THE SPATIAL ECOLOGY OF KING COBRAS (*Ophiophagus hannah*) IN THE SAKAERAT BIOSPHERE RESERVE, NORTHEAST THAILAND

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Environmental Biology

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นิเวศเชิงพื้นที่และการเลือกใช้ถิ่นที่อาศัยของงูจงอาง (*Ophiophagus hannah*) ณ พื้นที่สงวนชีวมณฑลสะแกราช ภาคตะวันออกเฉียงเหนือ ประเทศไทย

นายแม็กซ์ ดอลตัน โจนส์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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แม็กซ์ ดอลตัน โจนส์ : นิเวศเชิงพื้นที่และการเลือกใช้ถิ่นที่อาศัยของงูจงอาง (*Ophiophagus hannah*) ณ พื้นที่สงวนชีวมณฑลสะแกราช ภาคตะวันออกเฉียงเหนือ ประเทศไทย (THE SPATIAL ECOLOGY OF KING COBRAS (*Ophiophagus hannah*) IN THE SAKAERAT BIOSPHERE RESERVE, NORTHEAST THAILAND) อาจารย์ที่ปรึกษา : อาจารย์ ดร.คลอลิน โทมัส สไตร์น. 282 หน้า

นิเวศน์วิทยาเชิงพื้นที่/ การเลือกใช้ทรัพยากร/ นิเวศวิทยาของการทำรัง/ การตาย

งูจงอาง (*Ophiophagus hannah*) เป็นงูพิษในวงศ์ Elapidae ที่ยาวที่สุดในโลก ในงานศึกษาที่มีมาก่อนหน้ามักให้ความสนใจในองค์ประกอบของพิษและสายวิวัฒนาการของงูจงอาง แต่ในทางกลับกันการศึกษาด้านนิเวศวิทยาในสายพันธุ์ดังกล่าวมีเพียงส่วนน้อยและศึกษาในกลุ่มประชากรในประเทศอินเดียเท่านั้น โดยจุดมุ่งหมายในงานวิจัยนี้เพื่อศึกษานิเวศวิทยาเชิงพื้นที่ของประชากรงูจงอางภายในพื้นที่เขตสงวนชีวมณฑลสะแกราช ภาคตะวันออกเฉียงเหนือของประเทศไทยระหว่างเดือนมีนาคม พ.ศ. 2556 ถึงสิงหาคม พ.ศ. 2563

โดยทำการติดตามสัญญาณวิทยุระหว่างวันที่ 1 มีนาคม พ.ศ. 2556 ถึง 28 กรกฎาคม 2563 ในกลุ่มเป้าหมายจำนวน 24 ตัว โดยมีตัวโตเต็มวัย 17 ตัว (เพศผู้ 9 ตัว เพศเมีย 8 ตัว) และตัววัยเด็ก 7 ตัว (เพศผู้ 5 ตัว เพศเมีย 2 ตัว) และจำลองโมเดล dynamic Brownian Bridge Movement (dBBMM) ด้วยข้อมูล VHF พบว่า *O. hannah* มีค่าเฉลี่ยของการกระจายตัว 543.89 ± 81.75 ha (พิสัย = 82.09-1843.75 ha) และแสดงถึงความสัมพันธ์ระหว่างฤดูกาลและการเคลื่อนที่ในระดับบุคคล โดยเพศเมียตัวโตเต็มวัยจะเข้าสู่พื้นที่ป่าในช่วงฤดูผสมพันธุ์เท่านั้นและมีการกระจายตัวในพื้นที่การเกษตรในช่วงนอกฤดูผสมพันธุ์ ผู้วิจัยได้พิจารณาทรัพยากรเชิงลักษณะภูมิประเทศที่เฉพาะเจาะจงเช่น ป่า ถนน พื้นที่กึ่งธรรมชาติ พื้นที่ตั้งถิ่นฐานของมนุษย์และแหล่งน้ำ โดยดำเนินการ iSSF ในระดับบุคคลและประชากร ซึ่งส่งผลให้การคาดการณ์การเคลื่อนไหวในระดับบุคคลมีความแตกต่างกันสูง แต่โดยภาพรวมสามารถคาดการณ์ได้จากความพร้อมของพื้นที่กึ่งธรรมชาติและป่าสำหรับเพศเมียและเพศผู้ตามลำดับ อีกทั้งตรวจสอบพื้นที่ที่เป็นไปได้ในการอำนวยความสะดวกในการเคลื่อนย้ายระหว่างพื้นที่ของ *O. hannah* ตามถนนทางหลวงหมายเลข 304 ซึ่งตัดผ่านเขตสงวนชีวมณฑลสะแกราช พบว่ามีอุโมงค์ลอดผ่านจำนวน 32 แห่ง และทำการวิเคราะห์ recurse analysis และ dBBMMs ในแต่ละเหตุการณ์ที่ปรากฏพบว่า *O. hannah* เลือกใช้อุโมงค์ 19 แห่ง เพื่อเคลื่อนที่ผ่านถนนทางหลวงอย่างปลอดภัย

ผู้วิจัยได้บันทึกกรณีการตายของ *O. hannah* ภายในพื้นที่การศึกษาซึ่งแสดงให้เห็นว่าการตายโดยส่วนใหญ่มีสาเหตุมาจากกิจกรรมของมนุษย์แบ่งได้เป็น การจู่โจมโดยมนุษย์ 10 เหตุการณ์ และการถูกรถชน 7 เหตุการณ์ ซึ่งขอแนะนำให้มีการศึกษาเพิ่มเติมเพื่อบรรเทาปัญหาดังกล่าวและเชื่อว่าโครงสร้างพื้นฐาน เช่น รั้วและป้าย อาจพิสูจน์ได้ว่ามีประสิทธิภาพในการแก้ไขปัญหา แม้ในการศึกษานี้จะมีขีดจำกัดในด้านจำนวนของกลุ่มตัวอย่างและระยะเวลาของการศึกษาที่ยาวนาน แต่อย่างไรก็ตามผลการศึกษานี้จะเป็นรากฐานในการสนับสนุนการศึกษาอื่นในอนาคตเพื่อตรวจสอบระบบนิเวศของกลุ่มสัตว์เลื้อยคลานที่ยังไม่ชัดเจน

สาขาวิชาชีววิทยา ลายมือชื่อนักศึกษา________________

ปีการศึกษา 2563 ลายมือชื่ออาจารย์ที่ปรึกษา________________

ลายมือชื่ออาจารย์ที่ปรึกษาร่วม________________

MAX DOLTON JONES : THE SPATIAL ECOLOGY OF KING COBRAS (*OPHIOPHAGUS HANNAH*) IN THE SAKAERAT BIOSPHERE RESERVE, NORTHEAST THAILAND. THESIS ADVISOR : COLIN THOMAS STRINE, Ph.D. 282 PP.

SPATIAL ECOLOGY/ RESOURCE USE/ NESTING ECOLOGY/ MORTALITY

The King Cobra (*Ophiophagus hannah*), within the Elapidae family, is the longest venomous snake in the world. Many previous studies have focused on the composition of King Cobra venom, or have prioritized studying their phylogenies. However, very few studies have investigated the ecology of this iconic snake species, and of the studies that have, most were focused within Indian King Cobra populations. The aims of our study were therefore to investigate the spatial ecology of a population of King Cobras within the Sakaerat Biosphere Reserve, Northeast Thailand, between March 2013 and August 2020.

We tracked 24 King Cobras between 2013-03-01 and 2020-07-28, comprised of nine adult males, eight adult females, five juvenile males and two juvenile females. We performed dynamic Brownian Bridge Movement Models (dBBMM) using our VHF tracking data, which estimated King Cobras to have an average occurrence distribution of $\bar{x} = 543.89 \pm 81.75$ ha (range = 82.09-1843.75 ha). We showed clear seasonality in the movement frequency and associated space use of our individuals, with adult females only entering forested areas during the breeding season, and maintaining an occurrence distribution within an agricultural matrix throughout the non-breeding season.

We delineated resources as specific landscape features: forests, roads, semi-natural areas, human settlements and water. We performed iSSF at an individual- and population-level, which resulted in high individual heterogeneity in our estimates, though movement could largely be predicted by the availability of semi-natural areas and forests for females and males respectively.

We investigated potential areas along the Highway 304, bisecting the Sakaerat Biosphere Reserve, that could facilitate King Cobra mobility across the road. We discovered 32 underpasses along our survey area. We ran a *recurse* analysis and dBBMMs on subsets of tracking data during crossing events, which suggests that 19 underpasses have been used by telemetered King Cobras to safely traverse the highway.

We further recorded cases of King Cobra mortality within our study site. We show that natural deaths are rare, yet instances of anthropogenic causes of mortality are high. The main sources of anthropogenic deaths were persecution events (10) and vehicle collisions (seven). We suggest an education-based approach to alleviate the pressures acting upon King Cobras, and believe that road infrastructure, such as fencing and signage, may prove effective for mitigating future vehicle collisions. We are limited by our sample size and longevity of tracking durations; however, our results offer a foundation for future studies investigating the ecology of poorly-understood reptile taxa.

School of Biology Student's Signature____________________

Academic Year 2020 Advisor's Signature____________________

Co-advisor's signature____________________

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I thank the National Park, Wildlife and Plant Conservation Department, Thailand for providing permission to study a nationally protected species, and the National Research Council of Thailand for also providing permits to undertake this research. With these permissions, I am grateful for surgical expertise provided by Nakhon Ratchasima Zoo, Dusit Zoo, and Zoological Park Organization under the Royal Patronage of His Majesty the King, Thailand.

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LIST OF ABBREVIATIONS

AF = Adult female

AIC = Akaike's Information Criterion

aKDE = autocorrelated Kernel Density Estimates

AM = Adult male

AT = Anterior temporal

CLR = Case-controlled linear regression

dBBMM = dynamic Brownian Bridge Movement Model

F = Frontal

GPS = Global positioning system

HL = Head length

HW = Head width

ID = Identification

IL = Infralabial

IN = Internasal

IP = Inter parietal

iSSA = integrated Step-Selection Analysis

iSSF = integrated Step-Selection Functions

IUCN = International Union for Conservation of Nature

JF = Juvenile female

LIST OF ABBREVIATIONS (Continued)

JM = Juvenile male

KDE = Kernel density estimate

KM = Kaplan-Meier

MAB = Man and biosphere

MCP = Minimum convex polygon

N = Nasal

NW-TLC = Nong Weng – Ta Ling Chan

O = Occipital

P = Parietal

PF = Prefrontal

PoO = Post ocular

PrO = Pre ocular

PT = Posterior temporal

QGIS = Quantum Geographic Information System

R = Rostral

RSA = Resource selection analysis

SBR = Sakaerat Biosphere Reserve

SERS = Sakaerat Environmental Research Station

SL = Supralabial

SO = Supraocular

LIST OF ABBREVIATIONS (Continued)

SVL = Snout-to-vent length

TISTR = Thailand Institute of Scientific and Technological Research

TL = Tail length

UTM = Universal Transverse Mercator

VHF = Very high frequency

WGS = World Geodetic System

CHAPTER I

INTRODUCTION

1.1Background and problem

The King Cobra (*Ophiophagus hannah*) is the longest venomous snake in the world, and can be found all through-out Southeast Asia, including parts of India, Nepal and Southern China (Dolia, 2018), though remains understudied throughout its range. An overwhelming amount of studies have primarily focused on the composition of King Cobra venom (e.g. Joubert, 1973; Li *et al*., 1994; Huang *et al*., 1997; Rajagopalan *et al*., 2007; Vonk *et al*., 2013; Tan *et al*., 2020). In addition, there have been various studies which have incorporated King Cobras into phylogenetic analyses (Slowinski and Keogh, 2000; Pyron *et al*., 2013; Suntrarachun *et al*., 2014; Zaher *et al*., 2019). Ecological studies, on the other hand, have been largely misrepresented in the literature with most ecological information regarding the King Cobra being available within geographically focused field guides and books (Das *et al*., 2010; Cox *et al*., 2012; Charlton, 2018). The few ecology-focused studies on the King Cobra have been highly targeted, representing information from Indian populations (Barve *et al*., 2013; Rao *et al*., 2013; Shankar *et al*., 2013a; 2013b; Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018), Nepal (Baral *et al*., 2019; Thapa *et al*., 2019) and a population in Northeast Thailand as a result of this study (Marshall *et al*., 2018; Silva *et al*., 2018; Marshall *et al*., 2019; Jones *et al*., 2020; Marshall *et al*., 2020).

Space is incorporated into all aspects of ecology (Manel *et al.*, 2003; Guillot *et al*., 2009; Massol *et al*., 2011). Conservation biology specifically will infer spatial solutions where landscape features play a role in successful conservation planning; such as roads and protected areas (Dickman and Marker, 2005; Marker *et al*., 2008; Gaos *et al*., 2012). The implementation of these spatial solutions typically aligns with evidence from mammalian ecological studies (Coops and Catling, 2002; Boitani *et al*., 2011, Clément *et al*., 2014); or those involving similar charismatic vertebrate taxa with socio-economic interest (Wilson *et al*., 2007). Snakes, however, are rarely considered during long-term conservation strategies, partly owed to negative perceptions of snakes (Mullin and Seigel, 2009, Miranda *et al*., 2016), and the lack of ecological studies which have been undertaken on snakes, particularly within native tropical regions (Pawar, 2003).

Many studies have used very high frequency (VHF) radio telemetry to investigate the movements, and spatial requirements of snakes (Gardiner *et al*., 2013; Ward *et al*., 2013; Hyslop *et al*., 2014; Wolfe *et al*., 2018), which in turn, helps researchers investigate the ecology and natural history of snakes (Maritz *et al*., 2019). Boback *et al*. (2020) investigated the biases of visual encounter surveys for detecting brown tree snakes (*Boiga irregularis*) in Guam and reported a survey effort of 323 hours needed to locate one telemetered snake, extrapolated to a total of 6460 hours to re-discover their sample size of 20 telemetered snakes when relying on visual encounters alone. Radiotelemetry therefore lowers the need for extensive effort, manpower and ultimate high economic costs, of locating and studying snakes within a landscape.

Despite the success of VHF radio telemetry in elucidating snake ecology, there remains a bias of studies focused within the Americas (e.g. Roth, 2005; Moore *et al*., 2006; Kapfer *et al*., 2008; Kapfer *et al*., 2010; DeGregario *et al*., 2011; Glaudas and Rodríguez-Robles, 2011; Wastell and Mackessy, 2011; Vanek and Wasko, 2017; Delisle *et al*., 2019; Novak *et al*., 2020). In contrast, very few studies have performed comprehensive studies throughout Africa, Australia and Asia, and as a result, there have been few spatial ecology studies focusing on elapid snakes. In Australia, there have been such investigations on tiger snakes (*Notechis scutatus*; Butler *et al*., 2005), Stephens' banded snakes (*Hoplocephalus stephensii*; Fitzgerald *et al*., 2002); broad-headed snakes (*Hoplocephalus bungaroides*; Croak *et al*., 2013) and dugites (*Pseudonaja affinis*; Wolfe *et al*., 2018); and within Asia, studies have investigated banded kraits (*Bungarus fasciatus*; Knierim *et al*., 2019), Malayan kraits (*Bungarus candidus*; Mohammadi *et al*., 2014; Knierim *et al*., 2018) and King Cobras (*Ophiophagus hannah*; Barve *et al*., 2013; Rao *et al*., 2013; Silva *et al*., 2018; Marshall *et al*., 2019; 2020).

Although the abovementioned studies represent several different species, this is poor considering the high elapid diversity exhibited within these regions (Kelly *et al*., 2009). Furthermore, many of these studies present inconsistent tracking regimes and traditional space use estimators, such as Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE), which have been shown to include errors into space use estimates depending on tracking frequency and duration (Silva *et al*., 2020). Silva *et al*. (2018) specifically, investigated the potential to use statistical approaches originally catered to Global Positioning System (GPS) animal tracking, which provide a high number of location fixes, for coarser VHF tracking data. They introduced dynamic

Brownian Bridge Movement Models (dBBMM) as a method for calculating reptile space use and their results highlighted that dBBMMS outperformed MCPs and KDE across their simulated tracking regimes. The use of dBBMMs will allow future work to incorporate irregular movement behaviour exhibited by snakes into more accurate spatial estimates, allowing researchers to recommend more suitable conservation solutions (Péron, 2019).

My project therefore expands on work produced by Silva *et al*. (2018) and Marshall *et al*. (2018; 2019; 2020) to investigate the space use and movement patterns of King Cobras within the Sakaerat Biosphere Reserve, Northeast Thailand. The King Cobra is a large, vagile predator which exhibits movements comparable to large mammalian species, and thus provides an excellent model species to investigate novel analytical techniques to elucidate space use in large reptilian species. We primarily use dBBMMs and integrated step-selection functions (iSSF) to investigate movement patterns and resource use throughout a heterogeneous landuse matrix, among other statistical solutions. This thesis therefore provides the first comprehensive report on space use, resource use, nesting ecology, mortality risks and other relevant ecological information on King Cobras in Thailand.

1.2 Objectives

The objectives of this study are:

1) To investigate the space use and movement patterns of King Cobras throughout the Sakaerat Biosphere Reserve by examining individual occurrence distributions and motion variance, estimated with dynamic

Brownian Bridge Movement Models, to provide a greater understanding on King Cobra spatial ecology.

2) To assess the influence of landscape features (resources) on the movement (step length (m) and angle (º)) of King Cobras within the heterogeneous Sakaerat Biosphere Reserve landscape, using integrated step-selection functions.
3) To provide a novel understanding on the nesting ecology of King Cobras in the Sakaerat Biosphere Reserve, including seasonal movement patterns exhibited by reproductive female King Cobra using dynamic Brownian Bridge Movement Models, nest characteristics, incubation temperatures and biometric information on captured King Cobra hatchlings.
4) To identify potential areas that could facilitate King Cobra movement across the Highway 304 bisecting the Sakaerat Biosphere Reserve, and further investigate the interactions of King Cobras with major roads throughout the landscape, with particular focus on telemetered females during nesting movements.
5) To record cases of King Cobra mortality within the Sakaerat Biosphere Reserve, to identify the main threats acting on the population.

1.3 Scope and limitations

We investigated King Cobra spatial ecology via an intensive VHF radio telemetry study between 2013-03-01 and 2020-07-28, within the Sakaerat Biosphere Reserve, Northeast Thailand. We report on resulting occurrence distributions and motion variance estimates from dynamic Brownian Bridge Movement Models on individual telemetered King Cobra. We also investigated resource use and interactions between dominant landscape features (such as roads and semi-natural areas) and King Cobra movement. We further report on novel information regarding the nesting ecology of King Cobras at our study site, and the main threats acting on the population. We were limited by our ability to efficiently locate and capture King Cobras of adequate size for transmitter implantation, alongside being within a suitable location to commence tracking. In addition, we observed a high rate of mortality of our telemetered animals, coupled with many equipment malfunctions resulting in transmitter loss, which substantially limited the temporal value of our tracking data. We show this to be particularly true for telemetered females, with only one of our females remaining in the study for greater than one year. In contrast, we achieved a full year of data for many of our telemetered males. Due to the difficulty of locating suitable study animals, we opted to track both males and females, as well as suitably-sized juveniles and adults, which limited our inferences on specific King Cobra demographics, due to limitations in respective sample sizes.

1.4 Benefits of study

As the ecology and natural history of King Cobras has been largely under-represented within peer-reviewed literature, our study provides detailed results on their spatial ecology, the importance of specific landscape features on movement, a novel insight into King Cobra nesting ecology and threats acting upon the population. The data provided here can be applied to future work focusing on King Cobra ecology throughout its range. In addition, the results may also be applicable to further studies investigating King Cobra venom and taxonomic studies, as comprehensive ecological information may allow novel conclusions on evolutionary questions to be answered. Predominantly, we hope that our work may be considered and integrated into long-term conservation plans for King Cobras and other highly mobile ectothermic species. In addition to the research undertaken in this study regarding the King Cobra specifically, we have built a relationship with the local community and volunteers of the Udom Sab-Hook 31 rescue team to hopefully build a long-term respect and understanding for snakes within our study site, alongside giving the rescue teams the skills and confidence to efficiently and safely remove snakes from people's homes. We believe that our outreach efforts will have long-lasting effects for snake conservation with the Sakaerat Biosphere Reserve, limiting persecution events stemming from inevitable human-snake conflict.

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CHAPTER II

LITERATURE REVIEW

2.1 Spatial ecology

Studying the movements and spatial ecology of species can be essential for understanding their natural history, conspecific interactions and population dynamics (Fieberg *et al*., 2010; Gonzalez-Borrajo *et al*., 2016), the empirical data of which can be used to create informed and effective management decisions for long-term conservation plans (Sutherland *et al*., 2004; Balme *et al*., 2009; Grémillet and Boulinier, 2009; López-Bao *et al*., 2010; Segan *et al*., 2011). Specifically, investigating animal movements can elucidate information on spatial requirements (Hawkes *et al*., 2011), habitat selection (Moore *et al*., 2006; Wasko and Sasa, 2012), and resource use (de Knegt *et al*., 2007) alongside other important natural history information.

Studies investigating the spatial ecology of wildlife has been widely implemented across several taxa, many of which have focused on apex predators due to their role as ecosystem regulators (Estes *et al*., 2011; Ripple *et al*., 2014). For example, estuarine crocodiles (*Crocodylus porosus*) are highly mobile animals exhibiting territoriality and seasonal-dependent movement embedded within complex social structures (Campbell *et al*., 2013). These socio-spatial behaviours can be integrated within future management interventions.

Leopards (*Panthera pardus*), having the widest distribution amongst wild cats, exhibit large areas of space use and require contiguous expansions of habitat to facilitate natural mobility highlighting the need for concentrated conservation efforts outside of typical protected area boundaries (Marker and Dickman, 2005). Further research into free-ranging predators have shown behaviour-specific movements corresponding to resource abundance and key habitat features, both within a marine (Pinaud and Weimerskirch, 2005; Bailey and Thompson, 2006) and terrestrial ecosystem (Valeix *et al*., 2009).

Snakes are rarely considered as apex predators, largely owed to sympatric mammalian and avian predators, however, some large constrictors (Pittman *et al*., 2014) and highly venomous snakes (Radford *et al*., 2020) fit this ecosystem role. Although snake spatial ecology studies are many (e.g. Plummer and Mills, 2000; Baxley and Qualls, 2009; Do *et al*., 2016; Peterson *et al*., 2019; Yagi *et al*., 2020), few have investigated the movements of large snake apex predators. The studies that have are focused on invasive populations (Hart *et al*., 2015; Walters *et al*., 2016; Smith *et al*., 2018) or elapid snakes in Australia (Butler *et al*., 2005a; 2005b; Wolfe *et al*., 2018; Whitaker and Shine, 2003).

2.2 Elapid snakes

Elapidae is a large clade within the Caenophidia Infraorder, comprised of over 380 extant species (Uetz, 2020) across more than 60 genera (Golay *et al*., 1993, Keogh, 1998), containing the highest species diversity of any other venomous snake family. Many elapid species are considered medically significant to humans (Fry *et al*., 2009), possessing a pair of permanently-fixed tubular fangs typically allowing these snakes to administer potent neurotoxic venom (Kerkkamp *et al*., 2017). Species of Elapidae are widely distributed throughout the Old and New world, owed to a rapid biogeographic expansion during the late Eocene period (~31 million years ago; Kelly *et al*., 2009). Despite a large degree of ambiguity and inconsistency between taxonomic delineations within the Elapidae clade (Lawson *et al*., 2005; Vidal *et al*., 2007), lineages can broadly be categorised into the Asian/American coral snakes (Castoe *et al*., 2007; Lee *et al*., 2016), the Australasian and marine elapids (Lukoschek and Keogh, 2006; Strickland *et al*., 2016) and the Afro-Asian cobras (Wüster *et al*., 2007; Bittenbinder *et al*., 2019).

As a result of rapid evolutionary diversification (Sanders *et al*., 2008; Lee *et al*., 2016), elapid snakes exhibit a high degree of phenotypic, physiological, and behavioural diversity often linked to predator deterrence strategies (Grundler and Rabosky, 2014; Simões *et al*., 2020). For example, the high-contrasting body banding of coral snakes provides an aposematic signal for potential predators (Smith *et al*., 1977; Buasso *et al*., 2006). Furthermore, coral snakes are also known to perform characteristic body displays, such as elevating tails, body flattening and thrashing to further deter potential predators. (Greene 1979; Moore *et al*., 2020). In addition, true cobras, in the *Naja* genus, are infamously known to elongate ribs in their necks to present a “hood”, and many species within this genus are also able to spit venom (Westhoff *et al*., 2005). Elapid species in the monotypic genera *Hemachatus* and *Ophiophagus*, are also known to employ a defensive hooding display, alongside aposematic body patterning (Panagides *et al*., 2017).

The radiation of Asian elapids exhibits high diversity with true cobras (*Naja*), coral snakes (*Calliophis*, *Sinomicrurus*), kraits (*Bungarus*), sea snakes (*Acalyptophis, Aipysurus, Astrotia, Enhydrina, Hydrophis, Kerilia, Kolpophis, Lapemis, Laticauda,* *Pelamis, Thalassophis*) and the King Cobra (*Ophiophagus*; Das, 2010). Interestingly a large-scale phylogenetic analysis of over 4000 species of lizard and snakes places the King Cobra in a monophyletic clade with two mamba species: the black mamba (*Dendroaspis polylepis*) and the Eastern green mamba (*Dendroaspis angusticeps*; Pyron *et al*., 2013), both of which are endemic to Africa. Further ambiguity concerning the phylogenetic placing of *O. hannah* was reported by Zaher *et al*. (2019).

2.3 Elapid spatial ecology

Very high frequency radiotelemetry (VHF) is commonplace methodology when investigating the spatial ecology of snakes and has been widely applied to snake species worldwide (Tiebout III and Cary, 1987; Durner and Gates, 1993; Plummer and Mills, 2000; Baxley and Qualls, 2009; Do *et al*., 2016; Peterson *et al*., 2019; Yagi *et al*., 2020), and thus facilitates the study of a wide array of snake species, including highly variable pteroglyphs.

Elapid snakes have a broad global distribution, yet spatial ecology studies focused on this taxa are few mostly focusing on Australian species. In Australia, several studies have investigated the spatial ecology of species within the *Hoplocephalus* genus. For example, Webb and Shine (1997) investigated the spatial ecology and movements of broad headed snakes (*Hoplocephalus bungaroides*) highlighting several main points such as infrequent movements, individual heterogeneity in movement distances, high site fidelity, dependence of space use on body size and reproductive condition, and potential conspecific avoidance. Subsequently, Fitzgerald *et al*. (2002) performed radiotelemetric monitoring of Stephen's banded snake (*Hoplocephalus stephensii*) in eastern Australia and showed that individuals exhibited movement and shelter site selection likely attributed to foraging mode. The authors further showed a high degree of spatial overlap between telemetered snakes, though little concurrent overlap suggesting conspecific avoidance.

Translocation of animals has been shown to negatively impact the health and overall survival of individuals particularly among snake species (Reinert and Rupert Jr., 1999; Roe *et al*., 2010; Devan-Song *et al*., 2016). While presenting results on resident animals, Butler *et al*. (2005a; 2005b) investigated the effects of translocation on the space use, activity patterns and habitat preferences of tiger snakes (*Notechis scutatus*). The results from their papers show that translocated snakes exhibited larger areas of space use and did not remain to the confinements of protected area boundaries. Furthermore, although activity patterns were relatively consistent between resident and translocated animals, movement distance of the latter group were greater and exhibited a higher frequency of residential area use due to movements outside of the park within their study site. A similar study was subsequently conducted by Wolfe *et al*. (2018), also within Australia, on dugites (*Pseudonaja affinis*). Their results show similar findings to those of Butler *et al*. (2005a; 2005b) where translocated animals exhibited larger activity ranges, however, the dugites did not exhibit larger movement distances as was seen for tiger snakes. Wolfe *et al*. (2018) concluded two major points in their study: 1) occupied space exhibited by telemetered snakes appeared to be associated with high-risk areas, and 2) translocation negatively impacts the survival of telemetered snakes.

Whitaker and Shine (2003) investigated the movements and shelter-site use of brownsnakes (*Pseudonaja textilis*) and showed congruent movement and sheltering patterns as several other snake species which exhibit male-biased sexual dimorphism.

For example, male snakes in their study exhibited increased activity and movement during the local reproductive season, with males also utilising larger areas of space than females during this period. Furthermore, the reproductive state of females (gravid/non-gravid) also impacted the home ranges and movement frequency of telemetered individuals with gravid females restricting their movements in comparison. We also have some understanding of the space and habitat use of Australian blacksnakes (*Pseudechis porphyriacus*; Shine, 1987). Specifically, Shine (1987) showed a high degree of individual heterogeneity in habitat use, activity, space use and movement patterns within the sample, though results suggested that males utilise larger areas of space during the perceived breeding season. In addition, a severe drought during the Shine (1987) study resulted in a decrease in apparent population fecundity.

Further studies investigating elapid spatial ecology are beginning to emerge from a single study site in northeast Thailand. At the moment, these are limited to Malayan kraits (*Bungarus candidus*), banded kraits (*Bungarus fasciatus*) and King Cobras (*Opphiophagus hannah*). Mohammadi *et al*. (2014) radiotracked a single *B. candidus* for 22 days and showed the individual to have a 100% MCP home range of 12.3 ha and utilise space predominantly within deciduous forest. More recently, Knierim *et al*. (2019) investigated the spatial ecology of banded kraits, further elucidating important natural history of this species, including nest attendance. Specifically, their three snakes exhibited a mean 99% dBBMM occurrence distribution of 21.45 ± 19.56 ha, and selected less-disturbed habitats for diurnal sheltering. Although studies investigating the spatial ecology of King Cobras have been undertaken in India (e.g. Barve *et al*., 2013), the investigations out of the study site in northeast Thailand have stemmed from this current study.

2.4 King Cobras

2.4.1 Description and distribution

The King Cobra (*Ophiophagus hannah*), the only species recognised within the *Ophiophagus* genus, is the longest venomous snake in the world, exceeding lengths of 5.8 m (Das *et al*., 2010; Cox *et al*., 2012). Native to South and Southeast Asia, the King Cobra has a wide distribution across 15 countries: Bangladesh, Bhutan, Brunei Darussalam, Cambodia, southern China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Singapore, Thailand and Vietnam (Stuart *et al*., 2012; Dolia, 2018; Thapa *et al*., 2018; Figure 2.1). In addition, the altitudinal distribution of the King Cobra ranges between sea level and 2200m (Waltner, 1975; Bashir *et al*., 2010; Hrima *et al*., 2014). However, a King Cobra hatchling was discovered in October 2012 at the highest altitudinal record for the species of 2303m asl, in Mukteshwar, Nainital, India (Dolia, 2018).

Figure 2.1 Distribution of the King Cobra, modified from the IUCN website (https://www.iucnredlist.org/es/species/177540/1491874).

As is the case for many species within the Elapidae family, King Cobras are capable of administering large yields of neurotoxic venom (Li *et al*., 2006; Roy *et al*., 2010). Following the sequencing of the King Cobra genome, the only terrestrial venomous snake with a sequenced genome and one of only four elapids (Kishida *et al*., 2019), it was shown that King Cobras possess a venom and accessory gland containing a complex mixture of proteins across several toxin families, predominantly characterised by three-finger toxins and lectins (Vonk *et al*., 2013, Figure 2.2).

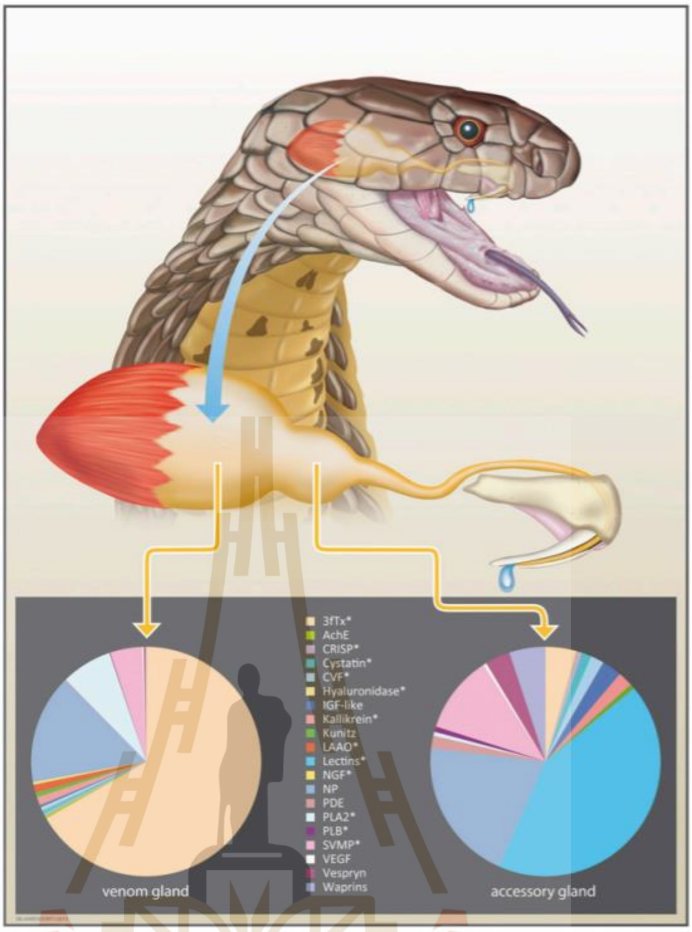

Figure 2.2 Profile of the King Cobras venom system and associated toxin families (Vonk *et al*., 2013).

Phenotypically King Cobras can be highly variable, though they are generally light-brown/black on their dorsum, which can be largely un-patterned or exhibit consistent white-yellow banding. Newly-hatched King Cobras have strongly contrasting yellow bands against a black dorsum. Ventrally the tail and body are typically grey, exhibiting a much lighter colouration than the dorsum (Das *et al*., 2010; Cox *et al*., 2012). King Cobras can elongate ribs in their necks to perform a defensive hooding behaviour as seen in species within the genus *Naja* (Panagides *et al*., 2017), exposing the yellow-orange venter of the hood.

2.4.2 Natural history

King Cobras have been largely associated with pristine forested habitat, with literature suggesting a preference for primary forests including evergreen, moist deciduous, tropical deciduous and mangrove swamps (Das, 2010). Rao *et al*. (2013) also showed telemetered King Cobras from a population in the Western Ghats, India, to primarily use evergreen forest (~83%), however, they also demonstrated a more generalist use of habitat types as King Cobras were also observed using plantation/orchard (~7%), degraded forest (~4%), agriculture (~3%), grasslands (~1%) and water bodies (~1%). Furthermore, Marshall *et al*. (2018; 2019; 2020) have shown telemetered King Cobras to use protected forested areas, alongside semi-natural areas, disturbed forest, human settlements and agriculture. This evidence suggests that King Cobras are habitat generalists and may use habitats opportunistically dependent on resource acquisition (Marshall *et al*., 2020).

As suggested by the generic epithet, King Cobras primarily predate on snakes (Bhaisare *et al*., 2010). During a radiotelemetry study based out of Agumbe Rainforest Research Station, Western Ghats, India, Bhaisare *et al*. (2010) observed a single adult male preying exclusively upon native pit vipers. Throughout a five-month study period, this adult male was observed preying upon two hump-nosed pitvipers (*Hypnale hypnale*) and 24 malabar pit vipers (*Trimeresurus malabaricus*). In addition, Tay (2019) observed a King Cobra actively foraging for, and subsequently begin ingestion of, a Sunda dog-faced water snake (*Cerburus schneiderii*), which further supports the

King Cobra as a snake specialist. However, few studies have also reported on King Cobras preying upon monitor lizards. For example, Siler *et al*. (2011) observed a male King Cobra ingesting a Cuming's water monitor (*Varanus cumingi*) in the Philippines. Furthermore, Jones *et al*. (2020) report on multiple instances of adult male King Cobras preying upon clouded monitor lizards (*Varanus nebulosus*) in northeast Thailand. This suggests that there is some plasticity in prey selection of King Cobras, though likely restricted to squamate taxa.

Another life-history trait unique to King Cobras, over other snake species, is their reproductive ecology as they are known to construct nests for oviposition, and further remain with the nests after laying. This behaviour has primarily been studied in populations throughout India, showing congruent behaviour of nest construction and females remaining with nests for varying periods of time (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). Hrima *et al*. (2014) report on general findings after locating 18 nests in the Aizawl district, Mizoram, India and provide evidence of King Cobras selecting oviposition sites on the edges of bamboo forests or other forest communities. In addition, the authors also state that nests were primarily constructed from dried bamboo leaves, on well-drained slopes near to water sources.

King Cobras are sexually dimorphic with males achieving longer lengths, and mass, than females (Cox *et al*., 2012; Marshall *et al*., 2018). This observed sexual dimorphism is likely attributed to the ritualistic male-male combat performed by King Cobras for mate acquisition (Shine, 1978; Figure 2.3). Male combat has been observed in over 120 snake species across four families (Boidae, Colubridae, Elapidae and Viperidae; Shine, 1994), for example: blacksnakes (*Pseudechis porphyriacus*; Shine *et al*., 1981) and Malayan pit vipers (*Calloselasma rhodostoma*; Strine *et al*., 2015).

Despite how well-known King Cobra male-male combat is, and many anecdotal reports on the matter, there is little to no information available within peer-reviewed literature.

Figure 2.3 King Cobra male-male combat as observed in India. Photo credit: Gowri Shankar.

2.5 King Cobra research

Many studies, using the King Cobra as a focal animal, have investigated the characteristics and properties of their venom (e.g. Joubert, 1973; Tan and Saifuddin, 1991; Li *et al*., 1994; Pu *et al*., 1995; Ahn *et al*., 1997; Huang *et al*., 1997; Pung *et al*., 2005; Jin *et al*., 2007; Rajagopalan *et al*., 2007; Zhang *et al*., 2010; Lee *et al*., 2011; Vonk *et al*., 2013; Petras *et al*., 2015; Tan *et al*., 2015; Wongtay *et al*., 2019; Tan *et al*., 2020), or feature them within phylogenetic and taxonomic studies (Slowinski and Keogh, 2000; Pyron *et al*., 2013; Suntrarachun *et al*., 2014; Zaher *et al*., 2019). In contrast, most ecological information regarding King Cobras are typically presented in broad field guides and focused books (Das *et al*., 2010; Cox *et al*., 2012; Charlton, 2018). Very few studies have performed comprehensive investigation into the ecology and natural history of King Cobra populations. The studies which have performed these investigations are primarily focused on King Cobra populations throughout India (Barve *et al*., 2013; Rao *et al*., 2013; Shankar *et al*., 2013a; 2013b; Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018) and a single study site in Northeast Thailand (Marshall *et al*., 2018; Silva *et al*., 2018; Jones *et al*., 2020; Marshall *et al*., 2019; 2020), stemming from data collected from this current investigation.

Barve *et al*. (2013) provide preliminary results on the spatial ecology of King Cobras in the Western Ghats, India. During this study, Barve *et al*. (2013) tracked three male King Cobras, one of which was translocated approximately 40 km away from the initial capture site. Their results show that the single translocated snake exhibited a much greater total distance travelled, and a larger minimum convex polygon (MCP) home range estimate; however, the individuals were all radiotracked for varying periods of time, which limited the inferences made about compared space use estimates. The non-translocated individuals exhibited an MCP area of 14.8 km^2 and 30.0 km^2. Also focusing on a population in the Western Ghats, India, Rao *et al*. (2013) present findings on the habitat and microhabitat use of telemetered King Cobras. They show that King Cobras exhibit a wide-range of habitat use, however, they recorded a predominant use of evergreen forests.

Three studies have investigated the nesting ecology of King Cobras in India, focusing on the states of Karnataka, Mizoram and Uttarkhand (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). The results from these three studies showed largely congruent results with adult females constructing nests of bamboo leaves, twigs and other forest debris, however, the size and exact construction varied across sites. All studies observed females sitting on top of the constructed nests for varying lengths of time. The exact reasoning for females remaining with the nests is largely ambiguous, though is postulated as a strategy of predator deterrence, to limit excess rainfall from reaching eggs, or to compact the nest for thermal stability.

Outside of India, studies have focused on a population of King Cobras at the Sakaerat Biosphere Reserve (SBR), Northeast Thailand. Marshall *et al*. (2018) highlighted the main threats posed on King Cobras as they move across a permeable protected area boundary. The results of their study showed that natural deaths were rare and cases of mortality were highly skewed towards anthropogenic sources, owed primarily to persecution events, and vehicle collisions, which is highly consistent with other studies which show that natural deaths are rare when anthropogenic pressures persist (Kapfer *et al*., 2008; Meek, 2012; Baker *et al*., 2016).

Marshall *et al*. (2019) radiotracked nine King Cobras over a 1765-day study period and estimated a mean 95% MCP space use of 337.47 ± 235.79 ha and a mean kernel density estimate (KDE) of 493.42 ± 335.60 ha. The smallest kernel estimate was exhibited by a juvenile male at 52.65 ha and the largest was from an adult male at 1073.55 ha. Marshall *et al*. (2019) further reported individual heterogeneity in habitat use, with individuals using protected areas and bordering human settlements, agriculture and semi-natural areas.

Silva *et al*. (2018) introduced dynamic Brownian Bridge Movement Models (dBBMM) as a method of investigating movement patterns and space use over traditional space use estimators typically used in reptile spatial ecology studies, namely

MCPs and KDEs. They found that these traditional methods incorporated greater omission and commission errors over novel dBBMM estimates. Furthermore, dBBMM's were effective at detecting movement corridors and long-term shelter sites. Using radiotelemetry data from one juvenile male and one adult male, Silva *et al.* (2018) calculated a 99% dBBMM occurrence distribution of 1040.1 ha and 940.9 ha respectively. In addition, they further recorded broad habitat use by telemetered King Cobras across multiple forest types and disturbed anthropogenic areas.

The studies undertaken by Silva *et al*. (2018) and Marshall *et al*. (2019) were further expanded upon in Marshall *et al*. (2020), using a bolstered dataset of telemetered King Cobras. They radiotracked seven King Cobras for an average of 649.47 ± 112.3 days, and recorded 99% dBBMM estimates between 149.28 ha and 1081.54 ha. In addition to these estimates, Marshall *et al*. (2020) presented results which suggest that King Cobras restricted movement when moving through an agricultural landscape, and will further remain near to potential anthropogenic threats provided that alternative habitat features are available.

A preliminary phylogenetic analysis was undertaken by Suntrarachun *et al.* (2014) using samples collected from multiple provinces, and localities, across Thailand. Through amplification of two mitochondrial loci, their results suggest that localities largely conformed to two unique clades representing King Cobras from North and South Thailand. The work conducted by Suntrarachun *et al*. (2014) provides a premise for the potential speciation which is present within King Cobra populations in Thailand. Further work will likely find similar disparity between populations throughout the King Cobra's wide distribution and suggests that studies focused in Thailand and India may actually represent the ecology of closely related species, or subspecies, under the *O. hannah* synonym.

2.6 Study site

2.6.1 Location and history

The Sakaerat Biosphere Reserve (SBR) was established in 1967 and accepted into the UNESCO Man and Biosphere (MAB) reserve network program, as one of 157 biosphere reserves worldwide, in 1977. The SBR is under the administrative authority of the Thailand Institute of Scientific and Technological Research (TISTR) and is situated approximately 300 km north-east of Bangkok, bordering the Khorat Plateau, Nakhon Ratchasima province (Figure 2.4). Designated biosphere reserves within the MAB program integrate three primary functions: conservation of cultural- and biological-diversity; sustainable economic development; and logistical support for research and education. These functions are implemented via three zones: Core Areas comprising a strictly protected area contributing to maintaining ecosystem functions, biodiversity and genetic variation; Buffer Zones which closely borders the core areas, offer less protection yet promote activities consistent with sustainable ecological practises, reinforcing further research and education; and Transitional areas allowing local communities to develop socio-culturally and ecologically sustainable practises (https://en.unesco.org/biosphere/about).

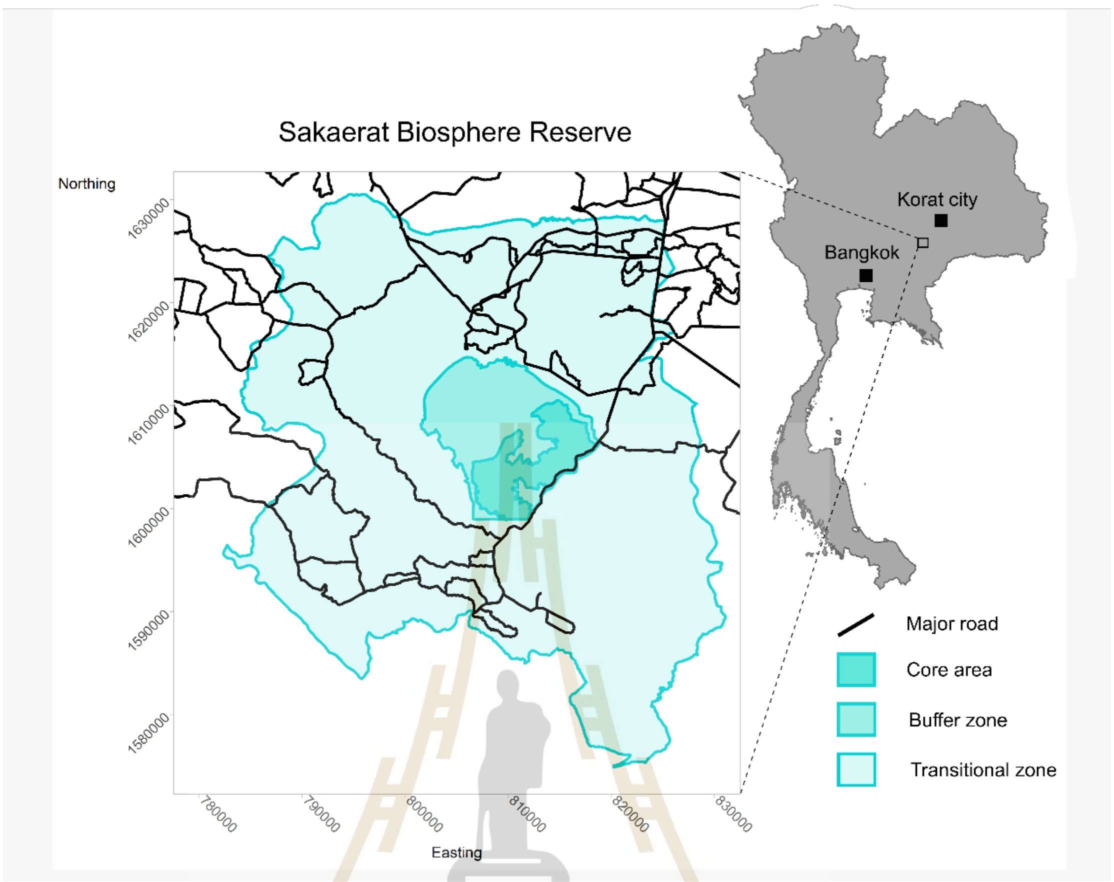

Figure 2.4 Sakaerat Biosphere Reserve in Northeast Thailand in relation to Bangkok and Korat City. Blue areas depict the boundaries of each area comprising the reserve. A greater level of protection is indicated with an increase in opacity: transitional zone, buffer zone and core area. Black lines show major roads throughout the reserve.

The core protected area of the SBR, offers the greatest level of protection for wildlife, with routine patrols by reserve rangers. Totalling an area of 80 km^2, the core area is dominated with two main forest types: dry evergreen forest makes up 60% of this area from the South-West throughout the North-East, containing trees predominantly in the *Hopea* and *Hydnocarpus* genera; and dry dipterocarp forest which constitutes 18% of the total core area to the North-East, characterised by widely-spaced trees in the *Dipterocarpus*, *Shorea* and *Gardenia* genera (Thailand Institute of Science and Technological Research, 2018). Also present within the core area are two patches of mature reforested plantation of *Acacia* and *Eukalyptus* trees, covering another 18%. Much of the remaining area contains small patches of bamboo (1%), open grassland (1%) and buildings (2%) within the Sakaerat Environmental Research Station (SERS). The buffer zone extends to the North from the core area, and further encompasses the regenerating plantation forest. The transitional zone is the largest area, which offers the lowest level of protection. There are over 72,000 residents occupying the transitional zone, distributed throughout 159 villages, where the land is primarily used for agriculture (most commonly rice, cassava, sugar cane and corn).

2.6.2 Wildlife

The SBR boasts high faunal biodiversity, likely attributed to the mosaic of available habitats and microhabitats within the core area/buffer zone and also within the transitional zone which partly envelopes parts of Thap Lan National Park. Within the entirety of the biosphere reserve, the landscape supports over 80 mammals from smaller shrew species (*Tupaia glis*, *Suncus etruscus*, *Hylomys suillus*), a variety of bat species (e.g. *Cynopterus* sp., *Rousettus leschenaultia*, *Megaderma spasma*), mid-sized primate species (*Macaca nemestrina*, *Hylobates lar*), to larger, iconic species such as tigers (*Panthera tigris*) and gaur (*Bos gaurus*; TISTR, 2020a). Bird diversity is exceptionally high within the reserve with approximately 235 species currently recognised (TISTR, 2020b), hosting the national bird of Thailand, the Siamese fireback (*Lophura diardi*), a major snake-predator the crested serpent eagle (*Spilornis cheela*), and iconic hornbill species (*Buceros bicornis*, *Anthacoeros albirostris*, *Rhyticeros undulatus*).

