# Ecology of the Reticulated Python (*Malayopython reticulatus*): Life in an Altered Landscape

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# Summary

Palm oil is one of the primary drivers of deforestation in Southeast Asia, causing widespread biodiversity loss. Reticulated pythons as large, widespread, generalist predators may play a key role at the interface between forest fragments and plantations, and are also the most heavily-traded species of snake in the world. This study occurred within forest fragments and oil palm plantations in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia.

The study explored the potential for visual encounter survey monitoring protocols as an effective tool for monitoring population changes resulting from trade dynamics by detailing population demographics, correlates of encounter rates, and by assessing occupancy and detectability. VHF telemetry was combined with LiDAR data to assess space-use, movement, and habitat selection in 16 pythons. Eight individuals were additionally trialled with experimental GPS devices. Data were collected from within forest fragments and plantations, aiming to compare python responses within differing landscapes.

Field surveys appear highly inefficient as a trade monitoring tool, with a mean encounter rate of 0.051 pythons/km surveyed. Encounter rates and movement responses of telemetered pythons were highly correlated with moon phase, suggesting that timing surveys to coincide with moon phases can improve efficiency. An overview is provided of the necessary considerations for future researchers wishing to adopt GPS technology for snakes. Males typically occupy larger home ranges than females, and home ranges within plantations appear smaller, and pythons move less often, compared to those in forests. Within forests, pythons often move in strong moonlight and low rainfall, while the opposite was observed for pythons in plantations. Pythons appear to select habitats closer to water and flood-prone areas. Habitat suitability within plantations is highly heterogeneous, and plantations showed lower suitability overall compared to forests.

The ecological implications of the underappreciated abundance and resilience of reticulated pythons warrant further study in the face of continued habitat alteration, and this work provides important and unique insights into python ecology and conservation.

## Acknowledgements

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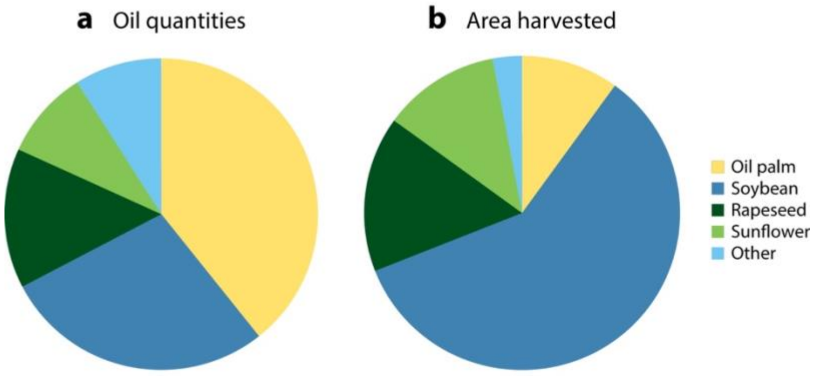
# 1 Pythons and Palms: A General Introduction

## 1.1 Deforestation and the pursuit of palm oil

Southeast Asia contains a large proportion of global biodiversity, and comprises several designated biodiversity hotspots (Myers et al., 2000). Concomitantly, it is experiencing high levels of deforestation and some of the highest rates of habitat loss in the world (Achard et al., 2002). Between 2001 and 2015 around 39Mha were lost in southeast Asia, representing about 13% of total global tree cover loss. Malaysia and Indonesia account for a major proportion of this (Curtis et al., 2018). Malaysia falls within in the top 10 countries for total forest area lost, with roughly 8.7Mha (almost 30%) of its remaining forest lost between 2001 and 2021. 2.8Mha of this was primary tropical forest, placing Malaysia in the top five countries worldwide for primary tropical forest loss (WRI, 2022).

Demand for palm oil (from the oil palm, *Elaeis guinensis*) is one of the primary drivers of habitat loss in Southeast Asia (Gaveau et al., 2016; Curtis et al., 2018). Malaysia and Indonesia account for roughly 80% of global palm oil production, but it is now expanding in other tropical regions, such as Africa and South America (Fitzherbert et al., 2008; Foster et al., 2011; Linder & Palkovitz, 2016). The island of Borneo was estimated to be covered by up to 7.9Mha of oil palm plantations in 2015 – about 11% of its total land area (Gaveau et al., 2016). Oil palm plantations greatly reduce biodiversity and connectivity, exacerbate erosion and pollution, increase the risk of flooding and forest fires, increase poaching, allow the spread of invasive species, and can increase the transmission rates of diseases to wildlife (Fitzherbert et al., 2008; Azhar et al., 2012; Hamilton et al., 2016; Afandi et al., 2017; Horton et al., 2017; Khatun et al., 2017; Guerrero-Sanchez et al., 2022). While there are major economic benefits to local and state revenues, there are also a range of negative social issues implicated in palm oil production, including land conflict with Indigenous and rural communities, human rights abuses, food insecurity, and increased socioeconomic inequality (Obidzinski et al., 2012; Meijaard & Sheil, 2013; Quaim et al., 2020). Despite some wildlife species being able to adapt to oil palm plantations, the biodiversity within oil palm plantations is greatly reduced relative to natural forests, and supports a lower diversity relative to other tree plantations, such as rubber (Fitzherbert et al., 2008). Vegetation structural complexity is greatly reduced, and temperatures can be up to 6.5˚C hotter than primary forest (Hardwick et al., 2015).



Qaim M, et al. 2020.
*Annu. Rev. Resour. Econ.* 12:321–44

***Figure 1.1*** *Global vegetable oil production (a) compared with the area of land that is harvested (b). The high productivity of oil palm (yellow) means that it comprises about 40% of vegetable oil production worldwide, but only uses 10% of the total land area dedicated to oil seed crops. However, its yield of protein (not shown) is lower than others. Figure from Quaim et al. (2020).*

While the negative effects of palm oil production for conservation are widely recognised, it is the most productive oil crop worldwide, producing up to eight times the amount of vegetable oil per unit area than the next most productive oil seed crop (Meijaard & Sheil, 2013) (figure 1.1). It also requires fewer fertilizers and pesticides, compounding its relative advantage (Quaim et al., 2020). The trees produce fruit (and therefore labour opportunities) year-round and can produce 15-30 tonnes of fruit (yielding 4-5 tonnes of oil) per hectare per year (Sheil et al., 2009). While deforestation rates are alarming, switching to alternative oil sources could lead to an increase in global rates of deforestation elsewhere to compensate (Meijaard & Sheil, 2013). Oil palm trees also store more carbon than other oil crops (Abram et al., 2016), although still considerably lower than primary tropical, and especially peat swamp, forest (Linder et al., 2016). Understanding how species are able to utilize this novel landscape is therefore a high research priority and could ultimately lead to improving management practices to promote higher levels of biodiversity, but such studies are still rare within the literature published on oil palm (Fitzherbert et al., 2008; Foster et al., 2011). A wide range of medium to large mammal species are now known to be able to utilize these landscapes to some extent, including elephants, orang-utans (*Pongo pygmaeus*), tigers (*Panthera tigris*), bearded pigs (*Sus barbatus*), sun bears (*Helarctos malayanus*), civets (*Viverra tangalunga* & *Paradoxurus hermaphroditus*), leopard cats (*Prionailurus bengalensis*), pangolins (*Manis javanicus*), and macaques (e.g., *Macaca fascicularis & M. nemestrina*)(Azlan & Sharma, 2003; Ancrenaz et al., 2014; Jennings et al., 2015; Love et al., 2017; Guharajan et al., 2018; Holzner et al., 2019; Othman et al., 2019; Chong et al., 2020; Evans et al., 2021). However, this tends to decline further away from remnant forest (Yue et al., 2015), and exacerbates human-wildlife conflict (Othman et al., 2019). Many species can supplement their diets with the oil-rich fruits, or predate upon the abundant rodents present. Predatory reptiles such as snakes, monitor lizards and crocodiles are also well documented to exploit these habitats (Akani et al., 2008; Evans et al., 2016; Natusch et al., 2016a; Guerrero-Sanchez et al., 2022). The extremely high densities of water monitors (*Varanus salvator*) and pythons (*Malayopython reticulatus*, and possibly *Python brongersmai*, *P. curtus* & *P. breitensteini*) (Shine et al., 1999a, Keogh et al., 2001; Natusch et al., 2016a, Khadiejah et al., 2019) experienced in some plantations may even have detrimental effects on biodiversity by predating on or outcompeting other species, but further research is required to determine if this is truly the case (D. Natusch, Pers. Comms).

Rodent pests are one of the most significant causes of damage to and loss of crops worldwide (Singleton et al., 1999), and this is also true for oil palm plantations. Losses due to rodents are estimated to be 5-30% without rodent control, and they can reach peak densities of 600 individuals per hectare (Wood & Gait Fee, 2003). Many predatory species are thus attracted into oil palm plantations to feed on this abundant prey resource. The use of chemical rodenticides is a common strategy to mitigate the damage caused by rodents, but comes with substantial economic and environmental costs, and may lead to resistance developing in the targeted pests, and secondary poisoning of wildlife feeding on them (Salim et al., 2014) (figure 1.2). Barn owls (*Tyto alba javanicus*) have been widely used as potential biological control agents in Malaysia through provisioning of nestboxes within oil palm plantations, and also breeding and releasing large numbers of these animals into plantations (Wood & Gait Fee, 2003; Puan et al., 2011). The potential to exploit other predators in this way has also been suggested, such as small carnivores (Silmi et al., 2013), macaques (Holzner et al., 2019), snakes and monitor lizards (Lim 1999). Generalist predators can be effective biological control agents in many cases (Symondson et al., 2002), and the potential of snakes for this purpose has been little explored. Owing to their low energy requirements and fasting abilities, snakes can have excellent temporal persistence when prey densities decline, so are less constrained by predator-prey population dynamics than endotherms (Madsen & Shine, 1996). Providing refugia and adopting management policies that benefit snakes and native rodent predators could also benefit other species, and lead to improvements in biodiversity and connectivity, thus synergistically benefitting both conservation and agricultural productivity (Burgstaller et al., 1992; Evans et al., 2021).

***Figure 1.2*** *A severely emaciated reticulated python found in oil palm plantation. The animal died not long after capture, and an autopsy showed that the blood was extremely pale and watery, indicating anti-coagulant poison may have been the cause. Photo by R. Burger.*

## 1.2 Study area

The Lower Kinabatangan floodplain (LKF) encompasses an area of roughly 16,800 $km^2$, although only 750$km^2$ of degraded and fragmented forests remain. While much of this remnant forest is protected (comprising the Lower Kinabatangan Wildlife Sanctuary, hereafter LKWS, and Class I Virgin Jungle Forest Reserves), still roughly one third remains unprotected (Ancrenaz et al., 2014). Twenty eight percent of all oil palm production in the state of Sabah is located within the Kinabatangan catchment area. The area experiences a warm, wet, tropical climate, with year-round temperatures of 21˚-34˚C, and annual precipitation averaging 3000mm (Ancrenaz et al. 2004; Abram et al. 2016). The forested habitat consists of freshwater swamp forests, semi-inundated forests, and riparian and mixed lowland dipterocarp forests, with mangrove and nipah palms closer to the river mouth. Much of the drier lowland forest has been cleared, primarily for oil-palm agriculture, and the remaining fragments have been repeatedly selectively logged in the past, removing mostly the larger, dominant dipterocarps (Abram et al. 2016).

Situated within the LKF, The LKWS is the only fully gazetted wildlife sanctuary in the Malaysian state of Sabah, under the jurisdiction of the Sabah Wildlife Department (SWD) (figure 1.3). It encompasses a series of 10 forested lots of various levels of degradation along the Kinabatangan river; the longest river in Sabah and second longest on the island of Borneo (Ancrenaz et al., 2014; Abram et al., 2016);

situated within a matrix of oil palm plantations. It forms the only corridor of forest that connects the coastal mangrove forests with the forests of the state interior, and as such is of high conservation importance within the region. Despite the high levels of degradation (most of the forest was previously logged for timber) the density and diversity of the LKWS is astounding and remains one of the best places for wildlife viewing in Sabah, and is frequented by large numbers of tourists (Chan & Baum, 2007). New species (e.g., Miller et al., 2014; Naruse et al., 2015; Miller et al., 2018) and new locality records (e.g., Evans et al., 2016; Wai et al., 2021) are still being discovered here. As an area for research, it provides a natural laboratory of a highly fragmented environmental landscape, and a model for research on wildlife responses to habitat fragmentation and the benefits of ecotourism. Within this locality, research centres have become established, including Danau Girang Field Centre (DGFC) and Sukau Ecotourism Research Centre (SERC) and NGOs such as KOPEL and HUTAN.

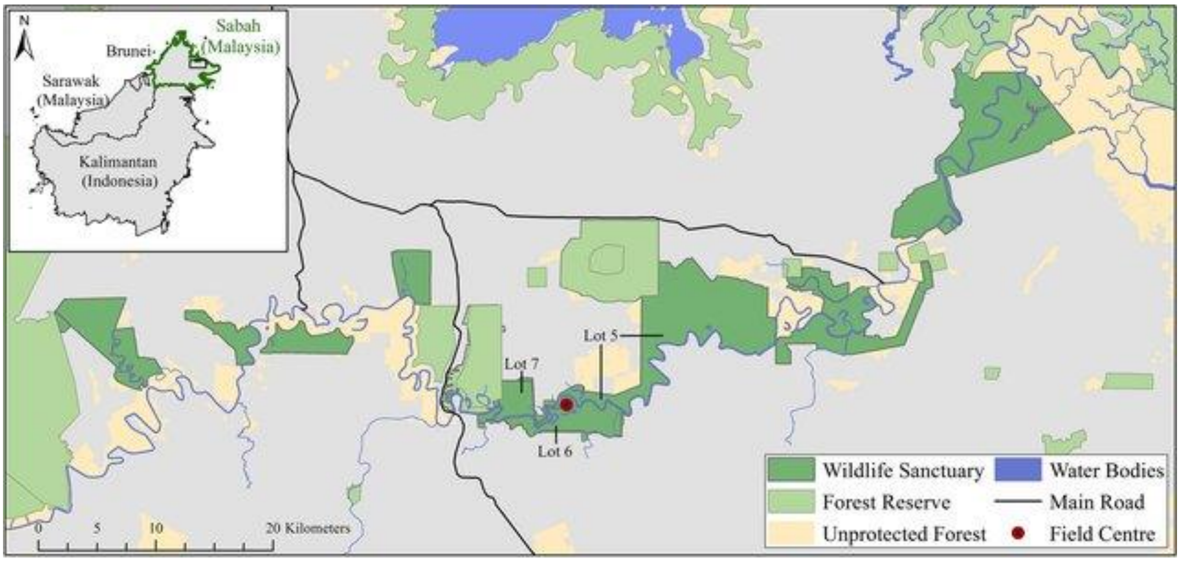


***Figure 1.3*** *A map of the Lower Kinabatangan Wildlife Sanctuary (LKWS), with the remaining protected and unprotected forests. Non-forest is shown in grey, and consists primarily of oil palm plantations. The location of the Field Centre within lot 6 is shown, and the majority of field work was carried out within lots 5, 6 & 7, and adjacent oil palm plantations, as well as along riverbanks adjacent to Pin-Supu forest reserves to the west of lot 7. Figure by Meaghan N. Evans (from Evans et al., 2021).*

## 1.3 Reptile conservation

There are more than 11,700 species of described reptile species worldwide (The Reptile Database, 2022), making them the most speciose group of terrestrial vertebrate taxa, yet conservation focus and efforts lag far behind those for mammals, birds and amphibians (Tingley et al., 2016). Globally, reptiles are a highly threatened taxonomic group (Gibbons et al., 2000) with around 21% of globally described species classed as threatened with extinction (Böhm et al., 2013; Cox et al., 2022), including 19.6% of squamates (Cox et al., 2022). The major threats that reptiles face are habitat loss, invasive species, pollution, disease, and unsustainable use (such as for skins, meat, or the pet trade) (Gibbons et al., 2000; Marshall et al., 2020). Climate change, and how its synergistic effects combine with these other pressures are another major threat, but limited research obfuscates the ability to make strong predictions (Cox et al., 2022). At least in terms of temperature increases, there may be net benefits to some species, particularly in temperate latitudes. However, tropical species are thought to have limited thermal acclimation capacity (Huey et al., 2012), and represent the highest proportion of reptile diversity (Huey et al., 2012; Böhm et al., 2013).

