enter and shelter in.
Liana	Climbing, twining or winding plants, usually with a woody stem.
Foliage	Leaves that constitute the crown of a tree.
Under bark	Under the bark of a tree trunk that has not detached from the tree yet, that is big enough to accommodate an adult <i>B. cyanea</i> under it.
Forest litter	Forest surface layer comprising loose, non-living organic debris
Open / low vegetation	An area of ground having no plants, or sparse, short vegetation growing on it.
Fallen log	Any naturally fallen trees or logs that are big enough to shelter an adult <i>B. cyanea</i> .
Termitarium	An aboveground termite nest growing beyond its initially concealing surface
Manmade	Any non-vegetative, manmade structure that is big enough to shelter an adult <i>B. cyanea</i> .

CURRICULUM VITAE

Name Natalia Anji D'souza
Date of Birth 3 October 1991
Education 2015. M.Sc. Conservation Biology, University of Kent, UK.

Publications

Hodges, C.W., D'souza, A., and Jintapirom, S. (2020). Diurnal observation of a Malayan Krait *Bungarus candidus* (Reptilia: Elapidae) feeding inside a building in Thailand. *Journal of Threatened Taxa* 12(8): 15947–15950. [On-line]. Available: <https://doi.org/10.11609/jott.5746.12.8.15947-15950>.

มหาวิทยาลัยเทคโนโลยีสุรนารี