The SBR further supports broad herpetofaunal diversity, with just under 30 recognised species of amphibians from miniscule microhylids (e.g. *Micryletta inornate*, *Microhyla pulchra*) to the common caecilian (*Icthyophis kohtaoensis;* TISTR, 2020c), and approximately 90 species of reptiles (TISTR, 2020d). Thirty-four of the reptilian species are represented by lizards from the families Agamidae (e.g. *Calotes mystaceus*, *Physignathus cocincinus*, *Acanthosaura cardomonensis*; Wood *et al*., 2010), Gekkonidae (e.g. *Cyrtodactylus intermedius*, *Hemidactylus frenatus*, *Ptychozoon trinotaterra*), Scincidae (e.g. *Eutropis macularia*, *Lygosoma quadrupes*), and Varanidae (*Varanus nebulosus*). Also present are two chelonian species in the families Bataguridae (*Cyclemys dentata*) and Testudinidae (*Indotestudo elongata*). The remainder of the herpetofaunal diversity contains over 60 species of snakes across multiple dominant families, however, only seven species are represented by members of the Elapidae family, namely kraits (*Bungarus candidus*, *Bungarus fasciatus*), coral snakes (*Calliophis maculiceps*, *Sinomicrurus maccellandi*), true cobras (*Naja kaouthia*, *Naja siamensis*) and the King Cobra (*Ophiophagus hannah*).

2.6.3 Climate

Under the authority of TISTR, there are five weather stations distributed throughout the core area of the SBR. Marshall *et al*. (2020) downloaded daily rainfall and temperature data from the SERS online repository (TISTR, 2020e) for the 2012 – 2018 period, and delineated the SBR climate into three main seasons: *hot* which falls between March and September showing a mean temperature of 33.8 ± 2.8 ºC and a mean rainfall of 2.5 ± 7.9 mm; *wet* which spans between September and January, exhibiting a mean temperature of 29.9 ± 2.2 ºC and a mean rainfall of 5.9 ± 11.1 mm; and *dry* that constitutes the remainder of the year between January and March, with mean temperature of 29.0 ± 3.5 ºC and a mean rainfall of 0.2 ± 0.8 mm (Figure 2.5; Figure 2.6). This is typical for a tropical climate, with clear seasonality throughout the year and no frost.

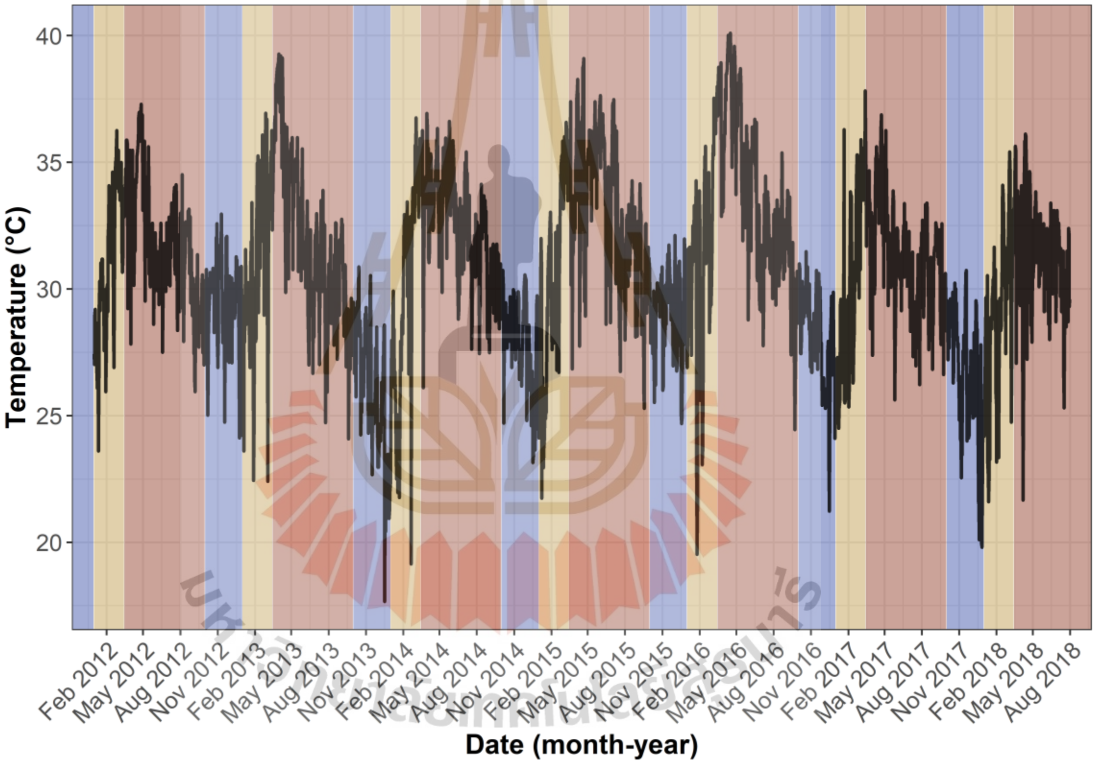

Figure 2.5 Temperature readings from SBR weather stations between 2012 – 2018.

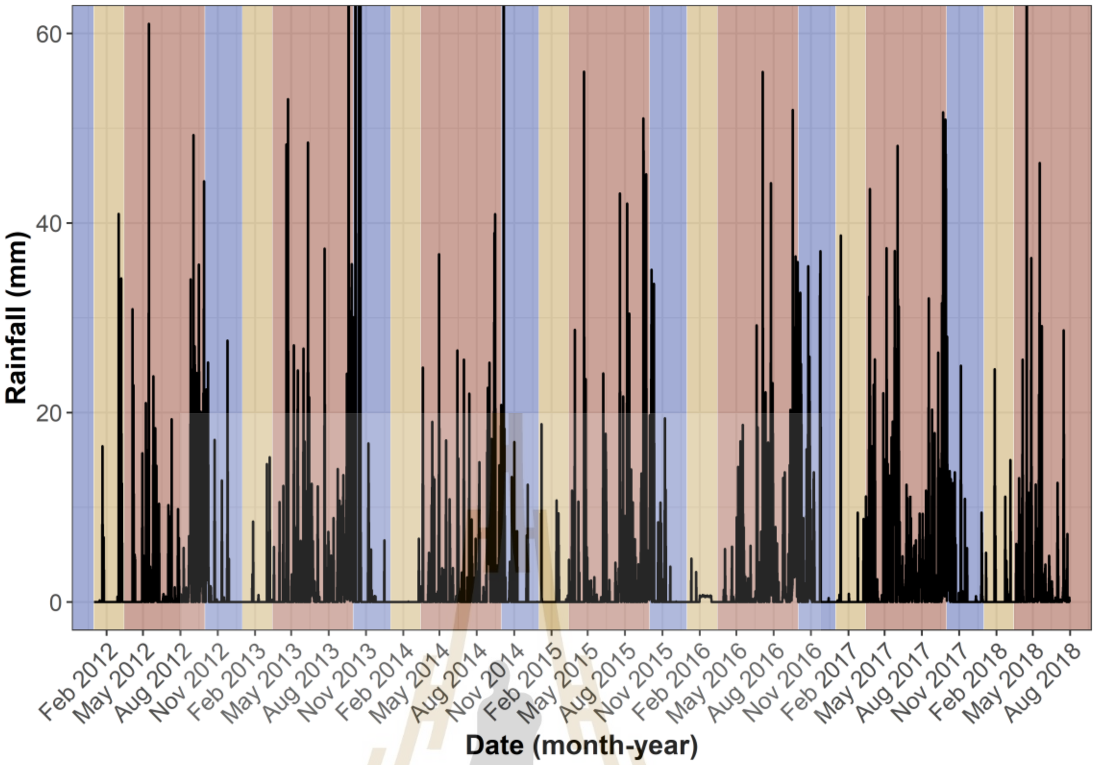

Figure 2.6 Daily rainfall collected from SBR weather stations between 2012 – 2018.

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CHAPTER III

KING COBRA SPATIAL ECOLOGY AND RESOURCE USE

3.1 Introduction

How animals utilise space is one of the most fundamental questions when investigating a population of conservation concern (Gremillet and Boulinier, 2009). Investigating animal movement can elucidate information concerning reproductive behaviours (Kamath and Losos, 2018), adaptations to anthropogenic infringement (Valeix *et al*., 2012; Loveridge *et al*., 2017), predator-prey dynamics (Courbin *et al*., 2016; Vogt *et al*., 2018) and interactions with conspecifics in the population (Jellen *et al*., 2007). Animal space use specifically can be directly correlated with landscape quality and the availability of resources (Breininger *et al*., 2011, Marshall *et al*., 2020).

Reptile studies have traditionally used space-use estimators, typically revolved around the home range of an animal (Row and Blouin-Demers, 2006a), defined by Burt (1943) “home range is the area than an individual traverses in its ‘normal’ activities of food gathering, mating and caring for young”. Specifically, previous studies have used minimum convex polygons (MCPs) and kernel density estimators (KDE; Worton, 1987).

Changes in tracking frequency or duration can result in errors in MCP home range estimates, whereas KDE estimates are highly sensitive to small or large datasets, resulting in omission and commission errors respectively (Fieberg and Börger, 2012; Silva *et al*., 2020). The issue specifically is due to the complicated nature of movement analyses, as the movement of individuals is inherently influenced by both spatial and temporal factors. Minimum convex polygons and KDEs do not include time within their estimates, and new estimators incorporating trajectory-based analyses are becoming more commonplace in understanding animal space use (Downs and Horner, 2012; Lyons *et al*., 2013; Silva *et al*., 2020).

Spatial ecology studies are now exploring the underlying behavioural mechanisms that influence animal movement over space and time (Schick *et al*., 2008; Kranstauber *et al*., 2012). Animals can adopt several behavioural states throughout a study period, such as mating, predator avoidance, sheltering and maintaining thermal optima (Morales *et al*., 2004; Jonsen *et al*., 2005; Gurarie *et al*., 2009; McClintock *et al*., 2012). To incorporate these transitions in behavioural states, Kranstauber *et al.* (2012) proposed dynamic Brownian Bridge Movement Models (dBBMM). Specifically, dBBMMs incorporate behavioural change point analysis to allow motion variance (σ^2m) to change in response to varying behavioural states (Gurarie *et al*., 2009).

Species which exhibit large areas of space use are required to move greater distances within a landscape, increasing energetic expenditure and the chance of encountering predators, competitors and conspecifics (Yoder *et al*., 2004; Lendrum *et al*., 2014). Larger areas of space use may be linked to sparse, or disjunct, resource availability particularly within landscapes heavily altered by anthropogenic development (Arrondo *et al*., 2018). Human-modified land can change the ecology of a landscape, which in turn, alters the behaviour of animals (Gaynor *et al*., 2018) and introduces new risks to taxa (Clark *et al*., 2011; Robertson *et al*., 2013, Karraker *et al*., 2018). Reptiles can be particularly vulnerable to land use change and are experiencing worldwide population declines as a result (Gibbons *et al*., 2000; Todd *et al*., 2010). Understanding how reptiles within modified landscapes are moving through space in relation to landscape features and resources will allow us to develop targeted conservation actions.

Resource selection analysis (RSA) offers a method for predicting spatial patterns in relation to available resources within a landscape (Manly *et al*., 2002). Through combining animal movement data with discrete spatial units (such as environmental information per pixel), studies have attempted to understand the relationship between available resources and observed movement patterns exhibited by focal animals (McDonald *et al*., 2013; Boyce *et al*., 2015). The concern with using RSAs is defining a spatial domain relevant to a study animal (Lele *et al*., 2013; Northrup *et al*., 2013). Case-controlled logistic regressions (CLRs) can address this issue by modelling utilised space as a function of observed movement and selection, limited to a pre-specified space (Boyce *et al*., 2003; Baasch *et al*., 2010). Avgar *et al*. (2016) introduced a CLR-based approach to simultaneously estimate movement alongside resource-selection, allowing the effects of environmental components on animal movement and selection to be differentiated, termed integrated step-selection analysis (iSSA). Following work presented by Avgar *et al*. (2016), further tools have been developed for conveniently modelling animal movement alongside resource selection, namely integrated step-selection functions (iSSF; Signer *et al*., 2019). Specifically, iSSF uses known locations used by individuals, and compares these to randomly generated locations (or steps) to evaluate the locations, and resources, used by an animal to un-used, yet available, resources within a limited spatial domain (Thurfjell *et al*., 2014; Avgar *et al*., 2016; Signer *et al*., 2019).

Although the implementation of movement data with resource selection has been broadly developed in spatial ecology studies (Manly *et al*., 2002; Boyce *et al*., 2003; Boyce *et al*., 2013; Avgar *et al*., 2016; Signer *et al*., 2019), there remains a paucity in the available literature regarding this topic concerning reptile populations. Snakes in particular exhibit several traits which make them an interesting model for investigating their space use and resource-associated movement. Firstly, snakes can show clear behavioural states linked to bouts of foraging (Reinert *et al*., 1984; Wasko and Sasa, 2012), digestion (Siers *et al*., 2018), thermoregulation (Brown *et al*., 1982; Row and Blouin-Demers, 2006b) and mating (Shine *et al*., 2004). In addition, snakes are not only located within human-modified areas (Smith *et al*., 2020; Marshall *et al*., 2020), but can be detrimentally impacted by associated land conversions (Gibbons *et al*., 2000). It is therefore important to understand how snake populations are adapting to heterogeneous landscapes, influenced by humans, while maintaining important behaviours linked to their natural history; all while accessing necessary resources within the landscape. The implications of which can inform wildlife managers on effective measures to conserve biodiversity.

The King Cobra (*Ophiophagus hannah*) presents as an ideal model to evaluate how space use is related to resource acquisition. King Cobras are large, highly mobile snakes that utilise large areas of space (Marshall *et al*., 2019; Marshall *et al*., 2020), which makes them similar to wide-ranging mammalian species of which conservation initiatives are often based-off, due to their sensitivity to landscape fragmentation (Henle *et al*., 2004). The population of King Cobras within the Sakaerat Biosphere Reserve (SBR) in northeast Thailand, in particular, are exposed to a highly heterogeneous landscape due to infringing human-modified area and roads adjacent to forested areas (Silva *et al*., 2018; Marshall *et al*., 2019; Marshall *et al*., 2020; Vaeokhaw *et al*., 2020).

We therefore set out to investigate the space use and resource acquisition by King Cobras within the SBR using several proxies: 1) Overall space use estimated using dynamic Brownian Bridge Movement Models; 2) The comparison of used locations versus randomly generated available locations using individual- and population-level integrated Step Selection Functions; 3) Changes observed in motion variance throughout individual King Cobras tracking regimes, output from dynamic Brownian Bridge Movement Models.

3.2 Methods

3.2.1 Study area

We conducted this research at the Sakaerat Biosphere Reserve (SBR), in the Nakhon Ratchasima Province in Northeast Thailand (14.44-14.55º N, 101.88-101.95º E, Figure 3.1). The reserve was established in 1967, and now functions under the Man and Biosphere (MAB) Program, becoming a UNESCO Biosphere Reserve in 1977. The SBR is comprised of three main areas offering varying levels of protection: a core area, buffer zone and transitional zone (Figure 3.1). The core protected area offers the greatest level of protection for wildlife, with routine patrols by reserve rangers. Totalling an area of 80 km^2, the core area is dominated with two main forest types: dry evergreen forest makes up 60% of this area from the South-West throughout the North-

East, containing trees predominantly in the *Hopea* and *Hydnocarpus* genera; and dry dipterocarp forest which constitutes 18% of the total core area to the North-East, characterised by widely-spaced trees in the *Dipterocarpus*, *Shorea* and *Gardenia* genera (Thailand Institute of Science and Technological Research, 2018). Also present within the core area are two patches of mature reforested plantation of *Acacia* and *Eukalyptus* trees, covering another 18%. Much of the remaining area contains small patches of bamboo (1%), open grassland (1%) and buildings (2%) within the Sakaerat Environmental Research Station (SERS). The buffer zone extends to the North from the core area, and further encompasses the regenerating plantation forest. The transitional zone is the largest area, which offers the lowest level of protection. There are over 72,000 residents occupying the transitional zone, distributed throughout 159 villages, where the land is primarily used for agriculture (most commonly rice, cassava, sugar cane and corn).

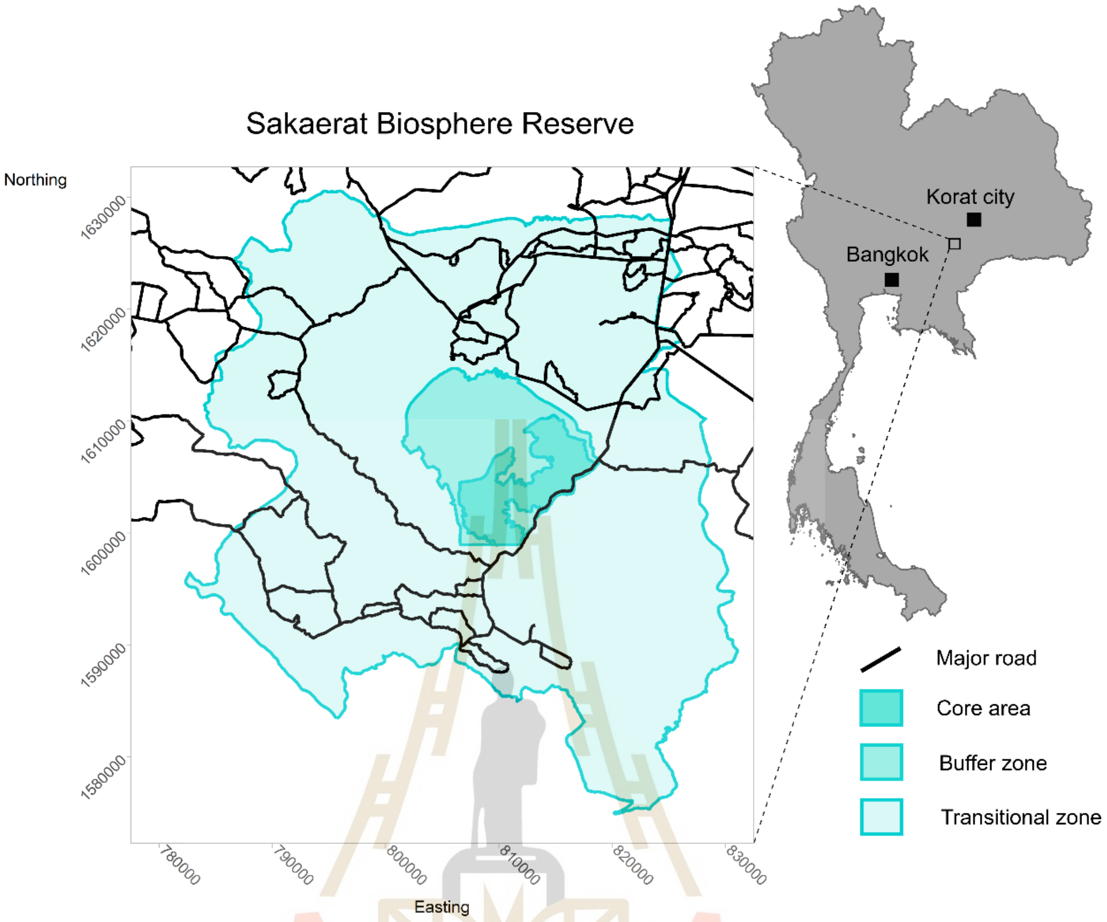

Figure 3.1 Sakaerat Biosphere Reserve in Northeast Thailand in relation to Bangkok and Korat City. Blue areas depict the boundaries of each area comprising the reserve. A greater level of protection is indicated with an increase in opacity: transitional zone, buffer zone and core area. Black lines show major roads throughout our study area.

All areas within the SBR were considered for radiotelemetry, though the inclusion of an individual depended heavily on the accessibility to a capture location. As a result, sampling efforts were generally limited to the core area, with adequate accessibility from SERS roads and trails; and the transitional zone which is webbed with many major and minor roads, including the large, four-laned Highway 304. The construction of the Highway 304 began in 1956, and was subject to further improvements in 1966, however, was only extended from two to four lanes in 2005 (Laurence, 2014; Vaeokhaw *et al*., 2020).

3.2.2 Snake capture for radiotelemetry

King Cobras are secretive and difficult to detect naturally. We therefore used several methods for locating and capturing study animals. In a separate study, based at SERS, we utilised 24 standardised Y-shaped 20 x 20 x 20 m trap arrays, connected to 360 50 cm funnel traps, which were opened for one-week intervals every month between March 2012 and April 2013. The placement of the traps was random throughout the core area of the SBR. In addition, we also used 36 T-shaped trap arrays, connected to 2 m funnel traps specifically designed to capture larger animals, such as the King Cobra. These latter 36 traps were placed in areas with a high perceived probability of capturing *O. hannah*. We also performed unstandardized visual surveys throughout all three zones of the SBR, where accessibility permitted. We conducted these surveys using motorcycles on major and minor roads, alongside walking surveys along paths and forested areas. Additionally, we heavily relied on a conservation initiative within the transitional zone of the SBR, giving local residents an opportunity to call researchers and staff based at SERS; alongside an option to contact locally trained rescue teams, who would bring study animals to the research station. As very little is known about the ecology and natural history of King Cobras, we conducted visual surveys at any time within a 24-hour period; however, as King Cobra are believed to be diurnal (Cox *et al*., 2012), we primarily performed these surveys in daylight hours (06:00am – 18:00pm). Lastly, following telemetry of adult males (described in 3.2.4

below), we attempted to use the Judas technique to capture adult females (Smith *et al*., 2016). As male King Cobras will actively search for reproductive females, we closely monitored the males during the King Cobra breeding season until we suspected that a male was interacting with a conspecific. This was determined by concluding that a snake is not moving from its current location (via triangulation), yet the radio signal exhibits inconsistencies common with a moving animal, suggesting that the snake is moving around in one location. At this time, we moved in to attain a visual on the telemetered snake to investigate if a conspecific could be located.

We recorded the location (Universal Transverse Mercator 47 N WGS 84 datum) of each capture location using handheld GPS units (Garmin 62 and 64 models), as well as capture time and date. We named unique individuals based on their age-class and chronological addition to the project (e.g. the fifty-eighth King Cobra captured, an adult female, is allocated the ID: AF058). We initially marked snakes 001 – 053, using a scalation branding method as used in Winne *et al*. (2006). From individual 054 onwards, we used passive internal transponders to distinguish unique snakes. We chose individuals to be included in the radiotelemetry study based on several factors: 1) King Cobras were large enough to have a transmitter implanted, which we evaluated as the transmitter weighed no more than 5% of the total body mass of a snake, 2) individuals appeared to be in good health, which was qualitatively assessed by the presence of a neural arch, the visibility of ribs and any un-healed wounds, 3) snakes were within a reasonable distance to SERS, with good accessibility surrounding the capture location.

3.2.3 Transmitter implantation

We maintained captured King Cobras at SERS using large, opaque plastic boxes, providing a water dish and shelter. Following assessment of a captured snake, and upon determining if an individual is to be added to the project, we contacted D.V.M. Wirongrong Changphet, a veterinarian at the Nakhon Ratchasima Zoo, to request that surgery is performed. We held snakes at SERS until the veterinarian was available to perform surgery. We prepared for surgery using aseptic protocols, which included boiling surgery tools in water for approximately 30 minutes, and subsequently placing the equipment in 95% ethanol until the veterinarian was ready to use them. We disinfected all surfaces with 95% ethanol, before introducing the snake to the surgery table. We then prepared snakes for surgery by using the inhalant anaesthetic isoflurane, until full muscle-tone was lost in the snakes. Upon tone-loss, we scrubbed the incision site on the snake with iodine, followed by 95% ethanol. Surgery was subsequently performed following methodology outlined in Reinert and Cundall (1982) and Hardy and Greene (2000), inserting the VHF radio-transmitter (Holohil SI-2T or AI-2T) in to the coelomic cavity and running the antennae laterally below the subcutaneous tissue (Figure 3.2).

Figure 3.2 The veterinarian (D.V.M. Wirongrong Changphet) performing transmitter implantation surgery on *O. hannah*.

The veterinarian made the incision approximately one-third of the total body length up from the cloaca, toward the anterior, cutting where the dorsal scales meet the ventral scales. She performed blunt incision using curved hemostats, to penetrate the coelomic cavity, and inserted the transmitter in to the coelom. She then fed the antennae in to a feeding tube and ran this laterally between the subcutaneous tissue and peritoneum, making another small incision between the dorsal scales to allow for the feeding tube to be pulled out. Once the veterinarian was pleased with the placement of the transmitter, she used soluble stiches to suture the muscle tissue. She then finished by using insoluble stiches to suture the scales using hemostats, and finished with square knots (Figure 3.3). Once sutures were tied off, the veterinarian applied antibacterial gel to the incision site, to reduce the chance of infection.

Figure 3.3 The incision site on a King Cobra following successful surgery.

3.2.4 Radio tracking snakes

We released implanted King Cobras within 24 hours post-surgery, as close to their capture location as possible. we attempted to record the location of release sites of all telemetered individuals; however, we report the first recorded location as a release location when we failed to do this (Figure 3.5).

We tracked individuals 001 – 005 using a continuous tracking method, following recommendations from a similar study being conducted in India. However, upon discovering the death of AM005 (Strine *et al*., 2014), we altered these protocols to allow for more standardised sampling intervals. We therefore relocated telemetered snakes, 006 – 034, four times per day, at approximately 06:00am, 11:00am, 16:00pm and 20:00pm. Due to staff and equipment limitations, we altered these protocols further and began tracking individual 054 onwards three times per day, at approximately 08:00am, 13:00pm and 18:00pm, with a combined mean time lag between tracks of 8.93 ± 0.06 hours. The time intervals are approximations and we had to track snakes early in the morning or late in to the night on occasion, depending on individual-based movement, terrain and accessibility to snake locations.

We used a triangulation method to determine a snake's location, maintaining a minimum distance of 10 m away, giving us reasonable confidence that a snake was within a 5 m^2 area. We performed triangulation via determining the direction that a snake is in, measuring a line on the GPS unit, and moving to another location surrounding the snake to perform again. We repeated this for three to five locations surrounding a snake, until an intersection corresponding to the snake's estimated location was achieved on the GPS (Figure 3.4). When individuals were in conspicuous locations (such as the edge of a busy road, or at the edge of a human settlement), we also homed-in on the signal to determine the exact location. We recorded the estimated location using a handheld GPS unit, and further recorded the accuracy of the unit in that location (important for subsequent spatial analyses). Lastly, we recorded the date and time that a snake was pinpointed in a specific location.

Figure 3.4 An intersection from measured lines on a Garmin 64s GPS unit.

3.2.5 Statistical analyses

3.3.5.1 Motion variance and space use

We ran dynamic Brownian Bridge Movement Models (dBBMM), implemented using the *move* package v.3.1.0 (Kranstauber *et al.*, 2016), to estimate the motion variance of all telemetered King Cobra. We also extracted 90, 95 and 99% contours using the *adehabitatHR* v.0.4.16 (Calenge, 2006) and *rgeos* v.0.4.2 (Bivand and Rundel, 2020) packages to estimate the space used by individuals. We opted to run dBBMM's as traditional home range estimates used in reptile studies, can over or under-represent the actual space used by an individual (Silva *et al*., 2020). Minimum Convex Polygons (MCP) specifically can result in errors depending on inconsistences with tracking frequency or study duration. Kernel Density Estimates (KDE) are highly sensitive to small or large datasets, resulting in omission and commission errors respectively (Fieberg and Börger, 2012; Silva *et al*., 2020).

3.2.5.2 Integrated Step-Selection Functions

We implemented integrated Step-Selection Functions (iSSF) using the *amt* package v.0.0.6 (Signer *et al*., 2019) to assess the influence of specific landscape features on King Cobra movement (i.e., avoidance or attraction). We used an inverted raster layer which expresses Euclidean distances from landscape resources within each pixel; which we inverted for facilitating the interpretation of model outputs (Marshall *et al*., 2020). The iSSF uses fixes from movement data where we know the animal was, and compares these true fixes with randomly generated fixes within an available spatial domain to the telemetered animal. Following reasoning in Fortin *et al*. (2005) and Marshall *et al*. (2020), we produced 200 random fixes for each step (move), which allowed us to sample a broad area surrounding each true location. Our telemetry data is very coarse when compared to GPS telemetry datasets, which is why we have opted for such a high number of randomly simulated fixes (Northrup *et al*., 2013; Thurfjell *et al*., 2014); which in turn, allowed us to sample rare resources within our chosen domain.

We estimated the avoidance and attraction of individual *O. hannah* by creating nine models, including step length and turning angle as a null model. Six of our models used a single resource type to predict selection and the final three models used multiple resources as predictors (Table 3.1).

Table 3.1 Model formula for the nine models used in the ISSF analysis.

Model	Model formula
model1	log_sl*cos_ta+strata(step_id_)
model2	log_sl*cos_ta+strata(step_id_)+dist_forest+dist_forest:log_sl+dist_forest:cos_ta
model3	log_sl*cos_ta+strata(step_id_)+dist_settle+dist_settle:log_sl+dist_settle:cos_ta
model4	log_sl*cos_ta+strata(step_id_)+dist_semiNat+dist_semiNat:log_sl+dist_semiNat:cos_ta
model5	log_sl*cos_ta+strata(step_id_)+dist_road+dist_road:log_sl+dist_road:cos_ta
model6	log_sl*cos_ta+strata(step_id_)+dist_water+dist_water:log_sl+dist_water:cos_ta
model7	log_sl*cos_ta+strata(step_id_)+dist_road+dist_forest+dist_semiNat
model8	log_sl*cos_ta+strata(step_id_)+dist_road+dist_forest+dist_settle
model9	log_sl*cos_ta+strata(step_id_)+dist_road+dist_forest+dist_water

We also assessed the resource acquisition of our sample on a population-level by using modified code supplied by Muff *et al.* (2020a; 2020b). Specifically, we incorporated a Poisson model with stratum-specific effects, and a prior precision of 0.0001 for slope coefficients. As JM002, AF004 and AM005 were tracked using a unique tracking method, we excluded these individuals from any individual- and population-level iSSF analyses. Furthermore, due to the homogenous nature of habitat selection exhibited by AM007, AM026 and JF055, we also removed these from the iSSF analyses. We fit Bayesian models using the *INLA* v.20.03.17 package (Rue *et al*., 2020) via integrated nested Laplace approximations. As per the individual-level iSSF, we simulated 200 random points for each step. However, we only incorporated single-factor models into the population-level iSSF: forest, roads, semi-natural areas, settlements and water.

We report estimates as attraction/association and avoidance, according to if the estimates are positive or negative respectively. We term resources as being "weakly" attracted to/avoided if confidence intervals overlap zero. In contrast, we term a "strong" attraction/avoidance if no overlap with zero is observed, giving us greater confidence in our estimates.

3.2.6 Software and data

We completed all analyses in R v.3.5.3 (R Core Team, 2019) and R Studio v.1.2.1335 (R Studio Team, 2019). We performed any data manipulation using R packages *dplyr* v.0.8.3 (Wickham *et al*., 2019), *lubridate* v.1.7.4 (Grolemund and Wickham, 2011), *readr* v.1.3.1 (Wickham *et al*., 2018), *reshape2* v.1.4.3 (Wickham, 2007), and *stringr* v.1.4.0 (Wickham, 2019). We worked with rasters and shapefiles using R packages *raster* v.2.8.19 (Hijmans, 2019), *rgdal* v.1.4.3 (Bivand *et al*., 2019) and *sp* v.1.3.1 (Pebesma and Bivand, 2005; Bivand *et al*., 2013). We created visuals using a combination of R packages *cowplot* v.0.9.4 (Wilke, 2019), *ggplot2* v.3.2.1 (Wickham, 2016), *ggspatial* v.1.0.3 (Dunnington, 2018), *scales* v.1.1.0 (Wickham and Seidel, 2019) and *scico* v.1.1.0 (Pederson and Crameri, 2018).

3.3 Results

3.3.1 King Cobra captures 2013 – 2020

We captured 24 King Cobras between 2013-03-01 and 2020-07-28, that were suitable for radiotracking, comprised of nine adult males, eight adult females, five juvenile males, and two juvenile females. We categorised female *O. hannah* with a snout-to-vent length (SVL) of <2000 mm as juvenile and >2000 mm as adult. We further categorised male King Cobras as juvenile if their SVL was <2200 mm and adult if >2200 mm. Three individuals, AM006, AM007 and AF010 were captured and lost from the project due to transmitter failure, but were subsequently recaptured after 842, 1405 and 280 days missing respectively. We therefore report on the information from the recapture event, due to improved data recording as time went on. Due to the varying methods deployed, we captured nine individuals from villager notations, seven opportunistically, three using the Judas method, three on active surveys and two individuals using passive traps; with seven discovered in the core area, four in the buffer zone and 13 in the transitional zone of the SBR (Figure 3.5).

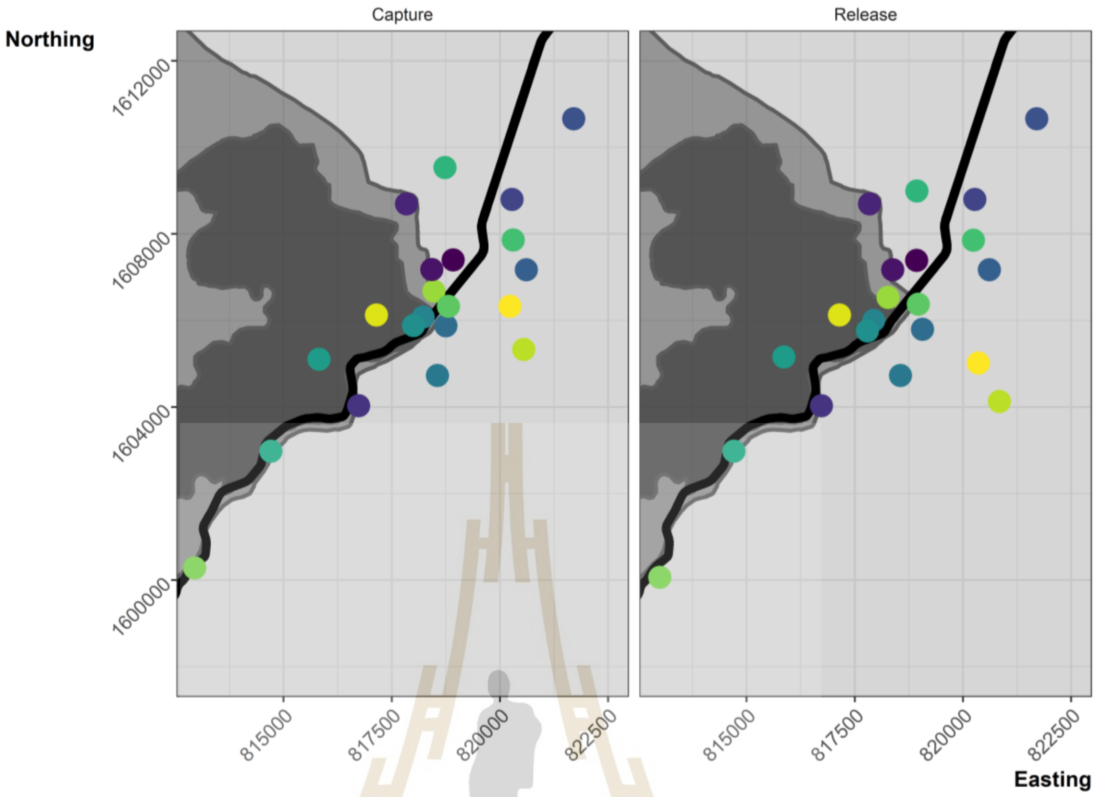

Figure 3.5 Capture and release locations for all telemetered *O. hannah* between 2013-03-01 and 2020-07-28. Coloured dots represent unique individual telemetered King Cobra. Grey areas depict the boundaries of each area comprising the reserve. A greater level of protection is indicated with an increase in opacity: transitional zone, buffer zone and core area. Black line shows the Highway 304.

3.3.2 King Cobra space use and resource use

We tracked 24 King Cobras between 2013-03-01 and 2020-07-28 for an average of 322.93 ± 51.2 days (range = 46.73 – 1176.1 days). We performed 869 ± 143 fixes (range = 120 – 3122 fixes) per individual on average, with a mean time lag of 8.93 ± 0.06 hours (range = 0.05 – 793.85 hours, Figure 3.6) between fixes. King Cobras relocated an average of 254 ± 43 times (range = 31 – 985 times) during their tracking duration and had a mean dBBMM 99% occurrence distribution of 543.89 ± 81.75 ha (range = 82.09 – 1843.75 ha). Fixes were broadly spread across our study area (Figure 3.7), though many were densely situated within semi-natural areas (Figure 3.8).

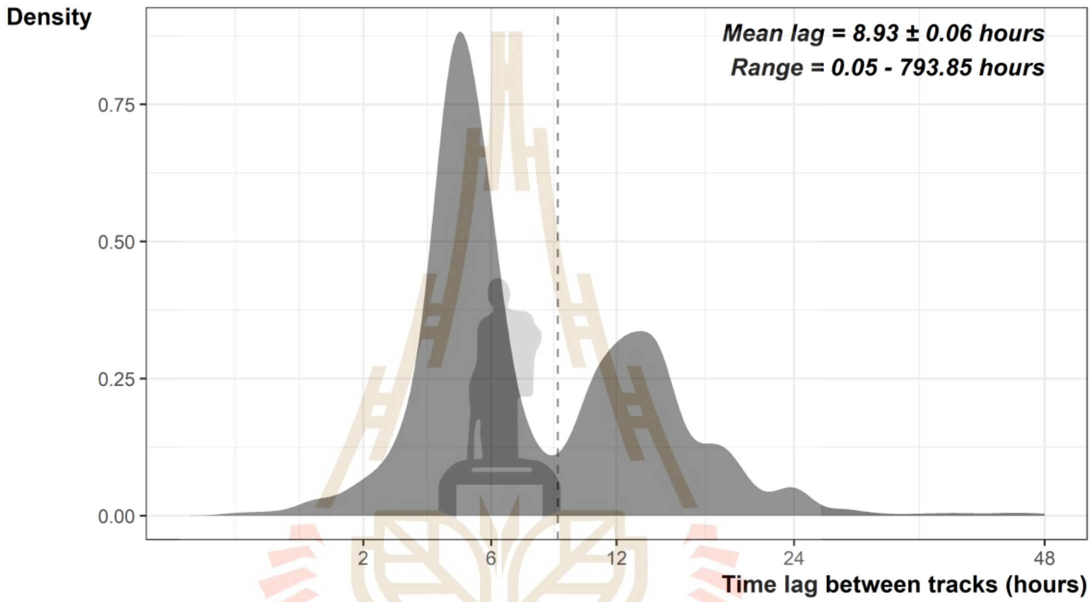

Figure 3.6 Time-lag between fixes on telemetered King Cobra.

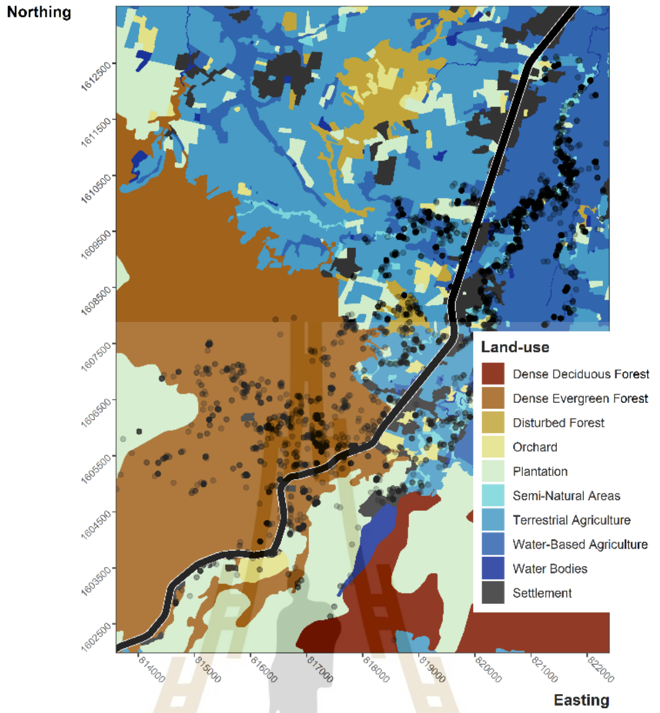

Figure 3.7 Land-use map with different colours depicting unique landscape features. Black dots show the locations of fixes made on all of our telemetered King Cobra.

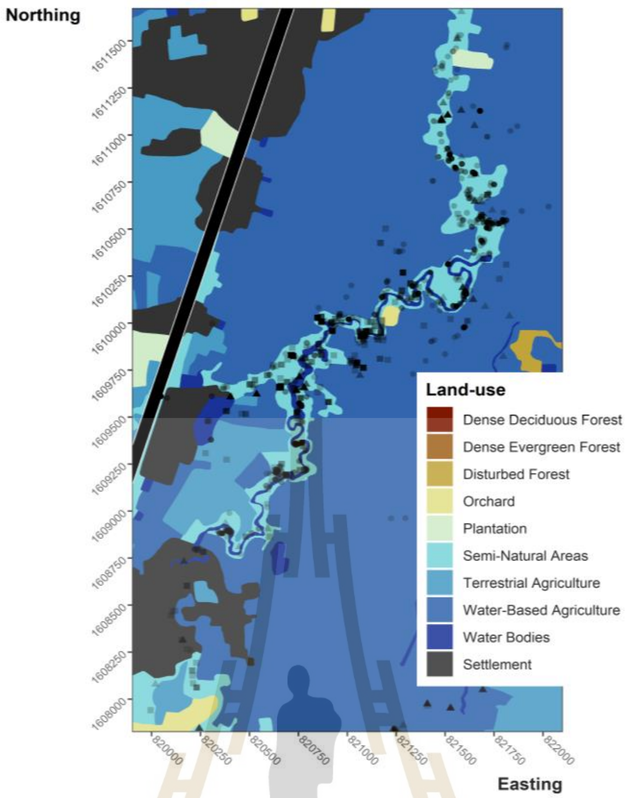

Figure 3.8 Land-use map with different colours depicting unique landscape features, illustrating a dominant use of semi-natural areas within the agricultural matrix. Black dots show the locations of fixes made on all of our telemetered King Cobra.

Our population-level iSSF suggests that the movements of male King Cobras can be mostly predicted by forest (Figure 3.9), showing a strong association (β = 0.001374, 95% CI 1.48^{-04} – 0.003397). We also found that male King Cobra movements were also weakly associated with settlements ($\beta = 1.13^{-04}$, 95% CI -4.22^{-04} – 6.20^{-04}), roads ($\beta = 1.50^{-04}$, 95% CI -8.93^{-04} – 0.001187), water ($\beta = 7.18^{-04}$, 95% CI -8.66^{-04} – 0.001568) and semi-natural areas ($\beta = 7.68^{-04}$, 95% CI -5.29^{-04} – 0.001917).

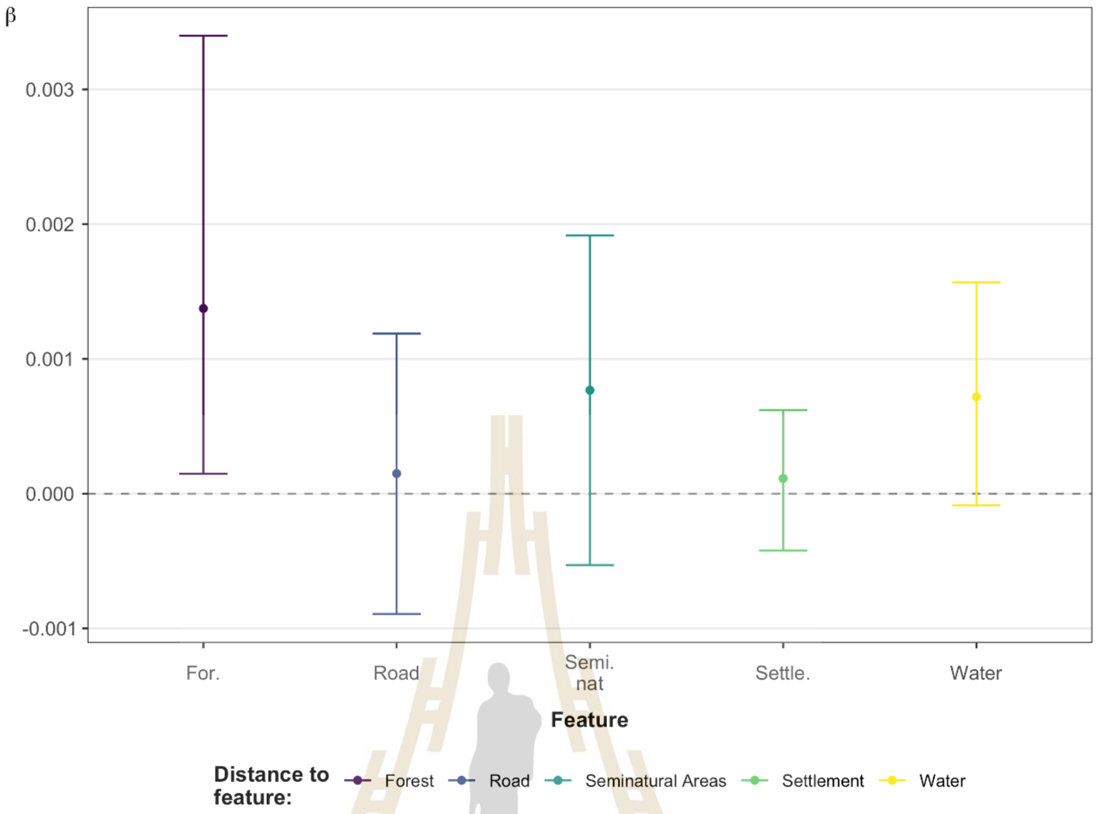

Figure 3.9 Population-level ISSF analysis on male King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

Our population-level iSSF suggests that the movements of female King Cobras can be mostly predicted by the availability of semi-natural areas (Figure 3.10), showing a strong association (β = 0.002273, 95% CI 0.001825 – 0.002728). We also found that female King Cobra movements were also weakly associated with water (β = 0.001416, 95% CI -2.50^{-04} – 0.003344) and forests (β = 2.49^{-04}, 95% CI -6.01^{-04} – 0.001045). However, our results suggest that female King Cobras show weak avoidance of settlements (β = -5.49^{-04}, 95% CI -0.00151 – 5.10^{-04}) and roads (β = -9.27^{-04}, 95% CI -0.00151 – 5.10^{-04}).

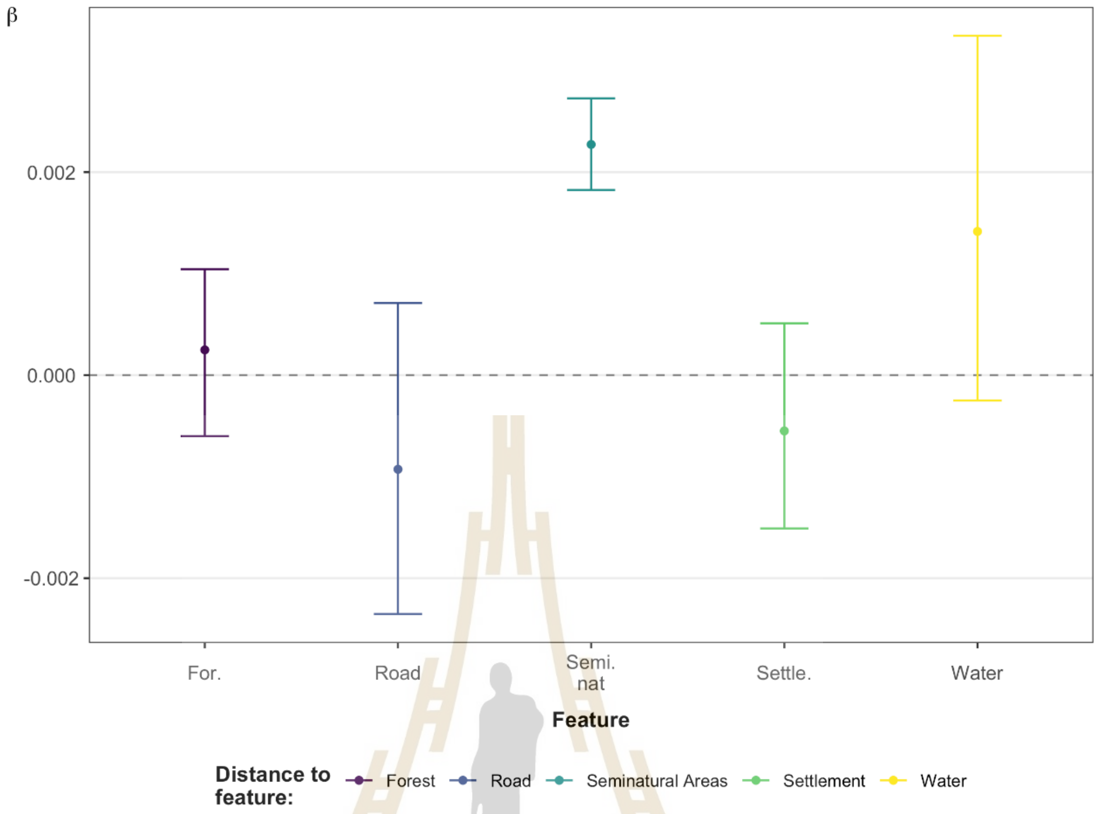

Figure 3.10 Population-level ISSF analysis on female King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

3.3.3 Juvenile male King Cobras

We tracked five juvenile male King Cobras between 2013-03-01 and 2020-08-28 for an average of 277.01 ± 77.73 days (range = 124.02 – 561.19 days). We performed 752 ± 210 fixes (range = 317 – 1497 fixes) and recorded 219 ± 53 relocations (range = 50 – 381 relocations) per individual on average (Table 3.4). The juvenile males had a mean estimated dBBMM 99% occurrence distribution of 406.09 ± 157.91 ha (range = 91.66 – 987.17 ha).