Southeast Asia has a high diversity of reptile species, with levels of endemism over 60% in the Sundaland, Philippines and Wallacea biodiversity hotspot regions (Sodhi et al., 2004) as well as a high proportion of both threatened and data deficient species (Böhm et al., 2013). Data deficiency is highest among snakes compared to other reptile taxa, and is higher in Asia than any other regions (Cox et al., 2022). Data deficiency for snakes is likely due to a tendency for larger geographical ranges among snakes (an important criteria in global assessments – IUCN, 2012), coupled with a greater difficulty to analyse long-term population trends. Lower numbers of preserved specimens in collections also reduce the ability of taxonomists to identify cryptic species (Böhm et al., 2013). Coupled with some of the highest global rates of habitat loss and wildlife harvesting, Southeast Asia as a region is of high concern when it comes to the conservation of reptiles, just as for many other taxonomic groups (Myers et al., 2000; Achard et al., 2002; Rosa et al., 2016; Cox et al., 2022).

## 1.4 Snakes as study organisms

Snakes are generally poorly studied, particularly in terms of their ecology. This can be partially attributed to a degree of “taxonomic chauvinism”, coupled with traditional Judeo-Christian beliefs and a potential innate propensity for fear responses in humans (Öhman & Mineka, 2003), leading to reduced research interest and funding, although attitudes are slowly improving (Shine & Bonnet, 2000). However, snakes are also notoriously difficult to study in their natural environment. Most species are shy, cryptic, occur at low densities and exhibit low levels of activity, leading to very low detection rates, and making accurate population estimates difficult (Rodda et al., 2005; Dorcas & Wilson, 2009; Steen, 2010; Durso et al., 2011; Willson et al., 2011; Durso & Seigel, 2015; Ward et al., 2017; Nafus et al., 2020). This is even more true in the tropics, where field conditions can exacerbate these issues (Shine et al., 1999b; Natusch et al., 2016a; Natusch et al., 2022), and some traditional temperate sampling techniques such as the use of cover boards and basking areas may be less effective due to more stable temperatures (Dorcas & Wilson, 2009; Halliday & Blouin-Demers, 2015; Asad et al., 2021). The proportion of ecological studies on snakes only reached levels that were commensurate with studies of other terrestrial vertebrates in the 1990s (Shine & Bonnet, 2000). However, the actual numbers of studies conducted remains relatively low, and knowledge of snake ecology therefore lags behind that for many other taxa.

Despite this, snakes are increasingly being seen as potential model organisms in ecological research (Shine & Bonnet, 2000), and in some cases may be particularly useful as bioindicators (see Beaupre & Douglas, 2009, for a full review). Snakes are often among the top predators in their environments, and therefore healthy snake population sizes and diversity, or their body conditions, can be potential indicators of overall ecosystem health. The importance that snakes play in trophic dynamics may be often overlooked or underappreciated due to perceived rarity, but is in fact substantial and of great ecological importance (Willson & Winne, 2016). Recent interest in snakes can also be partially attributed to their potential as invasive species, with studies on brown treesnakes (*Boiga irregularis*) on Guam and Burmese pythons (*Python bivittatus*) in Florida perhaps the best-known examples (e.g., Fritts & Rodda, 1998; Dorcas & Willson, 2012).

## 1.5 Study species: Reticulated Python

***Figure 1.4*** *A reticulated python resting in the open during the day on the forest floor, one of several pythons fitted with radio-telemetric devices in this study. Excellent camouflage helps them blend into leaf litter and vegetation. Iridescence can be seen on the scales, enhancing the beauty of their dorsal patterning in the light. But this beauty comes at a price, as their skins are highly prized for leather goods. Photo by R. Burger.*

### 1.5.1 Taxonomy

The reticulated python was first described as *Boa reticulata* (Schneider, 1801), with the specific epithet in reference to the net-like reticulations in its colour pattern. Reticulated pythons have largely been described under the taxonomic name *Python reticulatus* since 1842. However, Rawlings et al. (2008), Pyron et al. (2013) and Reynolds et al. (2014) identified the species as being closer evolutionarily to Australo-Papuan species than to the Afro-Asian species within the *Python* Genus, meaning a designation as *Python* would be paraphyletic (figure 1.5). Hoser (2004) had already described the reticulated python in self-published work as "Broghammerus reticulatus", but his prolific taxonomic revisions without scientific justification have caused consternation among herpetologists, and have largely been discredited (hence lack of italics for his nomenclature has been recommended) (Wüster et al., 2001, Kaiser et al., 2013; Pyron et al., 2013; Wüster et al., 2021). Reynolds et al. (2014) suggested the designation of a new genus, *Malayopython,* for reticulated pythons and their sister species (*M. timoriensis*). While all three synonyms may still be in use to some degree, recent studies have largely conformed to Reynolds et al. (2014) (e.g., Booth et al., 2014; Barker et al., 2015; Murray-Dickson et al., 2017; Wasserman et al., 2017; Kalki et al., 2018, Esquerré et al., 2020; Natusch et al., 2019; Natusch et al., 2020). This work therefore also follows the designation of *Malayopython reticulatus*.

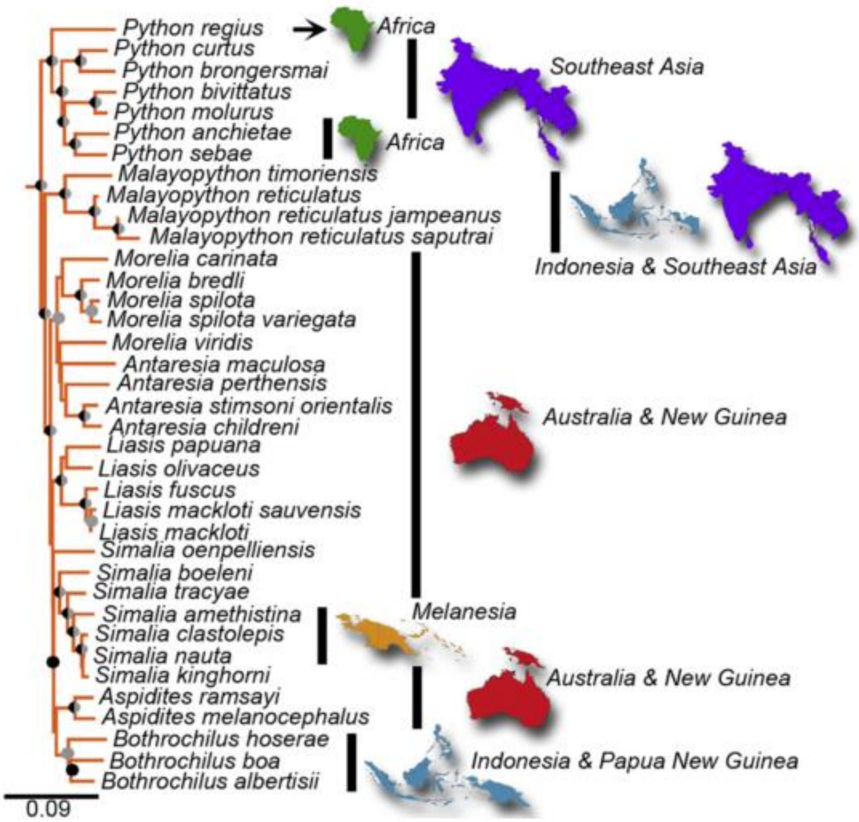


***Figure 1.5*** *Phylogenetic relationships of* Pythonidae*, and their regions of origin, taken from Reynolds et al. (2014).* Malayopython reticulatus *is clearly more closely related to the Australasian species than to the Afro-Asian species of the genus Python to which it has long been presumed to belong.* Python breitensteini*, which also occurs in Borneo, was not analysed, but belongs with* P. curtus *and* P. brongersmai*, based on other molecular studies*

### 1.5.2 Morphology

The reticulated python, *Malayopython reticulatus* (Schneider, 1801), is widely considered the longest species of snake in the world, with reports of lengths beyond 8.5m, and mass in excess of 150kg in exceptional specimens (Murphy & Henderson, 1997), although specimens above 5m in length are typically rare in the wild (Shine et al., 1999c). It (and *M. timoriensis*) is typically slender and has a lighter body mass/length ratio in comparison to many other species of giant constrictor, such as Burmese and African rock pythons (*Python bivittatus* and *P. sebae*) and the green anaconda (*Eunectes murinus*). Similar to most snakes, females are larger than males (Rivas & Burghardt, 2001), but the magnitude of sexual size dimorphism may be higher than any other snake species, except possibly the green anaconda (*Eunectes murinus*) (Shine et al., 1998b). Sexes cannot be determined from external morphological characteristics, however, due to overlap in traits at small and intermediate body sizes. Reticulated pythons mature to adulthood at relatively small sizes compared to their maximum attainable lengths, with males reaching maturity at around 1-2m in length, and females at around 2.5-3m, after roughly 2 and 3 years, respectively (Shine et al., 1998b;c; Natusch et al., 2016a). The species can exhibit exceptional growth rates in captivity. Hatchlings may be between 60 and 85cm in length (this current study measured 10 wild 1-day-old hatchlings ranging between 77 and 84.5cm – Burger, unpublished data), and may in some cases be able to reach 2.5-4m after only a year (Reed & Rodda, 2009), but this will certainly be slower in the wild, and is dependent on food availability and other environmental variables (Madsen & Shine, 2000).

### 1.5.3 Breeding

Breeding biology of the species is only known for a few localities, but appears to be highly seasonal (Shine et al., 1999b). Clutch sizes range between eight and 124 eggs, but are more typically between 20-40 (Reed & Rodda, 2009; and references therein), and the number of eggs is strongly positively correlated with body size (Shine et al., 1998b). Females probably reproduce every 2-3 years (Shine et al., 1999b), although Natusch et al. (2019), estimated every 3-5 years for one population, but this was possibly biased by the sampling method employed. Gestation takes 2-3 months, and females will guard their eggs after oviposition until they hatch (figure 1.6), usually not feeding during this time, with incubation also taking between 2-3 months (Reed & Rodda, 2009). While many other species of python can employ shivering thermogenesis to generate heat when incubating (Wolf et al., 2016), this has not been documented in reticulated pythons.

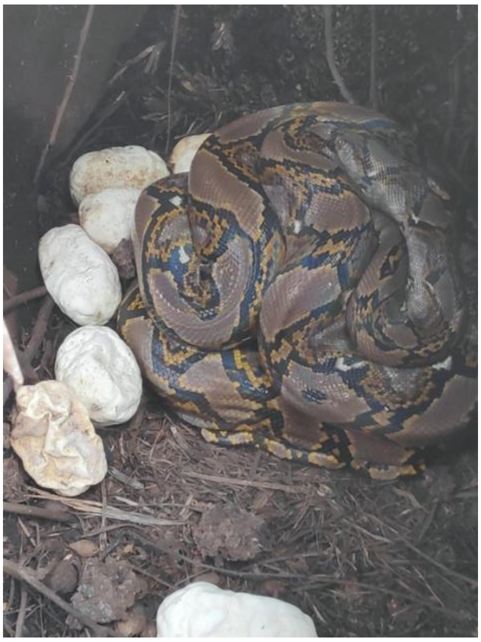


***Figure 1.6*** *A female reticulated python found during this study incubating eggs in her nest, under an oil palm tree after it had fallen in a storm. The disturbance may have caused the release of several eggs from her coiled protection – leading to desiccation and failure to hatch. Photo by R. Burger.*

### 1.5.4 Species distribution

Reticulated pythons are widespread in Southeast Asia, ranging from Bangladesh to Indonesia and the Philippines, although the northern limits of this range are poorly defined, and may also extend into parts of India (Kalki et al., 2018). This makes it one of the most widely distributed snake species in the world (Natusch et al., 2019). Three subspecies are described; the nominate subspecies *M. r. reticulatus*, which occurs across the majority of its range, and two “dwarf” forms each limited to small ranges in the lesser Sunda isles, *M. r. jampeanus* from the island of Tanahjampea and *M. r. saputrai* from the island of Selayar and the southern tip of Sulawesi (Auliya et al., 2002). There is considerable genetic divergence (94-96% similarity) between populations in the western portion of the range along mainland Southeast Asia and the Sunda shelf, and the eastern portion in the Philippines and Halmahera (Murray-Dickson et al., 2017), perhaps warranting these as being considered separate taxonomic units, but this has not yet been adopted. Several populations are postulated to have originated from past commensal or intentional human introductions, which complicates the biogeographical history (Murray-Dickson et al., 2017).