Table 3.2 Tracking summary of juvenile male King Cobras.

				dBBMM contours			
ID	Fixes	Days	Relocations	90	95	99	σ^2m
JM002	621	223.07	233	47.56	84.07	160.58	4.44 ± 0.39
JM013	1497	561.19	381	369.72	547.16	987.17	22.34 ± 1.11
JM019	890	311.79	228	52	105.96	366.24	7.8 ± 0.63
JM025	435	164.98	201	163.22	251.94	424.82	31.57 ± 3.26
JM034	317	124.02	50	30.93	49.98	91.66	21.51 ± 3.14

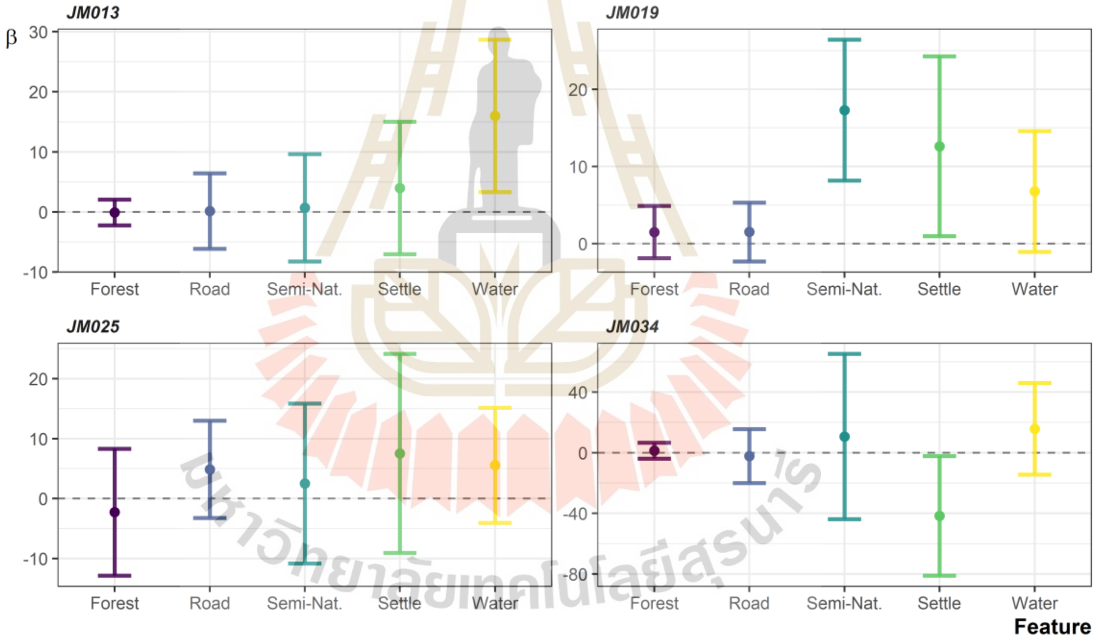

Figure 3.11 Resource selection of juvenile male King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

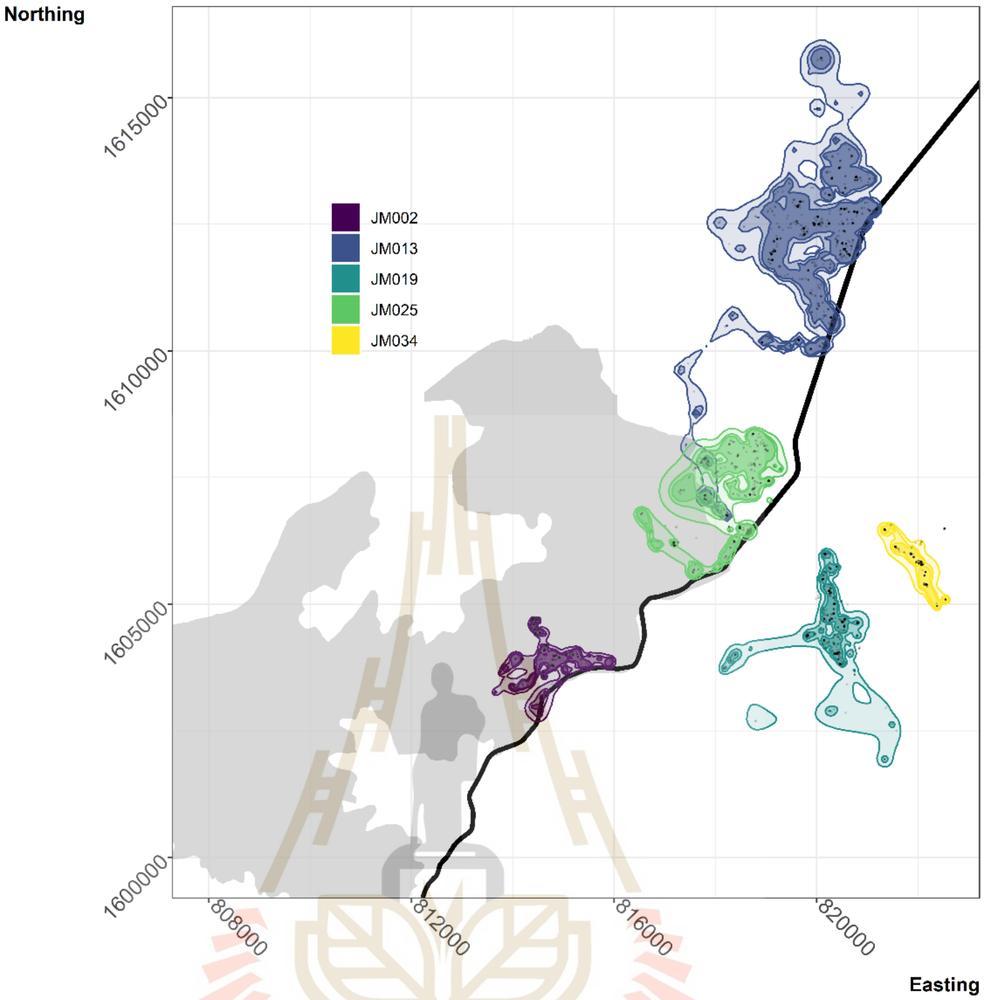

Figure 3.12 DBBMM occurrence distribution of juvenile male King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

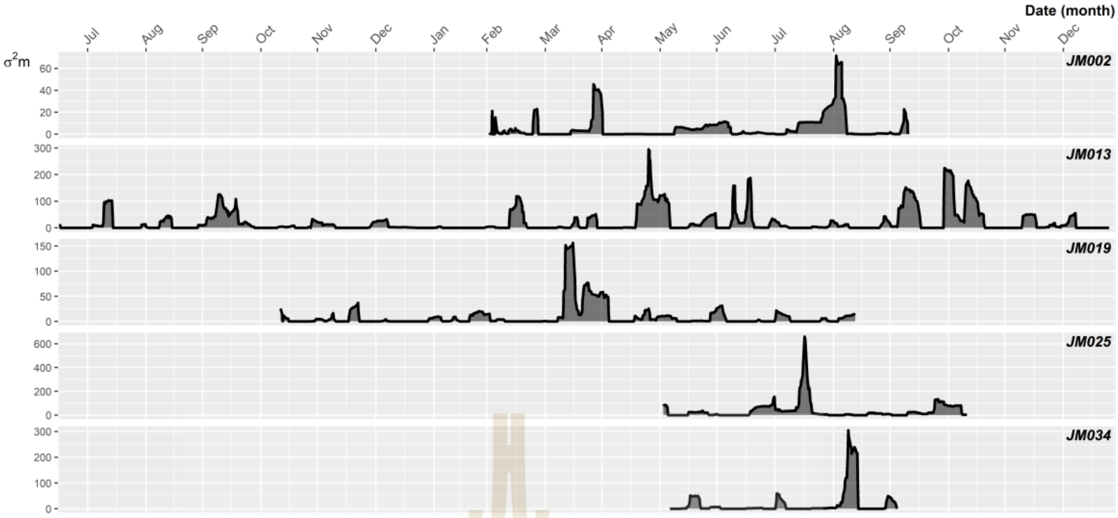

Figure 3.13 Motion variance exhibited by juvenile male King Cobras.

3.3.3.1 JM002

We tracked JM002 between 2013-03-01 and 2013-10-11 (223.07 days). We performed 621 fixes, and recorded 233 relocations. We estimated JM002 to have a dBBMM 99% occurrence distribution of 160.58 ha and a mean motion variance of 4.44 ± 0.39 σ^2m (Figure 3.13). We recorded JM002 using area exclusively within the core area of the SBR, occasionally moving towards and adjacent-to the Highway 304 (Figure 3.12), exhibiting periods of high and low motion variance, corresponding to different behavioural states.

3.3.3.2 JM013

We tracked JM013 between 2014-07-16 and 2016-01-26 (561.19 days). We performed 1497 fixes, and recorded 381 relocations. We estimated JM013 to have a dBBMM 99% occurrence distribution of 972.74 ha and a mean motion variance of

22.35 ± 1.11 σ^2m (Figure 3.13). Although JM013 was originally captured within the buffer zone of the SBR, we recorded him making large movements North, into the transitional zone where he utilised for the remainder of his tracking duration (Figure 3.12).

Resource selection for JM013 was best predicted by the single-factor Model 6 (Water; Figure 3.11). Our single-factor models show that JM013 has a weak association for settlements (β = 3.99, 95% CI -7.04 – 15.02), semi-natural areas (β = 0.69, 95% CI -8.24 – 9.62) and roads (β = 0.14, 95% CI -6.16 – 6.44), a strong association with water (β = 15.99, 95% CI 3.31 – 28.67) and a weak avoidance of forest (β = -0.08, 95% CI -2.22 – 2.07).

3.3.3.3 JM019

We tracked JM019 between 2015-11-07 and 2016-09-14 (311.79 days). We performed 830 fixes, and recorded 228 relocations. We estimated JM019 to have a dBBMM 99% occurrence distribution of 390.39 ha and a mean motion variance of 7.9 ± 0.63 σ^2m (Figure 3.13). We recorded an occurrence distribution for JM019 exclusively within the transitional zone of the SBR (Figure 3.12), primarily making use of an irrigation canal to traverse through village and agricultural area. Although we observed fairly low motion variance for JM019 throughout his tracking period, he exhibited large peaks between March – May (Figure 3.13).

Resource selection for JM019 was best predicted by the multi-factor Model 7 (Road, Forest and Semi-natural areas; Figure 3.11). Our single-factor models show that JM019 has a weak association for forests (β = 1.50, 95% CI -1.88 – 4.88), water (β = 6.77, 95% CI -1.05 – 14.59) and roads (β = 1.52, 95% CI -2.30 – 5.33), and a strong association with settlements (β = 12.63, 95% CI 0.98 – 24.28) and semi-natural areas (β = 17.30, 95% CI 8.18 – 26.42). We did not record any avoidance for landscape resources for JM019.

3.3.3.4 JM025

We tracked JM025 between 2016-05-31 and 2016-11-12 (164.98 days). We performed 435 fixes, and recorded 201 relocations. We estimated JM025 to have a dBBMM 99% occurrence distribution of 424.82 ha and a mean motion variance of 31.57 ± 3.26 σ^2m (Figure 3.13). We initially captured JM025 within the core area of the SBR, and then he moved towards the Highway 304 and subsequently North in to the transitional zone, where he remained (Figure 3.12). We recorded JM025 using irrigation canals, plantations and agricultural fields to move throughout the landscape. The movements North exhibited by JM025 were also characterised by a large peak in his motion variance, which was much higher than the motion variance estimates throughout his tracking period (Figure 3.13).

Resource selection for JM025 was best predicted by the multi-factor Model 9 (Road, Forest and Water; Figure 3.11). Our single-factor models show that JM025 has a weak association for settlements (β = 7.53, 95% CI -9.08– 24.14), semi-natural areas (β = 2.51, 95% CI -10.82 – 15.84), roads (β = 4.86, 95% CI -3.26 – 12.98) and water (β = 5.55, 95% CI -4.05 – 15.14) and a weak avoidance of forest (β = -2.28, 95% CI -12.86 – 8.30).

3.3.3.5 JM034

We tracked JM034 between 2017-06-04 and 2017-10-06 (124.02 days). We performed 317 fixes, and recorded 50 relocations. We estimated JM034 to have a dBBMM 99% occurrence distribution of 91.66 ha and a mean motion variance of 21.51 ± 3.14 σ^2m (Figure 3.13). We recorded an occurrence distribution by JM034 exclusively within the transitional zone of the SBR, using irrigation canals and agricultural fields (Figure 3.12).

Resource selection for JM034 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.11). Our single-factor models show that JM034 has a weak association for forests (β = 1.37, 95% CI -3.85– 6.60), semi-natural areas (β = 10.69, 95% CI -43.82 – 65.20) and water (β = 15.77, 95% CI -14.46 – 45.99), a weak avoidance of roads (β = -2.26, 95% CI -20.05 – 15.54) and a strong avoidance of human settlements (β = -41.58, 95% CI -81.03 – -2.13).

3.3.4 Adult male King Cobras

We tracked nine adult male King Cobra between 2013-03-01 and 2020-08-28 for an average of 443.93 ± 95.47 days (range = 68.73 – 1176.1 days). We performed 1214 ± 264 fixes (range = 134 – 3122 fixes) and recorded 350 ± 79 relocations (range = 66 – 985 relocations) per individual on average (Table 3.5). The adult males had a mean estimated dBBMM 99% occurrence distribution of 872.11 ± 131.21 ha (range = 376.51 – 1843.75 ha).

Table 3.3 Tracking summary for adult male King Cobras.

				dBBMM contours			
ID	Fixes	Days	Relocations	90	95	99	σ^2m
AM005	657	180.7	240	244.68	327.69	476.5	50.94 ± 3.28
AM006	736	346.02	232	668.44	1057.38	1843.75	47.61 ± 3.7
AM006_1	2173	723.05	542	513.68	694.71	1057.67	42.71 ± 1.74
AM007	782	349.03	171	620.7	858.96	1281.08	31.22 ± 2.84
AM007_1	969	320.66	220	212.78	327.91	600.31	51.41 ± 3.81
AM015	1944	680.13	587	383.53	607.88	1086.43	27.65 ± 1.26
AM018	3122	1176.1	985	265.29	502.8	984.34	33.57 ± 1.41
AM024	466	173.17	218	353.72	484.15	730.48	41.38 ± 2.24
AM026	134	68.73	66	187.94	249.03	376.51	69.99 ± 7.1
AM054	1381	520.62	378	130.82	217.34	477.05	26.73 ± 2.19
AM059	995	345.04	210	104.23	249.04	679.08	16.08 ± 1.3

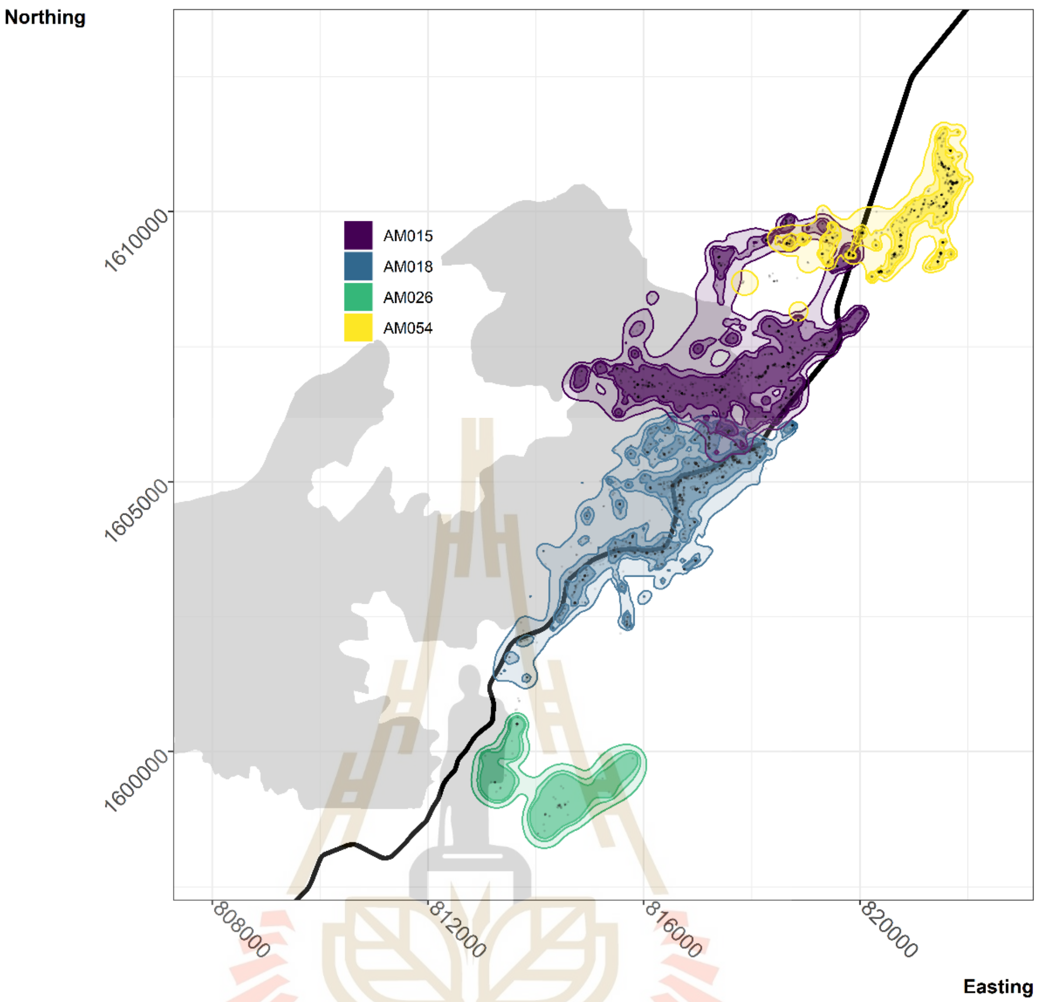

Figure 3.14 DBBMM occurrence distribution of adult male King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

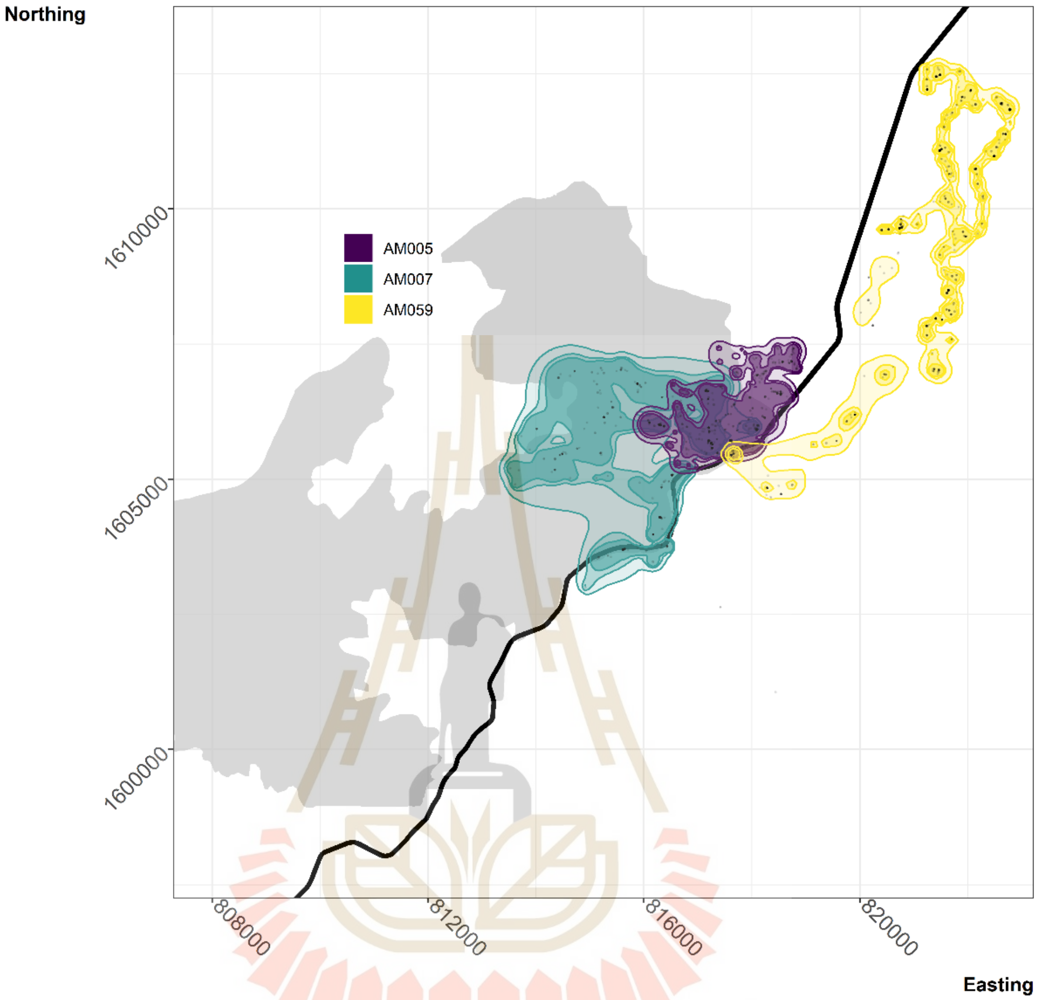

Figure 3.15 DBBMM occurrence distribution of adult male King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

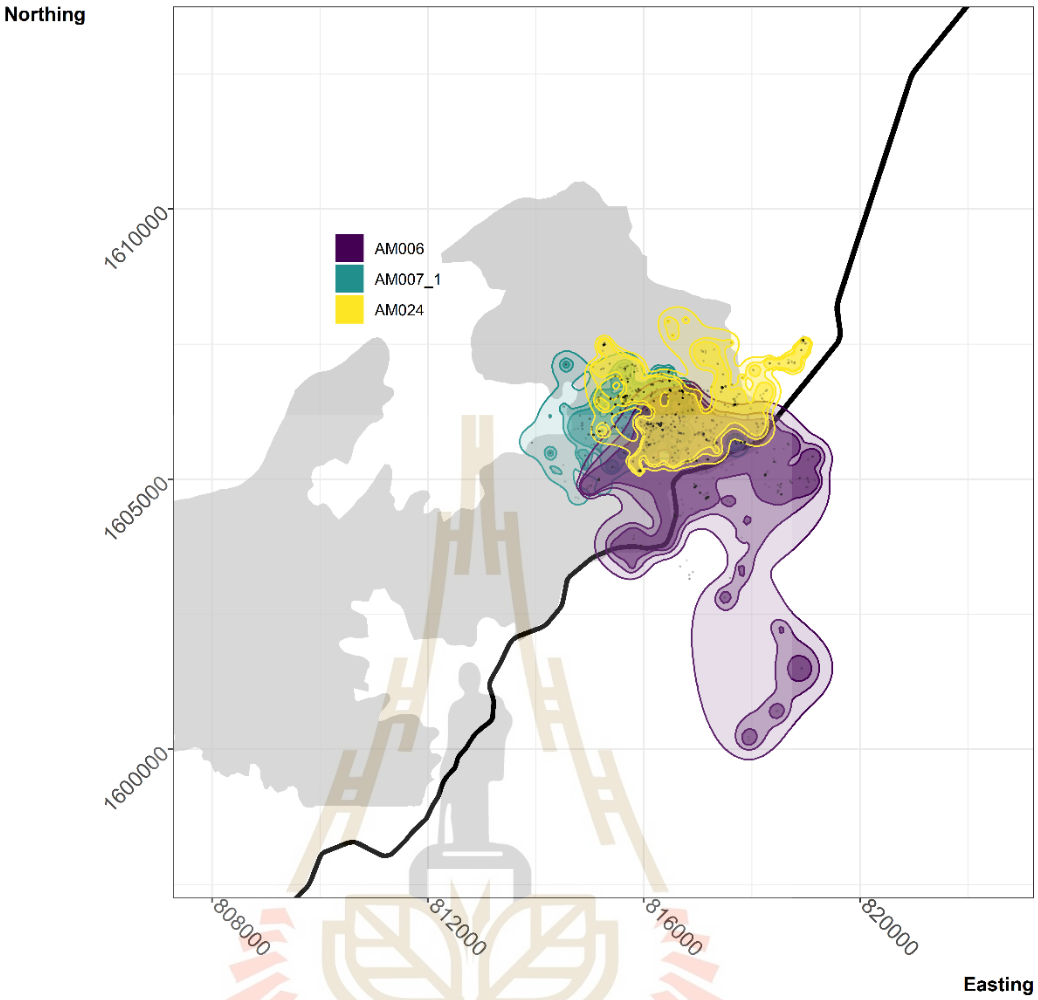

Figure 3.16 DBBMM occurrence distribution of adult male King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

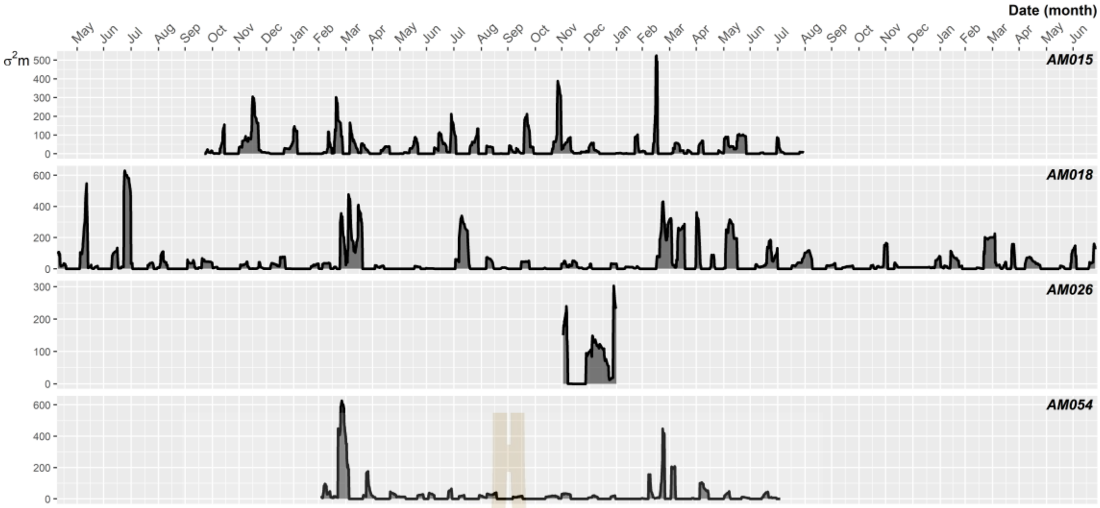

Figure 3.17 Motion variance exhibited by adult male King Cobras.

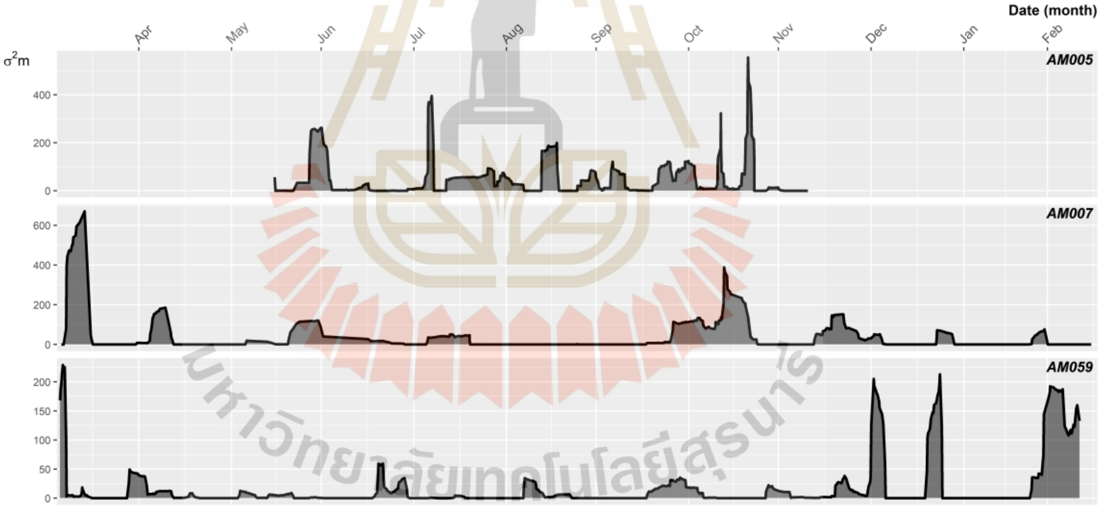

Figure 3.18 Motion variance exhibited by adult male King Cobras.

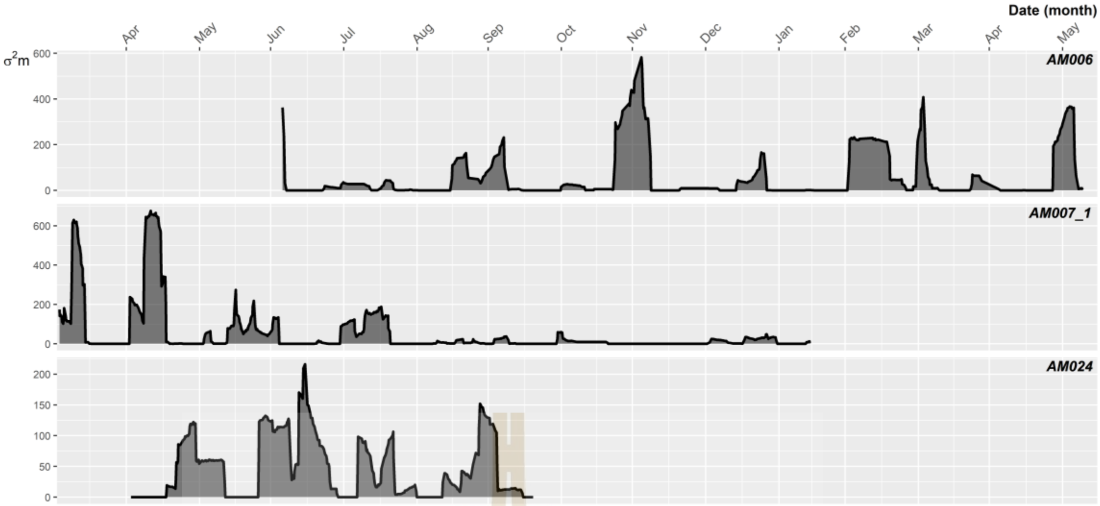

Figure 3.19 Motion variance exhibited by adult male King Cobras.

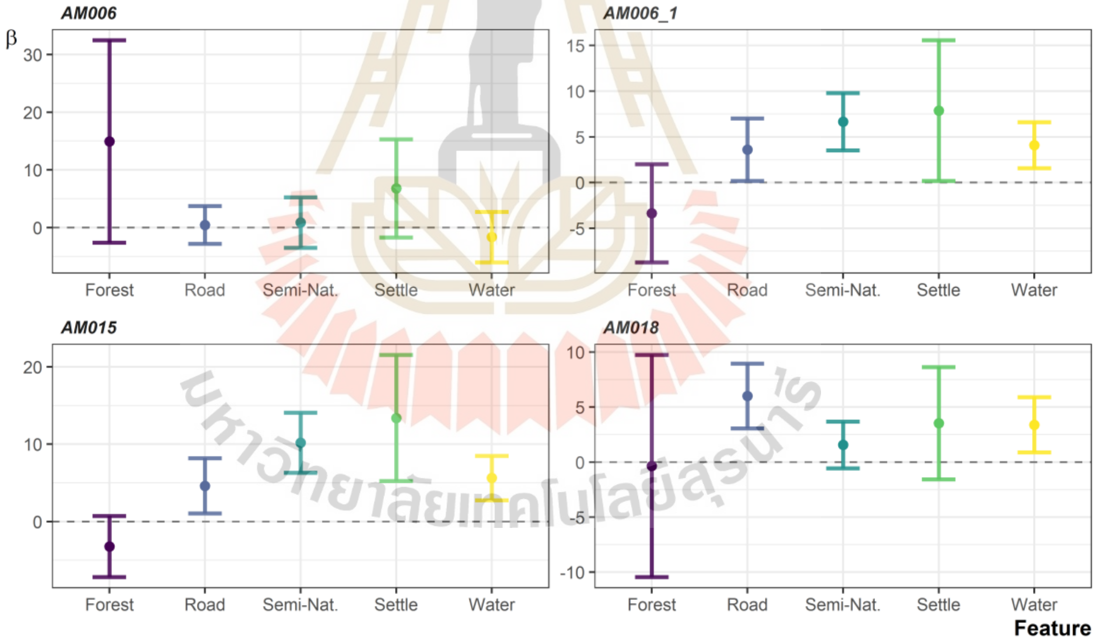

Figure 3.20 Resource selection of adult male King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

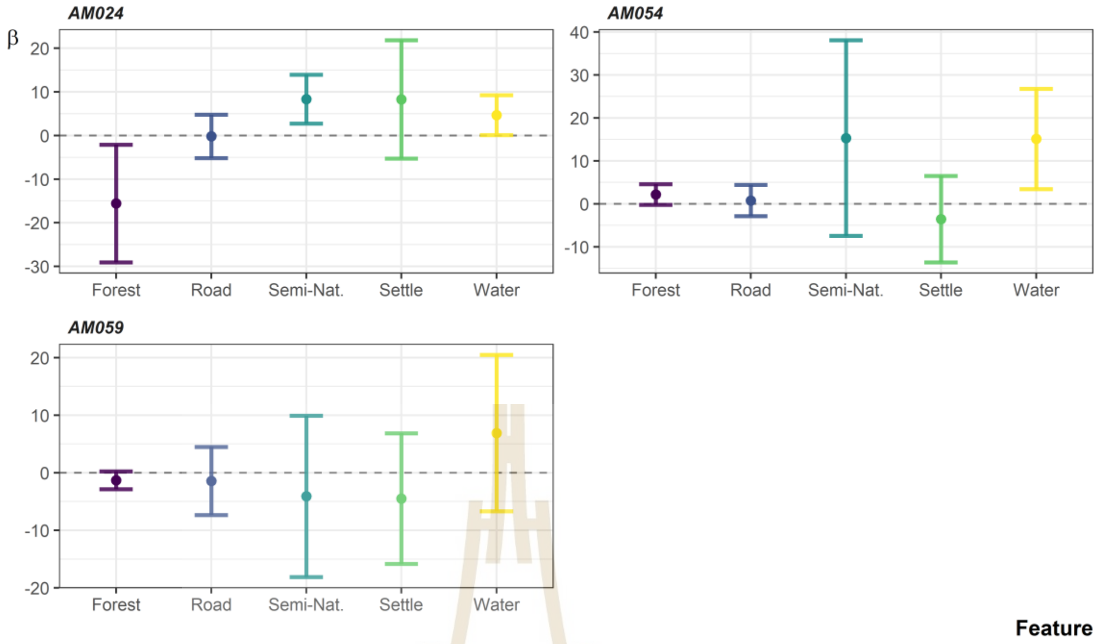

Figure 3.21 Resource selection of adult male King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

3.3.4.1 AM005

We tracked AM005 between 2014-03-29 and 2016-03-14 (180.7 days). We performed 657 fixes, and recorded 240 relocations. We estimated AM006 to have a dBBMM 99% occurrence distribution of 476.5 ha and a mean motion variance of 50.94 ± 3.28 σ^2m (Figure 3.17). We captured AM005 within the core area of the SBR, however, he would freely move between the core, buffer and transitional zones, utilising multiple habitat types (forests, agriculture, irrigation canals, human settlements; Figure 3.14).

3.3.4.2 AM006

We tracked AM006 between 2014-03-29 and 2016-03-14 (723.05 days). We performed 2173 fixes, and recorded 542 relocations. We estimated AM006 to have a dBBMM 99% occurrence distribution of 1063.42 ha and a mean motion variance of 42.61 ± 1.74 σ^2m (Figure 3.17). During this time, we recorded AM006 moving throughout the core, buffer and transitional zones of the SBR (Figure 3.14). Specifically, AM006 would make seasonal movements in to the transitional zone, likely corresponding to breeding behaviour. He primarily used dense forest habitat in the core area, but also made use of irrigation canals, human settlements and agriculture. Although AM006 maintained relatively high motion variance throughout his tracking period, we did observe peaks in the earlier months of the year, characteristic of breeding movements (Figure 3.17).

Resource selection for AM006 was best predicted by the single-factor Model 6 (Water; Figure 3.20). Our single-factor models show that AM006 has a strong association for settlements (β = 7.87, 95% CI 0.18 – 15.56), semi-natural areas (β = 6.65, 95% CI 3.51 – 9.79), roads (β = 3.60, 95% CI 0.17 – 7.03) and water (β = 4.09, 95% CI 1.57 – 6.60) and a weak avoidance of forest (β = -3.37, 95% CI -8.74 – 2.00).

Individual AM006 was lost from the study for 842 days and we subsequently tracked him between 2018-07-04 and 2019-06-15 (346.02 days). We performed 736 fixes, and recorded 232 relocations. We estimated AM006 to have a dBBMM 99% occurrence distribution of 1063.42 ha and a mean motion variance of 47.61 ± 3.81 σ^2m (Figure 3.17). During this second bout of tracking, AM006 exhibited similar movement patterns as his first tracking period. This was comprised of him using densely forested protected area, and moving in to the transitional zone (Figure 3.14). Although he also showed a propensity for forested area in the transitional zone, he would also make use of irrigation canals, human settlements and agriculture when available.

Resource selection for AM006, within this subsequent tracking period, was best predicted by the multi-factor Model 9 (Roads, Forest and Water; Figure 3.20). Our single-factor models show that AM006 has a weak association for forest (β = 14.93, 95% CI -2.60 – 32.45), settlements (β = 6.79, 95% CI -1.71 – 15.30), semi-natural areas (β = 0.89, 95% CI -3.49 – 5.27) and roads (β = 1.32, 95% CI -0.33 – 2.97) and a weak avoidance of water (β = -1.64, 95% CI -6.01 – 2.83).

3.3.4.3 AM007

We tracked AM007 between 2014-04-09 and 2015-04-29 (320.66 days). We performed 969 fixes, and recorded 220 relocations. We estimated AM007 to have a dBBMM 99% occurrence distribution of 616.9 ha and a mean motion variance of 51.9 ± 3.81 σ^2m (Figure 3.18). During this time, AM007 exhibited an occurrence distribution exclusively within the protected core area and buffer zone of the SBR. He moved throughout a large area, primarily using dense forested areas and plantation regrowth (Figure 3.15). We observed a clear increase in motion variance between March – May corresponding to breeding behaviour, which were much higher than subsequent peaks throughout his tracking period (Figure 3.18)

Individual AM007 was lost from the study for 1405 days and we subsequently tracked him between 2019-04-03 and 2020-03-17 (349.03 days). We performed 782 fixes, and recorded 171 relocations. We estimated AM007 to have a dBBMM 99% utilisation occurrence distribution of 1281.08 ha and a mean motion variance of 31.22

± 2.84 σ^2m (Figure 3.17). In this latter tracking period, AM007 typically exhibited the same movement patterns as first seen from initial tracking efforts, however, we also recorded him moving through the transitional zone early in his tracking period (Figure 3.15). Furthermore, we observed the same pattern in motion variance, exhibiting peaks in March – May (Figure 3.17).

3.3.4.4 AM015

We tracked AM015 between 2014-10-11 and 2016-08-31 (680.13 days). We performed 1944 fixes, and recorded 587 relocations. We estimated AM015 to have a dBBMM 99% occurrence distribution of 1081.54 ha and a mean motion variance of 27.3 ± 1.22 σ^2m (Figure 3.18). We recorded AM015 using all three zones of the SBR, showing seasonal movements into the forest (Figure 3.15). However, he would primarily make use of irrigation canals within the transitional zone and surrounding agricultural matrix. We observed several large peaks throughout the tracking period of AM015, however, we did also observe characteristic peaks in the suspected King Cobra breeding season (Figure 3.18).

Resource selection for AM015 was best predicted by the multi-factor Model 7 (Roads, Forest and Semi-natural areas; Figure 3.20). Our single-factor models show that AM015 has a strong association for settlements ($\beta = 13.39$, 95% CI 5.24 – 21.54), semi-natural areas ($\beta = 10.18$, 95% CI 6.30 – 14.06), roads ($\beta = 4.61$, 95% CI 1.04 – 8.18) and water ($\beta = 5.63$, 95% CI 2.76 – 8.49) and a weak avoidance for forest ($\beta = -3.23$, 95% CI -7.17 – 0.71).

3.3.4.5 AM018

We tracked AM018 between 2015-05-10 and 2018-09-30 (1176.1 days). We performed 3122 fixes, and recorded 985 relocations. We estimated AM018 to have a dBBMM 99% occurrence distribution of 977.84 ha and a mean motion variance of 33.56 ± 1.41 σ^2m (Figure 3.18). Throughout this long tracking duration, AM018 made use of the core, buffer and transitional zones of the SBR (Figure 3.15). He frequently traversed the Highway 304 to move throughout his observed occurrence distribution and primarily used dense forested area. We tracked AM018 over four consecutive breeding seasons (March – June) and he exhibited characteristically high peaks in motion variance in each year (Figure 3.18).

Resource selection for AM018 was best predicted by the multi-factor Model 8 (Roads, Forest and Settlements; Figure 3.20). Our single-factor models show that AM018 has a weak association for settlements (β = 3.54, 95% CI -1.57 – 8.64) and semi-natural areas (β = 1.56, 95% CI -0.50 – 1.19), a strong association for roads (β = 6.01, 95% CI 3.06 – 8.96) and water (β = 3.39, 95% CI 0.88 – 5.90), and a weak avoidance of forest (β = -0.35, 95% CI -10.44 – 9.74).

3.3.4.6 AM024 space use

We tracked AM024 between 2016-05-01 and 2016-10-21 (173.17 days). We performed 466 fixes, and recorded 218 relocations. We estimated AM024 to have a dBBMM 99% occurrence distribution of 730.48 ha and a mean motion variance of 41.38 ± 2.24 σ^2m (Figure 3.18). We captured AM024 within the core area of the SBR, he primarily moved through dry-evergreen and dry-dipterocarp forest until he began linear movements into the agricultural matrix via an irrigation canal (Figure 4.16). We recorded several dips and peaks in the motion variance of AM024, likely corresponding to bouts of foraging, digestion and ecdysis (Figure 3.18).

Resource selection for AM024 was best predicted by the single-factor Model 2 (Forest; Figure 3.21). Our single-factor models show that AM024 has a weak association for settlements (β = 8.28, 95% CI -5.26 – 21.83), a strong association with semi-natural areas (β = 8.32, 95% CI 2.72 – 13.92) and water (β = 4.69, 95% CI 0.13 – 9.25), a weak avoidance of roads (β = -0.18, 95% CI -5.16 – 4.79) and a strong avoidance of forest (β = -15.59, 95% CI -29.07 – -2.10).

3.3.4.7 AM026 space use

We tracked AM026 between 2016-11-30 and 2017-02-07 (68.73 days). We performed 134 fixes, and recorded 66 relocations. We estimated AM026 to have a dBBMM 99% occurrence distribution of 376.51 ha and a mean motion variance of 69.99 ± 7.10 σ^2m (Figure 3.19). We recorded AM026 moving through the transitional zone exclusively during his tracking period, using dense forested area and subsequently moved into Thap Lan National Park (Figure 3.16).

3.3.4.8 AM054

We tracked AM054 between 2018-03-02 and 2019-08-05 (520.62 days). We performed 1381 fixes, and recorded 379 relocations. We estimated AM054 to have a dBBMM 99% occurrence distribution of 489.48 ha and a mean motion variance of 29.17 ± 2.25 σ^2m (Figure 3.19). We observed AM054 exclusively using the transitional zone of the SBR. He primarily made us of a large irrigation canal bisecting the agricultural landscape, also following this feature to facilitate movement across the

Highway 304 (Figure 3.16). Similar to other tracked adult males, AM054 showed clear peaks in motion variance likely attributed to breeding movements, and exhibiting relatively small peaks and motion variance throughout the remainder of his tracking duration (Figure 3.19).

Resource selection for AM054 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.21). Our single-factor models show that AM054 has a weak association for forest (β = 2.18, 95% CI -0.24 – 4.60), semi-natural areas (β = 15.31, 95% CI -7.46 – 38.07) and roads (β = 0.78, 95% CI -2.87 – 4.42), a strong association with water (β = 15.12, 95% CI 3.44 – 26.80) and semi-natural areas (β = 47.72, 95% CI 36.45 – 59.00), and a weak avoidance of settlements (β = -3.57, 95% CI -13.62 – 6.48).

3.3.4.9 AM059

We tracked AM059 between 2019-04-03 and 2020-03-13 (354.04 days). We performed 995 fixes, and recorded 210 relocations. We estimated AM059 to have a dBBMM 99% occurrence distribution of 679.08 ha and a mean motion variance of 16.08 ± 1.30 σ^2m (Figure 3.19). Individual AM059 exclusively moved throughout the transitional zone of the SBR, making use of a large irrigation canal and water features within the agriculture. However, he also moved into the forest of the transitional area (Figure 3.16). We observed a high peak in motion variance at the beginning of AM059's tracking period in the suspected breeding season, with other large peaks observed almost a year later (Figure 3.19).

Resource selection for AM059 was best predicted by the single-factor Model 6 (Water; Figure 3.21). Our single-factor models show that AM059 has a weak association for water (β = 6.88, 95% CI -6.71 – 20.47), and a weak avoidance of forest (β = -1.30, 95% CI -2.86 – 0.26), settlements (β = -4.48, 95% CI -15.83 – 6.87), semi-natural areas (β = -4.09, 95% CI -18.11 – 9.93) and roads (β = -1.44, 95% CI -7.35 – 4.48).

3.3.5 Juvenile female King Cobras

We tracked two juvenile female King Cobra between 2013-03-01 and 2020-08-28 for an average of 276.12 ± 77.5 days (range = 198.62 – 353.62 days). We performed 635 ± 90 fixes (range = 542 – 722 fixes) and recorded 182 ± 66 relocations (range = 116 – 248 relocations) per individual on average (Table 3.6). The juvenile females had a mean estimated dBBMM 99% occurrence distribution of 263.46 ± 181.37 ha (range = 82.09 – 444.83 ha).

Table 3.4 Tracking summary for juvenile female King Cobras.

				dBBMM contours			
ID	Fixes	Days	Relocations	90	95	99	σ^2m
JF027	542	198.62	116	17.36	36.33	82.09	6.15 ± 0.54
JF055	722	353.62	248	174.52	277.22	444.83	20.48 ± 1.49

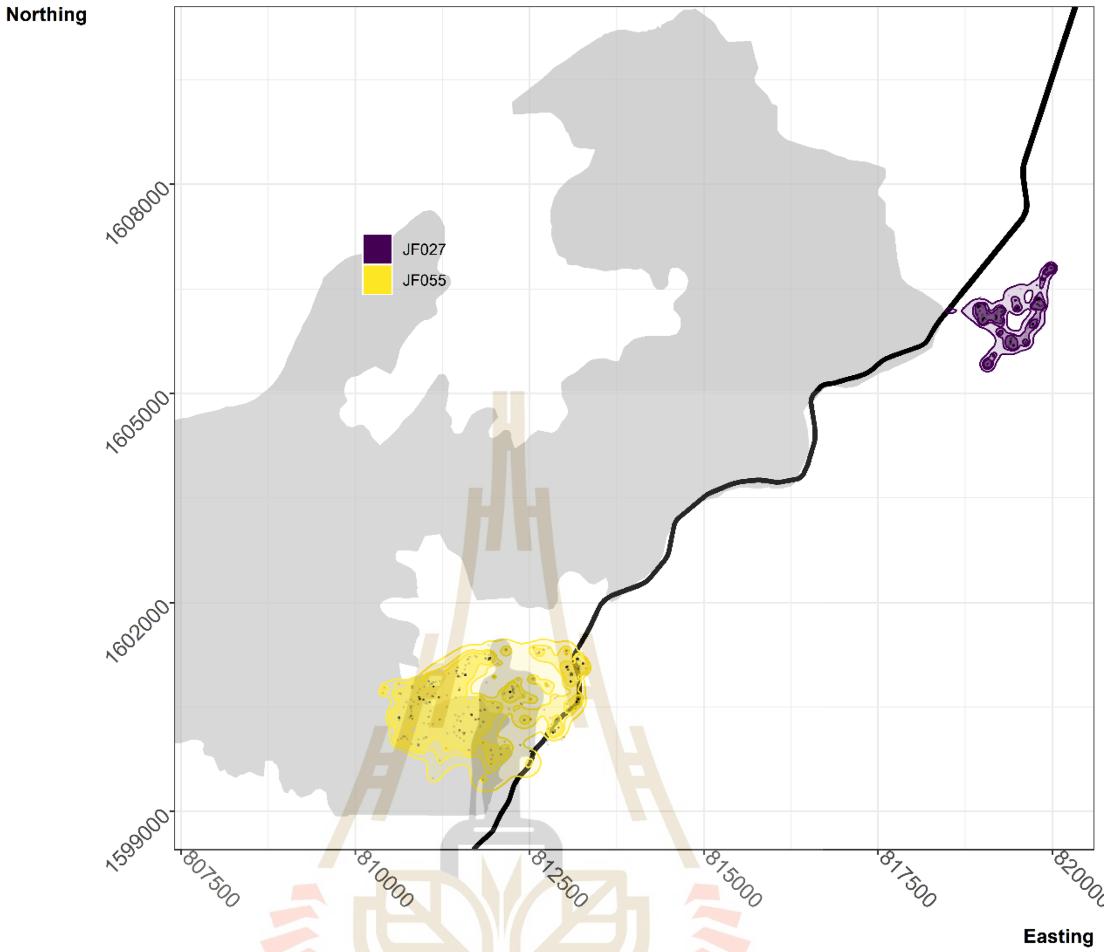

Figure 3.22 DBBMM occurrence distribution of juvenile female King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

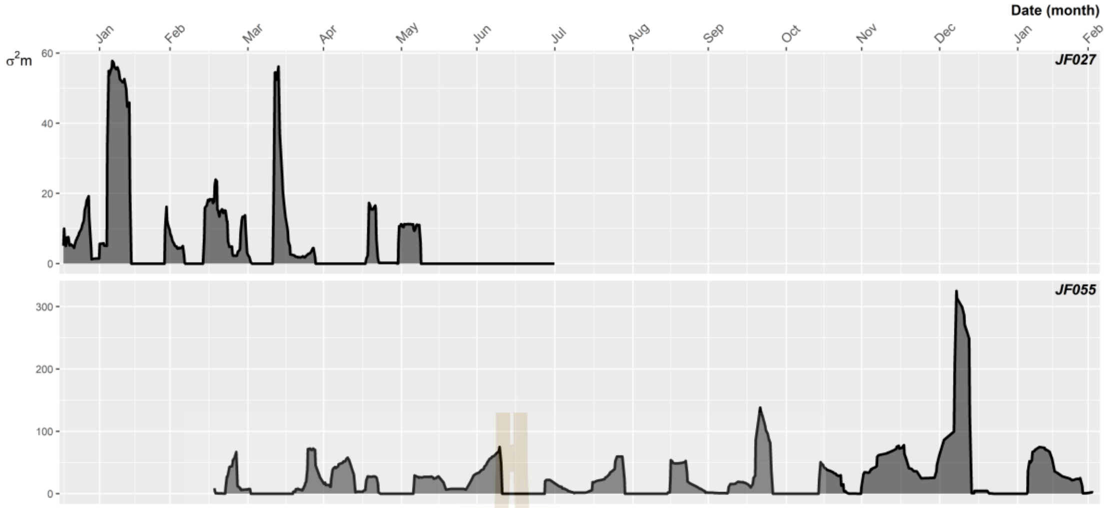

Figure 3.23 Motion variance exhibited by juvenile female King Cobras.

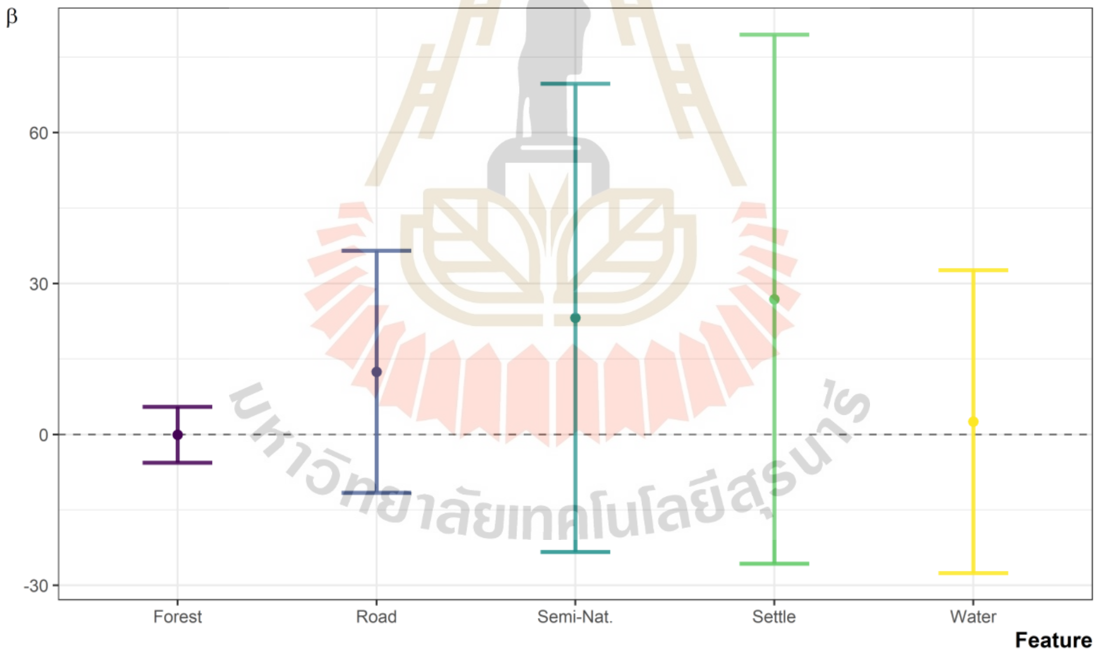

Figure 3.24 Resource selection of JF027. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

3.3.5.1 JF027

We tracked JF027 between 2017-01-15 and 2017-08-02 (198.62 days). We performed 542 fixes, and recorded 116 relocations. We estimated JF027 to have a dBBMM 99% occurrence distribution of 82.09 ha and a mean motion variance of 6.15 ± 0.54 σ^2m (Figure 3.23). We initially captured JF027 within the buffer zone of the SBR, but she promptly crossed the Highway 304 and moved into the transitional zone, where she primarily utilised an irrigation canal to move between human settlements and agricultural lands (Figure 3.22).

Resource selection for JF027 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.24). Our single-factor models show that JF027 has a weak association for forest (β = 0.25, 95% CI -5.31 – 5.80), settlements (β = 28.80, 95% CI -24.26 – 81.86), semi-natural areas (β = 21.13, 95% CI -24.43 – 66.68) and roads (β = 13.65, 95% CI -11.72 – 39.03), and a weak avoidance of roads (β = -0.14, 95% CI -25.96 – 29.69).

3.3.5.2 JF055 space use

We tracked JF055 between 2018-03-16 and 2019-03-05 (353.62 days). We performed 722 fixes, and recorded 248 relocations. We estimated JF055 to have a dBBMM 99% occurrence distribution of 444.83 ha and a mean motion variance of 20.48 ± 1.49 σ^2m (Figure 3.23). We recorded an occurrence distribution exclusively within the transitional zone of the SBR, for JF055. She made use of densely forested area, and occasionally traversed the Highway 304 to access fragmented forest (Figure 3.22). As JF055 had an occurrence distribution almost exclusively within dense forested area, unrestricted by human-modified barriers, she exhibited a broader spread of fixes, un-hindered by movement corridors (Figure 3.23).

3.3.6 Adult female King Cobras

We tracked eight adult female King Cobra between 2013-03-01 and 2020-08-28 for an average of 210.96 ± 74.80 days (range = 46.73 – 774.97 days). We performed 565 ± 219 fixes (range = 120 – 2245 fixes) and recorded 173 ± 74 relocations (range = 31 – 728 relocations) per individual on average (Table 3.7). The adult females had a mean estimated dBBMM 99% occurrence distribution of 281.60 ± 49.64 ha (range = 122.41 – 490.84 ha).

Table 3.5 Tracking summary for adult female King Cobras.

				dBBMM contour			
ID	Fixes	Days	Relocations	90	95	99	σ^2m
AF004	120	46.73	75	56.63	77.72	122.41	30.68 ± 3.39
AF010	289	83.53	47	0.52	31.14	487.94	135.13 ± 30.68
AF010_1	143	66.47	34	71.65	100.65	166.78	44.64 ± 11.85
AF017	2245	774.97	728	40.44	66.7	147.14	7.52 ± 0.33
AF056	428	162.07	138	78.25	110.32	176.5	15.61 ± 0.92
AF058	672	268.9	253	49.41	97.68	232.12	12.76 ± 0.74
AF086	623	241.02	197	103.32	153.9	284.32	11.26 ± 0.87
AF096	291	132.92	56	181.26	262.54	426.32	22.75 ± 3.08
AF099	276	122.02	31	169.5	268.64	490.84	15.52 ± 2.62

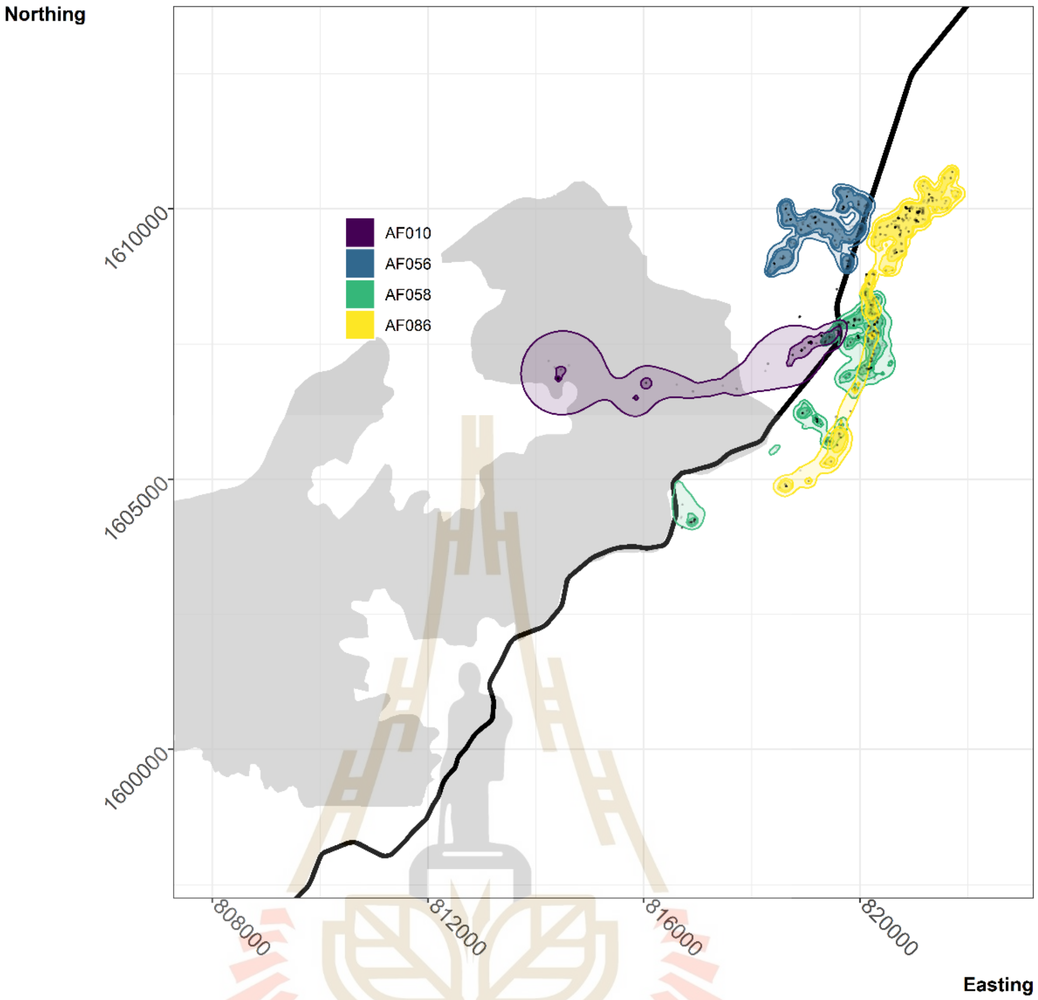

Figure 3.25 DBBMM occurrence distribution of adult female King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

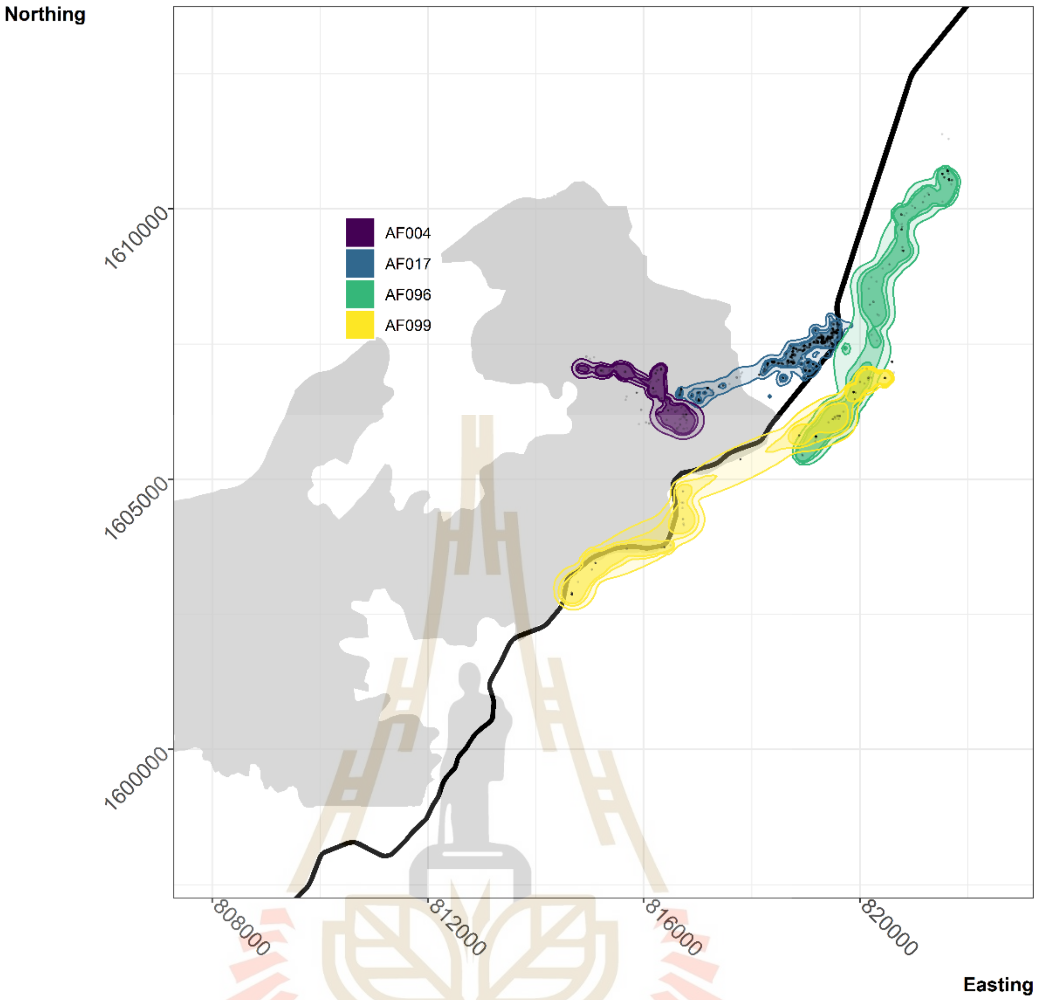

Figure 3.26 DBBMM occurrence distribution of adult female King Cobras. Ninety, 95 and 99% contours are shown with decreasing opacity.

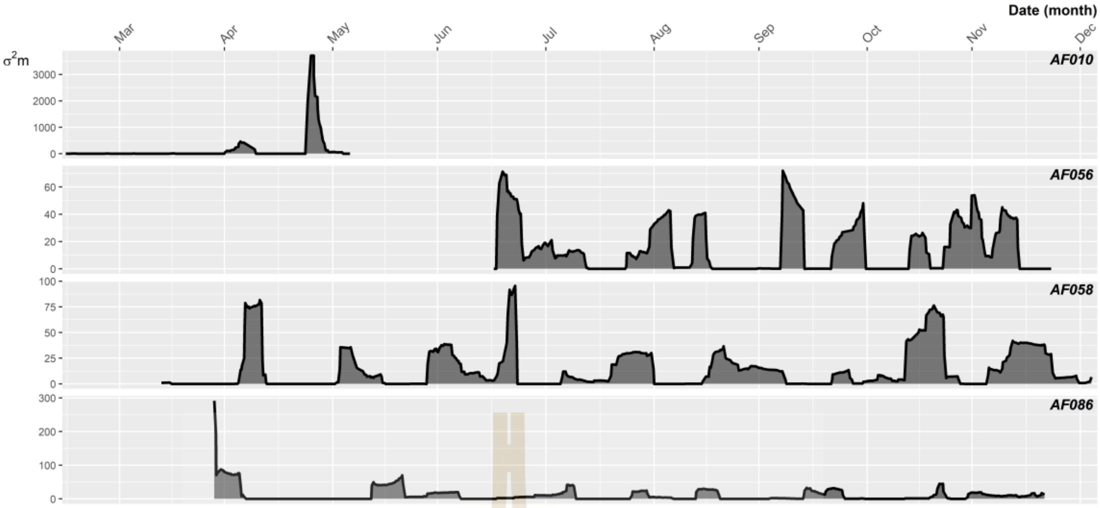

Figure 3.27 Motion variance exhibited by adult female King Cobras.

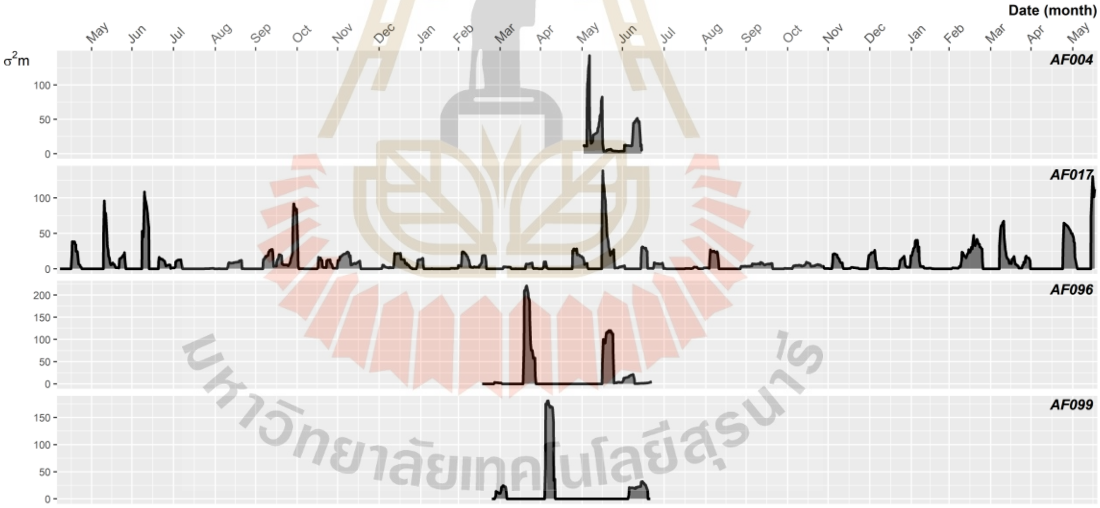

Figure 3.28 Motion variance exhibited by adult female King Cobras.

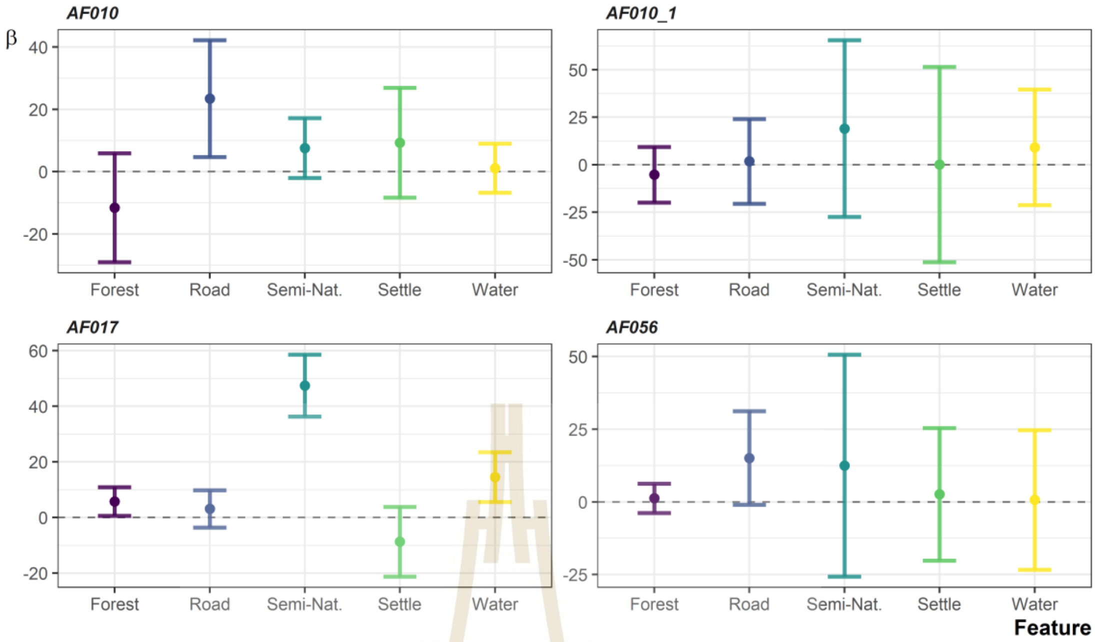

Figure 3.29 Resource selection of adult female King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

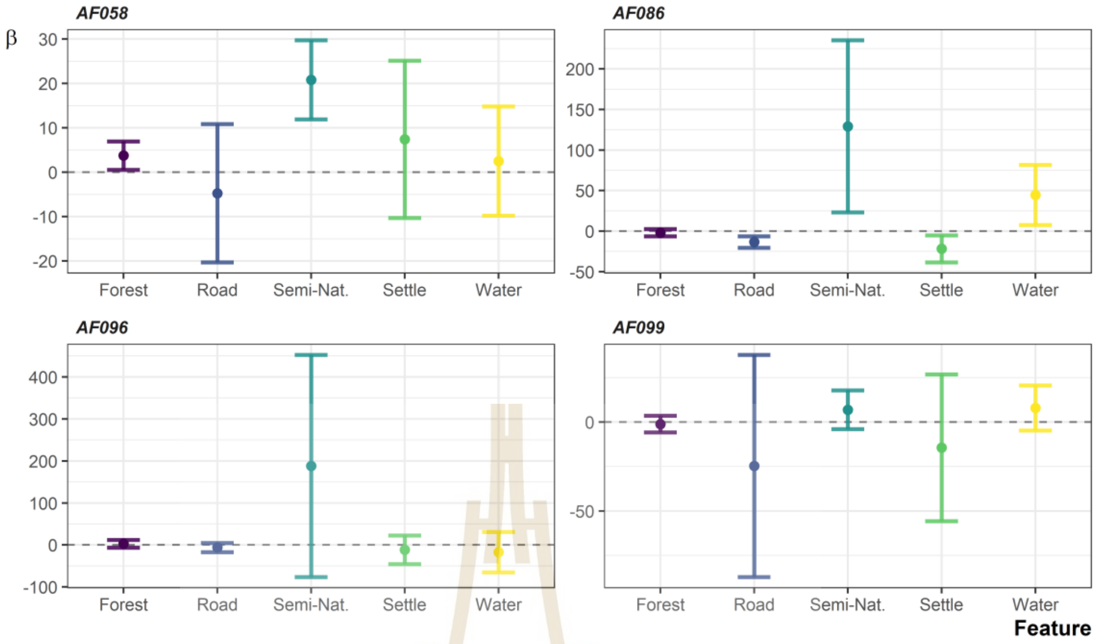

Figure 3.30 Resource selection of adult female King Cobras. Positive estimates suggest an association with the landscape feature. Error bars depict the 95% confidence intervals. Points show the ISSF estimate for each landscape feature.

3.3.6.1 AF004

We tracked AF004 between 2013-06-01 and 2013-07-17 (46.73 days). We performed 120 fixes, and recorded 75 relocations. We estimated AF004 to have a dBBMM 99% occurrence distribution of 122.41 ha and a mean motion variance of 30.68 ± 3.39 σ^2m (Figure 3.28). Individual AF004 exclusively moved throughout the core area of the SBR, utilising dry-evergreen forest (Figure 3.25).

3.3.6.2 AF010

We tracked AF010 between 2014-04-02 and 2014-06-08 (66.47 days). We performed 143 fixes, and recorded 34 relocations. We estimated AF010 to have a dBBMM 99% occurrence distribution of 166.78 ha and a mean motion variance of 44.64 ± 11.85 σ^2m (Figure 3.28). We recorded AF010 moving through the core, buffer and transitional zone of the SBR, making use of an irrigation canal to move through an agricultural matrix (Figure 3.25). We observed a very large peak in motion variance in late March, which were characterised by movements to locate an oviposition site, a long period of low motion variance (nesting), followed by another increase in motion variance as she moved away from her nest (Figure 3.28).

Resource selection for AF010 was best predicted by the multi-factor Model 7 (Roads, Forests and Semi-natural areas; Figure 3.30). Our single-factor models show that AF010 has a weak association for settlements (β = 0.09, 95% CI -51.25 – 51.43), semi-natural areas (β = 19.04, 95% CI -27.39 – 65.47), roads (β = 1.80, 95% CI -20.48 – 24.08) and water (β = 9.11, 95% CI -21.32 – 39.55), and a weak avoidance of forests (β = -5.25, 95% CI -19.88 – 9.39).

Individual AF010 was lost from the study for 280 days and we subsequently tracked her between 2015-03-15 and 2015-06-06 (88.53 days). We performed 289 fixes, and recorded 47 relocations. We estimated AF010 to have a dBBMM 99% occurrence distribution of 487.94 ha and a mean motion variance of 135.13 ± 11.85 σ^2m (Figure 3.28). In this second bout of tracking, we recorded similar movement patterns exhibited by AF010 where she moved out of the core protected area and into the transitional zone via an irrigation canal (Figure 3.25). However, we did observe AF010 traversing the Highway 304 during this time.

Resource selection for AF010 was best predicted by the multi-factor Model 6 (Water; Figure 3.30). Our single-factor models show that AF010 has a weak association for settlements (β = 9.28, 95% CI -8.31 – 26.88), semi-natural areas (β = 7.57, 95% CI -2.05 – 17.18) and water (β = 1.11, 95% CI -6.75 – 8.98), a strong association with roads (β = 23.44, 95% CI 4.72 – 42.17) and a weak avoidance of forests (β = -11.57, 95% CI -29.05 – 5.91).

3.3.6.3 AF017

We tracked AF017 between 2015-05-06 and 2017-06-19 (774.97 days). We performed 2245 fixes, and recorded 728 relocations. We estimated AF017 to have a dBBMM 99% occurrence distribution of 149.28 ha and a mean motion variance of 7.53 ± 0.33 σ^2m (Figure 3.28). We observed a seasonal pattern of AF017 moving into the core protected area during nesting season, and subsequently back into the transitional zone (Figure 3.26). During her time in the transitional zone, AF017 made use of a large irrigation canal, and other aquatic landscape features, almost exclusively. We observed the highest motion variance peaks by AF017 between April and July each year, corresponding to movements to and from oviposition sites (Figure 3.28).

Resource selection for AF017 was best predicted by the multi-factor Model 7 (Roads, Forests and Semi-natural areas; Figure 3.30). Our single-factor models show that AF017 has a weak association for roads (β = 3.14, 95% CI -3.59 – 9.86), a strong association with forests (β = 5.78, 95% CI 0.64 – 10.92), semi-natural areas (β = 47.43, 95% CI 36.31 – 58.55) and water (β = 14.53, 95% CI 5.57 – 23.49), and a weak avoidance of settlements (β = -8.67, 95% CI -21.19 – 3.85).

3.3.6.4 AF056

We tracked AF056 between 2018-07-15 and 2018-12-24 (162.07 days). We performed 428 fixes, and recorded 138 relocations. We estimated AF056 to have a dBBMM 99% occurrence distribution of 176.5 ha and a mean motion variance of 15.61 ± 0.92 σ^2m (Figure 3.29). We recorded an occurrence distribution exclusively within the transitional zone of the SBR, for AF056 (Figure 3.26). She moved throughout the agricultural landscape using an irrigation canal and connecting agricultural fields, typically near to major roads. We observed a typical pattern of periods with low motion variance, followed by small peaks likely corresponding to foraging, digestion and ecdysis (Figure 3.29).

Resource selection for AF056 was best predicted by the single-factor Model 6 (Water; Figure 3.30). Our single-factor models show that AF056 has a weak association for forest (β = 1.21, 95% CI -3.86 – 6.29), settlements (β = 2.58, 95% CI -20.22 – 25.38), semi-natural areas (β = 12.47, 95% CI -25.67 – 50.61), roads (β = 15.09, 95% CI -0.97 – 31.15) and water (β = 0.66, 95% CI -23.36 – 24.68).

3.3.6.5 AF058 space use

We tracked AF058 between 2018-04-11 and 2019-01-05 (268.9 days). We performed 672 fixes, and recorded 253 relocations. We estimated AF058 to have a dBBMM 99% occurrence distribution of 232.12 ha and a mean motion variance of 12.76 ± 0.74 σ^2m (Figure 3.29). We recorded AF058 moving exclusively throughout the transitional zone of the SBR (Figure 3.26). Although initially captured within forest, she moved into the agricultural matrix and heavily relied on irrigation canals to move through the landscape. She also made us of this canal to move across the Highway 304.

We did observe a peak in motion variance in May, due to AF058 moving away from her oviposition site, however, a larger peak was observed later in her tracking period (Figure 3.29).

Resource selection for AF058 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.31). Our single-factor models show that AF058 has a weak association for settlements (β = 7.43, 95% CI -10.27 – 25.13) and water (β = 2.51, 95% CI -9.78 – 14.81), a strong association with forests (β = 3.75, 95% CI 0.54 – 6.97) and semi-natural areas (β = 20.81, 95% CI 11.89 – 29.72), and a weak avoidance of roads (β = -4.72, 95% CI -20.29 – 10.85).

3.3.6.6 AF086

We tracked AF086 between 2019-04-26 and 2019-12-23 (241.02 days). We performed 623 fixes, and recorded 197 relocations. We estimated AF086 to have a dBBMM 99% occurrence distribution of 284.32 ha and a mean motion variance of 11.26 ± 0.74 σ^2m (Figure 3.29). We observed AF086 moving through the transitional zone exclusively (Figure 3.27). We captured her within the agricultural matrix, and she subsequently made linear movements into forested area to nest. She then moved back into the agricultural area and made use of irrigation canals and associated aquatic landscape features; characterised by a large peak in motion variance at the beginning of her tracking period (Figure 3.29).

Resource selection for AF086 was best predicted by the multi-factor Model 7 (Roads, Forests and Semi-natural areas; Figure 3.31). Our single-factor models show that AF086 has a strong association with semi-natural areas (β = 129.27, 95% CI 23.28 – 235.26) and water (β = 44.60, 95% CI 7.42 – 81.77), a weak avoidance of forests (β

= -1.91, 95% CI -6.46 – 2.65), and a strong avoidance of settlements (β = -21.79, 95% CI -38.44 – -5.14) and roads (β = -13.41, 95% CI -20.17 – -6.31).

3.3.6.7 AF096

We tracked AF096 between 2020-03-16 and 2020-07-28 (132.92 days). We performed 291 fixes, and recorded 56 relocations. We estimated AF096 to have a dBBMM 99% occurrence distribution of 426.32 ha and a mean motion variance of 22.75 ± 3.08 σ^2m (Figure 3.29). W recorded AF096 moving through a large irrigation canal of the transitional zone (Figure 3.27). She moved South after her capture, following the irrigation canal, and remained stationary within forest-adjacent agricultural area to nest. She subsequently moved back North, following the irrigation canal and into the agricultural matrix. Her nesting movements are characterised by a large peak of motion variance (locating an oviposition site), a long period of low motion variance (nesting) and another peak as she moved back towards her capture site (Figure 3.29).

Resource selection for AF096 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.31). Our single-factor models show that AF096 has a weak association with forests (β = 2.80, 95% CI -6.41 – 12.00) and semi-natural areas (β = 188.10, 95% CI -76.16 – 452.35), and a weak avoidance of settlements (β = -11.28, 95% CI -45.35 – 22.78), roads (β = -6.18, 95% CI -17.25 – 4.87) and water (β = -17.29, 95% CI -65.42 – 30.84).

3.3.6.8 AF099

We tracked AF099 between 2020-03-24 and 2020-07-24 (122.02 days). We performed 276 fixes, and recorded 31 relocations. We estimated AF096 to have a dBBMM 99% occurrence distribution of 490.84 ha and a mean motion variance of 15.52 ± 2.62 σ^2m (Figure 3.29). We recorded AF099 exclusively moving throughout the transitional zone of the SBR (Figure 3.27). She made linear movements via an irrigation canal and into dense forest area, where she remained for the remainder of her tracking duration. There are clear movement behaviours exhibited in AF099's motion variance where we observed a large peak as she was locating an oviposition site, followed by a long period of low motion variance during nesting, followed by an increase in motion variance as she moved away from her nest (Figure 3.29).

Resource selection for AF099 was best predicted by the single-factor Model 4 (Semi-natural areas; Figure 3.31). Our single-factor models show that AF099 has a weak association with semi-natural areas (β = 6.94, 95% CI -3.98 – 17.85) and water (β = 7.96, 95% CI -4.69 – 20.62), and a weak avoidance of forests (β = -1.14, 95% CI -5.83 – 3.55), settlements (β = -14.40, 95% CI -55.66 – 26.86) and roads (β = -24.67, 95% CI -87.07 – 37.73).

3.4 Discussion

We have now investigated the space use and interactions with landscape resources exhibited by King Cobras within the SBR using tracking data collected over the course of 7 years. Our results indicate that adult male (n = 9) *O. hannah* utilise larger areas than other demographics, likely attributed to large bouts of movement to locate females during the breeding season. This is followed by juvenile males (n = 5), adult females (n = 8) and then juvenile females (n = 2).

Males exhibiting a larger area of space use over female conspecifics is commonplace within snake radiotelemetry studies. Sutton *et al*. (2017) showed that male copperheads (*Agkistrodon contortrix*) had a larger 95% utilisation distribution than females (17.8 ± 2.3 ha; 7.1 ± 1.8 ha respectively). This is similar to other North American pit viper species, where Delisle *et al*. (2019) showed a significant difference in KDE between males and females (41.3 ± 6.8 ha; 7 ± 1.8 ha respectively) and DeSantis *et al*. (2019) highlighted the same pattern in western diamond-backed rattlesnakes (*Crotalus atrox*) with a greater 95% utilisation distribution estimated for males than females (42.6 ± 6.1 ha; 9.9 ± 1.8 ha respectively).

Few studies have investigated elapid spatial ecology and comparative inferences concerning other elapid species are lacking. Croak *et al*. (2013) present spatial ecology information for the broad-headed snake (*Hoplocephalus bungaroides*), an Australian endemic. Despite using more traditional space use estimators (MCP), the resulting areas of space use are much smaller than those exhibited by King Cobras in this study, and the largest area reported by Croak *et al*. (2013) was exhibited by a female during the spring/summer season (9.89 ha). Knierim *et al*. (2019) investigated the spatial ecology of a sympatric elapid snake to the King Cobras in this study, the banded krait (*Bungarus fasciatus*). The authors used the same statistical methods to estimate space use within the Sakaerat Biosphere Reserve, namely dynamic Brownian Bridge Movement Models, which showed their single male exhibiting a 99% occurrence distribution of 134.88 ha, which was considerably larger than the two females also studied (20.28 – 30 ha).

The estimated occurrence distributions of our telemetered King Cobra represent some of the largest areas of space-use by native snake species, however we are limited in making direct comparisons due to varying analytical techniques. This is only rivalled by areas exhibited by Indigo snakes (*Drymarchon couperi*), which had a maximum 100% MCP area of 1528 ha and a mean area of 359 ha (Hyslop *et al*., 2014); likely contributed to both Indigo snakes and King Cobras being large, actively foraging species. Though a true comparison cannot be made as MCP estimates are highly subjective to tracking regime and duration (Silva *et al*., 2018; 2020). Our telemetered King Cobras also exhibited much larger occurrence distributions than other large-bodied snakes within our study site, namely Burmese pythons (*Python* bivittatus; Smith *et al*., 2020). Burmese pythons at the SBR showed a mean dBBMM 99% occurrence distribution of 98.97 ± 35.42 ha and a maximum of 285.56 ha. Although Burmese pythons are large-bodied snakes, they exhibit a different foraging style than King Cobras, which likely explains the differences in occurrence distribution estimates (Spencer, 2012).

Our results suggest that reproductive events greatly influence movement as adult King Cobras will exhibit seasonal shifts in area use and motion variance corresponding to mate acquisition, locating oviposition sites and nesting behaviour. Seasonal shifts in space use have been observed in several other snake species, with males typically utilising larger areas than female conspecifics during breeding seasons (e.g. Timmerman *et al*., 1995; Waldron *et al*., 2006; Smith *et al*., 2009; Bauder *et al*., 2016). We also observed much larger areas of space use by our telemetered males than females, however our females also exhibited much greater occurrence distributions due to reproductive behaviour. Female King Cobras largely invest in the maternal care of eggs, and they are the only known snake species to actively build a nest for oviposition, alongside remaining with the nest (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). Prior to nesting, we observed large peaks in motion variance of females which we presume is due to females actively searching for suitable nesting sites. These peaks in motion variance were then followed by long durations of very low motion variance during nesting, and then another peak in motion variance when females were observed leaving oviposition sites.

Adult male King Cobras would also exhibit seasonal peaks in motion variance during the observed breeding season (March - April). This can be clearly observed in King Cobras tracked for multiple breeding seasons (e.g. AM018, Figure 4.36 and AM054, Figure 4.44). We typically did not observe this shift in motion variance estimates for juvenile males, with the exception of JM019 which exhibited a very large spike in the breeding season. We believe that this peak in motion variance is due to JM019 sexually maturing throughout his tracking period. We recorded an SVL for JM019, on his initial capture (2015-11-02), of 1823 mm; however, we measured his SVL on a subsequent re-capture (2016-06-20) as 2097 mm. This suggests that JM019 was already at reproductive size when he entered the 2016 breeding season, explaining the peak in motion variance typically exhibited by adult males.

Our movement analysis showed that telemetered *O. hannah* move throughout all three zones of the SBR, and that space use is not limited to the confinements of the ranger-patrolled protected area. We observed at least one individual represented by both life stages and both sexes moving between the protected core area and the transitional zone (e.g. JM025, JF055, AF017, AM018), often traversing the Highway 304 to do so. Protected areas, although designated as a method to counter the ever-growing pressure of human infringement, can be compromised due to permeable boundaries. Many studies have investigated the movement of wildlife throughout protected and non-protected areas, showing that animal movement is often unrestricted by the sanctuary of protected areas. This is particularly true for mammalian species such as elephants (Galanti *et al*., 2006; Wittemyer *et al*., 2007; Graham *et al*., 2009), wildebeest (Thirgood *et al*., 2004) and wolves (Vynne *et al*., 2014).

Movement throughout the agricultural area within the transitional zone was highly associated with semi-natural areas, which are densely vegetated areas bordering irrigation canals. We believe that these irrigation canals are acting as movement corridors, facilitating the movement through a human-dominated landscape, as these landscape features likely present areas of refuge (cover) throughout a human-dominated landscape (Marshall *et al*., 2020). Furthermore, the irrigation canals likely host a number of prey species for King Cobras, such as big-eyed pitvipers (*Cryptelytrops macrops*; Barnes *et* al., 2017; Strine *et al*., 2018), Burmese pythons (*Python bivittatus*; Smith *et al*., 2020) and several watersnakes (*Enhydris plumbea*, *Homalopsis mereljcoxi*, *Xenocrophic piscator*, *Cylindrophis rufus*; Murphy *et al*., 1999). Irrigations canals, or habitats near-to, have been shown as important habitat features for other snake species within human-disturbed landscapes. For example, Halstead *et al*. (2019) reported 74% of their observations of giant garter snakes (*Thamnophis gigas*) within irrigation canals at the Central Valley of California, USA.

Our population-level iSSF analysis suggests that the movement of male King Cobras can be largely predicted by the availability of forested areas. This observed association with forest may partly be due to the availability of a known prey item of male King Cobras: the clouded monitor lizard (*Varanus nebulosus*; Jones *et al*., 2020).

However, our individual-level iSSF analysis also suggested a high degree of individual heterogeneity exhibited in the associated movement in response to landscape resources by our telemetered males; particularly between different life stages. Our population-level iSSF on our telemetered females estimated semi-natural areas to be the best predictor for observed movement patterns. Again, we observed a high level of individual heterogeneity exhibited within our sample, though most individuals showed some association with semi-natural areas.

We are limited in our ability to make inferences about the exhibited differences between life stage and sex from our analyses, as the sampling effort was highly biased towards adult male King Cobra due to the high numbers of captures during increased breeding season movement. Furthermore, the temporal scale of our data including adult male King Cobras are much greater than any other demographic on average. Our iSSF analyses exhibit broad confidence intervals, which is likely contributed to our lack of relocations recorded for some individuals, limiting our sampling of available areas in contrast to true fixes. Although we can begin to make inferences on observed trends and behaviours, we suggest caution is taken when attempting to extrapolate results for similar studies throughout the distribution of *O. hannah*.

3.5 Conclusion

We have shown that King Cobras in the SBR utilise some of the largest areas of space when compared with other large snake species, worldwide. Our results suggest that male King Cobras use larger areas than females, though this inference is limited due to our sample bias (particularly temporal bias) towards telemetered males. In addition, reproductive individuals will shift their areas of space use and movement patterns during mate acquisition, and nesting behaviour. This demonstrates clear seasonality in the movement patterns of our King Cobra sample.

We also observed a high-degree of individual heterogeneity amongst our movement and resource acquisition analyses, suggesting that King Cobras exhibit characteristics of a generalist-species. This was particularly clear in the ability for our telemetered King Cobras to utilise almost any area within our study site, including protected and disturbed forest, aquatic/terrestrial agriculture, human settlements and areas rich with road networks.

This chapter begins to improve our understanding on the movement ecology of a large, highly mobile, reptilian predator. However, as our sample was limited to such a fine-scale spatial domain, we strongly suggest that that future studies attempt to replicate our study methods, particularly our spatial analyses, for other King Cobra populations so that we can begin to build a better understanding on this under-studied snake.

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CHAPTER IV

KING COBRA NESTING ECOLOGY

4.1 Introduction

Nesting ecology can refer to the factors influencing the fecundity of a species, particularly at a regional or population level (Beggs *et al*., 2007; Kamel and Delcroix, 2009). These factors can include the duration of the nesting season (Pike *et al*., 2006), size of nesting females (Congdon *et al*., 1987), clutch size and frequency (Tomillo *et al*., 2014), habitat selection for oviposition sites (Resetarits, 1998; Lor and Malecki, 2006) and other spatiotemporal patterns (Escalona *et al*., 2009).

Nesting ecology studies typically focus on the study of bird species, due to the broad complexity involving the nesting structures and behaviours exhibited (e.g. Pitman *et al*., 2006; Matsouka and Handel, 2010; Cassey *et al*., 2012; McNew *et al*., 2014). Reptile studies however, have largely focused on the nesting ecology of chelonians, which is attributed to the unique nesting behaviours exhibited by sea-turtle species aggregating on beaches to nest (Congdon *et al*., 1983; Reina *et al*., 2002; Cheng *et al*., 2009; Broderick and Godley, 2013; Thums *et al*., 2019; Gane *et al*., 2020). Very few reptile studies have focused on the nesting ecology of snakes, largely due to the lack of snake species which create nesting structures, as snakes will typically rely on natural oviposition sites.

For example, Nagy *et al*. (2017) showed that the forest vine snake (*Thelotornis kirtlandii*) will deposit eggs into parabiotic ant nests, which is believed to be advantageous due to thermal stability of the ant nests, and to prevent predation and fungal infection (Riley *et al*., 1985). Furthermore, the European grass snake (*Natrix natrix*) will oviposit in sites with rotting vegetation (Löwenborg *et al*., 2010; Baker *et al*., 2011) and even within roadside tunnels excavated by European moles (*Talpa europea*; Meek, 2017). Alexander (2018) also showed that southern African pythons (*Python natalensis*) oviposited within aardvark, warthog and porcupine burrow systems.

One snake species that is infamously known for creating nests for oviposition, is the King Cobra (*Ophiophagus hannah*). Many of the studies undertaken on the nesting ecology of the King Cobra have been focused on populations in India (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). Specifically, Whitaker *et al*. (2013) used information gathered from local residents to locate King Cobras oviposition sites, which resulted in a total of 15 nests between 2004 – 2010 within the states of Karnataka (n = 13), Mizoram (n = 1) and Uttarakhand (n = 1). The authors reported an average clutch size of 25 ± 0.5 eggs (range = 7-43 eggs), a mean incubation temperature of 23-27.1 ºC (range = 13.5 – 37.4 ºC), with females remaining with the nest for an average of 29 days (range = 2-77 days). Hrima *et al*. (2014), who also relied heavily on local information, discovered 18 nests between 2009 – 2012 in the Aizawl District of Mizoram. They report that the King Cobra nesting season within the Aizawl District occurs between late April and into July, with nests containing between 14-35 eggs and constructed on well-drained slopes primarily near to bamboo thickets; and further report an incubation temperature of between 26 – 29.5 ºC. In addition, Dolia (2018) recorded

18 nests between 2006 – 2017 within the Nainital district of Uttarakhand. Dolia (2018) report that nests were often in proximity to human habitation, disturbed forests and even fruit orchards, yet were only able to comprehensively report on a single nest which the female remained with for 2-3 weeks and contained 28 eggs within. They further captured and measured emerging hatchlings from this nest and report a mean total length of 50.8 cm (range = 46.7-55.9 cm; n = 27) and a mean mass of 22.7 g (range = 17-25 g; n = 27).

Of the studies reported above, adult female King Cobras were observed sitting within, or typically on top, of the nests for varying periods of time. This has largely been concluded as a method of deterring predators away from the nests (Daniel, 1983; Cox, 1991; Whitaker *et al*., 2013; Hrima *et al*., 2014). However, we can find no evidence of actual predator deterrence within the literature, which leaves the true reasoning for females sitting on-top of nests ambiguous. Females may be sitting upon nests to prevent excess amounts of water from reaching the eggs (as suggested in Whitaker *et al*., 2013), alternatively, females may be compacting the nest for greater thermal stability within the egg chamber.

Only one study has reported on nesting observations of King Cobras within Thailand, focusing collection efforts in the Nakorn Sri Thammaraj province, southern Thailand (Leakey, 1969). The authors show results from 16 nests between 3rd May 1966 – 31st May 1966, which contained a combined total of 484 eggs. Eggs and adult females were removed from the oviposition sites in Leakey (1969), and eggs artificially incubated which ultimately led to the death of all hatchlings. Most notably within this study, the largest clutch size reported was 43 eggs and nests were typically comprised of bamboo leaves that formed sealed structures presumably protecting nests from external temperature changes and excess moisture.

There is an evident paucity in the available literature concerning the nesting ecology of King Cobras, particularly within other populations of its distribution outside of India. Ambiguity remains concerning the nesting ecology of King Cobras, specifically in relation to the spatial ecology of King Cobras during nesting seasons, habitat requirements, the role of females post-oviposition and nest characteristics. This information is particularly interesting for populations within, or partly within, human-dominated landscapes. We therefore set out to investigate the nesting ecology of adult female King Cobras with the Sakaerat Biosphere Reserve (SBR), Northeast Thailand. As female King Cobras have been shown to heavily use space within an agricultural matrix within the SBR (Marshall *et al*., 2020), this gave us an opportunity to investigate how females residing within the agricultural landscape were adapting their nesting ecology in response to evident infringement into protected forested area. We investigate the nesting ecology of King Cobras within the SBR by: 1) comparing seasonal (breeding and non-breeding) occurrence distributions and motion variance via dynamic Brownian Bridge Movement Models, 2) using thermal dataloggers to compare temperatures within the egg chambers of nests with immediate environmental temperatures outside of the nest, 3) measuring nest characteristics of observed nests and further collecting biometric data on captured hatchlings from nests.

4.2 Methods

4.2.1 Study area

We conducted this study at the Sakaerat Biosphere Reserve (SBR), on the border of the Korat plateau within the Nakhon Ratchasima Province, Northeast Thailand (14.44-14.55º N, 101.88-101.95º E; see Chapter III for study site map). To investigate the nesting ecology of King Cobras, it is important to note that the SBR has three main zones which are afforded differing levels of protection under the Man and Biosphere (MAB) Program. The core area, which is routinely patrolled by reserve rangers, is afforded the greatest level of protection. The core protected area covers an area of 80 km^2 and is dominated by dry evergreen forest (60%) and dry dipterocarp forest (18%). This is followed by the buffer zone, which closely envelopes the core area with regenerating plantation forest. Lastly, the transitional zone offers the least protection, and is highly dominated by human settlements, agriculture (rice, cassava, sugar cane, corn), roads and other human infrastructure.