The species appears to be an excellent colonizer, known to traverse between islands, and was one of the first species recorded on Krakatau after the island emerged (Rawlinson et al., 1992). Owing to the species popularity in the pet trade, individuals have been found in Florida and Puerto Rico, and may have the potential to become invasive. Burmese pythons have already become invasive in Florida, while boa constrictors (*Boa constrictor*) have established in Puerto Rico (Reed & Rodda, 2009; Reynolds et al., 2013). While reticulated pythons occur in sympatry with Burmese pythons in their native ranges, it is not currently known whether they may be able to establish in Florida given the successful proliferation within the Everglades of Burmese pythons, which are better adapted to colder climes (Barker, 2008). Reticulated pythons may have been present in Puerto Rico for at least 10 years (John C. Murray, pers. comm.), and their establishment there or elsewhere could have severe implications for native fauna (Dorcas et al., 2012; Reed et al., 2012).

### 1.5.5 Habitat

Reticulated pythons appear to be remarkably adaptable, existing at relatively high densities within oil palm plantations and other forms of agriculture. They are regularly observed within urban areas, with large populations even in dense metropolitan areas such as Singapore (Low, 2018) and Bangkok (Reed & Rodda, 2009). Natusch et al. (2016a) suggested that reticulated pythons may have even undergone a population expansion due to human modifications, by increasing their densities in oil palm plantations. Within their more natural habitat, little is known of their specific habitat preferences, but they appear to inhabit most tropical habitat types, from dry open forests, grasslands and rocky scrub to dense lowland forests, swamps and marshes. They may, however, be particularly associated with riparian areas or found close to water (Auliya, 2006; Reed & Rodda, 2009; and references therein). They are excellent swimmers, as well as being found both terrestrially and arboreally. Juveniles may be more arboreal, while larger adults more terrestrial in nature (O'Shea et al., 2004).

### 1.5.6 Pythons as predators

Reticulated pythons exhibit a wide dietary breadth, feeding on a range of mammals and birds, but also occasionally reptiles, and possibly amphibians and fish (Murphy & Henderson, 1997; Shine et al., 1998c; Auliya, 2006; Reed & Rodda, 2009; Low et al., 2016), although mammals seem to be preferred. It is the only species of snake with regular, reliable evidence documented of them consuming adult humans (e.g., BBC News, 2017; 2018; Natusch et al., 2021), although attempts at predation have been noted in some other species (e.g., *Eunectes murinus*: Rivas, 1998; *Simalia amethystina*: Natusch et al., 2021). An anthropological study of hunter gatherers in the Philippines reported that around 26% of the men in one community had been attacked or killed by a reticulated python (Headland & Greene, 2011). Reticulated pythons have been reported feeding on a number of species of conservation concern, including civets (Viverridae), pangolins (*Manis* spp.), pigs (Suidae), slow lorises (Lorisidae), tarsiers (Tarsiidae), monkeys (Colobinae & *Macaca* spp.) bears (*Helarctos malayanos*), cuscus (Phalangeridae), porcupines (Hystricidae), deer (Cervidae) and bats (Chiroptera), as well as many birds (e.g., Columbiformes & Galliformes) (Shine et al., 1998c; Wiens & Zitzmann, 1999; Auliya et al., 2002; Gursky, 2002; Fredriksson, 2005; Reed & Rodda, 2009; Sukumal & Savini, 2009; Natusch et al., 2019). During the course of this study, reticulated pythons were observed having eaten radio-collared slow lorises (*Nycticebus menagensis*) on two separate occasions, as well as a 4.6m python that regurgitated a full-grown male pig-tailed macaque (*Macaca nemestrina*) upon its discovery (pers. obs). A GPS-collared leopard cat was also hypothesized to have been consumed as carrion by a reticulated python (Wilson et al., in press). They are also presumed potential predators of other endangered species, despite no published observations, such as gibbons (Hylobatidae), orang-utans (*Pongo* spp.), proboscis monkey (*Nasalis larvatus*), and felines such as the clouded leopard (*Neofelis diardi*) (Matsuda et al., 2008; Cheyne et al., 2012; Sunderland-Groves et al., 2021).

It is probably not unreasonable to assume reticulated pythons are theoretically able to feed on virtually all the terrestrial vertebrate species that occur within their range occasionally, or at least their young, except Asian elephants. A large proportion of the prey base, however, likely comes from rodents and other similar-sized small mammals. Natusch et al. (2019) and Shine et al. (1998b) carried out an analysis of stomach contents of over 7000 and 1000 pythons, respectively, in slaughterhouses, and rodents were by far the most common prey, but this shifts ontogenetically, so that pythons over 4m in length move away from rats to larger prey species. However, as the majority of the pythons studied were likely caught in human-modified landscapes such as oil palm plantations, the breadth of diet at a young age may be wider within more natural areas. Within human-modified landscapes, livestock and pets, such as chickens, ducks, cats, dogs, goats, and young cows are also regular or occasional prey (Auliya, 2006; Reed & Rodda 2009, and references therein; Shine et al., 1998c, Natusch et al., 2019), exacerbating the potential for human-wildlife conflict.

### 1.5.7 Predators of pythons

Adult reticulated pythons are among the top predators in their ecosystem, but may still occasionally fall prey to other species. Crocodiles are the most likely to be able to kill and eat large adult pythons, but tigers and leopards are also capable within the parts of their range where they overlap. An estuarine crocodile (*Crocodylus porosus*) was photographed feeding on a large reticulated python in the Lower Kinabatangan Wildlife Sanctuary in 2015 (see figure 1.7). King cobras (*Ophiophagus hannah*) have been documented consuming reticulated pythons, and with their maximum size of over 5m can easily predate on smaller adult pythons (Bhaisare et al., 2010). Young pythons hatch at a large size relative to other snakes, and grow very rapidly, which may somewhat limit their vulnerability to predation (Natusch et al., 2016a), but will still likely fall victim to many species that prey on snakes. Pigs, cobras (and other ophiophagous snakes), monitor lizards (*Varanus* spp.), birds of prey, herons, tarsiers, predatory fish, a wide range of mammalian carnivores, and larger species of rodent such as bandicoot rats (*Bandicota* spp.) are all documented eating snakes, and are therefore likely to also feed on hatchling pythons (Niemitz, 1973; Lyle & Timms, 1987; McConnell & McKilligan, 1999; Vorris & Murphy, 2002; Bhaisare et al., 2010; Jolley et al., 2010; Colon & Sugau, 2012; Phillips & Phillips, 2014; Guerrero-Sanchez, 2019). Humans, however, are the most well-documented predator of reticulated pythons, and many people consume them either as a delicacy, supplementary source of protein, or as a remedy in eastern medicinal practices (Groombridge &

Luxmoore, 1991; Shine et al., 1999b; Auliya, 2006; Headland & Greene, 2011; Aust et al., 2016; Natusch et al., 2019), in addition to their economic importance for their skins (see below).

***Figure 1.7*** *Estuarine crocodile,* Crocodylus porosus, *feeding on a large reticulated python in the LKWS, 2015. Photo by Danica Stark.*

### 1.5.8 Ecological importance

As both predators and prey, this leaves reticulated pythons in a complicated web of trophic dynamics interacting with a large proportion of vertebrate species in their ecosystem across most of Southeast Asia. They likely should be considered a keystone species (Murphy & Henderson, 1997), even though the term is often quite loosely defined (Cottee-Jones & Whittaker, 2012). If, as Natusch et al. (2016a) suggested, the species has increased in numbers in response to human habitat alterations, then this may have far-reaching consequences on relative abundances, or even extinction probabilities, of many other species, especially near the interfaces between natural and agrarian habitats, and in isolated fragmented forests. Wahab et al. (2020) reported numbers of pythons caught by snake hunters for the skin trade in Sulawesi, with one individual claiming to capture around 200 pythons per month in a small number of regular trapping locations, suggesting extremely high abundances in some locations.

### 1.5.9 Trade

Reticulated pythons are the most heavily-traded species of snake in the world (Kasterine et al., 2012; Natusch et al., 2019). This comes mostly from the value of their skins, to produce leather products. They are listed under CITES appendix II, allowing a quota to be harvested from the wild and exported each year, predominantly from Indonesia and Malaysia, amounting to >300,000 skins per annum from a global total of around 450,000 (Natusch et al., 2019). They are also bred in captivity for this purpose, particularly in Lao PDR and Viet Nam (Kasterine et al., 2012). Because pythons are often killed when encountered by people, as they are seen as a pest or a danger to children (Natusch et al., 2019), or as food (Kasterine et al., 2012; Headland & Greene, 2011; Natusch et al., 2016b), as well as a small but significant illegal trade in skins, the actual number killed by humans per year is substantially higher than CITES quotas. This raises questions of long-term sustainability of offtake, and has contributed to a number of studies attempting to address these concerns (Natusch et al., 2016b). The trade poses ethical and sustainability concerns for many, including calls for bans, and has led to a ban on imports from Peninsular Malaysia to the European Union. The benefits of trade to local livelihoods are not to be ignored, as it can represent important supplemental income for poor households (Nossal et al., 2016a,b). Rather than reducing the numbers of pythons caught, the ban led to a shift towards the less valuable Asian market, resulting in some hunters catching more pythons to maintain their income. This ban may have also resulted in increased illegal trade, reducing the ability to monitor and regulate offtake effectively (Natusch et al., 2016b).

Obtaining accurate population estimates for reticulated pythons is extremely difficult, more so than for many other snakes (Auliya 2006; Natusch et al., 2015; Natusch et al., 2019; Khadiejah et al., 2021). Encountering them in numbers over short survey periods is unfeasible, but this mostly reflects their low detectability rates, rather than their actual rarity. Natusch et al. (2016a;b) carried out an assessment of python slaughter facilities, and compared the results with those from 20 years earlier at the same two sites in Indonesia (Shine et al., 1998a;b;c; 1999b). During that 20-year period, over one million pythons had been removed in those two provinces alone. There was no evidence of a change in capture rates, sizes, nor of a shift towards smaller sizes of maturity, as might be expected if there were undue selective pressure. It appears as though this level of offtake represents only a small fraction of the pythons that inhabit those areas, and coupled with high breeding rates and fast growth rates, is unlikely to cause any severe decline in population levels. Indeed, the ineffectiveness of concerted efforts and novel methods to control and prevent the spread of Burmese pythons in Florida (e.g., Reed et al., 2011; Avery et al., 2014; Hunter et al., 2015;

Mazotti et al., 2016; Smith et al., 2016; Vaca-Castano et al., 2019) is a reflection of this, as the two species share many similar lifestyle traits. One study estimated that for every Burmese python encountered and removed from the Everglades, up to 10,000 go undetected (Nafus et al., 2020). Taken together, these results highlight that the potential ecological impact and predation pressure exerted by reticulated pythons on their environment is considerably higher than many biologists might assume.

### 1.5.10 Field studies

There are very few published studies addressing reticulated python ecology outside of the inferences that can be made from pythons collected in tanneries and slaughterhouses. As mentioned above, finding sufficient numbers of pythons within a limited survey period is generally not feasible (figure 1.8). One published field study was carried out over six months using live baited traps in Kalimantan (Indonesian Borneo) in 1996 (Auliya, 2006), generating a sample size of 19 individuals. A concurrent study in Sumatra used snare traps and caught 11 individuals within a similar time period (Abel, 1998). PERHILITAN (Department of Wildlife and National Parks, Peninsular Malaysia) carried out an initial assessment of population densities in several states by mark-recapture over four years between 2010 and 2013, using live-baited traps and nets. From a total 7,679 trap-days, they caught 44 individuals, and one recapture, while from ad hoc visual encounter surveys they encountered 20 individuals. Population estimates from this were unreliable, but they noted a higher capture rate in oil palm plantations than secondary forest (Khadiejah et al., 2021).

*Figure 1.8 Needles in haystacks: a reticulated python resting during the day with part of its body visible. Pythons spend a large portion of their time hidden among dense vegetation and detritus, and generally rely on their camouflage to avoid detection rather than attempting escape, even when an observer is standing over them. Visual encounter surveys lead to estimates of python density far below their true numbers. Photo by R. Burger.*

While at least two telemetric studies have been carried out (Low, 2018; D. Natusch, pers. comms), one on translocated conflict pythons in Singapore, and one in oil palm plantations in Peninsular Malaysia, neither of the results have been published to-date. Two unpublished Masters research projects were carried out examining the morphometry and microclimate of capture locations on 117 and 38 pythons caught by snake hunters in oil palm plantations in Kalimantan, finding some associations with particular plants species and humidity levels (Wardhani, 2012; Silalahi, 2014).

There has been some interest in parasite dynamics, as reticulated pythons are the definitive hosts of several species of the protozoan *Sarcocystis*, with rats as the intermediate hosts. Heavy infection with *Sarcocystis* in rats can be fatal, increasing the potential for reticulated pythons as agricultural biocontrol agents beyond simple predation (Jäkel et al., 1996; Paperna et al., 2004; Devan-Song et al., 2017; Wasserman et al., 2017). The species is also known to carry other parasites, including pentastomids, nematodes, cestodes, and protozoans, which may incur human health risks, particularly where they are regularly consumed. They also regularly carry ticks, and ticks collected from reticulated pythons in the LKWS have been found to test positive for Rickettsia (C. Jalius, unpublished data).

### 1.5.11 Why study reticulated pythons?

There is clearly a need for additional ecological research on the species. For robust trade monitoring purposes, it is probably not reasonable to assume that results from one location are applicable to the entire population, given the wide distribution and variety of habitats the species is found in. The current CITES guidelines on conducting non-detriment findings for snakes (published by the IUCN SSC boa & python specialist group, now the snake specialist group) cite reticulated pythons specifically, noting that for population field studies on this species: "The logistical difficulties involved…are insurmountable, meaning field studies for this species are not cost-effective or worthwhile" (Natusch et al., 2015). While accurate measurements of population density are probably unachievable in even a single field location, other information from field studies can be extremely useful for understanding the species ecology. This may include demographics, detectability rates, diet, home ranges, activity levels, and habitat preferences. These types of data are highly informative for improving monitoring efforts and mathematical modelling, and can complement inferences made from data collected in tanneries and processing facilities. More generally, this would improve our understanding of both natural and man-made ecosystem processes, and allow inferences for other, more endangered large constrictors (e.g., *Malayopython timorensis; Python bivittatus; Liasis savuensis*). The ecological processes underlying the relationships between reticulated pythons and their environment, both within natural systems and artificial environments such as oil palm plantations, are undoubtedly complex, and would require extensive study to fully understand. While the species itself is not threatened, and is unlikely to go extinct even if concerted effort were made to attempt to eradicate it across its range, the importance of reticulated pythons in the context of a holistic, systems approach to conservation should not continue to be undervalued.