4.2.2 Snake capture for radiotelemetry

Throughout our study, we have found King Cobras to be difficult animals to detect, particularly females, we therefore deployed several strategies for capturing King Cobras for radiotelemetry. Firstly, we performed unstandardised visual encounter surveys throughout accessible areas of the SBR zones, which we performed both on-foot and via motorcycles. This limited our detectability of King Cobras by restricting us to areas with substantial road- and path-networks. We primarily conducted surveys in daylight hours (06:00am – 18:00pm), though occasionally performed these at night. Secondly, we utilised a long-term conservation initiative, conducted by the Sakaerat

Conservation and Snake Education Team, where local residents would have an opportunity to contact us if a snake entered their home or surrounding property. Furthermore, we also trained local rescue teams to safely capture both venomous and non-venomous snakes in the area, which could also be called by local residents. We would bring captured King Cobras, either captured by us or local rescue team volunteers, to the Sakaerat Environmental Research Station (SERS) for assessment. Lastly, we used the Judas technique introduced by Smith *et al*. (2016), to locate female King Cobras using telemetered conspecifics. We performed radiotelemetry on male King Cobras (explained in detail in Chapter III), and used these individuals to locate females. Specifically, male King Cobras will actively pursue females during the breeding season, and we strictly monitored males during this time to aid with bolstering our sample size of female King Cobras. This comprised of monitoring radio-signals of telemetered males until it appeared that males were moving (fluctuations in the radio-signal), but no directional change was noted for the individual. This suggested that a male was moving around in a single location, and likely exhibiting a unique behaviour (such as interacting with a conspecific), allowing us to move in to attain a visual, in the attempt to capture a female.

Regardless of capture method, we recorded the location (Universal Transverse Mercator 47 N WGS 84 datum) of each captured female using handheld GPS units (Garmin 62 and 64 models), alongside the time and date of capture. We gave each King Cobra an ID corresponding to their age-class and chronological addition to the project (e.g. the ninety-ninth King Cobra captured, an adult female, is allocated the ID: AF099). We marked study King Cobras number 001 – 053 using ventral and dorsal scale branding, as described in Winne *et al*. (2006) and switched to using passive internal transponders from individual 054 onwards.

As we are interested in the nesting/reproductive ecology of King Cobras for this study, we aimed to track adult female King Cobras, and added individuals to the study by assessing the following criteria: 1) King Cobras had a snout-to-vent length (SVL) greater than 1800 mm, suggesting that the female is of reproductive size, 2) the transmitter did not exceed 5% of the snake's total body mass, 3) individuals qualitatively appeared to be in good health, 4) we are able to access capture locations and surrounding areas with relative ease in order to maintain a consistent tracking regime.

4.2.3 Transmitter implantation

We kept study animals in large, opaque plastic boxes, providing a water dish and shelter at SERS. When we were confident that the snake met our criteria, we contacted D.V.M Wirongrong Changphet, a veterinarian at the Nakhon Ratchasima Zoo, to perform surgery. We followed aseptic protocols when preparing for surgery, which consisted of boiling surgery tools in water for a minimum of 30 minutes, followed by placing the tools in 95% ethanol. We further disinfected the surgery table with 95% ethanol, prior to surgery. We anaesthetised snakes using the inhalant anaesthetic isoflurane, maintaining the exposure to anaesthetic until surgery was close to completion. We followed surgery protocols outlined in Reinert and Cundall (1982) and Hardy and Greene (2000), with the addition of isoflurane. We inserted the VHF radio-transmitter (Holohil SI-2T or AI-2T) into the coelomic cavity, running the transmitter antennae laterally below the subcutaneous tissue (further surgery protocols can be found in Chapter III).

Following successful surgery, we released implanted King Cobras, as near to reported capture locations as possible, which proved difficult when snakes were captured within human-settlements. We report the capture and release information for all telemetered adult female King Cobras, reporting the first telemetered location when release information is missing (Table 4.1).

Table 4.1 Capture and release information for telemetered adult female *O. hannah*. ID* depict individuals where true release sites were not recorded and the first datapoint was used. *Distance* Distance between capture and release UTM's.

ID	Capture Date	Capture Easting	Capture Northing	Release Date	Release Easting	Release Northing	Distance (m)
AF017*	28th April 2015	818424	1607178	6th May 2015	818376	1607172	48
AF058	6th April 2018	816730	1604030	10th April 2018	816730	1604030	0
AF086	23rd April 2019	820274	1608801	25th April 2019	820274	1608801	0
AF096	10th March 2020	821702	1610664	16th March 2020	821702	1610664	0
AF099	18th March 2020	820608	1607174	23rd March 2020	820608	1607174	0

4.2.4 Radio tracking snakes

We aimed to track AF017 four times per day, at approximately 06:00am, 11:00am, 16:00pm and 20:00pm, and the remaining snakes three times per day at approximately 08:00am, 13:00pm and 18:00pm, due to staff limitations. We achieved a mean time lag between tracks of 8.93 ± 0.09 hours (Range = 0.08 – 106.83; Figure 4.1). We tracked snakes using a triangulation method, attempting to maintain a minimum distance of 10 m away from a snake's true location, giving us reasonable confidence that a snake was within a 5 m^2 area. We performed triangulation using a method of measuring lines on our GPS units in the direction of the snake, and repeating at multiple points surrounding the snake. When adult females were sitting on-top of nests, we would frequently obtain visuals on the snake, breaking our typical protocol of 10 m away. We recorded each location on handheld GPS units, including GPS accuracy, date and time.

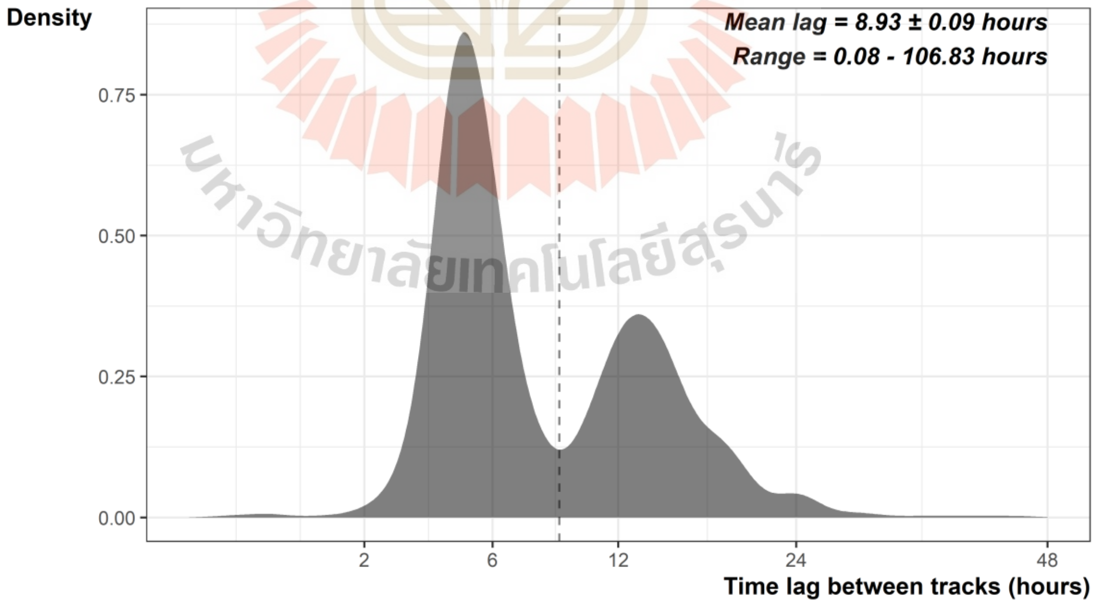

Figure 4.1 Time-lag between fixes for adult female King Cobras.

4.2.5 Nest monitoring

We closely monitored female King Cobras throughout our delineated breeding season (March 1st – July 15th). When we suspected that a female had begun nest-building, we moved in towards the exact location of the female in order to attain a visual to confirm the behaviour. We then deployed a minimum of one wildlife camera to monitor nest behaviours (Figure 4.2). We maintained the deployment of the wildlife cameras until we tracked the nesting female to a new location at a minimum of 200m away from the oviposition site, i.e., the snake had concluded nesting behaviour. Once we had confirmed the snake had moved away, we recorded the following measurements of the nest: *diameter* of the nest from North-South and East-West and *circumference* of the outer perimeter of the nest (qualitatively assessed via nest substrate).

Figure 4.2 Camera trap photo of AF086 sitting on top of her nest on 10-06-2019.

Immediately after measurements, we carefully opened up the nest to reveal the egg chamber. We took photos of the egg arrangement upon revealing the egg chamber prior to any manipulation to recreate the arrangement if we needed to move any eggs. We marked all of the eggs with a unique number using a non-toxic marker pen (Figure 4.3), in order to assess the subsequent hatching success. We removed and replaced eggs only in the event where we could not access lower eggs for counting/marking and recorded the total number of eggs present in the chamber. We carefully replaced any moved eggs, using our initial photo of egg arrangement as reference.

Figure 4.3 Marked eggs inside the egg chamber of a King Cobra nest.

Once all eggs were marked and counted, we proceeded to place pre-programmed HOBO MX TidbiT 5000 temperature-loggers inside of the egg chamber.

We programmed dataloggers to record temperatures every 15 minutes, chosen to record any fine-scale changes in temperature throughout the incubation period. When we only had the opportunity to monitor one nest in the year (i.e., AF058 and AF086's nests), we placed the internal dataloggers on the perimeter of the eggs in a North, East, South and West orientation (Figure 4.4). We were only able to place dataloggers in a North and South orientation for the nest of AF096 and AF099 due to equipment limitations. We then placed a small clump of nesting material back on top of the eggs and placed a final internal datalogger on top of this debris. Upon placement of all internal dataloggers, we recovered the nest with nesting substrate, attempting to recreate the integrity of the nest as we originally found it. We then proceeded to place external dataloggers surrounding the nest in the same orientation as the interior. We attached external dataloggers on natural structures surrounding the nests (vines, branches, stems), though used metal stakes when natural holdings were unavailable at a maximum distance of 2m away. This resulted in five internal and five external dataloggers for the nests of AF058 and AF086, and three internal (North, South and Central) and two external (North and Central) for the nests of AF096 and AF099.

Figure 4.4 Marked eggs inside the egg chamber of a King Cobra nest, showing the placement of four internal HOBO MX TidbiT 5000 temperature-loggers. Photo by Benjamin Marshall.

Following the placement of dataloggers, we erected an enclosure around the nest in an attempt to capture any newly-hatched snakes leaving the nest (Figure 4.5). We made the enclosure out of garden netting, using bamboo stakes and zip-ties to secure the structure, attempting to minimise any point of escape. Once we had erected the enclosure, we checked the nest two – three times per day to assess if any hatchlings had emerged. We captured any snakes that were leaving the nest by making a small incision into the enclosure and pulling them out using a snake hook or tongs, immediately placing them into a plastic box for processing. We were unable to capture any hatchlings from the nests of AF086 and AF096 (which we believe was due to the late erection of our enclosures). However, we processed hatchlings from AF058's nest in the field, and brought snakes from AF099s nest back to the Sakaerat Environmental Research Station (SERS) for processing.

Figure 4.5 An enclosure built around the nest of AF058 to prevent the escape of hatchling King Cobras.

4.2.6 Neonate processing

We chose not to anaesthetise neonate King Cobras as we were unsure if such small snakes would be able to wake up from anaesthetic, and wanted to minimise the risk of harming individuals. We therefore placed snakes into plastic snake tubes, in order to mitigate potential bites. We attempted to photograph all aspects of the snakes for subsequent scale counts, including head side (Figure 4.6), head dorsal, head ventral, ventral scales, subcaudal scales and body dorsals. We then placed string along the length of the snake and subsequently measured the piece of string to record the snout-to-vent length of the snake, we performed this over the top of the tube for safety purposes which may impact the accuracy of measurements. We then measured the tail length of neonates using the same method. We measured the mass of individuals by placing them into cotton snake bags and placing them onto weighing scales, and subsequently weighing the bag to assess the true mass of the snakes. We attempted to identify the sex of hatchlings using a snake probe, though this proved unsuccessful due to the size of the snakes. When processing snakes in the field, we immediately released them following processing within 1m of the nest. For individuals brought back to SERS, we released them within 24-hours of processing.

Figure 4.6 Head side photograph of a neonate King Cobra.

Once several individuals had begun emerging from the nest, we re-opened the nest to assess if all snakes had hatched, and capture any still remaining within the egg chamber. We counted and collected all eggs to assess the number that had successfully hatched. We also collected the dataloggers and downloaded the temperature readings for subsequent analysis.

4.2.7 Motion variance and space use

We investigated the seasonal changes in space use and motion variance by separating our tracking data into two main seasons: *breeding*, tracking period where mating and nesting were observed, and *non-breeding*, the remainder of an individual's tracking duration. We observed the earliest breeding behaviour by telemetered individuals on March 10th and further observed a female leaving her oviposition site as late as July 5th, throughout multiple years. We incorporated a 10-day buffer to each of these dates, which resulted in a breeding season between March 1st and July 15th and a non-breeding season between July 16th and February 28th.

Similar to methodology outlined in Chapter 3, we ran dynamic Brownian Bridge Movement Models (dBBMM) in the *move* package v.3.1.0 (Kranstauber *et al*., 2016), which allowed us to estimate the motion variance of telemetered King Cobra throughout the two seasons. We then extracted 90, 95 and 99% contours using the *adehabitatHR* v.0.4.16 (Calenge, 2006) and *rgeos* v.0.4.2 (Bivand and Rundel, 2020) packages to visualise estimated space use of individuals. We chose to run dBBMMS over traditional space use estimates due to evidence of omission and commission errors observed in minimum convex polygons (MCP) and kernel density estimates (KDE) respectively (Fieberg and Börger, 2012; Silva *et al*., 2020). We ran dBBMMs using a window size of 15 and a margin size of 3, which we chose due to the small temporal scale of the breeding season, allowing small changes in behavioural states to be efficiently factored into the models.

4.3 Results

4.3.1 Motion variance and space use

We tracked three adult female King Cobras in the non-breeding season (Table 4.2), which we tracked for an average of 197.3 ± 17.92 days. We performed an average of 535 ± 68 fixes and recorded a mean of 205 ± 28 relocations. We estimated an average dBBMM 99% occurrence distribution of 89.99 ± 26.36 ha. We tracked AF017 for two consecutive non-breeding seasons and report both separately, we also tracked AF058 and AF086 within a non-breeding season, though none were concurrently tracked.

Table 4.2 Tracking summary of adult female King Cobras within our two seasons: *breeding* and *non-breeding*. σ^2m: motion variance.

					dBBMM contour			
ID	Season	Fixes	Days	Relocations	90	95	99	σ^2m
AF017_1	Breeding	209	70.54	49	42.49	69.99	126.7	12.98 ± 2.12
AF017_2	Non-breeding	698	228.54	211	19.04	29.5	51	6.44 ± 0.54
AF017_3	Breeding	452	136.45	122	0.94	9.85	58.22	7.42 ± 1.06
AF017_4	Non-breeding	598	227.41	277	10.32	19.13	39.65	4.88 ± 0.37
AF017_5	Breeding	288	109.96	75	33.33	72.63	183.81	13.15 ± 1.57
AF058_1	Breeding	250	95.11	68	97.42	185.01	338.93	9.98 ± 1.43
AF058_2	Non-breeding	422	173.26	186	63.25	94.16	146.8	14.61 ± 1.09
AF086_1	Breeding	201	80.18	54	124.9	175.59	277.09	19.56 ± 2.76
AF086_2	Non-breeding	422	160	144	50.56	76.56	122.49	8.72 ± 0.7
AF096	Breeding	280	119.6	54	131.76	213.1	385.34	22.75 ± 3.47
AF099	Breeding	262	113.17	26	150.7	279.05	519.57	15.03 ± 2.87

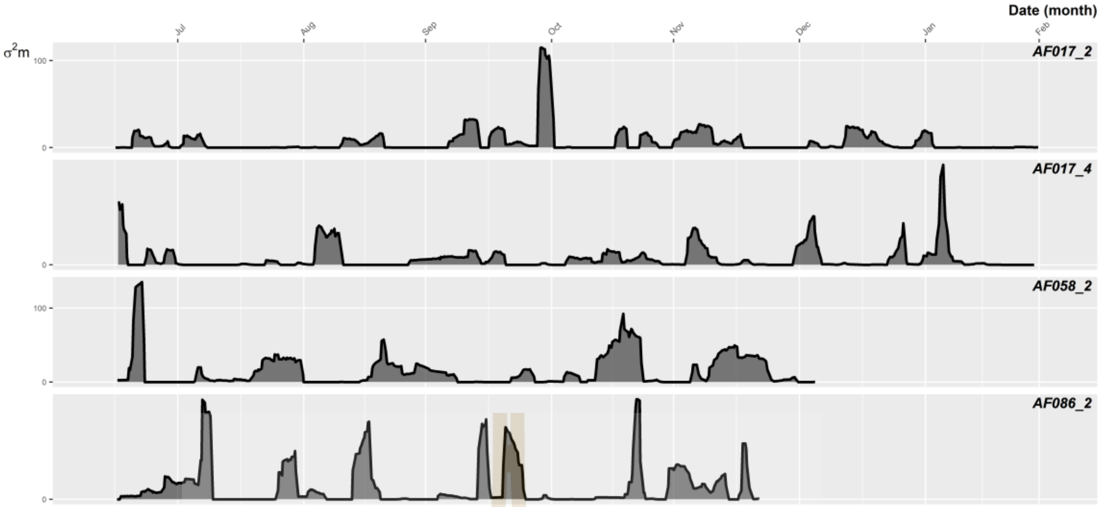

Figure 4.7 Motion variance of adult females during the non-breeding season.

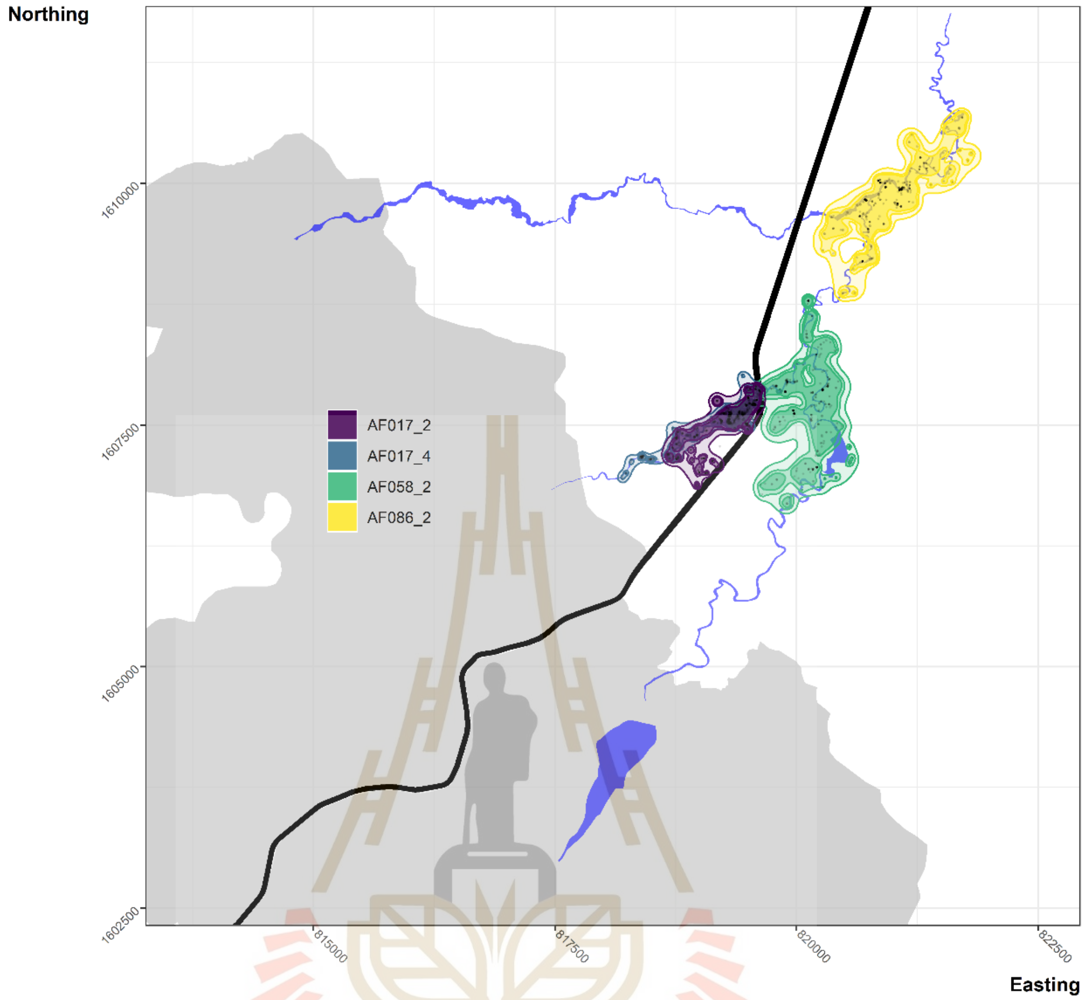

Figure 4.8 DBBMM occurrence distributions of adult females in the non-breeding season. Grey area depicts forested areas, the bold black line shows the Highway 304, blue shows the irrigation canals. Coloured contours show the 90, 95 and 99% contours in decreasing opacity respectively. Black dots show tracking fixes.

We tracked five adult female King Cobras in the breeding season (Table 4.2), which we tracked for an average of 103.57 ± 8.7 days. We performed an average of 277 ± 32 fixes and recorded a mean of 64 ± 11 relocations. We estimated an average dBBMM 99% occurrence distribution of 255.67 ± 51.61 ha. We tracked AF017 for three consecutive breeding seasons and report all separately, we also tracked AF058, AF086, AF096 and AF099 within a breeding season, though only AF096 and AF099 were concurrently tracked.

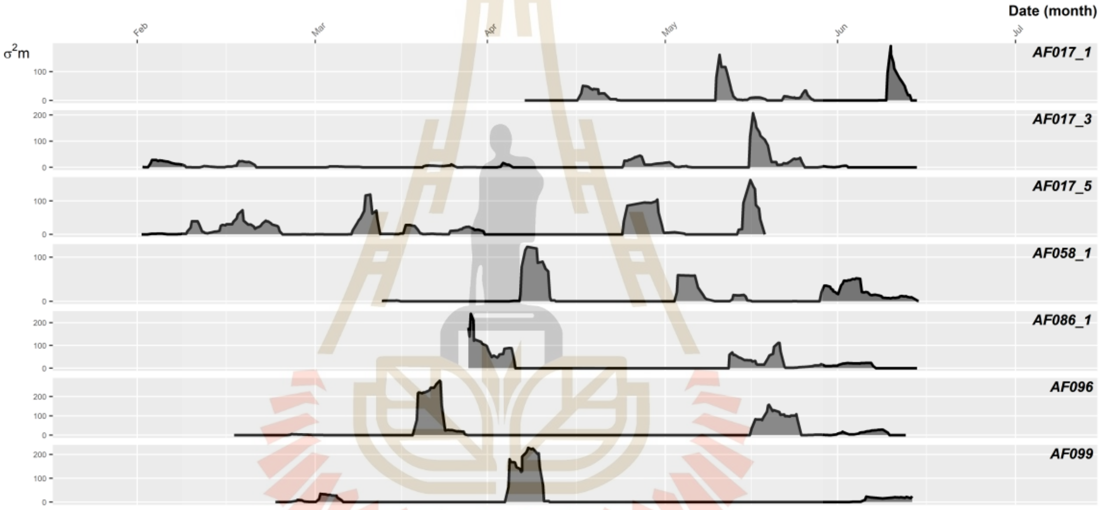

Figure 4.9 Motion variance of adult females during the breeding season.

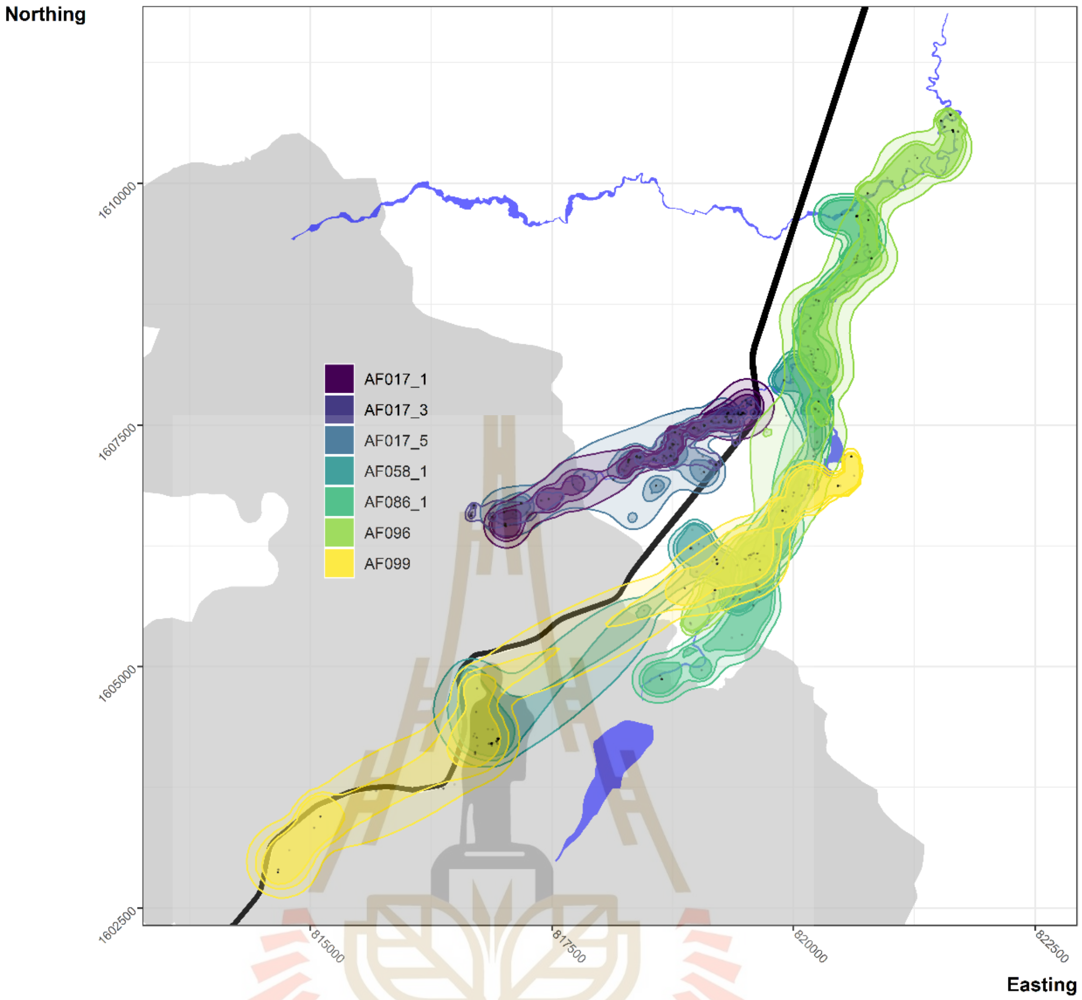

Figure 4.10 DBBMM occurrence distributions of adult females in the breeding season. Grey area depicts forested areas, the bold black line shows the Highway 304, blue shows the irrigation canals. Coloured contours show the 90, 95 and 99% contours in decreasing opacity respectively. Black dots show tracking fixes.

4.3.2 Nesting behaviours and processing

We discovered and processed four nests in total (Figure 4.33). We processed one nest by AF058 (Figure 4.29) in the 2018 breeding season which had a circumference of 1040mm, a North to South diameter of 740mm and an East to West diameter of 790mm and we discovered a total of 33 eggs inside of this nest. The nest of AF058 was comprised of forest floor debris, mainly leaf litter and twigs intertwined with small roots and branches. The nest was constructed at the base of a large vine, with other vines and dense vegetation surrounding. We recorded AF058 at her nesting location on 16-05-2018, where she remained until 02-06-2018, concluding nest construction, oviposition and nest-sitting in 17 days. We observed AF058 consistently moving off her nest in the evenings via camera trap footage, and taking shelter under a nearby rock, resuming nest-sitting at early day-break. We were unable to approach the nest, to change camera-trap batteries and sd cards, without the female fleeing to a nearby rock shelter.

Figure 4.11 Camera-trap photo of AF058 sitting on her nest on 02-06-2018.

We also processed one nest by AF086 (Figure 4.30) in the 2019 breeding season which had a circumference of 2640mm, a North to South diameter of 820mm and an East to West diameter of 990mm and we discovered a total of 36 eggs inside of this nest. The nest of AF086 was comprised of dried leaf litter and twigs, constructed amongst and within grassy vegetation. The nest was at the base of a Eucalyptus tree with densely vegetated grass surrounding the nest. We observed nest construction on 06-05-2019, and AF086 left her nest on 13-06-2019, allowing the construction of the nest, ovipositing and nest-sitting to be concluded within 38 days. We mostly observed AF086 sitting upon her nest for the majority of her nesting period post-construction, however, she would occasionally shelter under nearby vegetation for varying periods of time. This behaviour increased in frequency towards the end of her nest-sitting as she was undergoing ecdysis. We recorded AF086 moving into the nearby vegetation patch when overly disturbed by observers during camera-trap replacement. We observed AF086 leaving her nest shortly after ecdysis.

Figure 4.12 Telemetered female AF086 sitting upon her nest.

We then processed two nests in the 2020 breeding season by AF096 (Figure 4.31) and AF099 (Figure 4.32). We measured the nest by AF096 to have a circumference of 3019 mm, a North to South diameter of 1020mm and an East to West diameter of 1160mm, and discovered 50 eggs within. The nest of AF096 was constructed at the base of a large bamboo patch, amongst densely vegetated evergreen plants. We recorded bamboo leaves, other leaf litter and twigs comprising the main structure of the nest, which were intertwined with small roots and vines. The nest was near to a foot-path at the edge of an irrigation canal, the nest (and snake) could easily be seen from the path. We recorded AF096 constructing her nest on 27-04-2020 and leaving on 17-06-2020, resulting in 50 days performing nesting behaviours. Following nest construction, we barely noted any further movements from AF096 other than apparent repositioning. However, she entered ecdysis towards the end of her nest-sitting behaviour and would spend varying periods of time sheltering under nearby vegetation. We observed AF096 leaving the nest almost immediately following ecdysis. Despite the need for observers to get within 2m of the nest for camera-trap replacement, we never recorded AF096 fleeing from her nest.

Figure 4.13 Telemetered female AF096 sitting upon her nest.

We measured the nest of AF099 to have a circumference of 2400mm, a North to South diameter of 660mm and an East to West diameter of 950mm, and discovered

34 eggs inside. The nest of AF099 was constructed at the base of a young bamboo patch, within a large rock complex comprising the edge of a mostly-dried stream bed. We recorded that the nest was comprised of predominantly leaf litter and small twigs and partially enveloped the base of the young bamboo patch, with sparse vegetation surrounding. We recorded nest construction on 11-05-2020 from AF099, and observed her leaving the nest on 07-07-2020, resulting in 57 days of nesting behaviour. Although we recorded AF099 sitting upon her nest almost continuously throughout her nest-sitting, we also recorded her fleeing the nest during every radio-tracking fix, even when observers were >10m away, returning shortly after. We further recorded AF099 performing ecdysis towards the end of her nesting behaviours, leaving shortly after ecdysis had concluded.

Figure 4.14 Telemetered female AF099 sitting upon her nest.

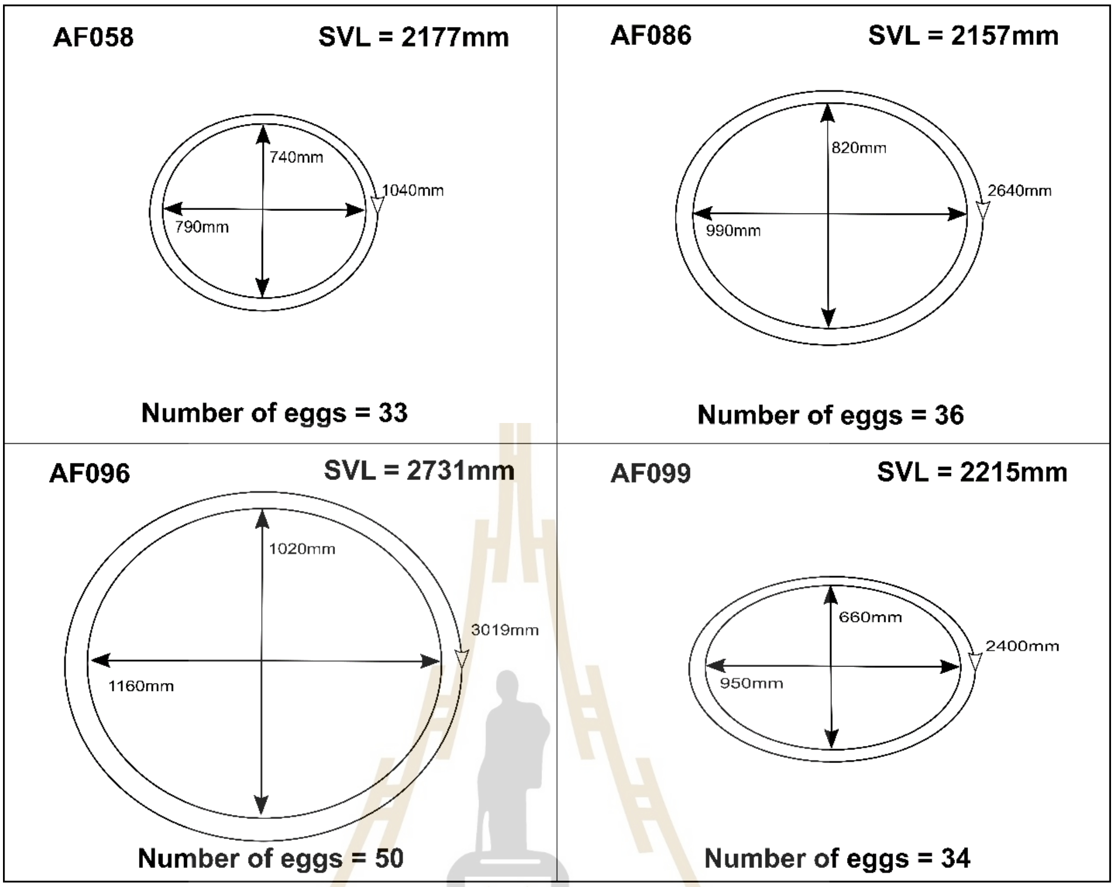

Figure 4.15 Measurements from four King Cobra nests. The size of the nest represents the scaled size in relation to the other nests.

4.3.3 Nest temperatures

We deployed dataloggers into four nests during this study, for the nests of AF058 (2018), AF086 (2019), AF096 (2020) and AF099 (2020). We recorded a mean internal temperature for the nest of AF058 of 26.32 ºC with a standard deviation of 0.005 ºC, and a mean external temperature of 25.42 ºC with a standard deviation of 1.72 ºC (Figure 4.34); comprised of five internal dataloggers and five external.

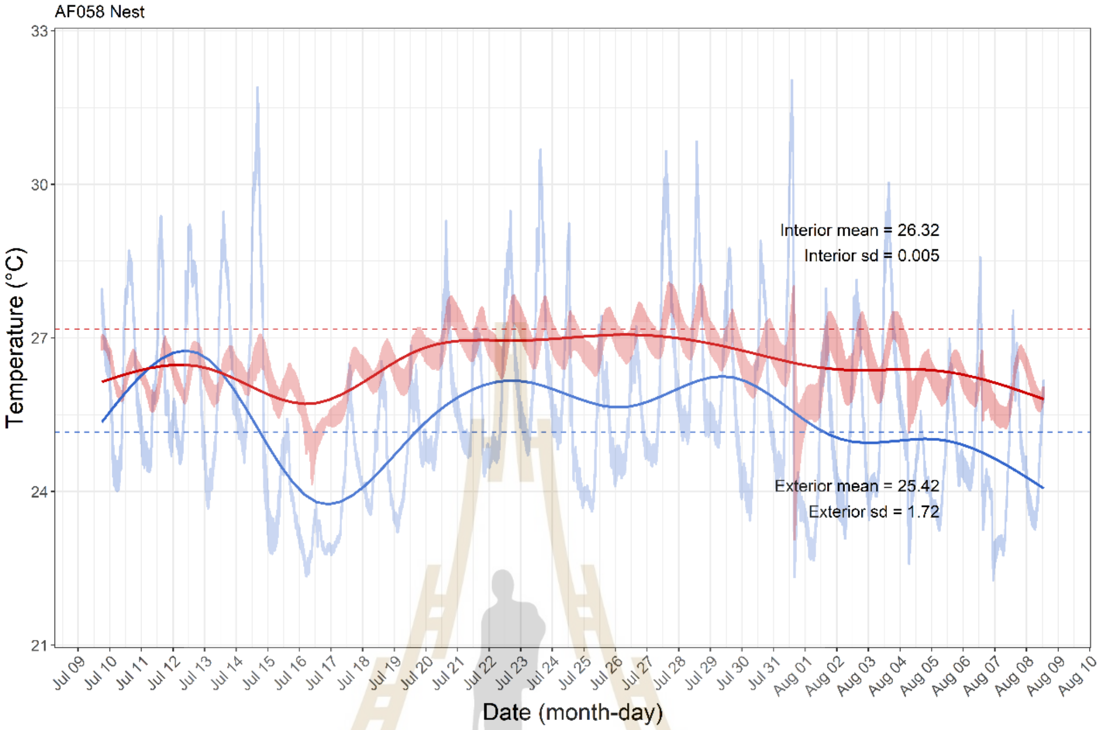

Figure 4.16 Temperatures of AF058's nest. Red lines show the internal temperatures and blue shows the external temperatures. *sd*: standard deviation.

We recorded a mean internal temperature for the nest of AF086 of 27.67 ºC with a standard deviation of 0.007 ºC, and a mean external temperature of 27.41 ºC with a standard deviation of 3.3 ºC (Figure 4.35); comprised of five internal dataloggers and five external.

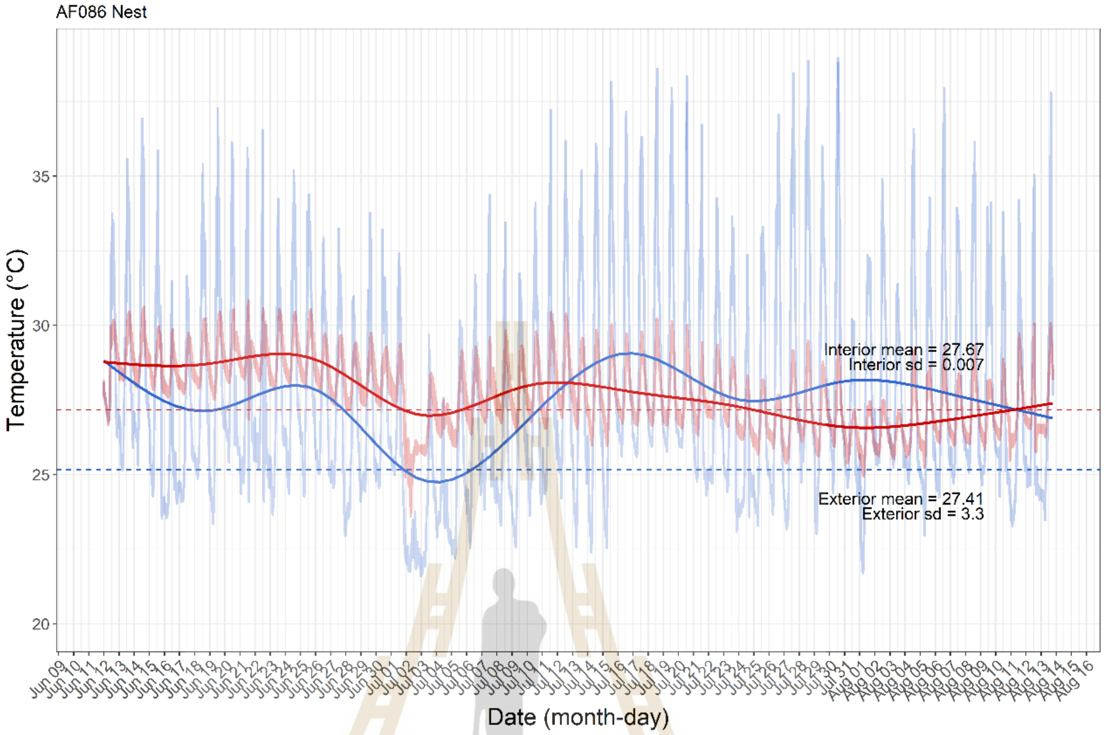

Figure 4.17 Temperatures of AF086’s nest. Red lines show the internal temperatures and blue shows the external temperatures. *sd*: standard deviation.

We recorded a mean internal temperature for the nest of AF096 of 27.88 ºC with a standard deviation of 0.009 ºC, and a mean external temperature of 27.09 ºC with a standard deviation of 2.72 ºC (Figure 4.36); comprised of three internal dataloggers and two external.

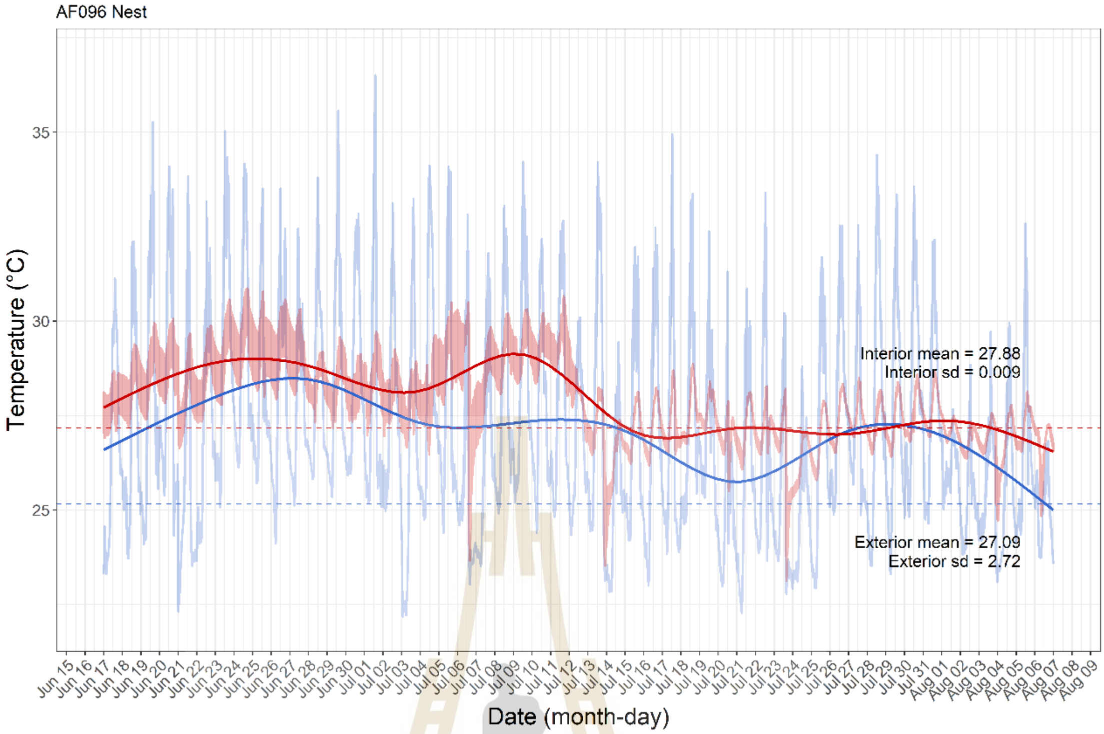

Figure 4.18 Temperatures of AF096's nest. Red lines show the internal temperatures and blue shows the external temperatures. *sd*: standard deviation.

We recorded a mean internal temperature for the nest of AF099 of 27.17 ºC with a standard deviation of 0.008 ºC, and a mean external temperature of 25.16 ºC with a standard deviation of 2.4 ºC (Figure 4.37); comprised of three internal dataloggers and two external.

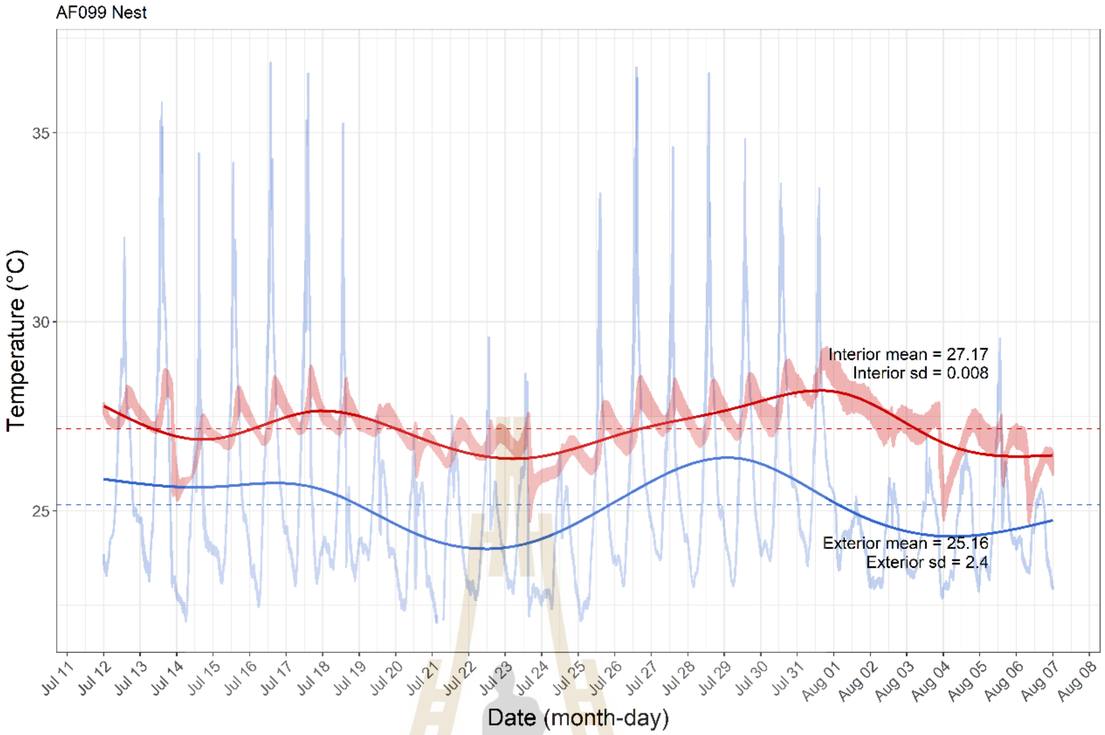

Figure 4.19 Temperatures of AF099's nest. Red lines show the internal temperatures and blue shows the external temperatures. *sd*: standard deviation.

4.3.4 Neonate processing

We captured and processed a total of 15 neonates across two nests (Table 4.3). We captured 12 hatchlings from the nest of AF058 which had a mean SVL of 371.5 ± 5.5 mm, a mean tail-length of 81.25 ± 1.67 mm and a mean mass of 17.74 ± 0.44 g. We then captured 3 hatchlings from the nest of AF099. We recorded these latter three hatchlings to have a mean SVL of 428.67 ± 6.96 mm, a mean tail-length of 87.33 ± 5.46 mm and a mean mass of 18.07 ± 0.96 g. We failed to capture any hatchlings emerging from the nests of AF086 and AF096.

Table 4.3 Bio-metric data of neonate King Cobras. *SVL*: snout-to-vent length, *TL*: tail-length.

Nest	ID	SVL (mm)	TL (mm)	Mass (g)
AF058	Hatchling 1	362	82	17.7
AF058	Hatchling 2	394	94	19.5
AF058	Hatchling 3	356	73	14.8
AF058	Hatchling 4	384	80	18.1
AF058	Hatchling 5	392	82	18.8
AF058	Hatchling 6	334	80	16.2
AF058	Hatchling 7	382	82	15.9
AF058	Hatchling 8	388	80	20
AF058	Hatchling 9	366	76	18.5
AF058	Hatchling 10	382	84	17.9
AF058	Hatchling 11	372	88	18.5
AF058	Hatchling 12	346	74	17
AF099	Hatchling 13	430	84	18.6
AF099	Hatchling 14	416	80	16.2
AF099	Hatchling 15	440	98	19.4

4.4 Discussion

In this chapter, we have provided clear evidence of seasonal shifts in occurrence distributions by adult female King Cobras between the breeding and non-breeding seasons. Our results showed that, despite the breeding season being a much shorter time-frame than the non-breeding season, females utilise larger areas of space, corresponding to movement into the forest for nesting. We did not observe our telemetered King Cobras moving into the forest during the non-breeding season, suggesting that adult females, with occurrence distributions primarily within an agricultural landscape, will only move into the forest for locating suitable oviposition sites. Our results also suggest that adult females will exhibit a greater movement variance during the breeding season. However, we did not observe this for AF058, though believe this is due to initially capturing AF058 within the forest suggesting that she may have already made large movements from the agricultural area. We also observed more linear movements during the breeding season, which is likely attributed to females moving directly into the forest for nesting. In contrast, females will use smaller, yet more evenly distributed areas of space during the non-breeding season. Furthermore, our motion variance estimates show clear shifts in behavioural states between the two seasons. Our non-breeding results generally show that females will exhibit regular small peaks in motion variance, likely corresponding to bouts of foraging, digestion and ecdysis. However, within our breeding seasons estimates, there are distinct peaks of high motion variance where females are moving into the forest, followed by long periods of low motion variance during nesting, and then another large peak as females move away from the forest and into the agricultural matrix.

Previous studies have generally shown that gravid females will reduce movement frequency, and distance, when compared to non-gravid females. For example, Charland and Gregory (1995) compared the movements of two species of garter snakes (*Thamnophis sirtalis* and *Thamnophis elegans*) in southeast British Columbia, Canada. Their results showed that gravid females adopted a more sedentary movement behaviour, exhibiting smaller movement distances and frequency than non-gravid conspecifics. Whitaker and Shine (2003) investigated the movements of brownsnakes (*Pseudonaja textilis*) in southeastern Australia and showed that reproductive females had smaller home ranges than non-reproductive females (0.38 ha and 2.16 ha respectively). However, Whitaker and Shine (2003) also showed that two of their telemetered gravid females made relatively large movements (maximum = 315 m) towards oviposition sites, similar to our observations of female King Cobras. In contrast, Buchanan *et al*. (2017) studied the spatial ecology of eastern hognose snakes (*Heterodon platirhinos*) in Massachusetts, USA, and showed that the movements of gravid females were substantially restricted prior to oviposition and significantly greater in the two-week post-oviposition period. In our King Cobra sample, we observed large movements pre- and post-oviposition, which was greater than those observed during non-breeding movements.

Based on our motion variance estimates, alongside personal observations of breeding behaviour, it appears than adult female King Cobras will breed between early March and mid-April and begin making movements towards an oviposition site between late March and late April. We observed females constructing nests between late-April and mid-May, and further remaining with the nest for between 17 and 57 days after commencing nest construction. Observation of nest building and sitting by females is largely congruent with nest observations made in Indian studies (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). Our telemetered females exhibited movements away from nests between early June and early July, prior to eggs hatching. Although the exact hatch dates from our nests are largely unknown, we suspect that this occurs between mid-July and early August due to our limited observations of emerging neonates.

We are limited in our inferences concerning nests and our resulting measurements due to our small sample size of located oviposition sites (n = 4). However, our results suggest that adult female King Cobras will use leaf litter, twigs and other forest debris to construct a nest of approximately 650 – 1200mm diameter and a circumference of 1000 – 3500mm. This appears to be dependent on the size of the female, which may directly correlate to the possible number of eggs laid. Our biggest clutch recorded was from AF096, our longest female ever recorded at the SBR with an SVL of 2731mm, which laid 50 eggs. Our other three females, which all had an SVL of approximately 2200mm, laid between 33 and 36 eggs. We recorded three of our nests within dense forested area (AF058, AF086 and AF099) and one nest on the edge of an irrigation canal adjacent to forested area. This suggests that King Cobras have an affinity to build nests within semi-disturbed areas, particularly as we personally observed agricultural workers, working within 50m from AF096's oviposition site. As the irrigation canals comprise an important component of the agricultural matrix, the ability for King Cobras to use the edge of these as nesting locations provides a promising aspect to the future of this population of King Cobras. However, despite this observed nest, AF096 still made clear movements South to be adjacent to forested area before building her nest.

Knierim *et al.* (2019) reported on nest attendance of banded kraits (*Bungarus fasciatus*), also within the Sakaerat Biosphere Reserve. Two females from Knierim *et al.* (2019) nested within the same burrow complex, with an overlap of 64 days and remaining in the burrow for 75 days and 77 days each in total, which is likely the first record of free-ranging elapid snakes exhibiting communal nesting. This, alongside our observations of King Cobra nesting, shows an evolutionary propensity for paternal care in Thailand elapid snakes, which may be true for other sympatric species, though further research is needed. Python species, such as the southern African python (*Python natalensis*), are also known to heavily invest in parental care (Alexander, 2018). Specifically, Alexander (2018) showed that *P. natalensis* remained with neonates for up to three weeks post-hatching, alongside other interesting maternal care traits, such as facultative melanism. Indian rock pythons (*Python molurus molurus*) are also known to exhibit maternal care for eggs, remaining with egg masses for up to 11-13 days prior to hatching (Ramesh and Bhupathy, 2010). The results presented for *P. m. molurus* represent a similar reproductive ecology as our King Cobra sample, where females will leave oviposition site prior to neonate emergence. Lastly, Hill III *et al*. (2006), also within our study area, report on nest attendance of a Malayan pit viper (*Calloselasma rhodostoma*) where the female remained coiled around eggs for the entirety of incubation, possibly exhibiting maternal thermogenesis.

Our temperature readings from our deployed dataloggers shows that the egg chamber of nests provide greater thermal stability when compared to immediate external temperatures. Although the mean temperature between the inside and outside of nests did not differ substantially, we observed much greater standard deviations surrounding our temperature readings for external temperatures when compared to readings from inside the egg chamber. As a result, external temperatures will reach much greater maximum and minimum temperatures. These results likely have a direct advantage to incubating eggs, as we observed a very high hatching success rate for our sampled nests. Again, we can only infer overall trends and cautiously extrapolate these results to other unsampled nests within our study site. Even though we are beginning to observe a clear relationship between the thermal stability within and outside of nests, we can only postulate that these provide a population-level pattern.

Our results, particularly due to our low sample size, do not allow us to answer the question of why females will remain with the nests following construction. Our temperature readings from dataloggers support the hypothesis that females will sit on top of nests to compact the nest and provide greater thermal stability within the egg chamber. However, one of our telemetered females, AF058, would often leave the nest for sheltering nearby throughout the night, alongside laying across a branch directly above the nest during the day. This would suggest that the female remains around for predator deterrence, however, we observed this same female, alongside two other females AF086 and AF099, often fleeing from their nests on approach by observers. This does not completely dismiss the notion of predator deterrence, as adult females will likely evaluate the benefits of defending the nest from a large mammalian predator and choose to flee, however, we cannot conclude the exact reasons with our limited sample size and observations.

We discovered that it was overall very difficult to capture neonate King Cobras emerging from the nest, while trying to cause as minimal disturbance as possible. Our enclosures proved generally ineffective for capturing neonates, resulting in a total of 15 captures across two nests; which is poor considering the maximum possible neonates of 153 (100% hatching success) across our four nests. The measurements from our captured neonates suggests that hatchlings within our population will emerge with an SVL of between 300-450mm and a mass of approximately 15-20g, which is largely consistent with measurements reported in Dolia (2018). We observed neonates rapidly ascending into the canopy upon release, suggesting that the hatchlings will exhibit an arboreal natural history, likely to reduce the risk of predation. We also observed the sloughed-skin of neonate King Cobras within the mid-story canopy, further supporting this hypothesis. Hatchling King Cobras also displayed a clear aposematic defense display by spreading their hood in response to observers, mirroring the behaviours observed in juvenile and adult King Cobras.

Although we present important findings for understanding the nesting ecology of King Cobras, we are greatly limited in extrapolating results to the population-level.

We strongly suggest that future studies aim to expand on this research within the SBR by implementing further research into female movement to and from nests, nesting structures and emerging neonates. For comparison, we also suggest that future studies investigating other King Cobra populations attempt to recreate our study design to further our understanding of King Cobra populations throughout their populations; though attempts should be made to bolster future sample sizes.

4.5 Conclusion

We have shown clear shifts in the movement frequency and corresponding space use for adult female King Cobras between two delineated seasons, *breeding* and *non-breeding*. We observed our telemetered adult females using forested areas only within the breeding season, corresponding to nesting behaviours. Although our telemetered snakes appeared to be acclimated to the disturbed agricultural landscape, the need for the females to move into forest specifically for nesting raises a conservation concern, particularly if further human infringement into forested areas occur. We did observe one of our adult females nesting on the edge of an irrigation canal, but this still resulted in large linear movement to be adjacent to forested areas.

We provide a preliminary understanding into the nesting behaviour and properties of nests for our population of King Cobras. Adult females will construct nests using leaf litter and other forest debris, of varying sizes likely corresponding to clutch size. The egg chambers of these nests provide thermal stability for incubation when compared to outside temperatures, allowing a high hatching success. We were only able to capture a few emerging hatchlings, which we provide basic measurements of. Our findings are mostly consistent with previous literature supporting the nesting behaviours by female King Cobras; however, we have now highlighted some basic resource requirements needed for successful nest building, alongside shifts in spatiotemporal patterns for nesting.

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CHAPTER V

KING COBRA ROAD INTERACTIONS

5.1 Introduction

Southeast Asia represents a global biodiversity hotspot that faces an array of human mediated threats that endanger the rich diversity of flora and fauna (Myers *et al*., 2000; Hughes, 2017; Ng *et al*., 2020). Rates of urbanisation are rapidly increasing linearly with a growing human population within Southeast Asia (Schneider *et al*., 2015), which is accompanied with an expansion of road networks needed to accommodate this urbanisation that presents a major threat to wildlife (Ascensão *et al*., 2018; Hughes, 2018). Roads can pose either a diffuse or hard barrier to wildlife movement (Shepard *et al*., 2008; Brehme *et al*., 2013), dividing habitats and resources, potentially undermining wildlife populations and genetic diversity (Aresco, 2005; Row *et al*., 2007; Balkenhol and Waits, 2009; Jackson and Fahrig, 2011; Clark *et al*., 2010; Herrmann *et al*., 2017). Furthermore, roads act as a direct source of mortality via vehicular collision (Bernardino and Dalrymple, 1992; Rosen and Lowe, 1994; Lodé, 2000; Aresco, 2005; Das *et al*., 2007; Row *et al*., 2007).

Motorists have been known to target specific taxa with their vehicles, such as snakes, which makes these taxa disproportionately affected by roads (Langley *et al*., 1989; Ashley *et al*., 2007; Beckmann and Shine, 2012; Secco *et al*., 2014). Specific life-history traits, such as an active foraging style and with high mobility, can further increase a species' risk from roads due to a demonstrated plasticity in their use of microhabitats (Forman *et al*., 2003; Hartmann *et al*., 2011).

The rates of road mortalities in snake populations is a thoroughly studied topic, showing strong evidence for an increased vulnerability to roads (Rosen and Lowe, 1994; Hartmann *et al*., 2011; Rincón-Aranguri *et al*., 2019). For example, Glista *et al*. (2007) recorded over 10,000 animals killed by vehicle collision, between March 2005 and July 2006 while performing bi-weekly surveys across four survey areas, 95% of which were species of herpetofauna. In addition, a study undertaken in the Dong Phayayen-Khao Yai World Heritage Site, which includes the Highway 304 (investigated in this study), discovered that snakes were the most frequently hit taxa by highway vehicles with 35.5% of road-kill discoveries being represented by snakes (Silva *et al*., 2020b). High rates of snake mortality can result in populations decline, inbreeding and local extinctions (Forman *et al*., 2003; Row *et al*., 2007).

Wildlife-crossing infrastructure has been widely suggested as a solution for mitigating wildlife-vehicle collisions, and further facilitating animal movement across fragmented habitats (Forman, 2003; Beckmann *et al*., 2010; Lister *et al*., 2015). Such infrastructure is generally comprised of underpasses, such as culverts or tunnels, or vegetated land bridges allowing wildlife to move over the top of roads (Dodd Jr. *et al*., 2004; Clevenger and Huijser, 2009; Glista *et al*., 2009). The longevity of wildlife-crossing infrastructure can further benefit wildlife populations over time, as individuals within a population can become acclimated to crossing structure designs and locations, which can aid in sustaining animal mobility between fragmented landscapes facilitating the acquisition of important resources, such as food and conspecifics for breeding (Clevenger and Barrueto, 2014).

Drainage culverts are commonly integrated structures into road construction plans, used to divert water away from the road's surface. Despite the intention, these structures may serve as important wildlife-crossing locations for a diversity of small taxa (Clevenger and Waltho, 2000; Ng *et al*., 2004; Aresco, 2005; Ascensão and Mira, 2007; Grilo *et al*., 2008; Sparks and Gates, 2017; Brunen *et al*., 2020). Baxter-Gilbert *et al.* (2015) assessed the effectiveness of ecopassages in central Ontario, Canada, which yeilded usage by three reptile species: painted turtles (*Chrysemys picta*), snapping turtles (*Chelydra serpentina*) and northern watersnakes (*Nerodia sipedon*). In addition, an under-highway culvert, augmented with drift fences and monitoring, proved to be an effective strategy for reducing turtle mortality as a result of vehicle collision (Aresco, 2005). Our current understanding of the importance of drainage culverts in Southeast Asia for facilitating the movement of animals across roads, is currently lacking.

In order to implement practical conservation strategies for mitigating wildlife mortalities, particularly for snakes which are known to exhibit high rates of road mortality (Hartmann *et al*., 2011; Rincón-Aranguri *et al*., 2019; Silva *et al*., 2020b), infrequently, and unpredictably, use ecopassages (Baxter-Gilbert *et al*., 2015) and are disproportionately targeted by road users (Ashley *et al*., 2007; Beckmann and Shine, 2012), we need to understand how individuals, and populations, are interacting with roads they inevitably come in to contact with. Smaller snakes have been shown to demonstrate a greater avoidance of roads than larger snakes (Andrews and Gibbons, 2005). In addition, venomous snakes (in a study from the southeastern U.S.) appear to move slower than non-venomous species, which increases the duration of time spent on a road's surface during a crossing event (Andrews and Gibbons, 2005). The King Cobra (*Ophiophagus hannah*), fits into the category of a large, venomous snake which is widely distributed throughout Southeast Asia and in parts of India, Nepal and southern China. Given the results of Andrews and Gibbons' (2005) study, King Cobras may be at a high risk of vehicle collision during road-crossing events. As King Cobras have been shown to freely move through permeable protected area boundaries, often moving across roads to reach fragmented habitats (Marshall *et al*., 2018; 2020), this may be further increasing their risk of vehicle collision. King Cobras are listed as vulnerable by the IUCN with decreasing populations and therefore urges investigation into pressures threatening King Cobras.

Marshall *et al*. (2018) provided preliminary data on the threats facing King Cobras within the Sakaerat Biosphere Reserve (SBR), Northeast Thailand. They concluded that anthropogenic sources of mortality far outweighed the few discoveries of natural deaths within the SBR. The majority of these anthropogenic sources occurred outside of the protected forested area of the reserve, of which four vehicle collisions were recorded, which prompts further investigation into the potential impacts that roads may have on the King Cobra in the SBR.

When researching populations of conservation concern, investigating females within the populations can provide valuable insight into the true threats facing the population due to the unique resource requirements for reproductive individuals (Brown and Weatherhead, 1997; Roth and Greene, 2006). Female King Cobras are known to uniquely invest in the maternal care of eggs by creating nests comprised of leaf litter and forest debris, and subsequently remaining with the nest post-laying (Whitaker *et al*., 2013; Hrima *et al*., 2014; Dolia, 2018). During such behaviours, adult female King Cobras can shift their movement frequency and associated space use (Marshall *et al*., 2020). Specifically, Marshall *et al*. (2020) showed a single adult female exhibiting an annual pattern of movement and habitat use associated with reproductive behaviour, characterised by spikes in individual motion variance and shifts in utilisation distribution. Due to the evident need for females to alter movement patterns to access unique resources for reproductive output, we suspect that this movement is putting females at greater risk of road mortality due to an increased need to interact with roads to access forested areas. This may be particularly true for individuals that primarily utilise space within anthropogenic landscapes and are required to perform linear movements into forested areas for locating oviposition sites.

With the evidence provided above, we aimed to identify potential areas that could facilitate the movement of King Cobras across a busy major road, the Highway 304, within the SBR. Using a long-term dataset on the spatial ecology of King Cobras in northeast Thailand, alongside novel data collection of potential road crossing structures, we explore the following: 1) Are King Cobras selecting for underpass locations to safely traverse across the Highway 304? 2) Are female King Cobras at risk of vehicle collision during breeding or nesting movements?

5.2 Methods

5.2.1 Study area

We conducted field work between 2014-03-22 - 2020-07-28, at the Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Thailand (14.44-14.55º N, 101.88-101.95º E; Figure 5.1). The SBR consists of three areas providing varying levels of protection: a core protected forested area covering 80 km^2 primarily comprised of dry dipterocarp forest and dry evergreen forest, a buffer zone of less-protected forest housing areas of plantation regrowth, and lastly a transitional area, offering the least wildlife protection, dominated by agriculture (rice, casava, corn, and sugar). The transitional area specifically hosts 159 settlements with 72,000 inhabitants as of 2018 (Thailand Institute of Scientific and Technological Research, 2018), including a network of major and minor roads. The forested areas of the core and transitional zones are fragmented by the Highway 304, which was initially constructed commencing in 1956, with further road improvement in 1966 and subsequent expansion from two to four lanes in 2005 (Laurence, 2014; Vaeokhaw *et al*., 2020).

In this study, we further investigate a major road of our study site transecting a village area in the transitional zone of the SBR, to the East of the Highway 304, named 304 Nong Weng – Ta Ling Chan (304NW-TLC; Figure 3.1). We investigate the 304NW-TLC road as it is the last major road (tarmac road with multiple lanes) separating the agricultural area from the un-protected forest fragment of the transitional zone, which we believe to have substantial conservation implications on the successful movement of female King Cobras during nesting behaviours.

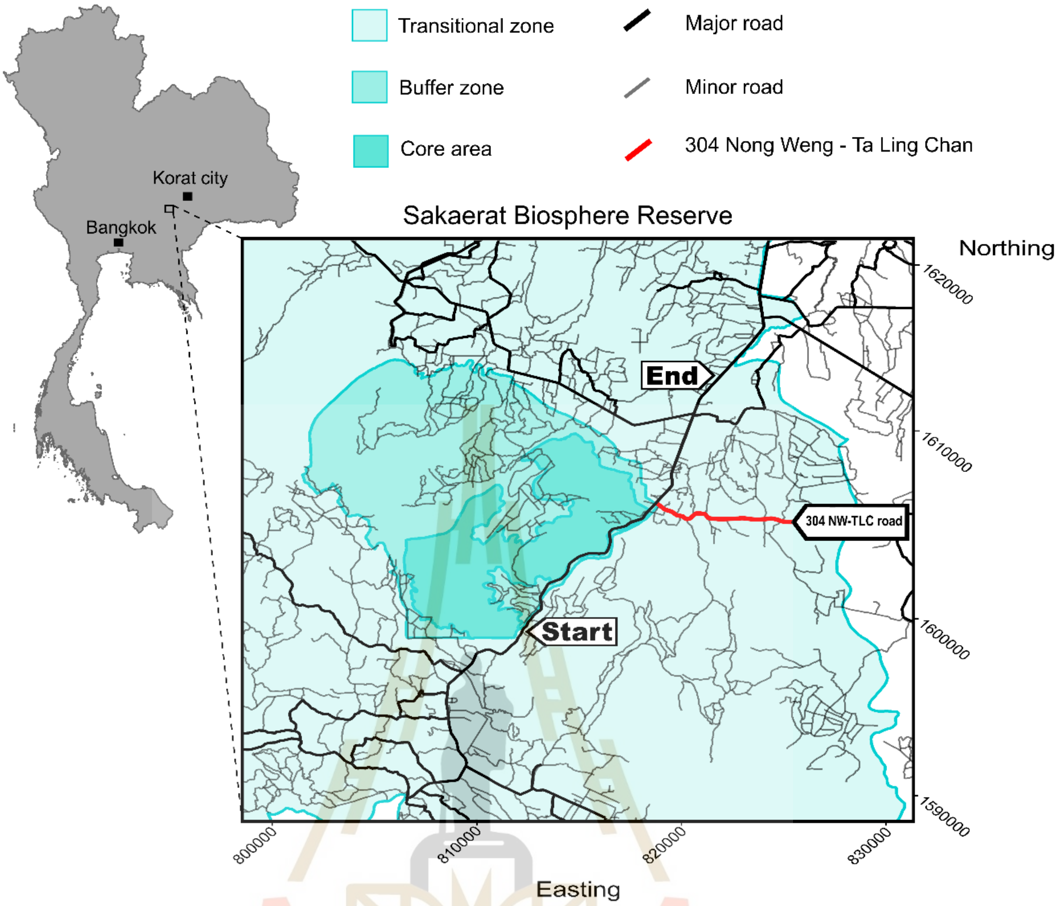

Figure 5.1 Study site map in relation to Bangkok and Korat city. The three zones of the Sakaerat Biosphere Reserve are highlighted by the level of protection offered via increased blue opacity. The bold red line shows the 304 Nong Weng – Ta Ling Chan Road. The *Start* and *End* mark the section of Highway 304 assessed during our study.

5.2.2 Snake capture for radiotelemetry

We located study animals using unstandardised visual surveys, which we primarily performed on foot throughout the core area and buffer zone, and via road-cruising surveys using motorcycles within the transitional zone. Furthermore, we heavily relied on local information provided by residents and rescue team volunteers to locate and capture individuals. As a result, we captured King Cobras between 2014-03-19 and 2020-03-18, using a combination of opportunistic captures, villager notations and visual encounter surveys. We provided individuals with a unique ID using the age-class and chronological capture number of each individual (e.g., AM018, an Adult Male and the 18th King Cobra captured, J standing for juvenile and F for female).

Following capture, we anaesthetised King Cobras using the inhalant anaesthetic isoflurane, to facilitate surgeries performed by a licensed veterinarian from the local Nakhon Ratchasima Zoo. We approximately followed methodology as outlined by Reinert and Cundall (1982), with the addition of isoflurane, implanting Holohil AI-2T or SI-2T transmitters into the coelomic cavity of snakes. We initially marked individuals with a unique brand (Winne *et al*., 2006), but switched to using passive internal transponders from individual AM054 onwards.

We maintained captured King Cobras at Sakaerat Environmental Research Station within opaque plastic boxes, providing water and a shelter until the veterinarian became available for surgery. We released snakes within 24 hours following surgery, as close to their reported capture site as possible, resulting in an average distance of 191.38 m (range = 0 – 1263 m, Table 5.1) from their capture site. We recaptured AM006, AM007 and AF010 after transmitter failures from their first implantations, and there provide capture and release information from this subsequent recapture, due to the improvement of data collection over the study’s duration (Table 5.1).

Table 5.1 Capture and release information for all telemetered King Cobra. ID* depict individuals where true release sites were not recorded and the first datapoint was used. *Distance* distance between capture and release UTM's.

ID	Capture Date	Capture Easting	Capture Northing	Release Date	Release Easting	Release Northing	Distance (m)
AM006	5th April 2018	818746	1605879	10th April 2018	819064	1605795	329
AM007	30th March 2019	818552	1604731	2nd April 2019	818552	1604731	0
AF010*	6th March 2015	818918	1607399	15th March 2017	818926	1607392	11
JM013*	6th July 2014	818471	1606679	19th July 2014	818267	1606533	251
AM015*	11th October 2014	818222	1606078	26th October 2014	817935	1606003	297
AF017*	28th April 2015	818424	1607178	6th May 2015	818376	1607172	48
AM018*	28th April 2015	818002	1605882	9th May 2015	817789	1605758	246
JM019*	1st November 2015	820547	1605330	7th November 2015	820842	1604127	1263
AM024	25th April 2016	815815	1605104	1st May 2016	815859	1605160	71
JM025	25th May 2016	817145	1606125	31st May 2016	817145	1606125	0

Table 5.1 (Continued).

ID	Capture Date	Capture Easting	Capture Northing	Release Date	Release Easting	Release Northing	Distance (m)
AM026	28th November 2016	814706	1602980	30th November 2016	814706	1602980	0
JF027*	14th January 2017	818809	1606327	15th January 2017	818968	1606376	166
JM034*	24th April 2017	820227	1606327	18th May 2017	820351	1605016	473
AM054	28th February 2018	818726	1609537	2nd March 2018	818933	1608996	582
JF055	14th March 2018	812944	1600279	16th March 2018	812993	1600065	221
AF056	24th March 2018	817836	1608698	29th March 2018	817836	1608698	0
AF058	6th April 2018	816730	1604030	10th April 2018	816730	1604030	0
AM059	28th March 2019	820302	1607863	2nd April 2019	820241	1607857	61
AF086	23rd April 2019	820274	1608801	25th April 2019	820274	1608801	0
AF096	10th March 2020	821702	1610664	16th March 2020	821702	1610664	0
AF099	18th March 2020	820608	1607174	23rd March 2020	820608	1607174	0

5.2.3 Radio tracking snakes

We provide two separate tracking protocols, which we altered due to staff and equipment limitations. We tracked individuals 001 to 026, between 2014-03-22 and 2018-07-28, four times a day (approximately 06:30, 11:00, 16:00, 20:00), with a mean time lag between tracks of 8.5 ± 0.1 hours. We tracked the subsequent, individuals 027 - 099, from 2018-07-28 - 2020-08-01 three times per day aiming for approximate five-hour intervals between successful pinpoints resulting in an achieved mean time lag of 9 ± 0.06 hours for all individuals (Figure 5.2). We performed the majority of tracks within daylight hours; however, we occasionally performed nocturnal tracks according to individual movement and habitat selection. We performed fixes using a triangulation method explained in Chapter III and IV, attempting to maintain a minimum distance of 10 m away (occasionally compromised by sub 10m GPS accuracy), to provide reasonable confidence that the snake was within a 5 m^2 area. We recorded a new location (Universal Transverse Mercator 47 N WGS 84 datum) using handheld GPS units (Garmin 62 and 64 models), further recording GPS accuracy, date and time of a completed track.

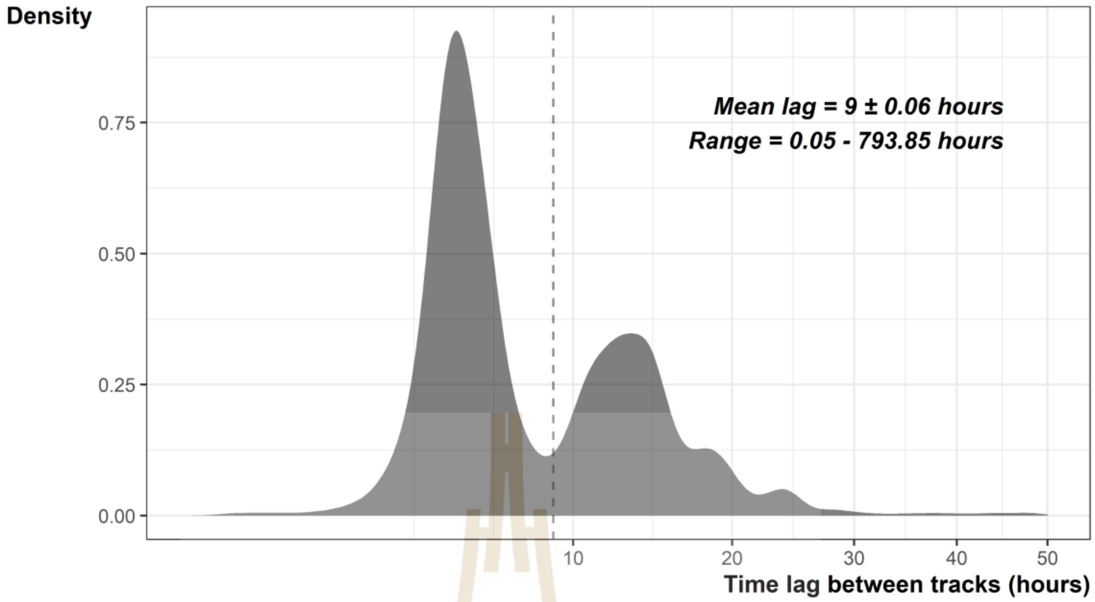

Figure 5.2 Distribution of time lags between datapoints. Horizontal line depicts the mean time lag.

5.2.4 Motion variance and space use

We ran dynamic Brownian Bridge Movement Models (dBBMM) to estimate the potential movement pathway and motion variance of telemetered adult female King Cobras caught after 2018-03-01 (individuals AF058, AF086, AF096 and AF099) using the *move* package v.3.1.0 (Kranstauber *et al*., 2016). We ran dBBMMs only on these four females as we have accompanying nesting information enabling an understanding of any observed patterns to be related to reproductive behaviour. We selected a window size of 25 and margin size of 5, as this timeframe typically allowed us to detect changes in movement states, specifically shifts between resting/sheltering and movement. Following methodology outlined in Marshall *et al*. (2020), we extracted 90, 95 and 99% contours (confidence areas), using R packages *adehabitatHR* v.0.4.16 (Calenge, 2006), and *rgeos* v.0.4.2 (Bivand and Rundel, 2020), to highlight King Cobra movement pathways. We used these extracted dBBMM contours to visualise the importance of landscape features (namely forest, roads and irrigation canals) for female King Cobra movement.

5.2.5 Quantifying crossing structure characteristics

We performed opportunistic surveys along our Highway 304 transect via motorcycles. We located any drainage culverts using roadside markers presumably set by construction workers, and visually defined locations of bridges. We recorded the location of both entrances of all potential road-crossing structures encountered, along with vertical diameter of entrance (mm), horizontal diameter of entrance (mm), length of structure (m), vegetation cover at entrance (yes/no), dominant substrate within the structure and connectivity to landscape feature (none, stream or irrigation canal) for each crossing. We measured the distance between adjacent potential crossing structures using the measuring tool in QGIS version 3.14.15 ‘pi’.

5.2.6 Identifying road crossing events

We manually created spatial polygons for all of the study area encompassing the side of the Highway 304 containing the core protected area, herein referred to as *North Side* (Figure 5.3) using QGIS version 3.14.15 ‘pi’. We calculated the frequency of road-crossing events of the main four-lane Highway 304 by showing the number of times each telemetered snake entered, or exited the North Side spatial polygon (Figure 3.4), using the *recurse* package v.1.1.0 (Bracis *et al*., 2018). We further created a spatial polygon encompassing the area South of the major 304NW-TLC road; herein referred to as *South Side* (Figure 5.4). We performed the same *recurse* analysis to record the number of times a nesting female King Cobra traversed the road, characterised by individuals entering, or exiting, the South Side spatial polygon (Figure 3.5).

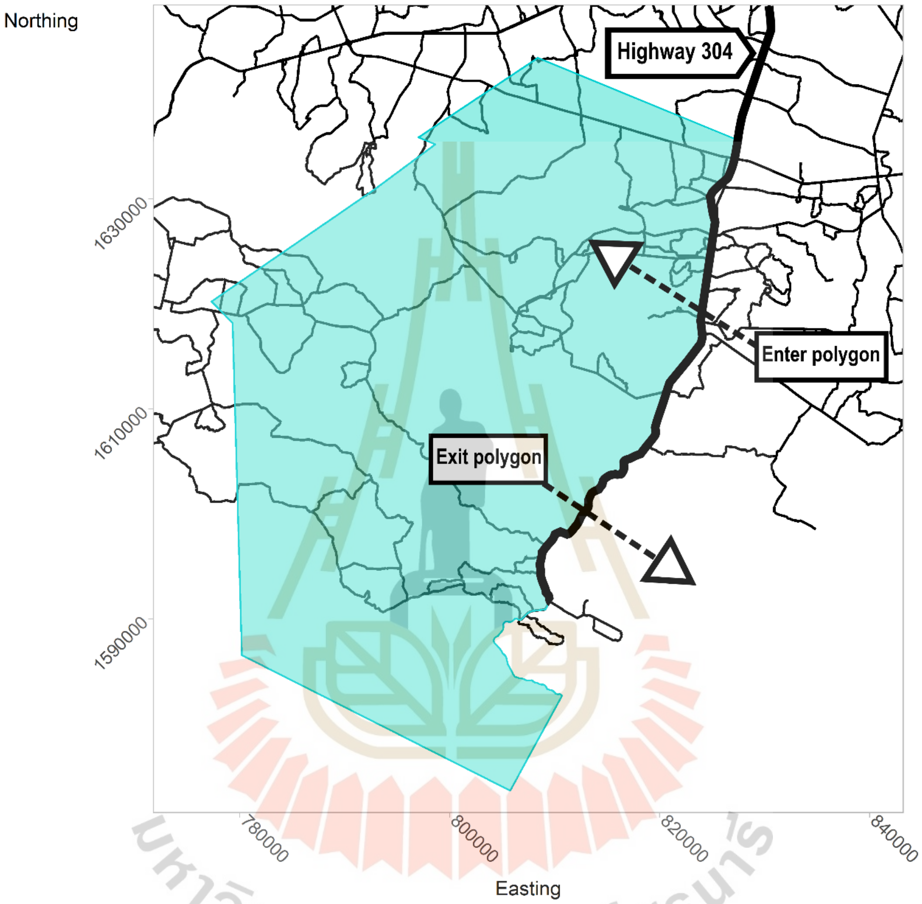

Figure 5.3 The North Side polygon (blue) used in the recurse analysis to determine road-crossings across the Highway 304.

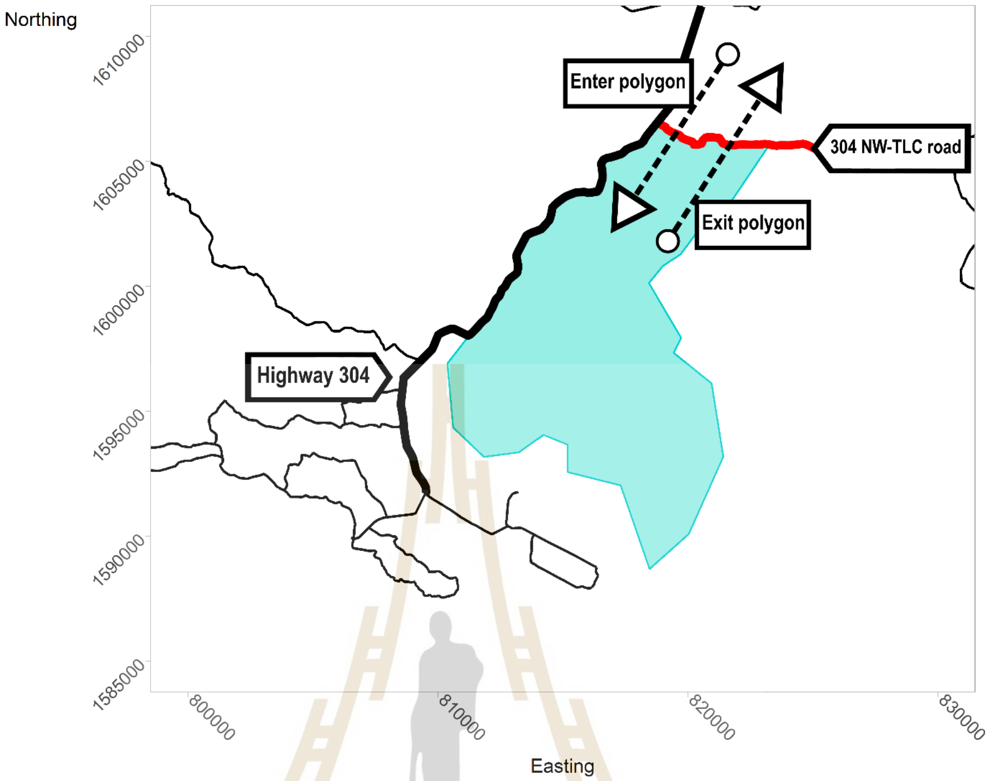

Figure 5.4 The South Side polygon (blue) used in the recurse analysis to determine road-crossings across the 304 NW-TLC road.

As our recurse analysis provided us with approximate timings of crossing events across the Highway 304, we subset the tracking data to show fixes taken two weeks prior to, and two weeks after, a recurse-estimated crossing event. We ran additional dBBMMs on these subsets to estimate an occurrence distribution describing the possible movement pathways taken during a crossing event. For these subsequent dBBMMs, we used a window size of 15 and margin size of 3 allowing us to detect temporally fine-scale changes in behavioural states when using underpasses. We created a mean occurrence distribution that described the likely movement areas used by our sample, derived from individual crossing dBBMM occurrence distributions.

5.2.7 Crossing structure use assessment

To assess if we could detect crossing structures which were used more frequently by telemetered King Cobras, we modelled the mean dBBMM occurrence values at crossing structure locations and the mean from (pseudo-) random locations elsewhere along the highway. We extracted dBBMM occurrence values at each crossing structure location, alongside 64 random locations. Using the *brms* v.2.13.0 (Bürkner, 2017) package, we ran a Bayesian regression model, aiming to predict scaled (0 to 1, centred) dBBMM occurrence distribution values by using two predictors: density of crossing structures and whether the point was a crossing structure or a random location. We would suspect that if King Cobras are actively choosing crossing locations, our dBBMM occurrence distribution values at each underpass location would be explained by our point variable.

To generate values corresponding to crossing structure density, we ran Kernel Density Estimates using the *adehabitatHR* v.0.4.16 (Calenge, 2006) on the estimated crossing locations, using least-squared cross validation to select the smoothing factor. To account for unequal spatial sampling of King Cobra movement we included an offset variable in the model. We ran a series of autocorrelated Kernel Density Estimates (aKDE) as a means of estimating the potential areas that our tracked King Cobras could have used during the study period. We ran aKDEs using the *ctmm* v.0.5.10 (Fleming and Calabrese, 2020) package, because to the large number of individuals we did not manually select the movement modelling method, instead relying on the movement modelling method with the lowest AICc. Once all aKDE utilisation distribution had been created, we created a mean utilisation distribution and from that extracted values at all points to be modelled to be used as offset values.

A Bayesian framework allows us to generate a multivariate posterior distribution across all covariates, alongside investigating the effect of informative priors to our model outputs (Lemoine, 2019; Ma *et al.*, 2008). We therefore ran ten models to assess the effect of weakly informative Cauchy priors on our regression model estimates (Table 5.3). We ran all models using a gaussian distribution with three chains over 5,000 iterations, using the first 1000 iterations as burn-in for each chain, resulting in 12,000 iteration post-burnin. Convergence of chains was confirmed using $\hat{R}$ values (convergence ~ 1.00 $\hat{R}$) and visual inspection of trace plots using the *tidybayes* v.2.1.1 (Kay, 2020) package.

Table 5.2 Bayesian regression model ID and weakly informative priors.

Model ID	Prior
Model 1	Non-informative
Model 2	Cauchy (0,1)
Model 3	Cauchy (1,1)
Model 4	Cauchy (-1,1)
Model 5	Cauchy (0,2)
Model 6	Cauchy (0,3)
Model 7	Cauchy (1,2)
Model 8	Cauchy (-1,2)
Model 9	Cauchy (-1,3)
Model 10	Cauchy (1,3)

5.2.8 Integrated step-selection function

We assessed the influence of major roads on adult female King Cobra movement (i.e., avoidance or attraction) by performing integrated Step-Selection Functions (iSSF) in the *amt* package v.0.0.6 (Signer *et al*., 2018). Following seasons delineated in Chapter 4, we separated tracking periods in to a breeding and nesting season, *breeding*, and the remainder of an individual's tracking duration in another, *non-breeding*. We personally observed breeding as early as March 10th, and recorded a female leaving her nest as late as July 5th, throughout different years. We added a 10-day buffer to each of these dates due to natural variation which gave us an annual breeding season between March 1st and July 15th. Our non-breeding season fell on days outside of this delineation, between July 16th and February 28th. We used an inverted raster layer which describes varying distances from major roads within the SBR; inverted to aid in the interpretation of model outputs (Marshall *et al*., 2020). As iSSF uses known locations from tracking data, and compares them with randomly-selected locations, we simulated 200 random points for each step, allowing a broad sampling of the surrounding landscape to be achieved (Fortin *et al*., 2005; Marshall *et al*., 2020). We opted for such a high number of random points due to our coarse VHF telemetry data when compared with GPS telemetry data, where the latter datasets could afford a single, or very few, random steps per used step (Northrup *et al*., 2013; Thurfjell *et al*., 2014), whereas 200 random points can allow us to sample rare, or discrete, landscape features.

We performed iSSF at an individual- and population-level, including step length, turn angle and (inverted) distance from major roads as predictors in all models. We investigated the population-level effects by modifying R script supplied by Muff *et* *al*. (2020): a Poisson model with stratum-specific effects, and a prior precision of 0.0001 for slope coefficients. Our breeding season model included data from six telemetered King Cobras, and our non-breeding models only included four individuals. This difference is due to the temporal limitations of our telemetry data, as some individuals were only tracked in either season. We used the *INLA* v.20.03.17 package (Rue *et al*., 2020) to fit Bayesian models via integrated nested Laplace approximations.

5.2.9 Software and data

We completed all analyses in R v.3.5.3 (R Core Team, 2019) and R Studio v.1.2.1335 (R Studio Team, 2019). We performed any data manipulation using R packages *dplyr* v.0.8.3 (Wickham *et al*., 2019), *lubridate* v.1.7.4 (Grolemund and Wickham, 2011), *readr* v.1.3.1 (Wickham *et al*., 2018), *reshape2* v.1.4.3 (Wickham, 2007), and *stringr* v.1.4.0 (Wickham, 2019). We calculated data means and standard error using the *pracma* package v.2.2.5 (Borchers, 2019). We worked with rasters and shapefiles using R packages *raster* v.2.8.19 (Hijmans, 2019), *rgdal* v.1.4.3 (Bivand *et al*., 2019) and *sp* v.1.3.1 (Pebesma and Bivand, 2005; Bivand *et al*., 2013). We created visuals using a combination of R packages *cowplot* v.0.9.4 (Wilke, 2019), *ggplot2* v.3.2.1 (Wickham, 2009), *ggspatial* v.1.0.3 (Dunnington, 2018), *scales* v.1.1.0 (Wickham and Seidel, 2019) and *scico* v.1.1.0 (Pederson and Crameri, 2018).

5.3 Results

5.3.1 Radiotelemetry

We tracked 21 King Cobras between 2014-03-22 - 2020-07-28, comprising of eight adult males, seven adult females, four juvenile males, and two juvenile females (Table 5.4). We rediscovered individuals AM006, AM007 and AM010, after 842, 1405 and 280 days missing from the study respectively, and we subsequently tracked following rediscovery. We tracked King Cobras for an average of 344.53 ± 55.65 days (range = 134 – 3122 days). We performed an average of 920 ± 157 fixes (range = 66 – 1176 fixes) on telemetered King Cobras, with an average of 9 ± 0.06 hours (range = 0.05 – 793.85 hours) between fixes. We recorded an average of 263 ± 48 relocations (range = 31 – 985 relocations; Table 5.4).

5.3.2 Road crossing and motion variance

We recorded nine out of the 21 telemetered King Cobras moving across the Highway 304 comprised of five adult males (AM006, AM007, AM015, AM018, AM054), three adult females (AF010, AF017, AF058) and one juvenile female (JF055; Figure 5.5). The adult males crossed the highway 15 times (range = 2 – 37 times per individual) on average, with the adult females crossing an average of twice (range = 2 – 3 times per individual) and the single juvenile female crossing four times.

Table 5.3 Summary of radiotelemetry and King Cobra space use.

ID	Datapoints	Days	Relocations	dBBMM space use (ha)			σ^2m
				90	95	99	
AF010*	143	66.47	34	71.65	100.65	166.78	44.64 ± 11.85
AF010	289	83.53	47	0.52	31.14	487.94	135.13 ± 30.68
AF017	2245	774.97	728	41.69	68.15	149.28	7.53 ± 0.33
AF056	428	162.07	138	78.25	110.32	176.5	15.61 ± 0.92
AF058	672	268.9	253	49.41	97.68	232.12	12.76 ± 0.74
AF086	623	241.02	197	103.32	153.9	284.32	11.26 ± 0.87
AF096	291	132.92	56	181.26	262.54	426.32	22.75 ± 3.08
AF099	276	122.02	31	169.5	268.64	490.84	15.52 ± 2.62
AM006*	2173	723.05	542	519.6	701.44	1063.42	42.61 ± 1.74
AM006	736	346.02	232	668.44	1057.38	1843.75	47.61 ± 3.7
AM007*	969	320.66	220	232.7	345.62	616.9	51.90 ± 3.81
AM007	782	349.03	171	620.7	858.96	1281.08	31.22 ± 2.84

Table 5.3 (Continued).

ID	Datapoints	Days	Relocations	dBBMM space use (ha)			σ^2m
				90	95	99	
AM015	1944	680.13	587	379.8	603.32	1081.54	27.3 ± 1.22
AM018	3122	1176.1	985	255.09	492.54	977.84	33.56 ± 1.41
AM024	466	173.17	218	353.72	484.15	730.48	41.38 ± 2.24
AM026	134	68.73	66	187.94	249.03	376.51	69.99 ± 7.1
AM054	1381	520.62	379	134.04	222.11	489.48	29.17 ± 2.25
AM059	995	345.04	210	104.23	249.04	679.08	16.08 ± 1.3
JF027	542	198.62	116	17.36	36.33	82.09	6.15 ± 0.54
JF055	722	353.62	248	174.52	277.22	444.83	20.48 ± 1.49
JM013	1497	561.19	381	354.33	533.26	972.74	22.35 ± 1.11
JM019	890	311.79	228	61.01	119.04	390.39	7.9 ± 0.63
JM025	435	164.98	201	163.22	251.94	424.82	31.57 ± 3.26
JM034	317	124.02	50	30.93	49.98	91.66	21.51 ± 3.14

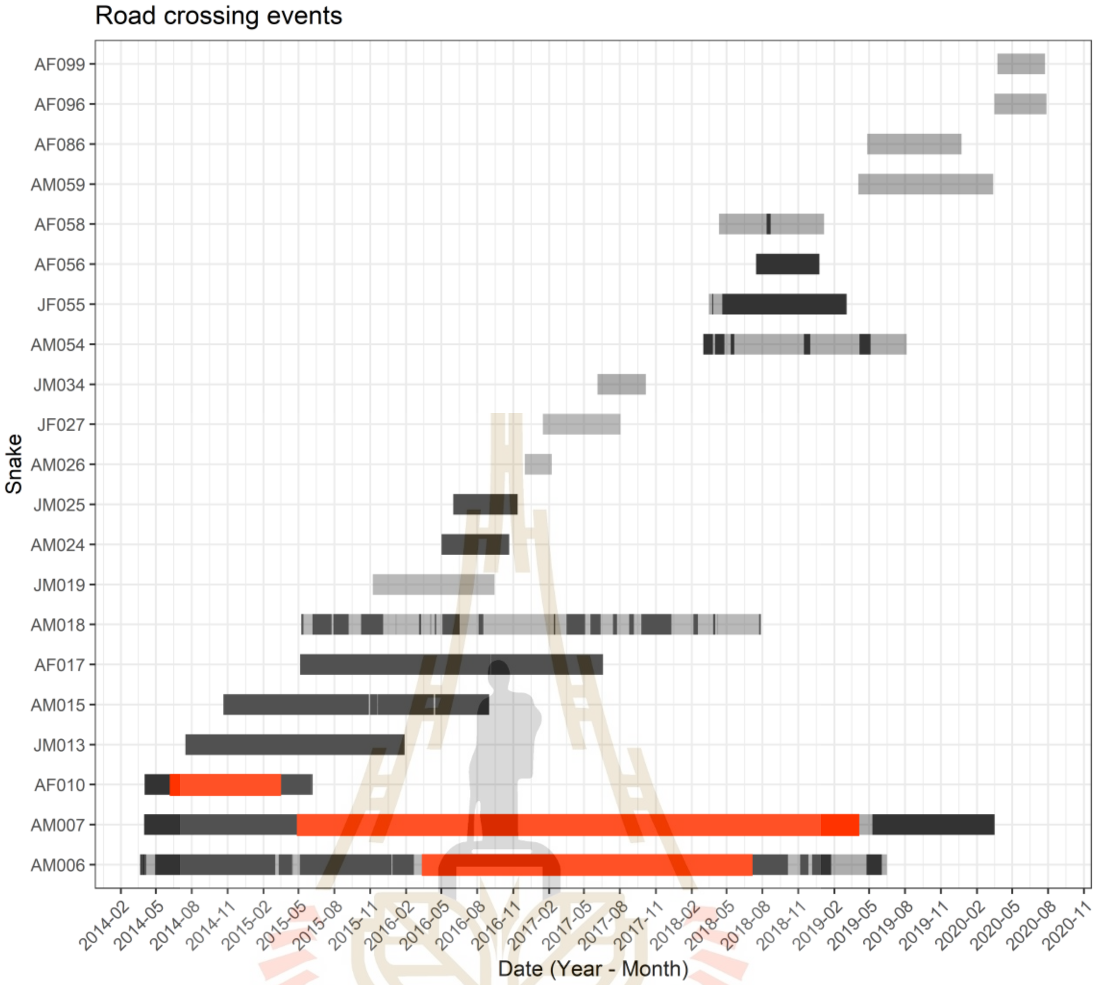

Figure 5.5 Road-crossing events from all 21 telemetered King Cobra. Each grey bar corresponds to a King Cobra individual, opaque bars show when individuals were inside of the North Side spatial polygon. Transitions from translucent to opaque therefore correspond to a snake crossing over the Highway 304. Red bars indicate periods of time where individuals were not tracked.

As a further result of our recurse analysis, we recorded all four of our telemetered females to have crossed the 304NW-TLC road at least once during our study period (Figure 5.6). The females entered the South Side spatial polygon, and the associated forested/forest-adjacent area, between mid-April (11th) and early May (5th), over multiple years. Three of these females subsequently exited the South Side spatial polygon, corresponding to an individual moving away from forested area and into the agricultural matrix, from mid-June (18th) to early July (2nd), throughout multiple years. We tracked AF099, moving North after leaving her oviposition site, making continuous movements towards the 304NW-TLC road; however, we lost the radio-signal from equipment malfunction on 2020-07-24 before crossing the road and leaving the forest. We tracked three females, AF058, AF086 and AF096, for 182, 188 and 40 days respectively after crossing back to the North side of the 304NW-TLC road, of which we recorded no further crossing over the 304NW-TLC road.