## 1.6 Thesis Overview and Aims

Overall, this thesis aimed to: i) assess field surveying as a viable option for population monitoring, and describe population demographics and assess covariates affecting capture rates,
ii) investigate the spatial ecology and habitat selection of reticulated pythons within a degraded and altered landscape; the Lower Kinabatangan Wildlife Sanctuary, including trialling GPS telemetry as an alternate means of collecting spatial data, and iii) compare results for individuals inhabiting oil palm plantations and those inhabiting forested areas.

The remainder of the thesis is divided into five chapters:

**Chapter 2** focusses on the development of a field survey protocol for reticulated pythons in riparian tropical forest. It has two main aims: i) to estimate detectability and seasonal and demographic trends in capture rates, and ii) to analyse data on morphological traits and demographics of the study population. The results present the most comprehensive field survey data on reticulated pythons to-date.

**Chapter 3** provides a review and guidelines for prospective snake biologists concerning the use of GPS transmitters for telemetric studies of snakes, with a case study of the methodology employed in this study to develop the technology for use on reticulated pythons.

**Chapter 4** aims to resolve python home ranges in the LKWS, and details the results of a telemetry study using VHF radio transmitters to characterize movement in response to climatic variables and space use of reticulated pythons and compare this between forested areas and oil palm plantations, under the hypothesis that pythons in plantations occupy smaller home ranges. It also provides a case study comparing the use of GPS and VHF data on space-use estimates.

**Chapter 5** uses telemetry and survey data to characterize habitat preferences of reticulated pythons at microhabitat, movement, and landscape scales, and estimate habitat suitability of the study area using airborne LiDAR data.

Finally, **Chapter 6** provides a synthesis summary and conclusion of the results presented within this thesis.

# 2 Detecting the Undetectable: Using Visual Encounter Surveys to Assess Population Demographics and Detectability of *Malayopython reticulatus* in an oil-palm-dominated landscape.

## 2.1 Introduction

The negative impacts of oil palm (*Elaeis guineensis*) plantations on wildlife in Southeast Asia are well-documented (e.g., Fitzherbert et al., 2008; Foster et al., 2011; Koh & Wilcove, 2008; Vijay et al., 2016), and the demand for palm oil is one of the primary drivers of deforestation and fragmentation in Borneo (Gaveau et al., 2016). Despite this, there are some generalist species that are able to adapt to inhabit or even thrive in these monocultures (e.g., Ancrenaz et al., 2014; Jennings et al., 2015; Rajaratnam et al., 2007; Shine et al., 1999a) (see chapter 1). In fragmented habitats, changes in population or behaviour of generalist species may have adverse consequences as the result of increased competition for resources with inflexible, specialist, or endangered species that remain isolated within fragments (Sverdrup-Thygeson et al., 2017). As one of these adaptable generalists, the reticulated python (*Malayopython reticulatus*) may play an important role in these dynamics (Natusch et al., 2016a;b).

Reticulated pythons primarily inhabit forests throughout their range, usually in areas associated with water, but are also regularly found in plantations, villages and even cities (Low et al., 2016; Natusch et al., 2016b). This adaptability may be due in part to a generalist diet consisting predominantly of a wide range of mammals, birds and occasionally reptiles (Shine et al., 1999b), as well as a rapid growth to maturity and high fecundity (Natusch et al., 2016a). As a predator interacting with a large range of terrestrial vertebrates, it may play a keystone role within the ecosystem, and further research is needed to understand some of the fundamental aspects of its biology and ecology in the wild (Stuart et al., 2018).

Progress in filling these gaps is limited because carrying out systematic surveys of most species of snakes is difficult due to their cryptic nature and low detectability; often being well-camouflaged, shy, with low levels of activity and preferring relatively inaccessible habitats (Durso et al., 2011; Natusch et al., 2015). In temperate regions, regular basking and hibernating in colonies can be exploited for studying some snake species, but these behaviours are rare in the tropics (Shine et al., 1999b; Natusch et al., 2021). Detectability of large-bodied constrictors, such as pythons, have been estimated in one controlled enclosure experiment on Burmese pythons (*Python bivittatus*), where only 2 detections from a possible 190 occurred (Dorcas & Wilson, 2013). Another study estimated

Burmese python detectability probability at between 0.0001 and 0.0146 using a combination of transect surveys and known locations of telemetered pythons in the vicinity of transects (Nafus et al., 2020). Reticulated pythons likely exhibit similarly low detection rates, and visual encounter surveys (VES) are typically not recommended as a feasible means to carry out population studies for this species (Natusch et al., 2015; 2016a;b; 2019). Alternatively, for many snakes, passive capture through the use of drift fences and traps, for example, can overcome any observer biases caused by VES, and this may be particularly effective for hard-to-detect species (but introduce other biases such as trap happy and/or trap shy individuals)(Dorcas & Willson, 2009). Passive live-baited traps and nets have been used in field studies of reticulated pythons, but the catch per unit effort was still extremely low (Auliya 2006; Khadiejah et al., 2021).

The multiple barriers that affect capture rates illustrate the difficulties of attaining a large enough dataset to be able to make population-level inferences of biology or ecology for reticulated pythons, and also implies that population densities are likely to be much higher than might be apparent from visual surveys. Gaps left by imperfect survey methods and low sample sizes have been filled by collecting data on animals brought to slaughter houses to get a better understanding of basic morphological characteristics (Shine et al., 1998a;b 1999b; Auliya, 2006; Natusch et al., 2016a;b; 2019; Khadiejah et al., 2021). Further, this allows for direct monitoring of trade dynamics. This approach does, however, suffer from potential biases associated with how the animals were collected. Juveniles are underrepresented in these samples as small individuals are not commercially viable in the leather trade, large individuals may be more likely to be heavily scarred and therefore not sold to tanneries, and gravid females may sometimes be left by hunters to ensure population sustainability (Nossal et al., 2016b; Natusch et al., 2019; Khadiejah et al., 2021). As many pythons caught by hunters may be sourced indirectly from local people inadvertently encountering them, and middlemen may be used for selling to tanneries, which makes it difficult to obtain accurate information on where the animal was captured (Natusch et al., 2016a; 2019; Khadiejah et al., 2021). However, it is believed that the vast majority of reticulated pythons caught for trade purposes originate in or near oil palm plantations and other human-modified landscapes. Elucidating any population differences between pythons inhabiting oil palm plantations and natural forests is therefore not only interesting ecologically with regard to the ways that they adapt to these landscapes, but it is also beneficial when it comes to the debate surrounding best monitoring practices to assess sustainability of harvesting and trade.

Trade of reticulated pythons from Sabah was historically carried out with a quota of 12,000 individuals per year, which was reduced to the current level of 3,000 in 2013 (Kasterine et al., 2012). However, currently Malaysian trade in the species effectively operates solely from Peninsular Malaysia (Natusch et al., 2016b). The European Union (EU) had previously been the largest importer of reticulated python skins from Malaysia, but banned the export of skins from Peninsular Malaysia to the EU in 2004 (Kasterine et al., 2012; Natusch et al., 2016b; Khadiejah et al., 2021). Following additional research data concluding trade levels to be sustainable (Natusch et al., 2016a;b), this ban was uplifted in 2016, but then reinstated again in 2019. This decision was upheld in 2021, citing that the current trade is "unsustainable by all assessments" (European Union, 2021) despite all previous assessments and scientific evidence declaring the trade as sustainable (Shine et al., 1999b; Natusch et al., 2016a; b; 2019; Khadiejah et al., 2021). Further recommendation was given to assess non-detriment findings (NDF – whereby scientific assessments should show that export levels will not be detrimental to the survival or maintenance of the ecological role of a species) through the use of population surveys of reticulated pythons throughout their geographical range, despite common sense and a large body of evidence suggesting this is not cost-effective or scientifically feasible. PERHILITAN performed a thorough study over four years to attempt a population estimate, but low capture/recapture rates made mark-recapture estimates unachievable despite considerable effort (Khadiejah et al., 2021).

Any further studies utilising systematic surveys of reticulated pythons in their natural habitat can provide additional evidence towards the feasibility (or lack thereof) of such a monitoring approach for assessing NDFs in the reticulated python trade, and for similar species (European Union, 2021; Nijman, 2022). A better understanding of encounter rates under different environmental conditions may allow for systematic surveys to improve capture/encounter rates by timing surveys to coincide with peak activity levels and improve sample sizes (Brown et al., 2002; Brown & Shine, 2002). The Lower Kinabatangan Wildlife Sanctuary (LKWS) is an appropriate potential area to carry out a study of such nature; reticulated pythons are often considered to be heavily associated with water and riparian habitats, and the heavy level of conversion of the nearby region to oil palm plantations may have bolstered the population size, so this may facilitate obtaining a sample size large enough to provide sufficient data. The mix of forest fragments and plantations within the LKWS further facilitates answering questions related to ecological differences that may occur in these two contrasting habitats. The lack of commercial exploitation for the skin trade in Sabah allows for a baseline assessment of population demographics and abundance without any of the changes that trade might cause. Population demographics and morphological data, while they may differ between regions (Natusch et al., 2019), can provide valuable insight into whether those analysed in slaughterhouses in Peninsular Malaysia and Indonesia are a reasonable representative sample of the wild population. Measures of detectability, while they will differ between locales and habitat types, can help to indicate the extent to which the true population size can be underestimated through encounter rates (Durso et al., 2011).

The study here aimed to: i) estimate the size distribution/morphology and growth rates of reticulated pythons; ii) quantify inter-annual and seasonal variation in capture rates, size distributions, and body condition; iii) quantify detectability and occupancy for pythons within the study site, and iv) examine how environmental variables affect python detectability. This was intended for two main purposes: i) to explore whether there are differences exhibited by reticulated pythons in oil palm plantations in comparison to forested areas, and ii) to evaluate whether visual encounter surveys can be an effective means for monitoring reticulated python populations, as an alternative or supplement to the current trade sustainability monitoring efforts in slaughterhouses that are already in place.

## 2.2 Methods

### 2.2.1 Study area

The study was conducted within the Lower Kinabatangan Wildlife Sanctuary (LKWS) and surrounding plantations and villages, in Eastern Sabah, Malaysian Borneo. The study focused on lots five, six and seven of the LKWS, and Pin-Supu forest reserve and surrounding plantations, encompassing a 64km stretch of the river (Figure 2.1). For further details of the study area, see chapter 1.

### 2.2.2 Surveying

The study area is most easily accessible via boat, and preliminary surveys identified pythons lying along the riverbanks at night, when they are most active (Reed & Rodda, 2009). Other studies (e.g., Auliya, 2006) have identified reticulated pythons as heavily associated with water bodies, and in many areas, road transects (e.g., Madsen & Shine, 2006; Wilson & Heinsohn, 2007; Hart et al., 2015;) and river transects (e.g., Plummer, 1997; Lind et al., 2005) have proven to be effective methods for surveying and sampling for snakes. The 64km stretch of river encompassing the study area was divided into 13 roughly equal sections, 4-6km in length, usually demarcated by obvious land features, such as tributaries, to aid navigation. Each river bank within each section was considered to be a separate transect, thus giving 26 transects totalling 128km in length. One section (therefore two transects – the north and south banks) was surveyed each night, between 19:00 and 22:00. If pythons were captured, then they were returned to their capture location the following night. Therefore, a fully randomised survey design was not used for logistical reasons (including fuel economy). River surveys were conducted by boat by a team of at least three people. Surveys were conducted at a low speed (4-6 km/h) and at close proximity to the riverbank (2-10 m, depending on water depth), while shining strong head torches (e.g., Ledlenser H14R.2 – 1000 lumens) and spotlights towards the bank looking for pythons among the undergrowth, detectable by their contrast against the mud, scale iridescence, and eye shine at close proximity. Surveys were not carried out in inclement weather, and only when the river level was low enough to expose the mud banks of the river. During long periods of drought, surveys were also not carried out if vegetation on the river banks became overgrown to the point that individuals could no longer be easily spotted. The formal surveys were augmented by opportunistic capturing of any pythons that were spotted in the study area, to gain a larger representative sample size of the population. This included whilst travelling between survey sites along the riverbank, and while walking along trails in forested areas. Within plantations, pythons were searched for on foot, visually searching along drainage ditches or by overturning piles of palm fronds. This was not standardised by constraining time, search effort or spatial pattern, however. Towards the end of the study, searches in plantation were made by car along roads between planting blocks, surveying road verges and drainage ditches using a spotlight. This was again not fully standardised as it was only carried out for a short period of time, and factors such as fallen palms, flooded areas and broken bridges prevented systemising the routes taken. Several pythons were also sampled opportunistically after being rescued by Sabah Wildlife Rescue Unit, located in Sepilok Orang-utan Rehabilitation Centre, and some were also found by local residents in nearby oil palm plantations.

Due to logistical constraints, transects were not all surveyed an equal number of times. As transects were also unequal in length, captures of new individuals resulting from surveys were recorded as the encounter rate of pythons for every kilometer surveyed, in order to standardize comparison between transects. This would mean that, for instance, if a 5km transect was surveyed 10 times, and one python was encountered, this would give a value of 0.02 (1/50) pythons per km.

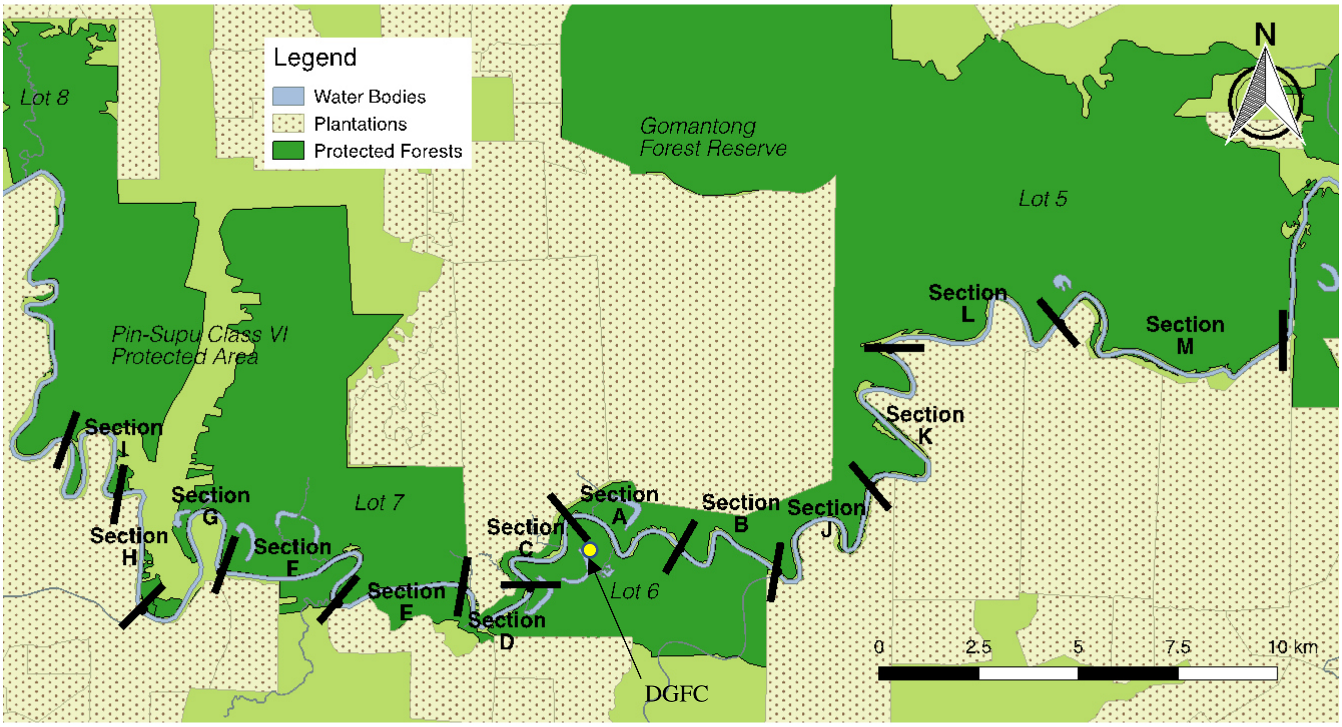


*Figure 2.1 Map showing survey sections along the Kinabatangan river. Each section comprises two transects, on the North bank, and South bank.*

### 2.2.3 Capture protocol

Upon locating a python, it was captured by holding it behind the head, securing it firmly, before the body was subsequently restrained with assistance from an additional member of the team. A third team member assisted with larger individuals, if necessary. The location of each python encountered (both captured and any that evaded capture) was recorded with a handheld GPS (Garmin GPSmap 64s). Pythons were placed into a cloth bag and transported back to the Danau Girang Field Centre (denoted in figure 2.1), and secured in a plastic container with breathing holes. Each animal was then sampled and measured (see below) the following day so that additional team members could assist with restraint if necessary, and released at the capture location within 24 hours following initial capture.

### 2.2.4 Sampling protocol

Pythons were weighed using electronic fishing scales (Wisefield, accurate to 5g) and sexed using lubricated ball-tipped sexing probes. Five dimensions were measured using Vernier callipers and a flexible plastic measuring tape: head length (HL) from snout tip to base of skull, head width (HW), snout-vent length (SVL), total length (TL) from snout to tail tip, and tail length (TaL) from vent to tail tip. Any apparent wounds or scars were noted. A passive integrated transponder (PIT) tag was inserted under the lateral skin at the mid-section for subsequent identification with radio frequency identification (RFID), should the animal be recaptured.

### 2.2.5 Environmental Variables

Daily temperature, humidity and rainfall were recorded from a weather station at Danau Girang Field Centre (DGFC). Temperature (to the nearest 0.5˚C) and relative humidity (to the nearest 0.5%) were recorded using an easylog datalogger (Lascar electronics), and recordings were always taken at 20:00, when surveys were carried out. Rainfall was measured to the nearest 0.5mm using a rain gauge, and given as the 24h total, measured at the end of a survey. Moon phase was also calculated using Moon Phase Calculator (Probadosoft) as percentage of the lunar surface illuminated at the study location at 20:00. Lux meters with a high enough sensitivity to calculate true luminosity during each survey were not available, and the moon may have been obscured by trees or clouds during surveying, so this was intended as a continuous variable to calculate the stage of the lunar cycle, rather than lunar brightness *per se*.

### 2.2.6 Data Analysis

Data analysis was carried out in R (version 3.5.0, R development core team 2020), while mapping was carried out with QGIS (version 3.4). For all models examined, continuous variables were checked using the package *olsrr* (Hebbali, 2020) for collinearity, and models were examined using the package *DHARMa* (Hartig, 2022) to perform residual diagnostics. Likelihood ratio tests for significance of fixed effects were performed by fitting equivalent models with and without the fixed effect of interest, using the package *lmtest* (Zeileis & Hothorn, 2002). Model predictions were calculated using the package *ggeffects* (Lüdecke, 2018) and data were plotted using *ggplot2* (Wickham, 2016). For mixed-effects models, marginal and conditional $R^2$ values were calculated with the package MuMIn (Bartoń, 2022).

*Morphology*

The use of ANOVA to assess differences in size between males and females was not possible due to non-normality of the data and residuals, so non-parametric Wilcoxon rank sum tests were used instead.

### *Growth rates*

Similar to the very small number of recaptures in the study by Auliya (2006), there was one individual measurement of SVL that actually decreased after recapture. Obtaining highly accurate length measurements of live pythons is difficult due to the animals wriggling or contracting their bodies (Murphy & Henderson, 1997). Linear regression was used to assess the degree of conformity between Head Length and SVL ($F_{1,114} = 3063$, $R^2 = 0.953$, p-value = <0.0001). Standardised residuals were normal, showed no heteroscedasticity, and a Durbin-Watson test showed no serial autocorrelation (D-W statistic = 2.11, p-value = 0.554). Overall, these results indicated that the ratio between Head length and SVL remains the same as pythons grow.

Head length measurements were therefore used for estimating growth rates, as these measurements were more reliable, even though relative changes are smaller. Growth rates were taken as the change in head length divided by the number of days between successive measurements of individuals. A quadratic linear regression was used to model growth rates with SVL as the explanatory term. As there were not enough recaptures of animals from plantations, it was not possible to compare growth rates between habitats.

### *Body condition index*

Body condition indices as a function of mass and length are used as correlative measures of energy stores and have important implications for health and fitness. For snakes, these indices are often derived from the residuals from a linear regression of log mass and log length, but this approach may not be the most appropriate method if fat stores change allometrically and it does not allow for comparison between populations, as regression parameters may differ (Weatherhead & Brown, 1996; Falk et al., 2017). Ratio measurements (e.g., body mass index, BMI, for humans) do allow comparisons between populations, but are generally poor measurements and suffer from biases (Falk et al., 2017). For snakes, but particularly large constrictors, energy reserves are more complicated because they have an unprecedented ability to regulate hypertrophy and atrophy of their organs to extreme levels in response to feeding and fasting (Secor, 2008). Therefore, the amount of fat on an animal does not represent the full picture in terms of energy storage.

The aim in this instance was to examine the overall difference in body condition between pythons in oil palm plantations and forest, and between sexes, rather than obtain individual values. Therefore, a general linear model (GLM) examining log mass as the dependent variable, with explanatory variables of habitat (either oil palm plantation or forest), sex, log SVL and both sex and habitat in interactions with log SVL, was used instead of the more typical residuals from a linear regression or ratio measurement of body condition. For most snakes, the relationship between body mass and length does not differ much between the sexes (Weatherhead & Brown, 1996), but the interaction term between sex and log SVL was included here because while females are larger, male reticulated pythons have been shown previously to have higher mass than females at similar body sizes, necessitating different slope parameters in the model (Shine et al., 1998a). Similarly, as there were proportionately fewer small individuals caught in the plantation, and fat body scores tend to increase with size (Shine et al., 1998a), the interaction term allowed comparison of pythons from plantations and forests, while controlling for this size effect.

### *Annual and seasonal trends of captures*

To assess capture rates across months, a General Additive Model (GAM) with log link and Poisson errors was used to assess captures frequency across months, using the package *mgcv* (Wood, 2017). Month was modelled as a cyclic cubic regression spline, while year and the number of surveys carried out in a particular month were also included as covariates. Model comparisons were performed using AIC where sex was used as either an interaction term (monthly splines were allowed to vary between sexes) or as a covariate to assess whether capture rates differed for males and females in different months. If there were noticeable seasonal differences for males and females (e.g., because of breeding activities), then this pattern would be important to consider in future monitoring efforts.

Examining differences in body sizes across time is a central tenet for monitoring trade sustainability (Natusch et al., 2016a). As the capture rates within any single month were generally low, and the number of surveys carried out differed between months, estimates of length by month were quite variable. Lengths were examined in GLMs with year as an explanatory variable and sex as a covariate due to sexual size dimorphism. Models with and without month as a covariate were examined for fit using AIC, and against a general linear mixed model (GLMM), carried out using the package *lme4* (Bates et al., 2015), with month included instead as a random effect, to explore if this better accounted for potential stochasticity by shrinking values towards the mean. The GLMM was selected as the better fit.

To compare whether body condition showed annual trends, a GLM was used with log mass as the dependent variable, with an interaction term for both sex and year with log SVL. As for the model exploring trends in SVL between years, models were examined with and without month, and as a GLMM with month as a random effect, using AIC as the model selection criterion. The linear model without month as a covariate was selected.

For all the models assessing trends, *post hoc* contrasts of marginal means (for categorical variables) or marginal trends (for where slopes were allowed to vary between categories) were carried out using the package *emmeans* (Lenth, 2022), using the Tukey adjustment for p-values.

### *Encounter probability*

A binomial GLMM was used to explore the effects of weather and moon phase on the probability of encountering pythons along riverbanks. A starting global model was used with a binomial outcome variable of at least one python being encountered along a surveyed transect, or no encounter. Explanatory fixed effects were total rainfall that day (mm), rainfall the previous day (mm), moon phase (as the percentage of illumination of the moon surface, relative to the study location), temperature (˚C) and relative humidity (%) at the field station at the start of the survey. The transect surveyed was included as a random effect to account for differences in encounter probabilities in different river sections. All possible fixed effect combinations were examined using the package *MuMIn* (Bartoń, 2022), and ranked by AICc (all candidate models within <2 AICc were considered equivalent).

### *Occupancy and detectability*

Occupancy modelling is an effective technique for monitoring species that are hard to detect, or where detectability is variable, and is therefore a particularly useful tool for studying snake populations as it incorporates an estimate of detectability (Dorcas & Willson, 2009; Durso et al., 2011). Similarly, N-mixture models can also incorporate estimates of detectability to produce abundance estimates from count data (Royle, 2004), but they have been shown to be often poor for use on snakes (Ward et al., 2017). In contrast to the mixed model method used above, occupancy models can use site-level covariates to estimate whether transects where no captures occurred are likely to be real absences or just a result of the difficulty of detection.

Occupancy modelling was carried out using the R package *unmarked* (Fiske & Chandler, 2011). Standardised riverbank surveys were examined for each transect (n=26), with counts of encounters. Observation-level covariates examined were moon phase, temperature, humidity, total rainfall that day, rainfall the previous day, and month and year as categorical variables. Site-level covariates examined were the transect length (in km), proportion of agricultural land within buffer zones of both 250 and 500m, calculated within QGIS, a categorical variable to indicate whether the transect was on the north or south side of the river, and a categorical variable to indicate whether the transect bordered a forest lot or a forest corridor. A global model with all covariates was used, and then all possible covariate combinations examined using the dredge function in the package *MuMIn* (Bartoń, 2022), and ranked by AIC corrected for sample size. All models within <2AICc of the top performing model, as well as the starting and null models, were reported. The top performing model was checked for goodness-of-fit using a bootstrapped Mackenzie-Bailey test, with 50 simulations, using the package *AICcmodavg* (Mazerolle, 2020).

## 2.3 Results

This study reports encounter rates when assessing presence along riverbanks during systematic surveys, which are controlled by the length of transect (pythons per km). Where additional morphological variables are required for analysis, the term *capture rates* is used instead to reflect the potential disparity due to not all encountered pythons being caught/sampled. The term *detection rates* is also used in reference to occupancy modelling, which reflects the chance of one or more encounter per transect, so are uncontrolled for distance.

### 2.3.1 Captures & Encounters

A total of 527 riverbank surveys were carried out, covering a survey distance of 2,427.3km. A total of 159 individual *M. reticulatus* were sampled and measured (75 females, 74 males, and 10 unassigned hatchlings). Of these, 83 were found during systematic surveys along riverbanks, while the remaining 76 were captured or sampled opportunistically, including one that had been freshly killed by a plantation worker. 25 individuals were recaptured on at least one occasion, either during surveys or opportunistically, across 40 total recapture events. One further marked individual was 'recaptured' after finding its carcass in the forest. There were 10 occasions where a python was visually located, and the animal escaped capture, giving a 95.2% capture success rate overall (of 209 total capture attempts). There were also four occasions where captured pythons were transported back to the field centre, and escaped their enclosures before measurements could be taken.

Seventy-nine python encounters (Including recapture events) occurred on the southern bank of the Kinabatangan River, while 18 were encountered on the northern bank. A chi-square test found this to be a significant difference in the number of encounters overall ($X^2 = 34.37$, $p = <0.001$), but when split by transects the difference was found not to be significant ($X^2 = 8.68$, $p = 0.666$), suggesting this may be largely due to the very high encounter rates along one single transect on the southern bank. Pythons were found on the southern bank along 12 out of 13 transects, while only within 6 out of 13 transects along the northern bank (figure 2.2), despite both banks being surveyed equally.