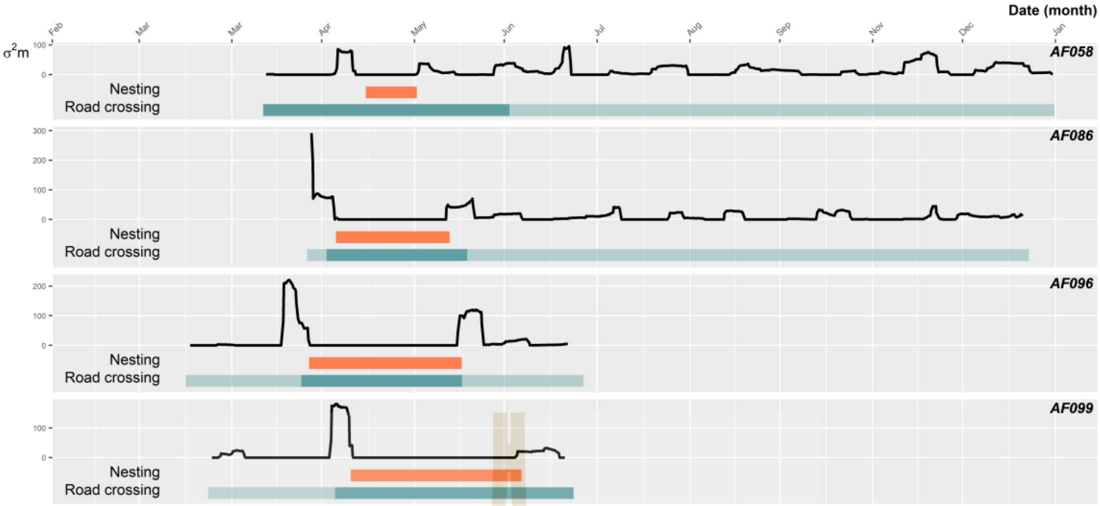

Figure 5.6 Adult female King Cobra movement variance. Black lines show the motion variance of each individual, faceted by individual ID. Orange bars highlight the duration of time females remained with their nests. Opaque blue bars represent when an individual was within the South Side spatial polygon (South of 304NW-TLC road and therefore within forested area for nesting). Transitions from translucent to opaque blue bars show road crossing events.

We recorded an average motion variance for our four adult females of 14.20 ± 0.73 σ^2m (range = $5.6e^{-05}$ – 291.49 σ^2m), and further observed a peak in the motion variance values of three of these females prior to nesting (AF086: 291.49 σ^2m, AF096: 220.98 σ^2m, AF099: 180.64 σ^2m; Figure 5.6); only one female, AF058, showed a motion variance peak later in her tracking duration (95.58 σ^2m).

5.3.3 Road-crossing structures and characteristics

We discovered and measured 32 potential road-crossing locations (underpasses) along a 15.31 km section of highway (Euclidean distance from the first and last crossing point; Figure 5.8), 21 single drainage culverts, seven double drainage culverts (two culverts side by side) and four bridges. We recorded 26 of these crossing points (24 drainage culverts and two bridges) within an 8.07 km section of the highway adjacent to the forest comprising the protected area of the SBR. The road-crossing features were spaced out along the highway at a mean distance of 536.3 ± 88.4 m (range = 191 – 2620 m). Through inspecting movement data surrounding each *recurse*-identified crossing event we observed telemetered King Cobras using 19 crossing structures to traverse the Highway 304 (15 drainage culverts and all four bridges).

We measured crossing structures to have a mean length of 40.94 ± 1.75 m (range = 26 – 82 m), a mean entrance height of 1138.16 ± 127.13 mm (range = 194 – 3000 mm), and a mean entrance width of 3792.22 ± 1418.51 mm (range = 543 – 30000 mm; Table 5.6). All crossing points were constructed using concrete, except one metal drainage culvert (C24), and structures typically did not contain any substrate build-up (n = 17). The structures we did record with dominant substrate build-up had gravel (n = 5), rocks (n = 4), water (n = 3), soil (n = 2) and anthropogenic waste (n = 1). Only nine structures were connected to stream beds and three to irrigation canals (three out of the four bridges were connected to irrigation canals). All crossing structures had evidence of anthropogenic waste either at the entrance, or within. Only four culverts were void of any vegetation cover connecting to the entrances (C4, C6, C14 and C28).

Table 5.4 Characteristics of road crossing structures. *Type* structure types. *Times used* the number of times the structure was used to traverse the Highway 304 by telemetered King Cobra. *Length* straight line distance of the structure from entrance one to entrance two. *Width* the horizontal measurement of the structure entrance. *Height* the vertical measurement of the structure entrance. *Substrate* the dominant substrate type present within the structure. *Material* the dominant material types the structure is comprised of. *Vegetation* whether or not there was vegetative cover at the entrance of the structure. *Waste* whether there was anthropogenic waste immediately outside, or within, the structure. *Feature* the aquatic landscape feature that the structure led into. *Distance* mean Euclidean distance to the two nearest crossing structures.

ID	Type	Times used	Length (m)	Width (mm)	Height (mm)	Substrate	Material	Vegetation	Waste	Feature	Distance (m)
C1	Culvert	1	35	942	851	None	Concrete	Yes	Yes	None	230
C2	Culvert	0	37	981	986	None	Concrete	Yes	Yes	None	227
C3	Culvert	1	53	983	995	None	Concrete	Yes	Yes	Stream	231
C4	Culvert	0	52	975	984	None	Concrete	No	Yes	None	449
C5	Bridge	2	26	22000	2422	Gravel	Concrete	Yes	Yes	Klong	623
C6	Culvert	0	42	962	992	None	Concrete	No	Yes	None	459
C7	Culvert	1	37	898	874	None	Concrete	Yes	Yes	None	322
C8	Culvert	1	41	943	782	None	Concrete	Yes	Yes	None	338
C9	Culvert	0	42	966	667	Rocks	Concrete	Yes	Yes	None	324

Table 5.4 (Continued).

ID	Type	Times used	Length (m)	Width (mm)	Height (mm)	Substrate	Material	Vegetation	Waste	Feature	Distance (m)
C11	Culvert	0	33	514	194	None	Concrete	Yes	Yes	None	386
C12	Culvert	0	82	930	597	None	Concrete	Yes	Yes	Stream	397
C13	Double Culvert	2	42	906	643	Gravel	Concrete	Yes	Yes	Stream	303
C14	Culvert	1	34	2100	1790	None	Concrete	No	Yes	Stream	316
C15	Double Culvert	1	35	975	960	Rocks	Concrete	Yes	Yes	Stream	263
C16	Culvert	2	39	990	985	None	Concrete	Yes	Yes	Stream	212
C17	Culvert	0	33	982	984	None	Concrete	Yes	Yes	None	444
C18	Double Culvert	3	38	897	967	None	Concrete	Yes	Yes	None	630
C19	Culvert	1	32	970	993	None	Concrete	Yes	Yes	None	464
C20	Culvert	3	35	950	979	Rocks	Concrete	Yes	Yes	None	607
C21	Double Culvert	14	45	1040	951	Gravel	Concrete	Yes	Yes	Stream	231

Table 5.4 (Continued).

ID	Type	Times used	Length (m)	Width (mm)	Height (mm)	Substrate	Material	Vegetation	Waste	Feature	Distance (m)
C22	Culvert	3	39	960	942	Waste	Concrete	Yes	Yes	Stream	225
C23	Culvert	1	37	972	930	None	Concrete	Yes	Yes	None	338
C24	Double Culvert	3	35	925	935	None	Metal	Yes	No	Stream	402
C25	Bridge	1	40	12000	1750	Rocks	Concrete	Yes	Yes	None	447
C26	Double Culvert	20	41	965	983	Soil	Concrete	Yes	Yes	None	1579
C27	Bridge	18	38	30000	3830	Soil	Concrete	Yes	Yes	Klong	1827
C28	Culvert	0	49	800	480	Water	Concrete	No	Yes	None	910
C29	Bridge	6	37	30000	3000	Gravel	Concrete	Yes	Yes	Klong	2131
C30	Culvert	0	49	850	980	Water	Concrete	Yes	Yes	None	1321
C31	Culvert	0	51	1000	1000	Gravel	Concrete	Yes	Yes	None	881
C32	Double Culvert	0	48	1000	1000	Water	Concrete	Yes	Yes	None	465

5.3.4 Bayesian regression models

We detected only a slight variation in estimates from our introduced Cauchy priors within our ten models (Figure 5.7), and therefore report on the estimates produced from our non-informative prior model.

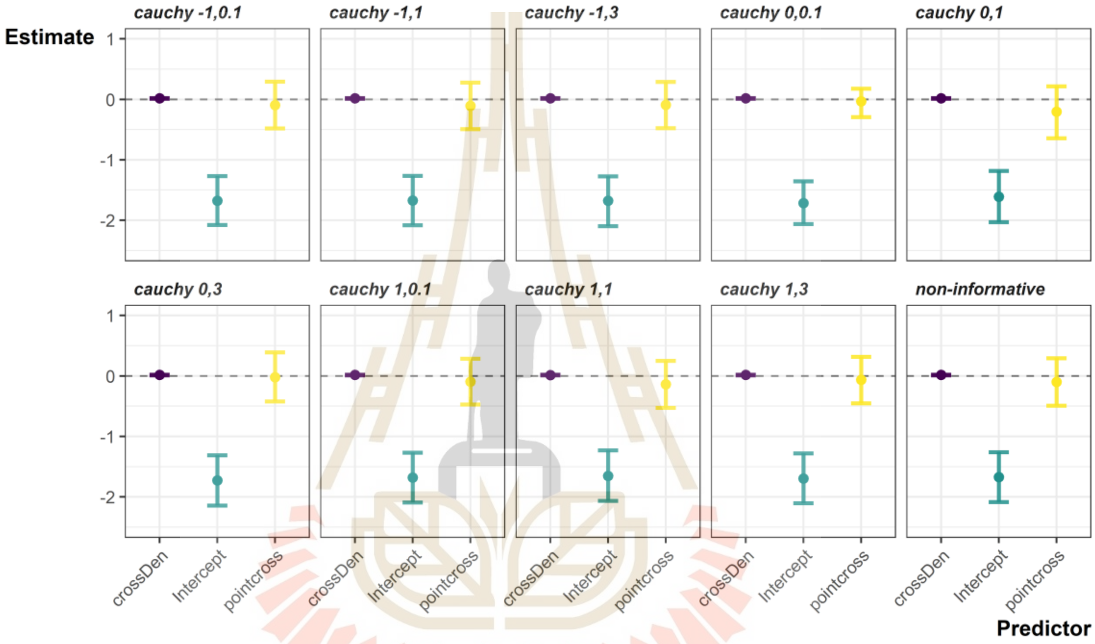

Figure 5.7 Results of weakly informative priors applied to Bayesian regression models. Circles show the β estimate from the model and error bars show the associated 95% credible intervals for each estimate.

The Bayesian regression model showed no apparent effect from our point variable (i.e., underpass location or random, estimate = -0.1 95%CI -0.49 – 0.29) indicating that the movement paths we recorded and the dBBMM estimates (Figure 5.8A) are inadequate in detecting the exact crossing structure used. However, we did detect a small positive association with the density of crossing structures (Figure 5.8C) on our dBBMM occurrence distribution response variable (estimate = 0.02 95%CI 0.01 – 0.02). This suggests that while we cannot discern underpasses use in relation to randomly generated locations on the road, we can connect the concentration of King Cobra occurrence (i.e., crossing events) to stretches of the highway where crossing structures exist.

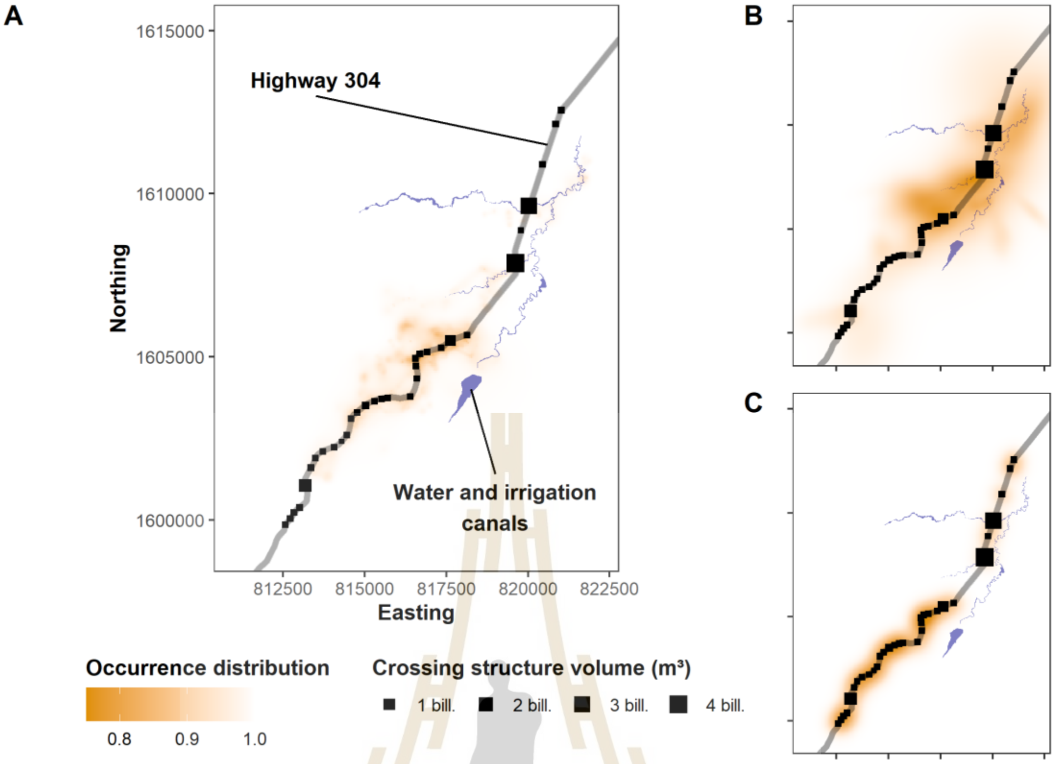

Figure 5.8 The variables used in Bayesian regression models to investigate highway crossing usage. Black squares indicate crossing structure location and volume. All maps are North oriented and display the same extent. A) Mean dBBMM occurrence distribution based on two-week subsets either side of a *recurse* detected crossing event. B) Mean aKDE utilisation distribution generated from all King Cobra tracking data. C) KDE depicting the density of crossing structures.

5.3.5 Female movement pathways

We extracted 90, 95 and 99% contours from four adult females, AF058, AF086, AF096 and AF099 as our recurse analysis showed that these females interacted with the 304NW-TLC road. By overlapping extracted contours with spatial polygons of the irrigation canal, roads and forested area within our study site, we demonstrate the importance of irrigation canals to move throughout the agricultural landscape (Figure 5.9). Furthermore, as these contours overlapped with the 304NW-TLC road, we further highlight the importance of this major road on the nesting movements of female King Cobras. The plotted locations furthest South on the maps (Figure 5.9) approximately show the nesting locations of AF058, AF086 and AF099; however, AF096 moved 434 m (straight line distance) Southeast along an irrigation canal when searching for a suitable oviposition site, prior to moving back North to nest.

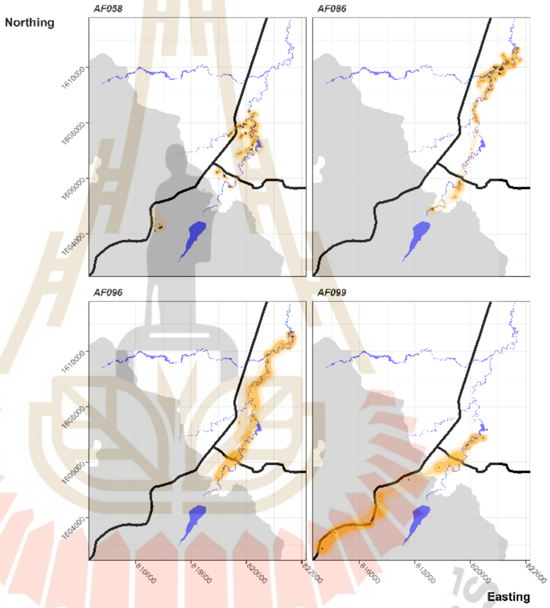

Figure 5.9 DBBMM estimates of occurrence distribution contours. Polygons with increasing orange opacity represent the 99, 95 and 90% confidence areas during the study period. Black dots are tracked locations of King Cobras. The shaded grey area highlights the forest areas within our study site. Solid black lines show the Highway 304 (central) and the 304 Nong Weng – Ta Ling Chan road (East). Blue polygons represent the irrigation canals.

5.3.6 Integrated step-selection function

As we had inverted the raster layer, any positive coefficients represent a positive association with roads (i.e. attraction). The locations of four adult female King Cobra showed a positive association to major roads during the breeding season (AF010, AF017, AF058 and AF096; Figure 5.10), whereas our analysis demonstrated an avoidance of major roads by the movement of our two remaining females during the breeding season (AF086 and AF099, Figure 5.10). Our non-breeding season models suggest that the movements of our adult females tracked during this time showed an avoidance to major roads (AF017, AF056, AF058 and AF086; Figure 5.10). However, many of our estimates, and resulting confidence intervals, overlapped zero, limiting our inferences.

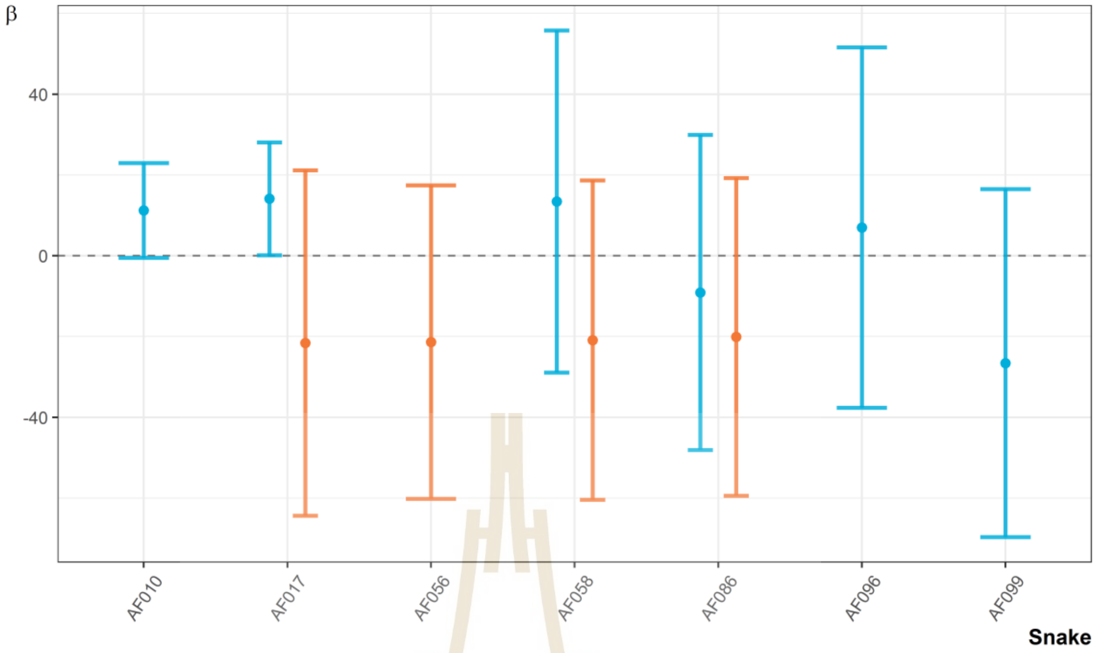

Figure 5.10 The coefficient from the non-breeding season integrated step-selection function analysis. Breeding and non-breeding season are depicted by blue and orange respectively. Circles show the β estimate from the model and error bars show the associated 95% confidence intervals for each estimate.

Our population-level ISSF models resulted in a very low association with major roads within our study site during the breeding season (β = 4.38^{-04}, 95% CI -1.98^{-04} – 0.001; Figure 5.11); however, we observed a slightly lower association during the non-breeding season (β = 1.43^{-04}, 95% CI -0.00105 – 0.00129; Figure 5.12). As seen in our individual-level models, our population-level results exhibited confidence intervals which overlapped zero limiting our inferences.

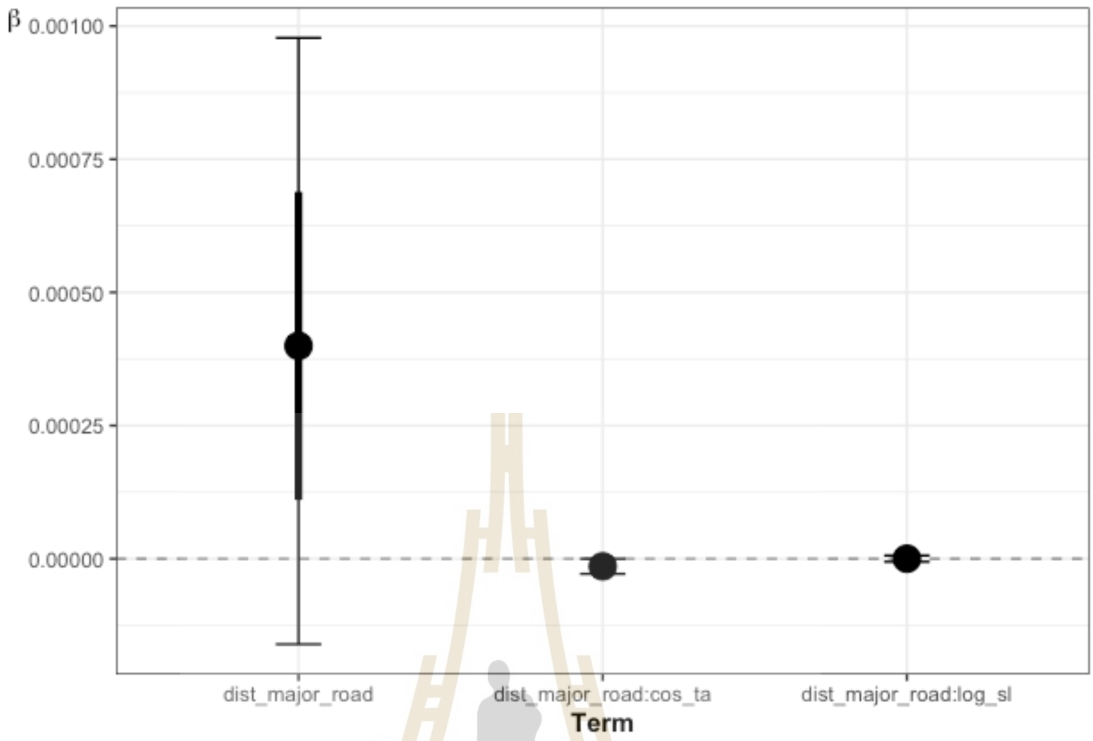

Figure 5.11 The coefficient from the breeding season, population-level, ISSF analysis. Circles show the β estimate from the model and error bars show the associated 95% credible intervals for each estimate.

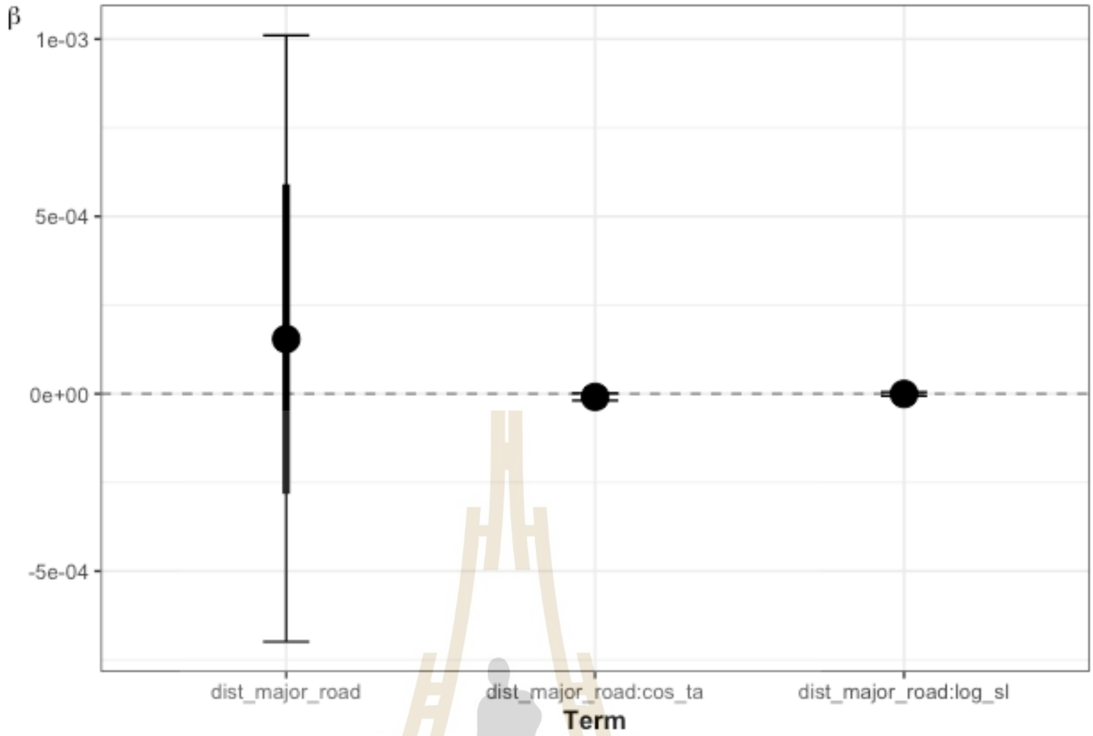

Figure 5.12 The coefficient from the non-breeding season, population-level, ISSF analysis. Circles show the β estimate from the model and error bars show the associated 95% credible intervals for each estimate.

5.4 Discussion

We investigated the interactions between telemetered King Cobras and two major roads in the SBR, both of which closely border a protected forested area. Our results show that King Cobras repeatedly traverse a major four-lane highway, with large individual heterogeneity crossing frequency (e.g. AM054 crossed nine time over 520.27 days and AM018 moved across a total of 37 times over 1176.1 days). Although direct observations of King Cobra crossing the road are very infrequent, our investigations suggest that 19 out of 32 potential crossing-locations over 15.31 km of the highway, are used by telemetered King Cobra to traverse the road. However, the few cases of direct crossing observations show King Cobras will use both drainage culverts and bridges to safely traverse. (Figure 5.13). Results of our Bayesian regression models suggest that crossing structure density is a small but significant factor in where King Cobras cross the highway, but failed to provide further evidence on the exact structures used. Individual- and population-level iSSF showed negligible changes in movement in relation to major roads for nesting female King Cobras within and outside of breeding season, despite female King Cobras having to cross the busy 304NW-TLC road when locating oviposition sites. Major roads dividing female King Cobras usual occurrence distributions with areas for suitable oviposition may present a particular mortality risk during a demanding time.

Figure 5.13 Use of road-crossing structures by telemetered King Cobra. *Top* Use of a drainage culvert by AM015. *Bottom* Movement underneath a bridge by AM054. King Cobras in frame are highlighted with dashed-white circles.

Overall, we recorded relatively infrequent instances of King Cobras moving across the Highway 304. However, we did record our adult males traversing the highway at greater frequency than any other demographic. Furthermore, adult males appeared to move across the road more regularly during the earlier months of each year (February to May), corresponding to when males would be actively seeking receptive females for breeding, as can be seen in results for AM006, AM007, AM015, AM018 and AM054 (Figure 4.1). Our results therefore suggest that male King Cobras could be prioritising breeding attempts over the risk that the busy highway may pose. Other species have also shown greater propensity to cross roads during breeding periods (Bonnet *et al*., 1999).

We did not record any designed wildlife crossing locations within our highway transect, however, we present evidence that King Cobras will use a combination of drainage culverts and bridges to safely cross. As we typically recorded a location of a King Cobra on one side of the road, and then on the other side during a subsequent track, we cannot directly confirm that individuals are using the underpasses as opposed to moving over the road, for most cases. However, we have observed some individuals actively moving underneath the bridges (Figure 5.12), obtained fixes where snakes were directly underneath the Highway 304, and provide a model suggesting the location of crossing structures is related to dBBMM movement pathways. Due to the death of AM015, an adult male that has previously shown an ability to safely move across the highway, we suspect that there is a very high probability of vehicle collision when snakes come into contact with the road's surface. The Highway 304 is one of the busiest roads in Thailand, in 2006 there were approximately 7,488 vehicles/day recorded (Srikrajang 2006). Wildlife crossing infrastructure is a widely researched and implemented strategy to mitigate wildlife-vehicle collisions (Beckmann *et al*., 2010; Dodd Jr *et al*., 2004; Glista *et al*., 2009; Lister *et al*., 2015), however, few studies have investigated the use of drainage culverts as effective crossing structures for wildlife within Southeast Asia.

Although the evidence presented in this study is promising, the use of road-crossing structures does not necessarily mean that the impacts of the Highway 304 are being mitigated (Cunnington *et al*., 2014; Rytwinski *et al*., 2016). Underpasses, on their own, do not reduce road mortality in small, secretive taxa such as amphibians and implementing underpasses as a mitigation measure may be difficult without further installing fencing and directive infrastructure to accompany them (Rytwinski *et al*., 2016). Throughout our study, we have encountered seven incidents of King Cobra road-mortality, five of which occurred on the Highway 304. Out of these five highway-mortalities two were juvenile males, two were young of the year and one was a telemetered adult male. The newly-hatched and juvenile snakes may be less acclimated to the presence of the crossing structures and distances between underpasses would be relatively greater and more challenging for smaller snakes to access therefore potentially making them more vulnerable to road mortality. The discovery of our telemetered adult male, AM015, was worrying, particularly as our recursive analysis suggests that AM015 crossed underneath the same bridge on seven different occasions, showing a capacity to safely traverse the road.

The dBBMMs for each telemetered female King Cobra highlights three main points. 1) telemetered females (at least those tracked South of the highway) depend greatly on the refuge that the man-made irrigation canals provide, with dBBMM confidence areas following irrigation canal spatial polygon, 2) movements increase when females are required to move for locating suitable oviposition sites, this can be seen by the linear movements southward for each female (except AF058 who was captured near to her most southern point), 3) and when females move towards, and away, from the forested area to the South, they are required to cross over the main road, 304NW-TLC road, likely putting each female at greater risk of road-mortality during these annual bouts of movement.

Concluding from our long-term observations of King Cobra movement, females will shift their space-use during the 'nesting season' in order to find a suitable location for oviposition (Marshall *et al.*, 2019; 2020). Southward movement (Figure 5) corresponds to the need for females to enter forested, or otherwise heavily vegetated, area for oviposition. These large spikes in motion variance shown by three of our adult females (Figure 5.6) prior to nesting, likely put female King Cobras at greater risk of mortality. Therefore, the evidence presented in this study for increased movement during oviposition site location, alongside the need to traverse a busy main road within our study area, presents a conservation concern for the SBR population of King Cobras. The potential death of even a single gravid female King Cobra could have detrimental impacts on overall population stability (Bonnet *et al*., 1999; Row *et al*., 2007). Our adult females have been seen moving underneath a bridge allowing safe passage across the 304NW-TLC road, but have also been observed moving directly over the road, narrowly escaping collision with oncoming vehicles.

It is difficult to ascertain any true association with major roads and the movement of our adult female King Cobras, as the iSSF suggests both attraction and avoidance between the breeding and non-breeding seasons (Figure 5.11; Figure 5.12). Furthermore, many of the confidence/credible intervals exhibited for each estimate, overlapped zero which limits our inferences concerning the true relationship between major roads and individual movement. However, failing to detect clear avoidance throughout the two different seasons is a concern. Telemetered King Cobras are freely moving throughout the landscape, irrespective of the presence of major roads is a conservation concern considering the road mortalities observed (Marshall *et al*., 2018) and that major roads are not guaranteed to house crossing structures.

The interactions presented above adds to a growing base of road ecology literature attempting to decipher how animals interact with anthropogenic obstacles to their movement. It is encouraging that unintentional ecological underpasses are likely providing some level of permeability and preventing complete fragmentation of habitats, for snakes especially, given their reluctance to cross roads and their vulnerability if doing so (Andrews and Gibbons, 2005; Shine *et al*., 2004). King Cobras being larger and ranging further than most other reptiles likely makes them additionally vulnerable to habitat fragmentation and the dangers posed by roads (Bonnet *et al*., 1999; Rytwinski and Fahrig, 2012).

5.5 Conclusion

King Cobras have been required to adapt to the many roads webbed through a human-dominated landscape adjacent to a protected area. The presence of crossing structures (drainage culverts and bridges) along a major four-lane highway appears to enable King Cobras to traverse the road providing a level of permeability. Despite this, we are still discovering individuals that have died due to vehicle collision on Highway 304. We suggest that future studies investigate the potential use of long-term drainage culverts by other snake species in order to gain a better understanding of how important this road infrastructure may be for population mobility and thus survival.

In order to mitigate some of the risks posed on King Cobras crossing busy roads, and to reduce the impact that infrastructure has on the mobility of this highly mobile snake, we suggest that more targeted research is required to confirm that crossing structure density can boost road permeability. Further, investigations into roadside fencing will be needed to ascertain methods of reducing the road mortality we observed despite the presence of road crossing structures. We have highlighted season vulnerability of adult females that any conservation action should recognise.

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CHAPTER VI

KING COBRA BIOMETRICS AND MORTALITY

6.1 Introduction

As snake populations continue to decline, the need to develop long-term conservation plans increases (Reading *et al*., 2010; Saha *et al*., 2018). Prior to developing such conservation strategies, we need to identify the risks and threats posed on these populations (Peery *et al*., 2004; Steinmetz *et al*., 2006; Maritz *et al*., 2016). Declines are typically linked to anthropogenic pressures, of which the introduction of invasive species, unsustainable harvesting practises, habitat degradation, pollution and direct mortality via road networks and persecution are among some of the highest impacting causes (Gibbons *et al*., 2000; Trombulak and Frissell, 2000). A proposed mitigation strategy to alleviate some of these pressures is the integration of protected areas within dominant landscapes (Bruner, 2001; Watson *et al*., 2014; Gray *et al*., 2016). However, efficient management designs of how to designate and maintain protected areas are complex, particularly when attempting to protect highly mobile species that freely move across permeable protected area boundaries (Rodrigues *et al*., 2004; Baldi *et al*., 2017). As individuals from a population move across protected area boundaries, they increase their probability of human-wildlife conflict, which in turn can result in a direct impact to their survival (Swanepoel *et al*., 2015; Smith *et al*., 2016b; Belote and Wilson, 2020).

As protected areas become increasingly infringed by anthropogenic areas, typically resulting in fragmented areas of protection, the likelihood of individuals within a population using these anthropogenic areas also increases (DeFries *et al*., 2005; Clark *et al*., 2013; Geldmann *et al*., 2019); particularly within tropical regions where the rate of habitat loss is so high (Sodhi *et al*., 2010; Hughes, 2017; Roll *et al*., 2017). This evidence prompts further understanding of how animals may persist when traversing permeable protected area boundaries, bringing species into more frequent contact within humans (Hansen and DeFries, 2007). Snake populations have exhibited particular adaptability to increased habitat loss by utilising novel anthropogenic landscapes (French *et al*., 2018; Smith *et al*., 2020). This affinity for human-dominated landscapes can increase the likelihood of human-snake conflict, which largely results in the translocation or death of snakes (Anguiano and Diffendorfer, 2015; Miranda *et al*., 2016; Marshall *et al*., 2018; Hauptfleisch *et al*., 2020).

Due to a limited understanding about snakes, people will typically resort to killing snakes when encountered in their homes or place of work, particularly as many people will presume a snake to be venomous if they cannot confidently identify the species (Marshall *et al*., 2018). However, human-snake conflict events, such as these, can not only lead to an increased frequency of snake mortality, but can further result in envenomations as a direct consequence (Nonga and Haruna, 2015; Longkumer *et al*., 2016; Pandey *et al*., 2016). An evident predisposition to persecute snakes presents a conservation concern for species inhabiting anthropogenic areas (Akani *et al*., 2002; Shankar *et al*., 2013; Wolfe *et al*., 2018).

Persecution of snakes during human-snake conflicts may be largely dependent on the phenotypic characteristics of the species, such as aposematic markings or size

(Miranda *et al*., 2016; Souchet and Aubret, 2016). The King Cobra (*Ophiophagus hannah*) possesses clear aposematic signalling in the form of hooding, as seen in true cobras (*Naja* sp.; Nasoori *et al*., 2016), and is a large snake possessing potent neurotoxic venom (Li *et al*., 2006; Roy *et al*., 2010). King Cobras are widely distributed throughout Southeast Asia, India, southern China and Nepal (Das, 2010), and are habitat generalists being shown to use pristine natural areas (Stuart *et al*., 2012), alongside human-dominated/degraded habitat, particularly within agricultural landscapes (Rao *et al*., 2013; Marshall *et al*., 2019; 2020).

King Cobras exhibit several life history traits that exacerbate their risk of extinction, such as a specialist diet (Jones *et al*., 2020), large body size (Marshall *et al*., 2018) and slow rate of maturation (Böhm *et al*., 2016, Todd *et al*., 2018). Alongside these traits, the affinity for King Cobras to utilise large areas of space, particularly within an agricultural matrix may further increase their risk of human-snake conflict, and thus rate of mortality due to direct persecution and from other human-mediated threats (Marshall *et al*., 2018; 2019; 2020). We therefore investigated the risks faced by King Cobras within a permeable protected biosphere reserve in Northeast Thailand by using data from a long-term radiotelemetry study. We collected biometric data for captured King Cobras, and further recorded cases of mortality within the reserve in order to identify the main risks acting on the population in relation to individual traits (sex, biometrics, age class and movement patterns).

6.2 Methods

6.2.1 Study area

We conducted this study at the Sakaerat Biosphere Reserve (SBR), in northeast Thailand (14.44-14.55º N, 101.88-101.95º E; see Chapter 3 for study site map). The SBR is comprised of three main zones: a core area, buffer zone and transitional zone which offer decreasing protection for wildlife respectively. The core area is almost exclusively forested area dominated by dry-evergreen forest (60%) and dry-dipterocarp forest (18%); however, it is also sporadically webbed with road and path networks which stem from the Sakaerat Environmental Research Station (SERS). The buffer zone closely borders the core area and primarily encompasses area of regenerating plantation forest. The transitional zone, is predominantly occupied by human settlements, and is netted with many major and minor road networks, including the Highway 304. The construction of the highway commenced in 1956, with further construction in 1966 and ultimately becoming a four-lane highway in 2005 (Laurence, 2014; Vaeokhaw *et al.*, 2020). Furthermore, the transitional zone also contains vast areas of agricultural land of rice, cassava, sugar cane and corn primarily.

6.2.2 Snake capture

We deployed several strategies for capturing King Cobras within our study site. We attempted to locate individuals using unstandardised visual encounter surveys throughout all three zones of the SBR. We primarily performed surveys within the core and buffer areas on foot via paths created by other research teams. When surveying through the transitional zone, we relied on motorcycles to cruise major and minor roads. Many of our surveys, when actively searching for King Cobras, were conducted in daylight hours (06:00am – 18:00pm), however, we also conducted surveys at night particularly as we were also searching for other research animals during this time, namely Burmese pythons (*Python bivittatus*; Smith *et al*., 2020). We concurrently relied on the information from local residents to locate King Cobras. Specifically, we offered a service to residents of the transitional zone where we would respond to villager notifications to remove snakes from their homes. We responded to snake-calls to remove any species of snake, though brought captured King Cobras to the research station in such an event. The local villagers also had the opportunity to contact a locally trained rescue team, trained by us, to remove snakes from their homes. The rescue team volunteers would bring King Cobras to the research station to aid in our study. Lastly, we implemented a method highlighted in Smith *et al*. (2016a) named the Judas technique. This technique relies on radio-tracking King Cobras until they are observed interacting with a conspecific, which we can then capture (radiotelemetry and the Judas technique is explained in more detail in Chapter III and IV).

We recorded the capture location (Universal Transverse Mercator 47 N WGS 84 datum), date and time of each King Cobra capture via handheld GPS units (Garmin 62 and 64 models). We named unique King Cobras using a nomenclature system corresponding to the snake's age class and chronological addition to the project (e.g. juvenile male 025: JM025; adult female 086: AF086). We marked captured King Cobras using ventral and dorsal scale branding (Winne *et al*., 2006) from individuals 001 – 053 and subsequently used passive internal transponders.

6.2.3 Biometric data collection

We brought captured King Cobras to SERS and maintained them within opaque plastic boxes, further providing snakes access to water and a shelter site, prior to processing. We prepared snakes for biometric data collection by anaesthetising them using the inhalant anaesthetic isoflurane. The use of isoflurane renders a snake to lose all muscle-tone, allowing us to record accurate measurements. Furthermore, as there is an associated risk of envenomation from a King Cobra bite, this allowed us to record measurements while minimising the risk to ourselves. Upon the full loss of muscle-tone, we collected the following biometric measurements: snout-to-vent length (mm; SVL), tail length (mm; TL), head length (mm; HL), head width (mm; HW) and mass (g). We determined the sex of study animals using a metal snake probe of appropriate thickness. Probes would generally extend to two or three subcaudal scales if female and beyond four or five in males.

We took the opportunity to photograph anaesthetised King Cobras for subsequent scale counts, which included photographs of the head side, head dorsal, head ventral, body dorsal, body ventral and subcaudal scales (Figure 6.1). We counted the subcaudal and ventral scales of each King Cobra using these photographs. We also recorded the scalation pattern on all aspects of the head. We performed scale counts twice for each individual, referring to a third count when we determined an inconsistency between the first two counts. We repeated measurements and photographs for each individual upon subsequent recapture to assess growth rate and consistency between scale counts, we recaptured telemetered King Cobras every 6-8 months.

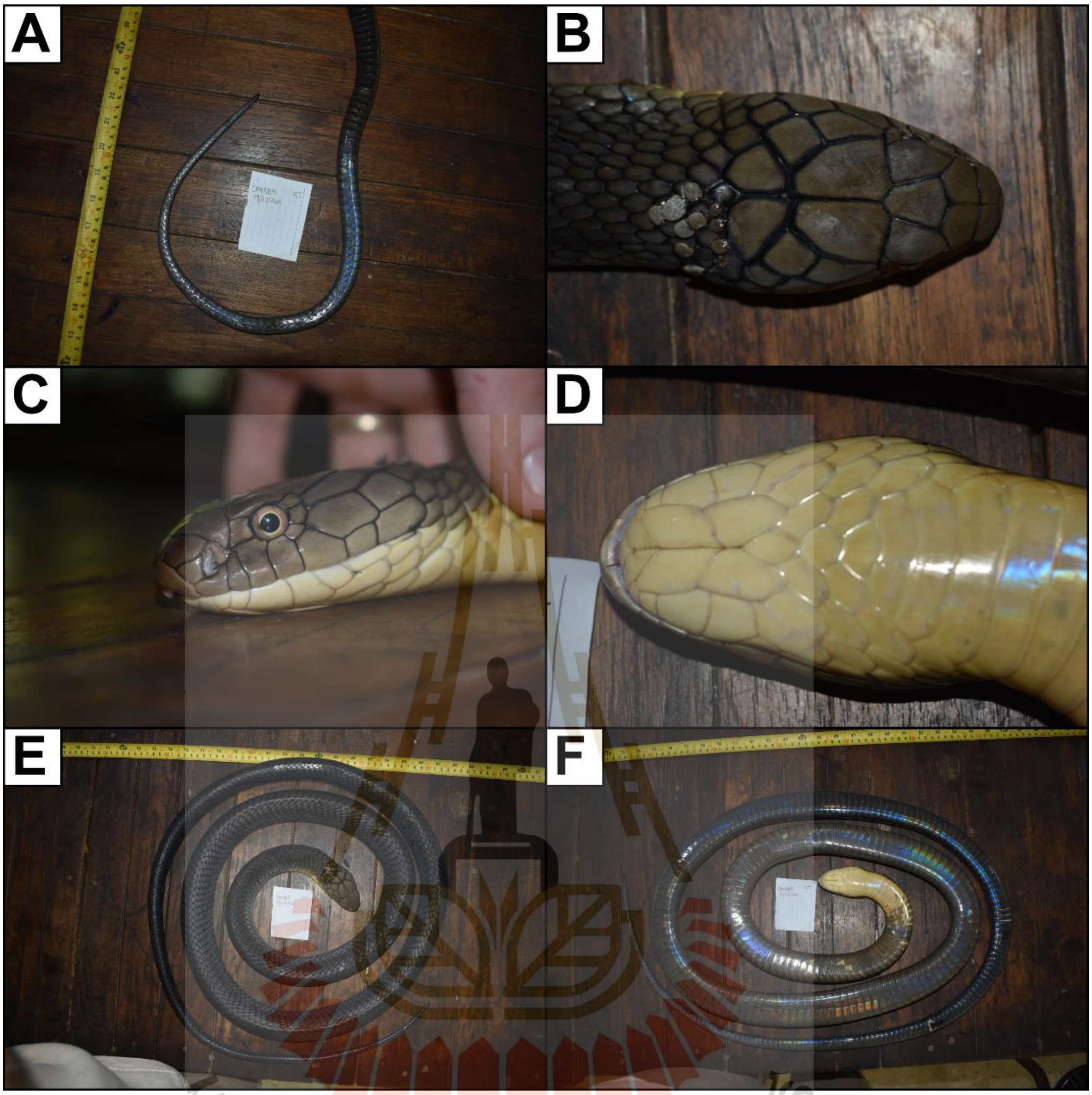

Figure 6.1 Processing photos of King Cobras under isoflurane anaesthetic. *A* subcaudal scales, *B* head dorsal, *C* head side, *D* head ventral, *E* body dorsal, *F* body ventral.

6.2.4 King Cobra mortality

We discovered King Cobra mortalities opportunistically throughout our study site and period. This included discovering King Cobras via villager notation, radio-tracking a telemetered King Cobra that has died and opportunistically encountering dead individuals on road surveys. We recorded the location of the mortality using handheld GPS units (Garmin 62 and 64 models) and the time and date of discovery.

During our 330-weeks study, we partitioned the data into one-week intervals, designating the week that each snake entered and exited the study (*Week start* and *Week end* Table 3.1), and the fate of the King Cobra by the end of the study. We estimated the survival probability of telemetered King Cobra per week, using a staggered-entry Kaplan-Meier survival estimator (Pollock *et al*., 1989; Palmer and Wellendorf, 2007). We investigated the effect of two binary variables: sex (male/female) and age class (adult/juvenile) on the survival of telemetered King Cobra throughout the 330-week period, using a Cox proportional hazards regression model (Goodrich *et al*., 2008; Maran *et al*., 2009). We also included two numeric variables into the latter model, the snout-to-vent length (SVL) of individuals (averaged over multiple recaptures) and the mean motion variance from our dBBMM analysis per week/per snake (calculated in Chapter 3). We report on the final fate of all of our telemetered King Cobra, denoting *Dead* if the snake was known to have died during the study and *Alive* if the snake was released following telemetry, or the transmitter failed prior to final recapture (Table 6.1).

Table 6.1 Known-fate data for telemetered King Cobra. *Start week* the week that the snake entered the study. *End week* the week that the snake left the study.

ID	Start week	End week	Fate
AM006	0	272	Dead
AM007	1	312	Alive
AF010	0	63	Dead
JM013	15	96	Alive
AM015	29	127	Dead
AF017	58	169	Dead
AM018	58	236	Dead
JM019	84	129	Dead
AM024	109	134	Dead
JM025	113	137	Dead
AM026	140	149	Alive
JF027	146	175	Dead
JM034	166	184	Alive
AM054	205	280	Dead
JF055	207	258	Dead
AF056	224	248	Alive
AF058	210	249	Dead
AM059	261	311	Alive
AF086	265	300	Dead
AF096	312	331	Alive
AF099	313	330	Alive

6.3 Results

6.3.1 King Cobra captures

We captured a total of 74 King Cobras between 17-02-2020 and 08-08-2020, comprised of 37 adult males, 18 juvenile males, 13 adult females and six juvenile females (Figure 6.2). We captured 46 individuals via villager notations, 18 opportunistically, five during active surveys, three using the Judas technique and two using passive traps.

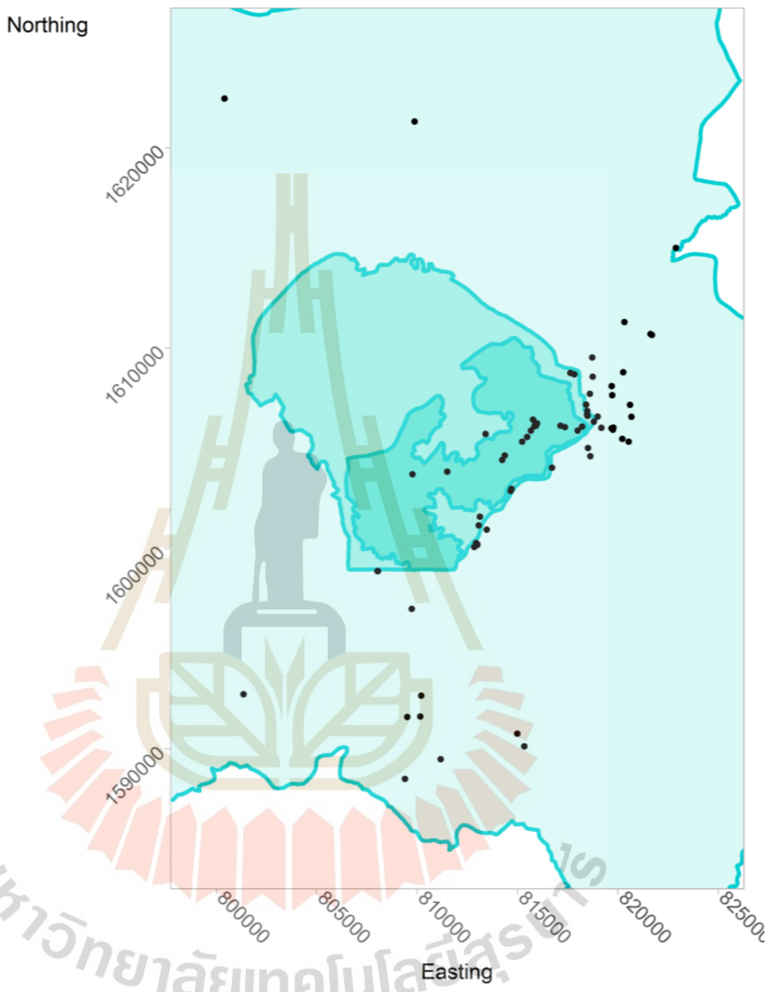

Figure 6.2 Capture locations for King Cobras within the SBR. The three zones of the SBR are depicted by blue area of increasing opacity for the transitional zone, buffer zone and core area respectively. Black dots show the capture locations for unique King Cobras.