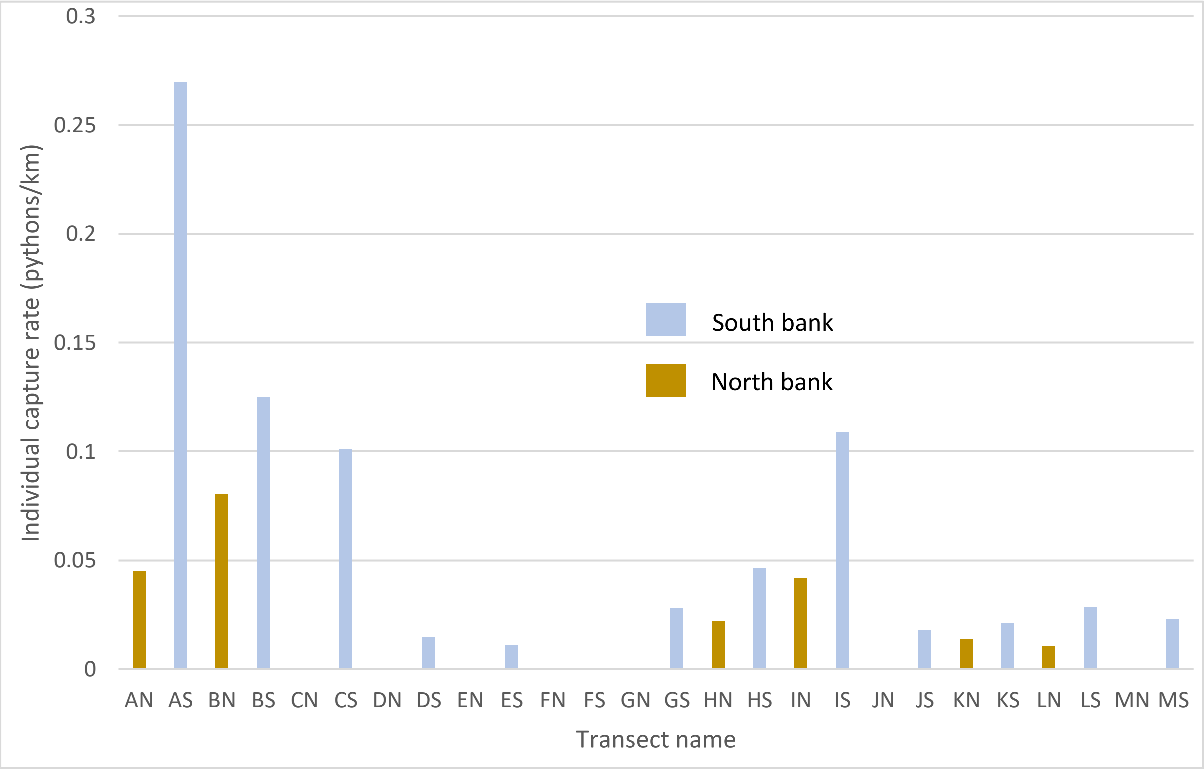


***Figure 2.2*** *Capture rate of individuals (i.e., excluding recaptures and uncaught encounters) - controlled for differing transect distance and number of surveys - for each transect. N = North Bank, S = South Bank, for each transect section (A-M). Transects in sections G-M were not surveyed during the first year of data collection.*

### 2.3.2 Morphology

A full set of morphological measurements was obtained from 146 individuals (74 females and 72 males). The highest number of measured individuals occurred in the size range 180-200cm (Figure 2.3). Mean SVL was 226.7 cm (± SD 85.4 cm), while mean mass was 5.74 kg (± SD 4.89 kg). The relationship between SVL and other measurements taken are depicted in figure 2.4 .

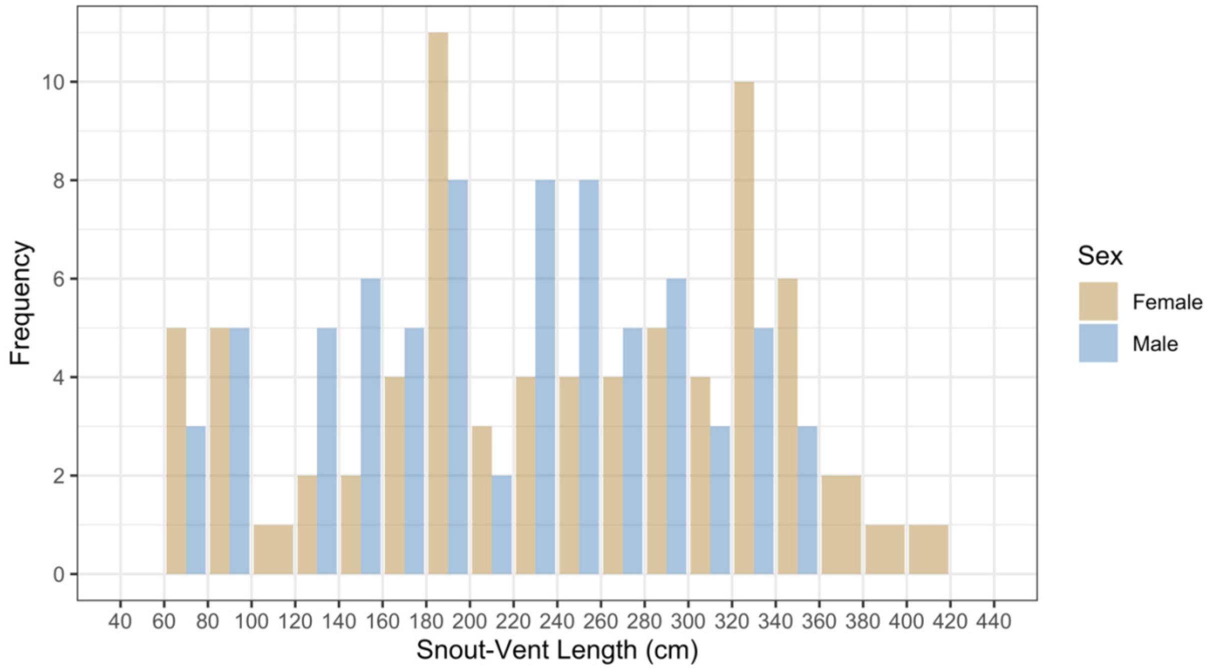


***Figure 2.3*** *Frequency distribution showing SVL measurements of all sampled individuals (excluding recaptures) during the study. The peak in frequency of pythons 180-200cm in length was also apparent in the dataset from Auliya (2006).*

Females were longer than males, with female SVL averaging 236.3cm (±SD 92.9) and males averaging 216.9cm (±SD 76.2). Female mass averaged 6.31kg (±SD 5.40) and males 5.14kg (±SD 4.26). Wilcoxon rank sum tests were not significant at the 5% level (SVL: W = 3043, p-value = 0.138. Mass: W = 2966.5, p = 0.303).

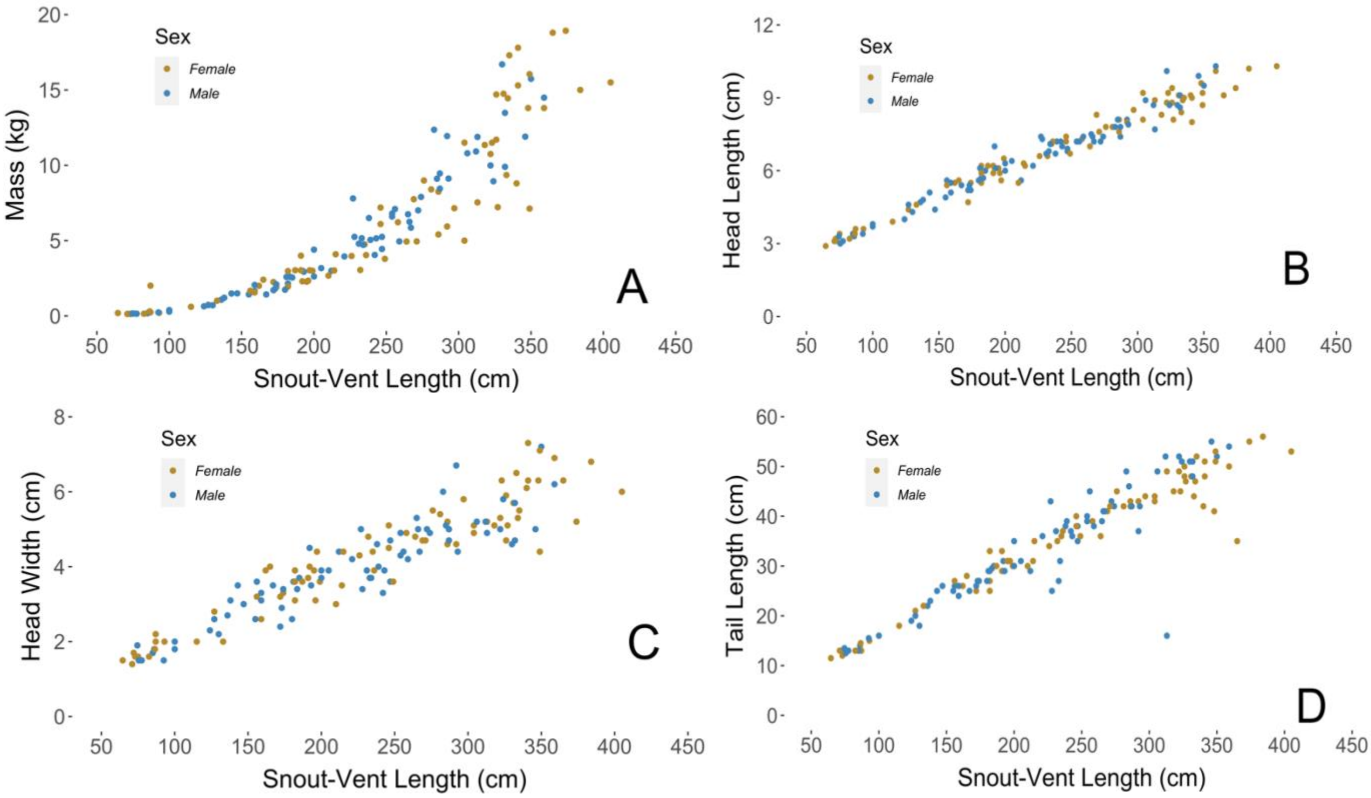


*Figure 2.4 Plots depicting the relationship between Snout-Vent Length (SVL) with other morphometric measurements. Mass increases exponentially with increasing SVL, at least at the sizes measured in this study. Head Length and Head Width increase linearly with length. Tail length also shows this trend, but it is common for tail ends to be lost through injury.*

### *Body condition*

The body condition model allowed for the interpretation of mass differences between males and females and between habitat types whilst controlling for the changing effect with length. Males tended to have a higher mass for a given length on average (i.e., body condition) than females (t = 2.550, p = 0.012), when controlled for by habitat type (Figure 2.5). Pythons caught in plantation appeared to have slightly higher mass at a given length (Figure 2.6), e.g., at 400cm SVL, males were predicted to have a mean mass of 23.2 ±0.07kg, while in plantation this was 25.2 ±0.09kg. However, the difference overall was not significant (t = 0.983 p = 0.327).

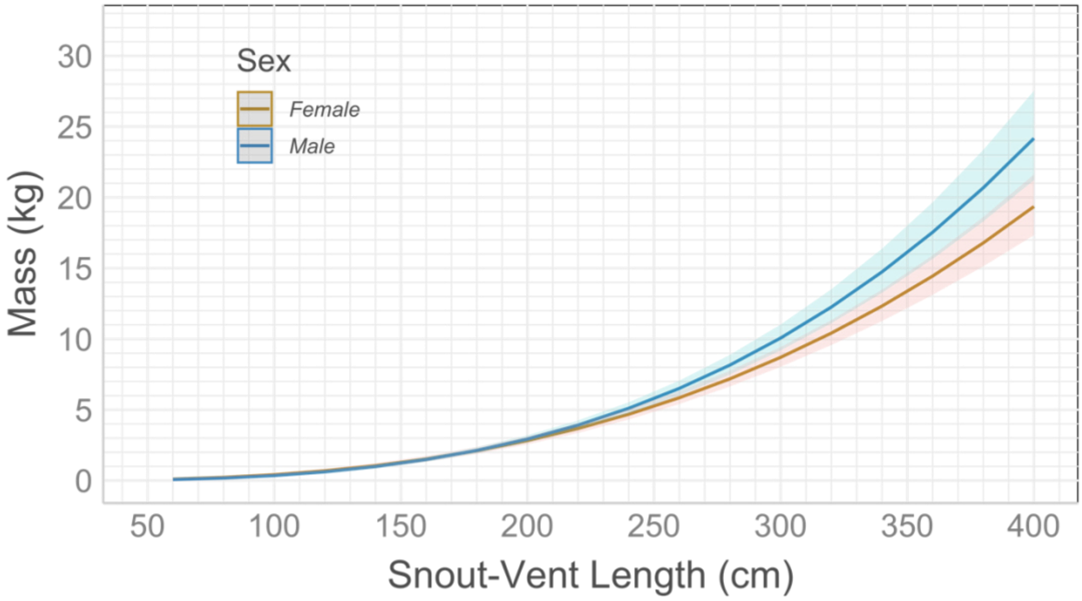


***Figure 2.5*** *GLM predictions of the relationship between mass and SVL for males and females, controlled for by habitat type.*

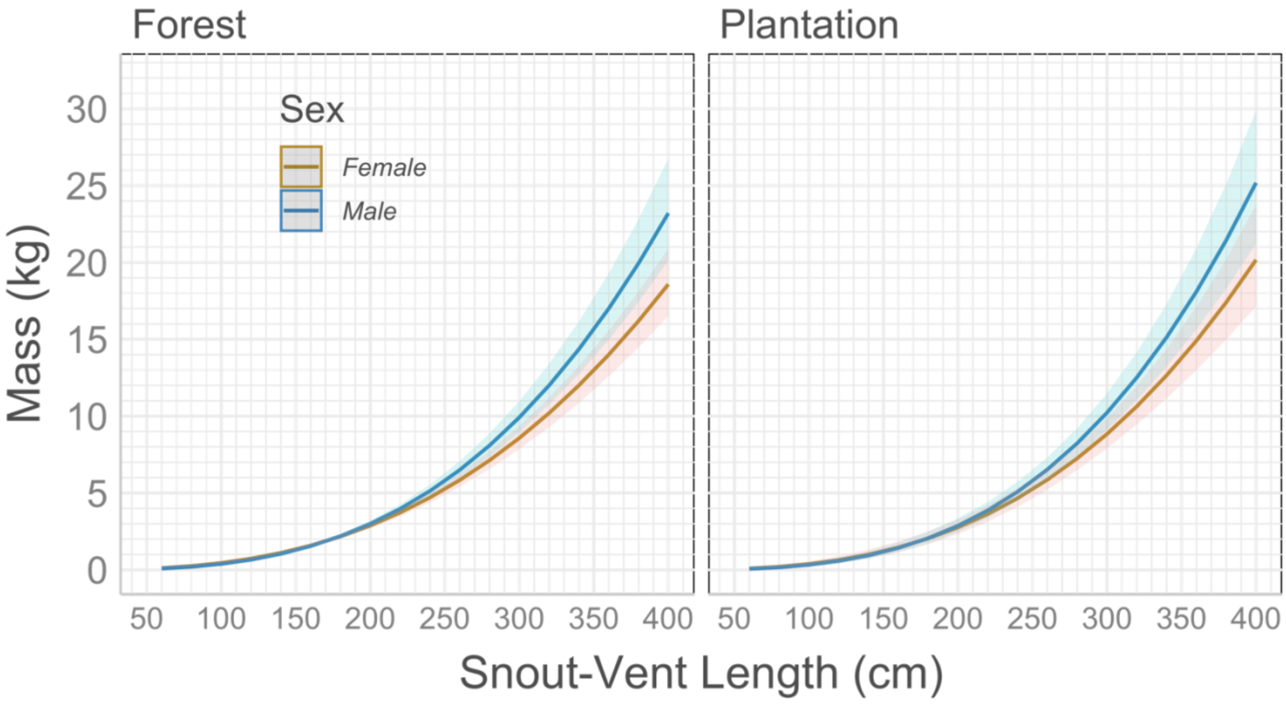


***Figure 2.6*** *Predictions of body condition compared between pythons caught in plantations versus pythons caught in forest, controlled for by length.*

*Growth rates*

For animals recaptured at least once, the growth rate was calculated as the change in head length divided by the number of days between successive measurements. A linear regression with quadratic term for SVL was significant ($F_{1,34}$ = 7.87, P = 0.008) (figure 2.7), but the model did not meet assumptions of normality of residuals, and the adjusted $R^2$ value of 0.164 indicates considerable unexplained variation. This appears to be due to lower than expected growth rates for pythons between 200 and 300cm SVL (figure 2.8).

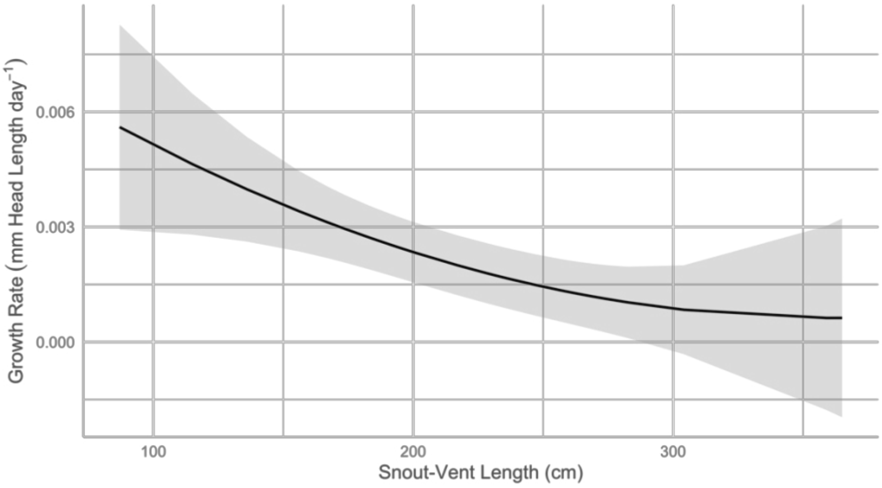


***Figure 2.7*** *Predicted values from a quadratic regression. The model residuals are a poor fit, so this is not indicative of a real trend from the observed data.*

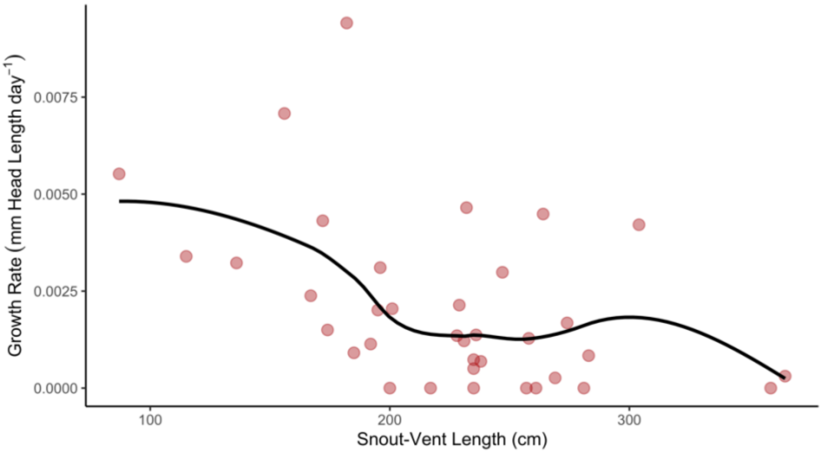


**Figure 2.8** Values of growth rate recorded for recaptured reticulated pythons. A Loess smoother shows the moving average trend in the data, where individuals between 200 and 300cm SVL were observed to have lower growth rates than might be expected.

### 2.3.3 Annual and Seasonal Trends in captures/encounters

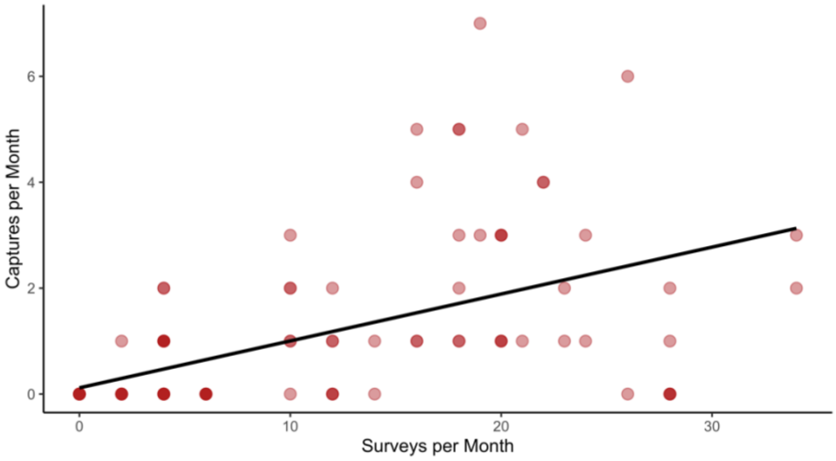


*Figure 2.9 The relationship between the number of surveys carried out per month and the number of pythons captured per month. Darker coloured dots represent overlapping points.*

Riverbank surveys were carried out across five years, from April 2016 to March 2021. As surveys were carried out only when weather and river level permitted easily spotting pythons, the number of surveys carried out in different months differed considerably, ranging between 0 and 34. A linear regression did not meet assumptions of normality of residuals, and Spearman's rank showed a significant monotonic relationship between the number of surveys and number of captures per month (S = 96960, rho = 0.663, p = <0.0001) (figure 2.9). This potential bias needed to be incorporated into the assessment of the number of pythons caught over time.

GAMs assessing trends in capture rates showed that the model without sex as an interaction term was a better fit (ΔAIC = 18.88) and model checks showed the model with interaction of sex had a k-value that was too low. These results suggest that there were not enough data to effectively model any differences between male and female capture rates over time if they were to exist as a result of seasonal differences in activity. *Post hoc* pairwise contrasts carried out with estimated marginal means indicated that sex was not significant (t = 0.095, p = 0.925), while capture rates by year (controlling for differences in monthly capture rates) were only significantly different between years 1 and 3 (table 2.1; figure 2.11). The model spline terms were highly non-linear (edf = 6.39), with a peak around September and October, and two smaller peaks around March/April, and July (figure 2.10). The model overall showed moderate fit, with 53.6% of deviance explained.

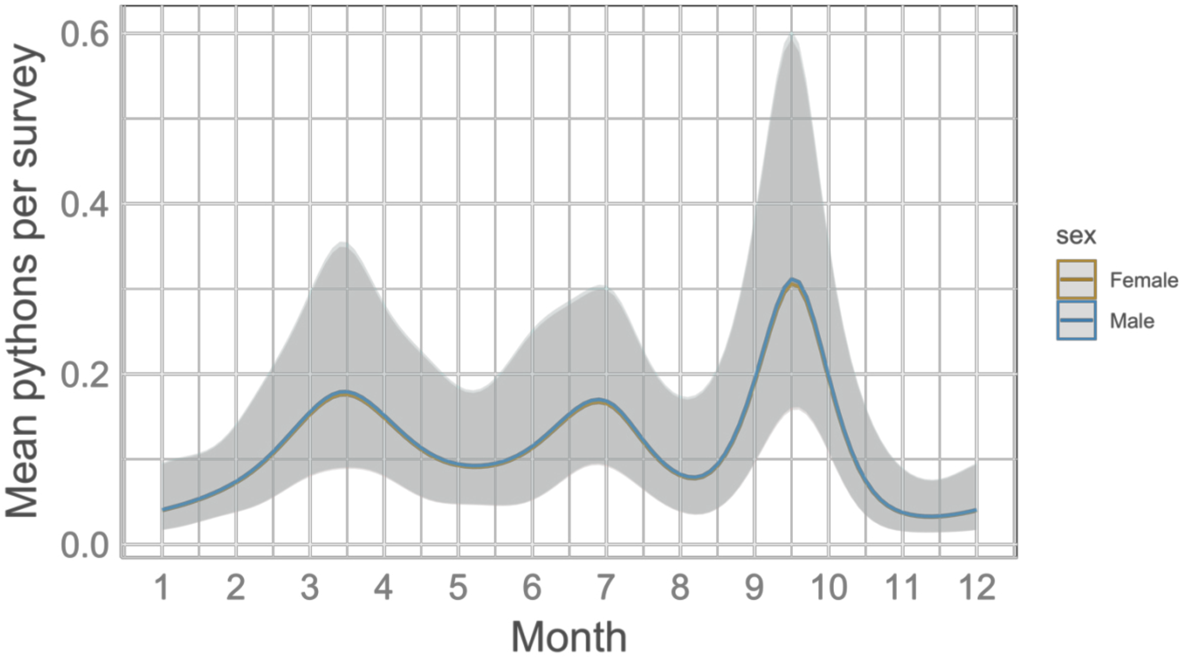


***Figure 2.10*** *The trend in capture rate across months for males and females, based on predictions from a General Additive Model. Capture rate is given as the number of pythons caught per survey, by controlling for number of surveys and setting the value for model predictions at 1. Male and female capture rates did not differ within the model and therefore overlap completely.*

***Table 2.1*** *Capture rate contrasts between years. Estimates of slope differences and associated statistics are shown, given that capture rate varies non-linearly with month, and the number of surveys carried out.*

| *Contrast of Years* | *Coefficient Estimate* | *SE* | *df* | *T ratio* | *P value* |
|---|---|---|---|---|---|
| *1 - 2* | 0.641 | 0.288 | 107 | 2.222 | 0.1795 |
| ***1 - 3*** | **1.198** | **0.330** | **107** | **3.632** | **0.0039** |
| *1 - 4* | 0.382 | 0.319 | 107 | 1.197 | 0.7533 |
| *1 - 5* | 0.848 | 0.438 | 107 | 1.937 | 0.3043 |
| *2 - 3* | 0.558 | 0.299 | 107 | 1.862 | 0.3440 |
| *2 - 4* | -0.259 | 0.302 | 107 | -0.857 | 0.9119 |
| *2 - 5* | 0.207 | 0.462 | 107 | 0.449 | 0.9915 |
| *3 - 4* | -0.817 | 0.337 | 107 | -2.424 | 0.1169 |
| *3 - 5* | -0.350 | 0.489 | 107 | -0.716 | 0.9523 |
| *4 - 5* | 0.466 | 0.463 | 107 | 1.008 | 0.8513 |

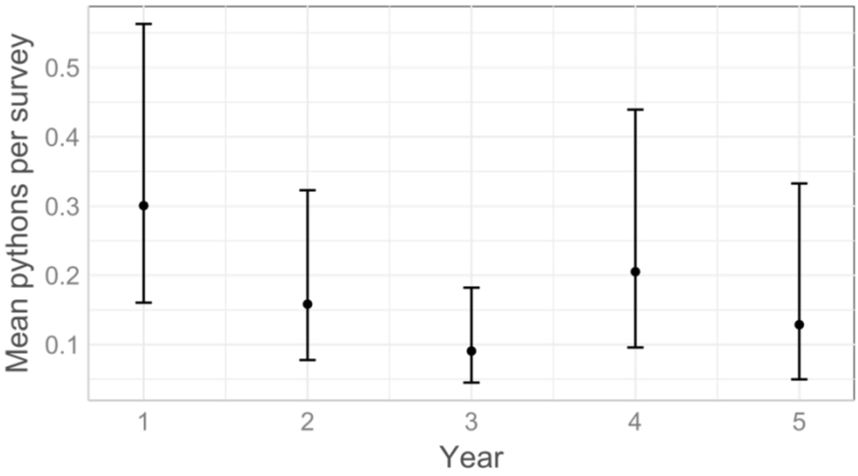


***Figure 2.11*** *Mean capture rate in each year from a GAM. Year 3 had a significantly lower capture rate than year 1. Capture rate is given as the number of pythons caught per survey, by controlling for number of surveys and setting the value for model predictions at 1. Here, the numbers are the sum of males and females, hence higher rates than in figure 2.10.*

The GLMM examining changes in sizes between years indicated that year was significant in a likelihood ratio test ($X^2$ = 54.50, p = <0.0001). *Post hoc* pairwise contrasts indicated that captures in years 3 and 4 had significantly lower mean values than those in year 1, and year 4 was also significantly lower than year 2, while sex as a covariate was also significant ($X^2$ = 8.95, p = 0.003) with females 18.5 ± 13.1cm larger than males on average (table 2.2 and figure 2.12). The difference in size of, for example, 57.5 ± 30.0cm between years 1 and 5 was not significant, suggests an overall poor statistical power for detecting trends without a very large effect size. Marginal $R^2$ of the model was 0.206, while conditional $R^2$ was 0.327.

***Table 2.2*** *Snout-Vent length contrasts between years. Estimates of differences in means of SVL and associated statistics are shown, from a GLMM that included sex as a covariate and month of capture as a random intercept. The values here are averaged across sex.*

| *Contrast of years* | *Estimated difference in SVL* | *SE* | *df* | *T ratio* | *P value* |
|---|---|---|---|---|---|
| *1 - 2* | 13.6 | 18.7 | 104 | 0.725 | 0.9504 |
| ***1 - 3*** | **66.7** | **20.1** | **107** | **3.316** | **0.0107** |
| ***1 - 4*** | **87.7** | **20.6** | **103** | **4.255** | **0.0004** |
| *1 - 5* | 57.5 | 30.0 | 106 | 1.916 | 0.3156 |
| *2 - 3* | 53.1 | 20.4 | 107 | 2.606 | 0.0764 |
| ***2 - 4*** | **74.1** | **20.8** | **105** | **3.573** | **0.0048** |
| *2 - 5* | 43.9 | 29.8 | 104 | 1.473 | 0.5821 |
| *3 - 4* | 21.0 | 20.4 | 108 | 1.030 | 0.8409 |
| *3 - 5* | -9.2 | 31.0 | 106 | -0.297 | 0.9983 |
| *4 - 5* | -30.2 | 30.4 | 106 | -0.995 | 0.8569 |

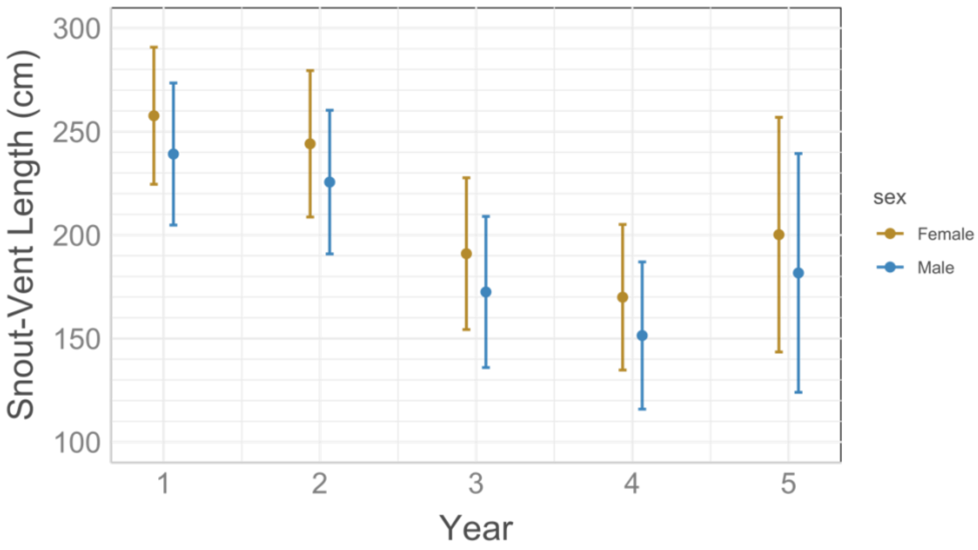


***Figure 2.12*** *Predicted values from a GLMM examining the sizes (as SVL) of pythons caught between years.*

The seasonal body condition model showed a good fit with an adjusted $R^2$ value of 0.965, and showed that year 3 and year 4 had significant differences in body condition from other years. *Post hoc* pairwise contrasts, carried out with estimated marginal means of linear trends, indicated that pythons caught in year 3 experienced higher body condition than those in years 1 and 2, while those in year 4 had higher condition than year 2 (table 2.3 and figure 2.13).