6.3.2 Male biometrics

Our adult males had a mean mass of 4340.49 ± 267.73 g (range = 1920 – 8440 g), a mean SVL of 2721.6 ± 52.19 mm (range = 2200 – 3714 mm), a mean tail length of 639.68 ± 11.98 mm (range = 429 – 790 mm), a mean head length of 78.3 ± 1.29 mm (range = 62 – 95 mm) and a mean head width of 53.49 ± 1.13 mm (range = 43.2 – 67 mm; Table 6.2; Figure 6.3).

Our juvenile males had a mean mass of 1276.78 ± 115.83 g (range = 420 – 2250 g), a mean SVL of 1881.67 ± 42.47 mm (range = 1543 – 2177 mm), a mean tail length of 439.94 ± 26.98 mm (range = 141 – 559 mm), a mean head length of 53.98 ± 1.52 mm (range = 40 – 67.2 mm) and a mean head width of 35.61 ± 0.98 mm (range = 28.4 – 45.9 mm; Table 6.3; Figure 6.3).

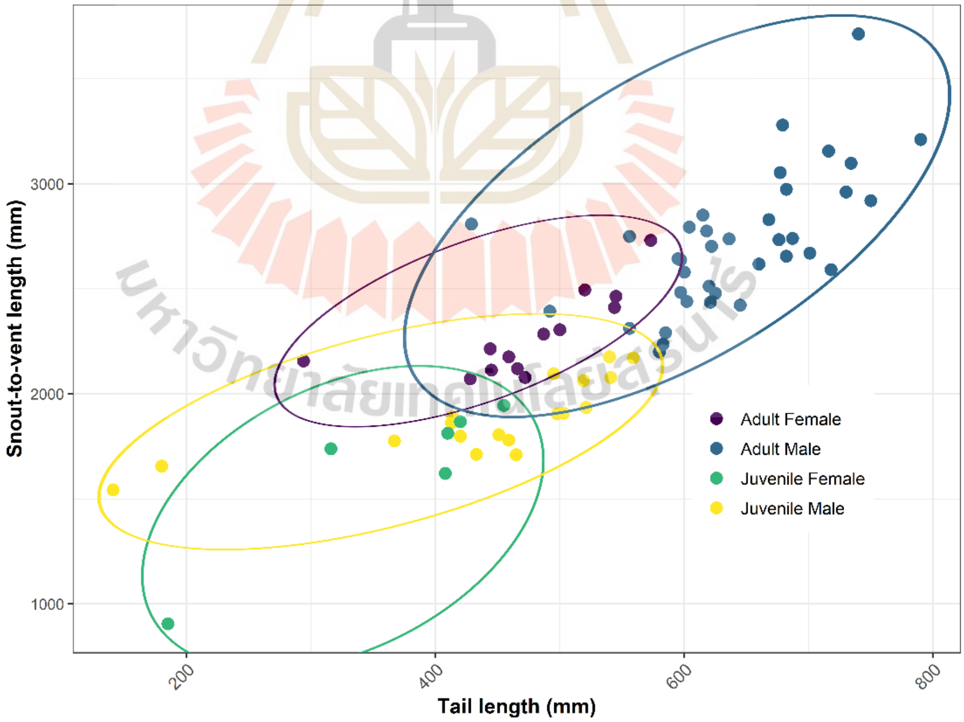

Figure 6.3 Comparison of snout-to-vent length and tail length of King Cobras.

Table 6.2 Biometric data from adult male King Cobras, showing the first capture event. *SVL* snout-to-vent length, *TL* tail length, *HL* head length, *HW* head width.

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)
AM005	2013-06-04	Adult	Male	6200	3714	740	88.4	60
AM006	2014-03-22	Adult	Male	4620	2794	604	70.2	49.7
AM007	2014-03-28	Adult	Male	5320	2656	682	84.4	54.7
AM009	2014-04-10	Adult	Male	5040	2618	660	72.9	48.6
AM011	2014-04-11	Adult	Male	5441	2734	676	80.2	52.6
AM015	2015-05-05	Adult	Male	3120	2580	600	72.9	52
AM016	2015-04-01	Adult	Male	1920	2440	602	69.5	43.5
AM018	2015-05-03	Adult	Male	3393	2740	687	71.5	52
AM020	2016-01-18	Adult	Male	3140	2436	621	70.2	44.1
AM021	2016-03-08	Adult	Male	2500	2479	625	71.8	45.2
AM023	2016-03-25	Adult	Male	5860	3054	677	95	60
AM024	2016-05-01	Adult	Male	2920	2513	620	76	46
AM026	2018-03-28	Adult	Male	7110	3156	716	91.7	63.8
AM029	2017-10-25	Adult	Male	5460	2750	556	78	63
AM030	2017-04-08	Adult	Male	8440	3280	679	80.6	63.8
AM031	2017-04-09	Adult	Male	4340	2670	701	75.3	51.9
AM032	2017-04-14	Adult	Male	5860	2920	750	81.5	63
AM033	2017-04-14	Adult	Male	4650	2703	622	83.6	51.7

Table 6.2 (Continued).

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)
AM034	2017-04-24	Adult	Male	2060	2200	580	62	43.2
AM035	2017-04-24	Adult	Male	6880	3211	790	79.5	67
AM036	2017-05-03	Adult	Male	4100	2738	636	73	57.5
AM054	2018-03-01	Adult	Male	2900	2394	492	70	50
AM059	2018-04-10	Adult	Male	4870	2776	618	84	54.8
AM079	2018-12-30	Adult	Male	4255	2809	429	81.5	60.2
AM082	2019-03-07	Adult	Male	3080	2638	597	83.8	51
AM084	2019-03-25	Adult	Male	4535	2644	595	79.9	53.2
AM085	2019-04-01	Adult	Male	4735	2830	668	86.1	53
AM089	2019-09-29	Adult	Male	5925	2851	615	90.3	64.3
AM090	2019-10-19	Adult	Male	2630	2422	645	72.7	47.5
AM091	2019-11-06	Adult	Male	5075	3098	734	88	60.8
AM095	2020-03-09	Adult	Male	2200	2592	718	72.4	50.3
AM097	2020-03-13	Adult	Male	6700	2961	730	90	57.5
AM100	2020-03-21	Adult	Male	3720	2483	597	76.9	51.3
AM101	2020-03-26	Adult	Male	3110	2312	556	70.4	46.6
AM102	2020-05-08	Adult	Male	4249	2974	682	83.7	57.9
AM104	2020-06-24	Adult	Male	2110	2237	583	71.1	43.5
AM105	2020-07-19	Adult	Male	2130	2292	585	68	43.9

Table 6.3 Biometric data from juvenile male King Cobras, showing the first capture event. *SVL* snout-to-vent length, *TL* tail length, *HL* head length, *HW* head width.

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)
JM002	2013-02-26	Juvenile	Male	420	1656	180	40	30
JM013	2015-01-17	Juvenile	Male	150	1936	521	56.4	36.3
JM014	2015-01-14	Juvenile	Male	627	1543	141	43.5	28.4
JM019	2016-06-20	Juvenile	Male	1440	2097	495	49.8	36.7
JM022	2016-03-23	Juvenile	Male	2180	2177	540	57	40.5
JM025	2016-05-26	Juvenile	Male	1202	1908	503	53.7	34
JM028	2017-03-06	Juvenile	Male	2040	2078	541	61.7	41.1
JM072	2018-08-11	Juvenile	Male	840	1776	367	48.6	32.4
JM073	2018-09-04	Juvenile	Male	1445	1710	465	51	36
JM074	2018-09-15	Juvenile	Male	980	1862	413	50.7	31.3
JM075	2018-11-03	Juvenile	Male	2250	2172	559	67.2	45.9
JM080	2019-01-02	Juvenile	Male	1168	1780	459	53.1	34.3
JM081	2019-01-26	Juvenile	Male	1410	2063	519	60.8	37.9
JM083	2019-03-18	Juvenile	Male	1120	1712	433	53.5	35.2
JM087	2019-08-04	Juvenile	Male	1030	1799	420	54.6	34.6
JM092	2019-12-26	Juvenile	Male	1195	1905	49.8	59.3	37.7
JM093	2019-12-26	Juvenile	Male	1120	1890	414	56.3	35.7
JM094	2020-01-13	Juvenile	Male	1015	1806	451	54.5	33

6.3.3 Female biometrics

Our adult females had a mean mass of 2360.92 ± 266 g (range = 1426 – 5140 g), a mean SVL of 2278.92 ± 54.84 mm (range = 2072 – 2731 mm), a mean tail length of 475.15 ± 19.49 mm (range = 294 – 573 mm), a mean head length of 61.8 ± 1.7 mm (range = 54.1 – 76 mm) and a mean head width of 39.49 ± 1.48 mm (range = 32.8 – 50.6 mm; Table 6.4; Figure 6.3).

Our juvenile females had a mean mass of 843.67 ± 176.82 g (range = 118 – 1445 g), a mean SVL of 1648.83 ± 155.28 mm (range = 906 – 1945 mm), a mean tail length of 365.67 ± 40.74 mm (range = 185 – 455 mm), a mean head length of 44.45 ± 3.59 mm (range = 29.5 – 50.9 mm) and a mean head width of 29.4 ± 2.52 mm (range = 17 – 33.5 mm; Table 6.4; Figure 6.3).

Table 6.4 Biometric data from female King Cobras, showing the first capture event. *SVL* snout-to-vent length, *TL* tail length, *HL* head length, *HW* head width.

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)
AF004	2014-05-31	Adult	Female	/	2110	500	52	38
AF008	2014-04-10	Adult	Female	2230	2120	466	57.5	35.2
AF010	2015-03-06	Adult	Female	2827	2495	520	62	37.9
AF017	2015-10-25	Adult	Female	1426	2078	472	56.6	34
AF056	2018-03-25	Adult	Female	2005	2072	428	54.1	32.8
AF058	2018-04-07	Adult	Female	2740	2177	459	59.5	41.1
AF077	2018-12-10	Adult	Female	1629	2114	445	61.2	36.8
AF086	2019-04-24	Adult	Female	2175	2157	294	59.3	33.8
AF088	2019-08-13	Adult	Female	2555	2465	545	69.4	47.8
AF096	2020-03-10	Adult	Female	5140	2731	573	76	50.6
AF098	2020-03-18	Adult	Female	2510	2305	500	64.4	42
AF099	2020-03-19	Adult	Female	2335	2215	444	54.7	39.5
AF103	2020-06-24	Adult	Female	1455	2412	544	65.7	40.1
AF106	2020-07-19	Adult	Female	1665	2285	487	63	41.8
JF003	2013-04-06	Juvenile	Female	770	1622	408	38	31
JF012	2014-06-07	Juvenile	Female	118	906	185	29.5	17
JF027	2017-01-15	Juvenile	Female	1020	1868	420	47.7	33.5
JF055	2018-03-15	Juvenile	Female	1445	1945	455	50.9	32
JF076	2018-11-13	Juvenile	Female	935	1813	410	50.5	30.5
JF078	2018-12-22	Juvenile	Female	774	1739	316	50.1	32.4

6.3.4 Recaptures and growth rates

We recaptured seven adult males, four adult females, two juvenile males and two juvenile females (Figure 6.4), allowing us to calculate the average growth rates of individuals SVL's. Our adult males grew an average of 0.22 mm/day (range = 0.06 – 0.55 mm/day), adult females grew 0.3 mm/day (range = 0.12 – 0.73 mm/day) on average, our juvenile males grew an average of 1.31 mm/day (range = 1.19 – 1.42 mm/day) and juvenile females grew 0.21 mm/day (range = 0.12 – 0.3 mm/day) on average (Table 6.5; Table 6.6; Figure 6.5).

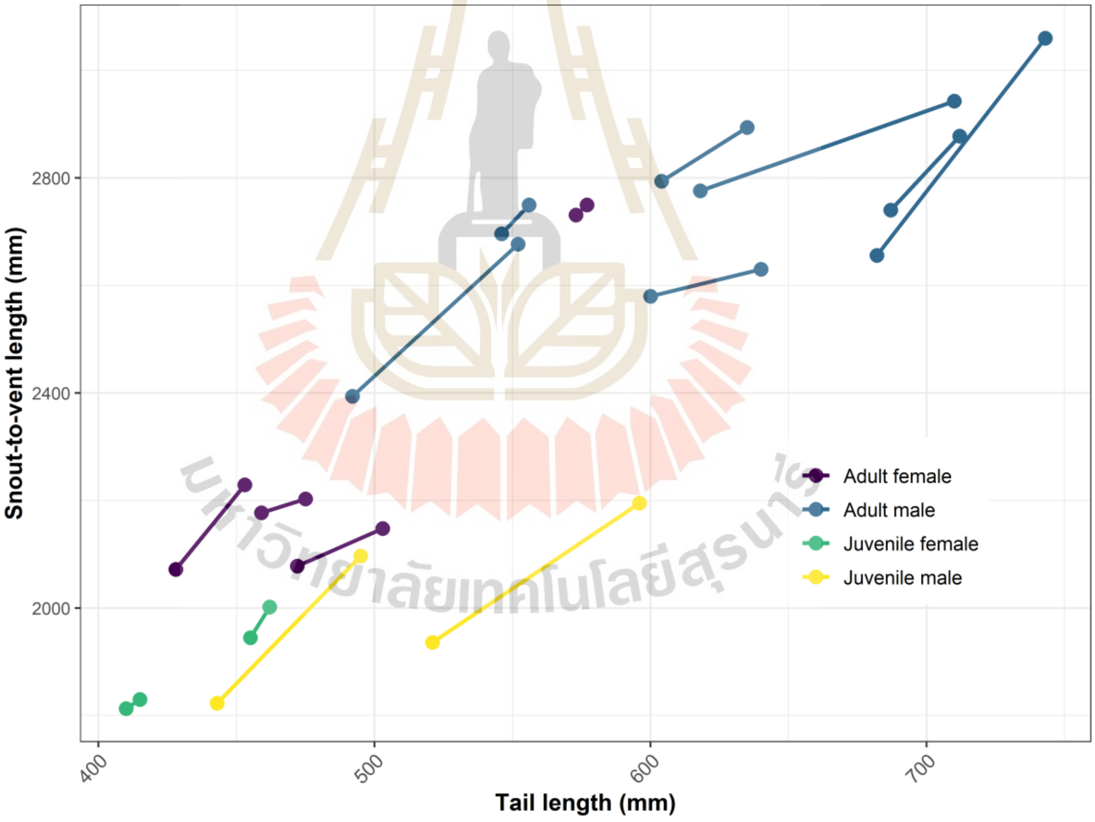

Figure 6.4 Increase in snout-to-vent length and tail length of recaptured King Cobras.

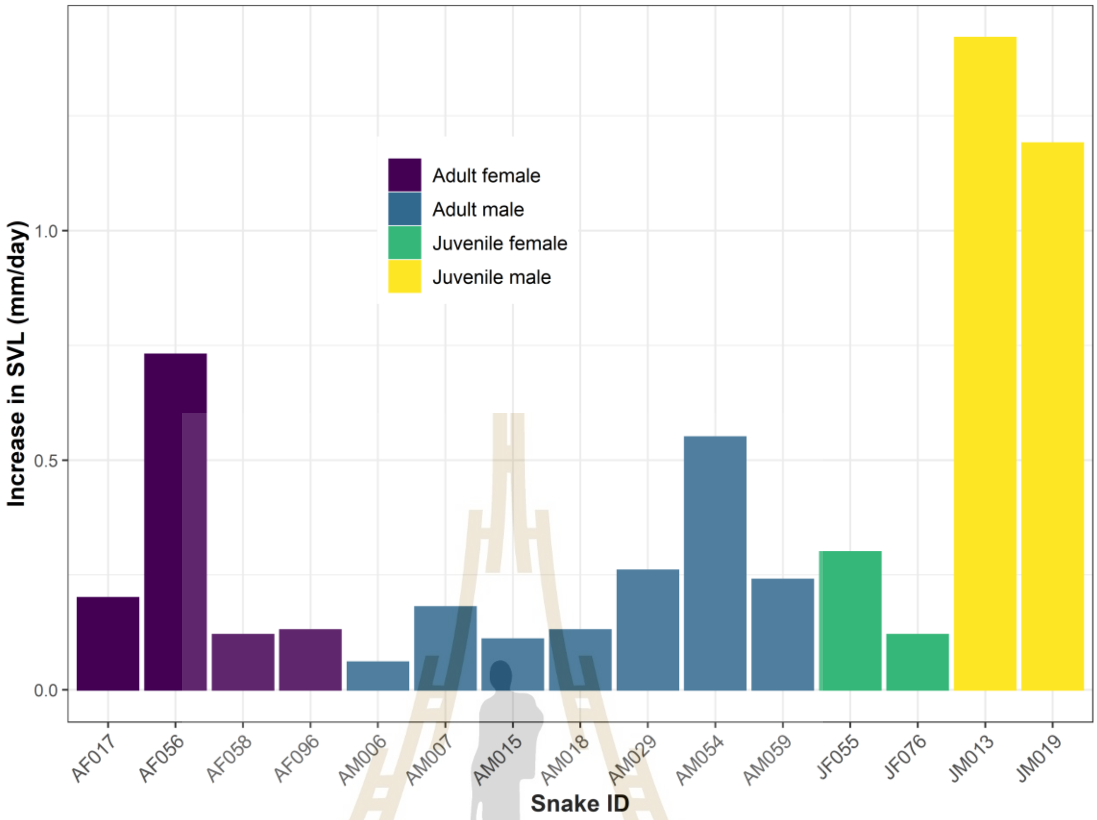

Figure 6.5 Mean increase in snout-to-vent length of recaptured King Cobras.

Table 6.5 Biometric data from recaptured male King Cobras, showing the first and last capture event. *SVL* snout-to-vent length, *TL* tail length, *HL* head length, *HW* head width.

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)	SVL increase (mm/day)
AM006	2014-03-22	Adult	Male	4620	2794	604	70.2	49.7	
AM006	2018-10-08	Adult	Male	6155	2894	635	88.8	61.6	0.06
AM007	2014-03-28	Adult	Male	5320	2656	682	84.4	54.7	
AM007	2020-03-21	Adult	Male	7535	3060	743	95.3	68	0.18
AM015	2015-05-05	Adult	Male	3120	2580	600	72.9	52	
AM015	2016-07-23	Adult	Male	3720	2630	640	73.7	53.3	0.11
AM018	2015-05-03	Adult	Male	3393	2740	687	71.5	52	
AM018	2018-05-11	Adult	Male	4130	2878	712	86.4	53.6	0.13
AM029	2017-04-04	Adult	Male	6105	2696	546	76	52.7	
AM029	2017-10-25	Adult	Male	5460	2750	556	78	63	0.26
AM054	2018-03-01	Adult	Male	2900	2394	492	70	50	
AM054	2019-07-26	Adult	Male	4710	2677	552	80.3	57.3	0.55
AM059	2018-04-10	Adult	Male	4870	2776	618	84	54.8	
AM059	2020-03-15	Adult	Male	6475	2943	710	87.3	63.6	0.24
JM013	2015-01-17	Juvenile	Male	1500	1936	521	56.4	36.3	
JM013	2015-07-18	Juvenile	Male	2000	2195	596	66.18	41.4	1.42
JM019	2015-11-02	Juvenile	Male	1045	1823	443	49.71	32	
JM019	2016-06-20	Juvenile	Male	1440	2097	495	49.8	36.7	1.19

Table 6.6 Biometric data from recaptured female King Cobras, showing the first and last capture event. *SVL* snout-to-vent length, *TL* tail length, *HL* head length, *HW* head width.

ID	Date (yyyy-mm-dd)	Age class	Sex	Mass (g)	SVL (mm)	TL (mm)	HL (mm)	HW (mm)	SVL increase (mm/day)
AF017	2015-10-25	Adult	Female	1426	2078	472	56.6	34	
AF017	2016-10-10	Adult	Female	2740	2148	503	57.4	39.5	0.2
AF056	2018-03-25	Adult	Female	2005	2072	428	54.1	32.8	
AF056	2018-10-26	Adult	Female	2050	2229	453	62.5	42	0.73
AF058	2018-04-07	Adult	Female	2740	2177	459	595	41.1	
AF058	2018-11-06	Adult	Female	1910	2203	475	60.9	41.2	0.12
AF096	2020-03-10	Adult	Female	5140	2731	573	76	50.6	
AF096	2020-08-01	Adult	Female	3490	2750	577	76.6	51.1	0.13
JF055	2018-03-15	Juvenile	Female	1445	1945	455	50.9	32	
JF055	2018-09-24	Adult	Female	1425	2002	462	56.3	35.4	0.3
JF076	2018-11-13	Juvenile	Female	935	1813	410	50.5	30.5	
JF076	2019-04-03	Juvenile	Female	940	1830	415	51.1	30.7	0.12

6.3.5 King Cobra scalation

Our scale counts showed relatively consistent scalation patterns on captured King Cobras. We counted a range of 237 – 252 ventral scales, 74 – 106 subcaudal scales, eight infralabials, seven supralabials (infrequently eight), one preocular, three postoculars, two anterior temporals, two posterior temporals, two prefrontals, two internasals, one rostral, a divided nasal, two supraoculars, one frontal, two parietals and two occipitals (Figure 6.6; Figure 6.7). We also observed a small inter parietal scale, however, this was infrequently present on captured King Cobras (Figure 4.5).

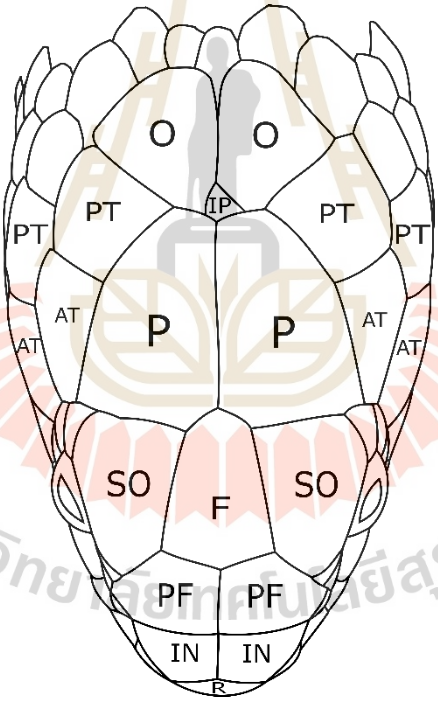

Figure 6.6 Head dorsal scalation pattern of a King Cobra. *R* rostral, *IN* internasal, *PF* prefrontal, *F* frontal, *SO* supraocular, *P* parietal, *AT* anterior temporal, *PT* posterior temporal, *IP* inter parietal, *O* occipital.

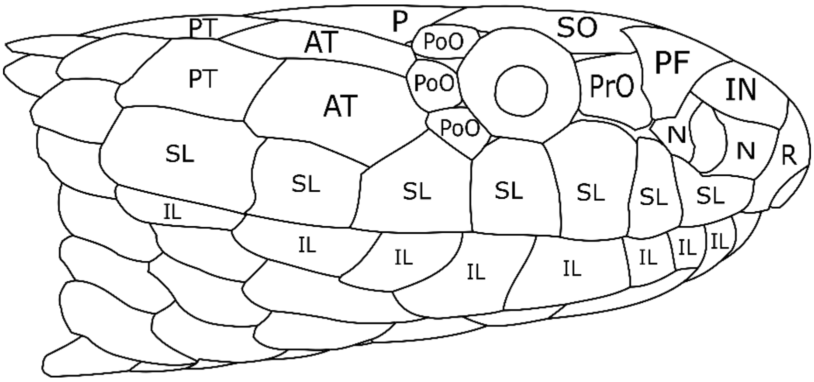

Figure 6.7 Head side scalation pattern of a King Cobra. *AT* anterior temporal, *PT* posterior temporal, *P* parietal, *SO* supraocular, *PoO* post ocular, *PrO* pre ocular, *PF* pre frontal, *N* nasal, *R* rostral, *IN* internasal, *SL* supralabial, *IL* infralabial.

6.3.6 Known-fate analysis

We discovered 19 cases of mortality from our telemetered king cobra during our study. We released four individuals following a successful tracking regime and we lost four individuals due to transmitter failure. We calculated a mean survival probability over our 330-week study period of 0.459 (95%CI 0.337 - 0.774) and 0.527 (95%CI 0.375 - 0.899) for our Kaplan-Meier and Cox proportional hazards regression models respectively (Figure 6.8). In addition, we did not discover any effect of age (χ^2 = 0.516, p = 0.47), SVL (χ^2 = 1.076, p = 0.30), sex (χ^2 = 0.054, p = 0.82) or motion variance (χ^2 = 0.124, p = 0.72) on the survival rates of telemetered King Cobra.

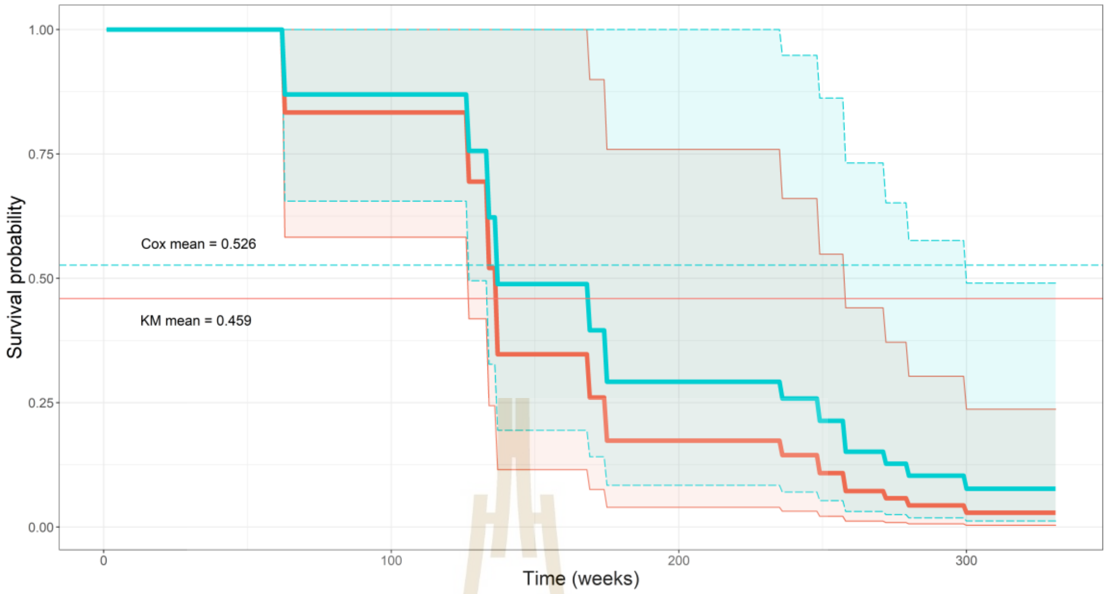

Figure 6.8 Survival probability over the study period of telemetered King Cobra. Blue line depicts the estimated survival probability using the Cox proportional hazards model, and the shaded blue area shows the 95% confidence intervals. Red line depicts the estimated survival probability using the Kaplan-Meier model, and the shaded red area shows the 95% confidence intervals.

6.3.7 Natural deaths

We only recorded four natural deaths during our study period, three telemetered individuals JM002, AF004 and AF077, and an un-tracked adult female. We recorded three of these deaths as predation events on our telemetered females, and one unknown cause. We discovered the bodies of JM002 and AF004 with wounds on their bodies which appeared to be from mammalian predators. We tracked AF077 for only 7 days (hence no inclusion within the other aspects of our study) when we discovered that she was sheltering with one of our other telemetered snakes, AM006, on 2019-01-06. We placed a camera trap on the shelter site and observed only one very large snake leaving, and later witnessed a convergence of tracking frequencies, confirming our first case of King Cobra cannibalism within our study site. We retrieved the transmitter after it was passed by AM006 within a rock complex. We found the un-tracked female within the dry-evergreen forest with no evident wounds or sign of trauma.

6.3.8 Anthropogenic sources of mortality

We recorded the deaths of 22 King Cobras in the anthropogenic landscape: sixteen telemetered individuals and six we discovered opportunistically. We discovered a previously captured adult male (AM079) on 2019-06-13 after initially being notified by a villager to remove the snake from their home, upon arriving the snake was discovered decapitated by a passer-by (Figure 6.9). We observed the remaining five opportunistic mortalities of non-telemetered King Cobras as vehicle collisions on the Highway 304. We found the first individual, a juvenile male (mass = 700 g, SVL – 1610 mm) on 2015-04-30. We found the second individual, a neonate of unknown sex (mass = 20 g, SVL – 480 mm), on 2017-08-20. We subsequently located another neonate of unknown sex (biometric data uncollected) in approximately the same location on the road, exactly a year later on 2018-08-20 (Figure 6.9). We discovered another juvenile male (mass = 332 g, SVL – 1280 mm) on 2019-09-27. Lastly, we discovered an additional juvenile male (mass = 590 g, SVL – 1450 mm) on 2019-09-09 with an evident food bolus (subsequently identified to be a *Cryptelytrops* sp.).

Altogether we have discovered a total of 26 King Cobra mortalities between 2013-03-01 and 2020-07-28, comprised of 19 telemetered individuals (Table 6.7) and seven opportunistic discoveries. The causes of mortality are distributed as follows: 10

persecution events, seven vehicle collisions, three unknown, three natural predations, one due to agricultural practises, one ingestion of a plastic bag (Strine et al., 2014) and one individual that seemingly starved after moving outside of the protected area (Marshall et al., 2018; Figure 6.10).

Figure 6.9 Some of the King Cobra mortalities discovered within the SBR transitional zone. White boxes show the snake ID and cause of death.

Table 6.7 Cause of mortality of telemetered King Cobras.

ID	Cause of death
JM002	Natural - predated
AF004	Natural - predated
AM005	Anthropogenic - consumed plastic bag
AM006	Anthropogenic - death from apparent blunt trauma
AF010	Anthropogenic - killed and eaten
AM015	Anthropogenic - highway road mortality
AF017	Anthropogenic - persecuted and left in plastic bag
AM018	Unknown/anthropogenic - remains founds under vegetation in dried-up irrigation canal
JM019	Anthropogenic - agricultural road mortality
AM021	Anthropogenic - caught in fish trap and stabbed
AM024	Natural/anthropogenic - starved after leaving the protected area
JM025	Anthropogenic - death from apparent blunt trauma
JF027	Unknown/anthropogenic - transmitter found in irrigation canal
AM029	Anthropogenic - found beheaded near logging access road
AM054	Unknown/anthropogenic - found dead on its back at edge of irrigation canal
JF055	Unknown/anthropogenic - remains found in rock complex on edge of highway
AF058	Anthropogenic - persecuted and left in plastic bag
AF077	Natural - predated
AF086	Anthropogenic - lacerated by agricultural vehicle

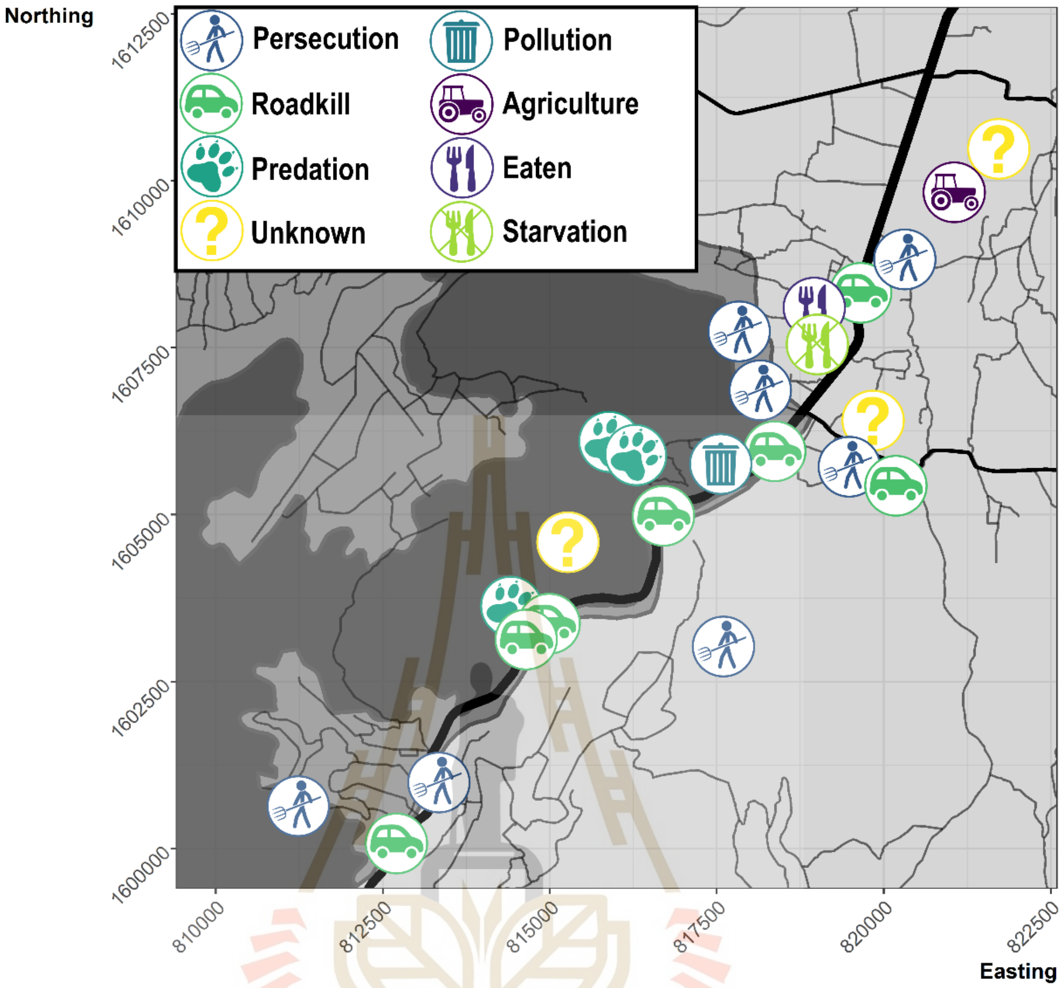

Figure 6.10 Discovered King Cobra mortalities within the Sakaerat Bisophere Reserve.

6.4 Discussion

We have reported on the biometric measurements for King Cobras captured within the SBR. Overall, we observed a low rate of King Cobra discoveries, which was highly biased towards the capture of adult males. We have previously shown King Cobras to exhibit seasonal shifts in space use corresponding to breeding behaviour (explored in Chapter III and Chapter IV), and during the breeding season males will typically move in greater frequency and distance. We captured many of our adult males during these breeding season movements, particularly as King Cobras will more-readily move into people's homes during this time. Our data, congruent with previously published and anecdotal reports on King Cobras, shows clear sexual dimorphism within the population. We measured adult males to have a mean SVL of 2721.6 ± 52.19 mm (range = 2200 – 3714 mm; n = 37), whereas we measured adult females at a mean SVL of 2278.92 ± 54.84 mm (range = 2072 – 2731 mm; n = 13) showing that males achieve much longer lengths than our captured females.

We also recorded adult males to have much larger head lengths and widths than those of adult females. The size of an individual's head appears to grow proportionately with overall length and mass increases, however, the increase in head width likely contributes positively to gape size leading to wider prey availability (Forsman and Lindell, 1993; King, 2002, Vincent *et al*., 2006). Mode of predation is likely to be a primary mechanism driving morphological adaptations, particularly concerning head width and thus gape size, in snakes (Tamagini *et al*., 2018). Jones *et al*. (2020) showed multiple events of adult male King Cobras preying upon clouded monitor lizards (*Varanus nebulosus*), however, the authors presented evidence that female King Cobras only preyed upon snakes within the Sakaerat Biosphere Reserve. The differences in head size particularly width, of King Cobras in our study likely contributes to the dietary differences in demographics reported in Jones *et al*. (2020), allowing adult males to broaden their prey availability.

We achieved a low frequency of recaptures from individuals in our population, resulting in six recaptured females and nine recaptured males. Out of these individuals, we estimated a daily growth rate of less than 1 mm/day for almost all individuals, with the exception of out two recaptured juvenile males, JM013 and JM019 which showed a daily growth rate of 1.42 mm/day and 1.19 mm/day respectively. Although we have a very small sample size to compare with, the growth rates exhibited by our two juvenile males suggests that this demographic grows at a faster rate. This further supports our observed sexual dimorphism, as young males will grow faster to achieve larger sizes for competing with conspecifics for breeding upon sexual maturity. There can be further benefits from an increased growth rate of juvenile snakes, such as a decreased susceptibility to predation through successful fleeing (Jayne and Bennet, 1990), improved performance of defensive tactics (Erickson *et al*., 2014), or increased foraging success due to a positively associated gape size discussed above (Forsman and Lindell, 1993). However, when investigating free-ranging animals, there may be unforeseen factors influencing growth rates, such as prey availability which we were unable to quantify in this study (Forsman and Lindell, 1996; Madsen and Shine, 2008).

Our data shows an increased risk of mortality as snakes move out of the protected area. We discovered few instances of natural deaths, and three out of the four we did discover were victim to natural predation events. However, other studies suggest that natural predations are infrequent when populations are also subject to increased anthropogenic threats (Kapfer *et al*., 2008; Meek, 2012; Baker *et al*., 2016). We recorded the natural predation of JM002, AF004 and AF077. We are unable to identify the potential predator of JM002, however, we believe that AF004 was killed by a hog badger (*Arctonyx collaris*) due to characteristic bite marks found on the transmitter (Marshall *et al*., 2018). We recorded the natural predation event of our other adult female as our first record of cannibalistic behaviour by a larger conspecific, AM006. As we only recorded natural predations on a single juvenile and adult females, we suspect that smaller individuals in the population are more vulnerable to such events

(Meek, 2014). However, we cannot discern accurate inferences due to our highly skewed and limited dataset on the true frequency, or patterns, of natural predation.

We recorded many instances of anthropogenic sources of mortality during our study period. This was primarily a result of direct persecution (10), followed by vehicle collisions (seven), unknown causes (three), plastic pollution (one; Strine *et al*., 2014), apparent starvation (one) and collision with agricultural machinery (one). As King Cobras utilise large areas of space and can exhibit large singular movements (Marshall *et al*., 2019; 2020), individuals may be at greater risk of road mortality (Bonnet *et al*., 1999; Akani *et al*., 2002). Two telemetered individuals we discovered on the road were adult males which exhibited large occurrence distributions (see Chapter 3), which suggests that these large areas of space use may have increased their risk of vehicle collision. However, three of the opportunistic discoveries of road mortality were juvenile males and considerably smaller than our telemetered individuals. Furthermore, the remaining two discoveries of vehicle collision were newly-hatched individuals, likely dispersing from nest sites. These discoveries suggest that roads may be impacting several life-stages of King Cobras, and not only far-ranging adult males.

We only recorded one anthropogenic source of mortality within the core protected area of the SBR, AM029. There was a newly cleared road adjacent to the mortality site of AM029 which we believe to have facilitated his death via increased accessibility into dense forested area by poachers and illegal harvesters (Clements *et al*., 2014). As we could not locate the remains of a head for AM029, and found recently placed anthropogenic waste nearby, we believe this individual was beheaded.

We recorded persecution events as the second highest cause of mortality within our study site. Three of these instances occurred to adult females following a successful nesting season, of these three, one was killed an eaten by a local resident and the other two were discovered in plastic bags after evidently being persecuted. As we have shown clear seasonality in the movement patterns of reproductive females in Chapter 4, we assume that large seasonal movements placed these individuals at an elevated risk of mortality by increasing their exposure to anthropogenic threats (Bonnet *et al*., 1999; Hyslop *et al*., 2009). Another of our recorded persecution events occurred on a large non-telemetered adult male, AM079. We were notified of this snake by a villager and rushed to the location to safely remove the snake from outside the villager's home, however, upon arrival we discovered that the snake had been beheaded by an inebriated passer-by. Although disappointing, the fact that the villagers attempted to remove the snake by calling us, prior to the persecution event, presents hope for the impact that our conservation initiative is having within the transitional zone.

We did not discern any trends from our biometric data collection on the observed mortalities in our study. We observed broad instances of mortality across all life stages and both sexes. This suggests that mortality risk is more likely driven by individual-level heterogeneity in movements, habitat use and behaviour. Furthermore, we did not observe a single mortality cause impacting a single life-stage or sex, apart from independent mortality causes (such as plastic pollution). Our results therefore illustrate a diverse array of mortality sources for King Cobras within the SBR. The findings of this study can be used to implement detailed conservation plans on conserving this large elapid. Based on our findings, we suggest that future conservation plans focus on an education-based approach to reduce direct persecution events. Furthermore, ecopassages, alongside directive fencing may help mitigate future road mortalities.

6.5 Conclusion

We report on cases of mortality of King Cobras observed in a permeable protected area in northeast Thailand, alongside biometric data for captured individuals. Our results show a diversity of mortality causes for King Cobras, which are highly skewed towards deaths outside of the protected area. The sources of mortality we have described likely represent a fraction of the true survival observed in the SBR, which suggests that the population may be at risk. We could not discern any patterns of mortality for a particular demographic, suggesting that anthropogenic threats are impacting King Cobras at a broad population level, likely attributed to individual movement traits and behaviour.

We suggest further research is dedicated to understanding the mortality sources acting on King Cobras throughout their wide distribution. This will allow a broader understanding of the threats acting on the species as a whole. Furthermore, conservation plans should factor in the causes of mortality described above, and further research should attempt to quantify their effectiveness on reducing King Cobra mortality, and thus survival probability over time. An education approach, alongside novel road infrastructure and improved signage of the current conservation initiative may prove to be an effective start to reducing the mortality rate in the SBR.

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CHAPTER VII

CONCLUSION AND RECOMMENDATION

7.1 Conclusions

This study presents a comprehensive investigation into the ecology of King Cobras, with a particular focus on spatial ecology, within the Sakaerat Biosphere Reserve, Northeast Thailand. We introduce a paucity in peer-reviewed literature on reptile spatial ecology studies in Asia, which reflects on a lack of ecological information for elapid snakes. Our results highlight important patterns of space use and associated movement of a single King Cobra population. Specifically, we show a high degree of seasonality in the movements of adult King Cobras, with males exhibiting larger movement distances and frequency when searching for mates; and females performing large linear movements into forested areas for nesting. We further highlight baseline information on the nesting ecology of King Cobras in Thailand, presenting results which suggest that females have specific habitat/microhabitat requirements for oviposition sites outside of the disturbed human-dominated areas.

We provide evidence of how specific landscape features are both limiting (roads, settlements) and facilitating (semi-natural areas, forests) movement for King Cobras throughout a highly heterogeneous landscape. Lastly, we highlight sources of mortality acting on King Cobras in the Sakaerat Biosphere Reserve, and show that anthropogenic sources of mortality have been common throughout our study period. Our results can be used as a foundation for future studies investigating the ecology of poorly-understood reptile taxa.

7.1.1 King Cobra Spatial Ecology and Resource Use

Our dBBMM 99% occurrence distribution estimates ($\bar{x}$ = 543.89 ± 81.75 ha, range = 82.09 – 1843.75 ha) represent some of the largest areas of space use by a snake species. On average, our telemetered adult males (872.11 ± 131.21 ha, range = 376.51 – 1843.75 ha) exhibited the highest occurrence distribution estimates over other King Cobra demographics. We further recorded that male King Cobras typically exhibited larger occurrence distributions than female conspecifics. We provided evidence of seasonal shifts in movement patterns, with males exhibiting large peaks in motion variance during the breeding season, and characteristics peaks and periods of low motion variance exhibited by females during nesting movements and oviposition. We observed King Cobras utilising various habitats throughout the Sakaerat Biosphere Reserve, included dense forested areas, semi-natural areas and human-dominated agricultural/village areas. We did not record any single landscape feature (resource) which unanimously predicted movement of our telemetered King Cobras, with results showing a high level of individual heterogeneity. However, our population iSSF estimates suggest that the movement of our sampled females could largely be predicted by the availability of semi-natural areas, and movements of our males could primarily be predicted by forested areas. Although our results present a vastly improved understanding on the movement patterns of King Cobras, we are limited by our sample size and fine-scale spatial domain. We therefore suggest that future studies replicate our intensive tracking regime in other King Cobra populations, alongside our statistical analyses, in order to build a better understanding on the ecology of King Cobras throughout their range. Further insight into King Cobra ecology, supplemented with the results presented in this study, will allow for more informed decisions to be made on the status of King Cobra populations, and corresponding conservation strategies.

7.1.2 King Cobra Nesting Ecology

Our results show that adult female King Cobras will exhibit seasonal shifts in occurrence distribution estimates and motion variance between two delineated seasons: *breeding* and *non-breeding*. Areas of space use exhibited in the breeding season (255.67 ± 51.61 ha, range = 58.22 – 519.57 ha) were larger than our non-breeding estimates (89.99 ± 26.36 ha, range = 39.65 – 146.8 ha). In addition, we only recorded our telemetered adult females entering forested area during the breeding season, remaining within an agricultural matrix inside the non-breeding season. As a result of radiotelemetry efforts, we monitored four nests between 2018 – 2019. We recorded three nests inside of forested areas, and one nest adjacent to forest at the edge of an irrigation canal. Nests were constructed of leaf litter, twigs and other forest debris, and the size of the nest varied, likely attributed to the body length of nesting females and associated clutch size. Our thermal dataloggers showed greater thermal stability inside of the egg chambers when compared to immediate outside temperatures. We provide basic measurements of captured neonates, however, our method of capturing individuals proved generally ineffective and future work should implement earlier, and more secure, construction of nesting enclosures if attempting to replicate our study design. Our results show some basic resource requirements for nesting females, alongside a better understanding of the nesting ecology of King Cobras in the Sakaerat Biosphere Reserve. We are extremely limited to make broad inferences from our results due to our small sample size, however, our preliminary results are largely congruent with nesting ecology studies previously undertaken in India. We suggest that future studies aim to bolster our current sample size to provide a greater understanding into King Cobra nesting ecology at the Sakaerat Biosphere Reserve, in order to elucidate overall nesting patterns and requirements for informed conservation and wildlife management decisions to be implemented.

7.1.3 King Cobra Road Interactions

We discovered 32 underpasses on a 15.31 km section of the Highway 304 which could facilitate movement across the road. Our results from our *recurse* analysis, and via visual inspection of dBBMM movement pathways, suggest that 19 of these underpasses have been used by telemetered King Cobras to safely traverse the road. Underpasses consisted of drainage culverts (21), double drainage culverts (seven) and bridges (four). We recorded 26 underpasses (24 drainage culverts and two bridges) within an 8.07 km section of highway adjacent to the protected core area. We recorded infrequent use of underpasses by telemetered King Cobras, with some individuals performing many road crossings throughout their tracking duration (e.g. AM018 moved across the road 37 times over 1176.1 days). We also investigated the frequency of crossings on another major road at our study site, the 304 Nong-Weng Ta Ling Chan (304 NW-TLC), by reproductive females. All of our sampled females moved over this road at least once during their tracking period, corresponding to movements to and from oviposition sites, suggesting that females are placed at greater risk of vehicle collision during these movements. We show that locations of culverts can significantly predict where King Cobras cross the highway, though regression models failed to provide further evidence on exact structures used. Our results suggest that underpasses can alleviate the risk of vehicle collision along the Highway 304, however, we still uncovered cases of road mortality across our survey area. We therefore suggest that future investigations attempt to confirm that underpass density can boost road permeability, while integrating new infrastructure to guide wildlife into these underpasses, such as roadside fencing.

7.1.4 King Cobra Biometrics and Mortality

We highlight the primary sources of mortality within the Sakaerat Biosphere Reserve, Northeast Thailand. The permeable boundary of the protected core area permits the movement of King Cobras into human-dominated areas where they are subject to many anthropogenic pressures. We therefore recorded anthropogenic sources as the main causes of mortality within our study site, with 22 deaths recorded as anthropogenically-caused and only four natural deaths. This is congruent with previous studies showing that natural deaths are rare when populations are subject to anthropogenic pressures. Out of our observed anthropogenic sources of mortality, persecution events (10) and vehicle collisions (seven) were the most frequently observed mortality cause. We also recorded biometric data on any located King Cobras, dead or alive, which we further report on in this chapter. We could not discern any pattern of mortality affecting a specific King Cobra demographic, which suggests that mortality risk is subject to individual movement patterns, habitat use and behaviours. However, as a result of our biometric data collection, we support previous reports on sexual dimorphism in our King Cobra population, with males achieving greater lengths and mass than females, owed to exhibited male-male combat. We suggest that future investigations into King Cobra ecology also record detailed accounts of individual mortality events in order to create a broader understanding of the threats acting on the species throughout its wide distribution. As we have mitigated many events of persecution and human-snake conflict via education-based approaches, we recommend that further effort is undertaken on an education approach to alleviating future conflict. Novel road infrastructure, and signage may further aid in reducing the high rate of vehicle collisions observed along the Highway 304 and other major roads.

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