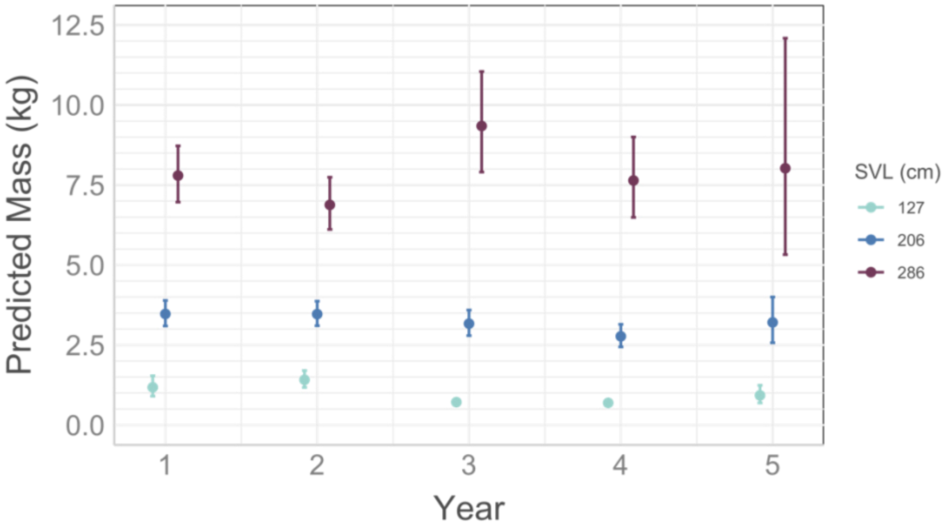


***Figure 2.13*** *Body condition trends across years, as predictions of mass at given sizes. Relative differences in body condition do not appear to be shared among differently sized individuals, and differences between years are more pronounced among larger individuals.*

*Table 2.3 Body condition contrasts between years. Estimates of slopes and associated statistics are shown, given that body condition varies with length, and different years had different mean lengths of pythons caught.*

| *Contrast of years* | *Difference in Coefficient Estimate* | *SE* | *df* | *T ratio* | *P value* |
|---|---|---|---|---|---|
| *1 - 2* | 0.00183 | 0.001097 | 102 | 1.671 | 0.4565 |
| ***1 - 3*** | **-0.00406** | **0.001212** | **102** | **-3.348** | **0.0099** |
| *1 - 4* | -0.00305 | 0.001192 | 102 | -2.558 | 0.0861 |
| *1 - 5* | -0.00161 | 0.002069 | 102 | -0.776 | 0.9371 |
| ***2 - 3*** | **-0.00589** | **0.000944** | **102** | **-6.237** | **<.0001** |
| ***2 - 4*** | **-0.00488** | **0.000907** | **102** | **-5.383** | **<.0001** |
| *2 - 5* | -0.00344 | 0.001949 | 102 | -1.764 | 0.4003 |
| *3 - 4* | 0.00101 | 0.000668 | 102 | 1.504 | 0.5621 |
| *3 - 5* | 0.00245 | 0.001886 | 102 | 1.3 | 0.692 |
| *4 - 5* | 0.00145 | 0.001867 | 102 | 0.774 | 0.9375 |

### 2.3.4 Environmental predictors of encounter rate

After examining potential models from the global starting model, five candidate models were within 2 AIC of each other (shown in table 2.5). The model chosen had moon and temperature as fixed effects, and was chosen based on the most parsimonious model having significant quantile deviations when model checks were performed. Only the moon illumination percentage was found to correlate significantly with capture probability in a likelihood ratio test (table 2.5), and showed that capture probability tends to decrease with increasing moon illumination (i.e. a fuller moon). Temperature, although not a significant effect, suggested the possibility of an increased encounter rate with higher temperatures (figure 2.14).

***Table 2.4*** *Model comparisons for binomial GLMM determining the effects of weather and moon phase on encounter probability. Only models within <2AICc of the top model, and the null model without specifications, are shown. The single model chosen is shown in bold.*

| *Model specifications* | *k* | *LL* | *AICc* | *ΔAICc* | $w_i$ | $R^2m$ | $R^2c$ |
|---|---|---|---|---|---|---|---|
| ***Moon + temperature + (1\|transect)*** | **4** | **-125.89** | **259.93** | **0** | **0.31** | **0.080** | **0.326** |
| *Moon + (1\|transect)* | 3 | -127.39 | 260.88 | 0.95 | 0.19 | 0.064 | 0.308 |
| *Moon + rain + temperature + (1\|transect)* | 5 | -125.37 | 260.97 | 1.04 | 0.18 | 0.082 | 0.336 |
| *Moon + previous day rain + temperature + (1\|transect)* | 5 | -125.39 | 261.02 | 1.09 | 0.18 | 0.084 | 0.336 |
| *Moon + rain + (1\|transect)* | 4 | -126.73 | 261.61 | 1.68 | 0.13 | 0.068 | 0.321 |
| *Null + (1\|transect)* | 2 | -132.77 | 269.59 | 9.66 | 0.00 | 0 | 0.278 |

*k: number of parameters*
*LL: Log-Likelihood*
*AICc: Model fit corrected for sample size*
*ΔAICc: Change in AICc from the best model*
$w_i$*: Akaike weight – strength of model in relation to other models*
$R^2m$*: marginal R-squared value – proportional of variance explained by fixed effects alone*
$R^2c$*: conditional R-squared value – proportion of variance explained by fixed and random effects combined*

***Table 2.5*** *Individual likelihood ratio results for each fixed effect in the chosen mixed model to examine abiotic effects on capture probability.*

| ***Variable*** | $X^2$ | ***P-value*** |
|---|---|---|
| ***Moon*** | **10.075** | **0.0015** |
| *Temperature* | 2.224 | 0.1359 |

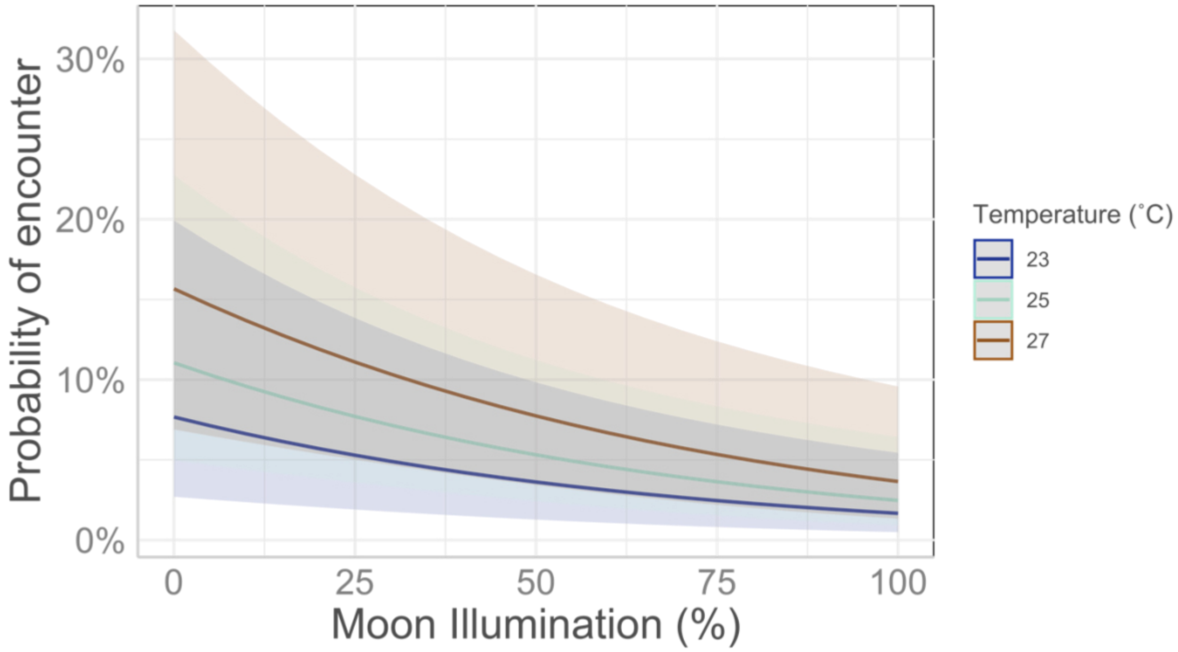


***Figure 2.14*** *Predictions of how moon illumination affects the probability of capturing at least one python during any given survey, whilst statistically controlling for the differing capture rates in different transects, using a binomial mixed model. When setting temperature to its mean value, during a new moon (0% illumination) the probability of catching a python is 12.0% (CI's 5.5 and 43.2%) while during a full moon (100% illumination) the probability is 2.7% (CI's 1.0 and 6.9%).*

### *Occupancy modelling and detectability*

Overall null mean site occupancy across all transects (i.e., with no covariates included) was estimated as 0.662 ± 0.094, while null detection probability was estimated as 0.221 ± 0.021. With the addition of environmental variables, three candidate models were within <2AICc of each other (table 2.6), but only the top model showed good fit after performing a Mackenzie-Bailey goodness of fit test (c-hat = 1.45, p = 0.18). The chosen model had a mean occupancy probability across all transects higher than the null model at 0.718 ±0.136, while the mean detection probability was lower than the null model at 0.205 ±0.024. The occupancy rate differed between the north and south banks of the river (z = 2.54, p = 0.0112), with an estimated occupancy rate of 0.933 ± 0.075 for the south bank, and 0.318 ± 0.132 for the north (figure 2.15). While transect type (forest or corridor) was included in one model, this was not significant (z = 0.71, p = 0.478). The proportion of adjacent areas consisting of plantation and the transect length were not included in any candidate models, so did not appear to have any effect on the probability of a transect being occupied.

Detection rate decreased with moon illumination (z = -3.80, p = 0.0001), with a full moon having only 28.6% of the detection probability of a new moon (figure 2.16). Humidity was included in one candidate model, but was not significant (z = -0.99, p = 0.323). Month, year, temperature, and daily rainfall on the day of the survey and the previous day did not appear to correlate with detection probability.

***Table 2.6*** *Occupancy model comparisons assessing site-level covariates on probabilities of occupancy (ψ) and survey-level covariates on detectability (p). The model chosen is shown in bold.*

| *Model specifications* | *k* | *LL* | *AICc* | *ΔAICc* | $w_i$ | *ψ* | *p* |
|---|---|---|---|---|---|---|---|
| ***~ moon*<br>*~ riverbank*** | **4** | **-187.821** | **383.64** | **0.00** | **0.41** | **0.718 ±0.136** | **0.205 ±0.024** |
| *~ moon + humidity*<br>*~ riverbank* | 5 | -186.877 | 383.75 | 0.11 | 0.39 | 0.718 ±0.136 | 0.202 ±0.023 |
| *~moon*<br>*~ riverbank + type* | 5 | -187.562 | 385.12 | 1.48 | 0.20 | 0.748 ±0.132 | 0.205 ±0.023 |
| *~ moon + temperature + humidity + rain + previous day's rain + month + year*<br>*~ Plantation proportion within 250m + plantation proportion within 500m + transect distance + riverbank + type*<br>*(Global model)* | 16 | -185.139 | 402.27 | 18.63 | 0.00 | 0.748 ±0.135 | 0.203 ±0.024 |
| *~1*<br>*~1*<br>*(Null model)* | 2 | -201.314 | 406.63 | 22.98 | 0.00 | 0.632 ±0.098 | 0.223 ±0.023 |

*k: number of parameters*
*LL: Log-Likelihood*
*AICc: Model fit corrected for sample size*
*ΔAICc: Change in AICc from the best model*
*$w_i$: Akaike weight – strength of model in relation to other models*
*ψ: Occupancy rate – probability of occurrence in a site*
*p: Detectability – probability of detecting a python in a given survey*

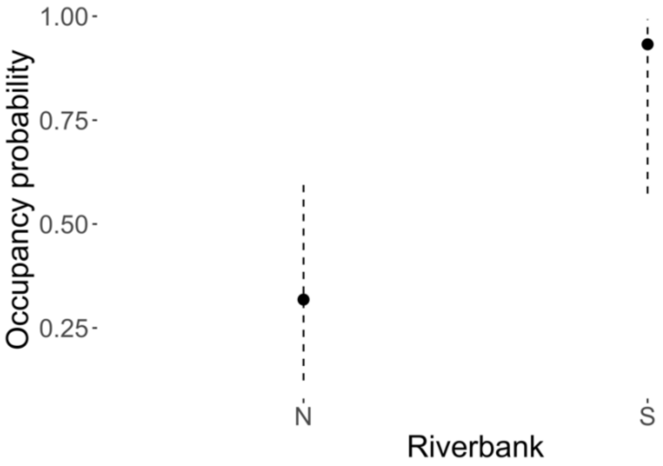


***Figure 2.15*** *Model predictions from the chosen single-season occupancy model showing the differences in occupancy probability for transects on the north (N) and south (S) banks of the Kinabatangan river.*

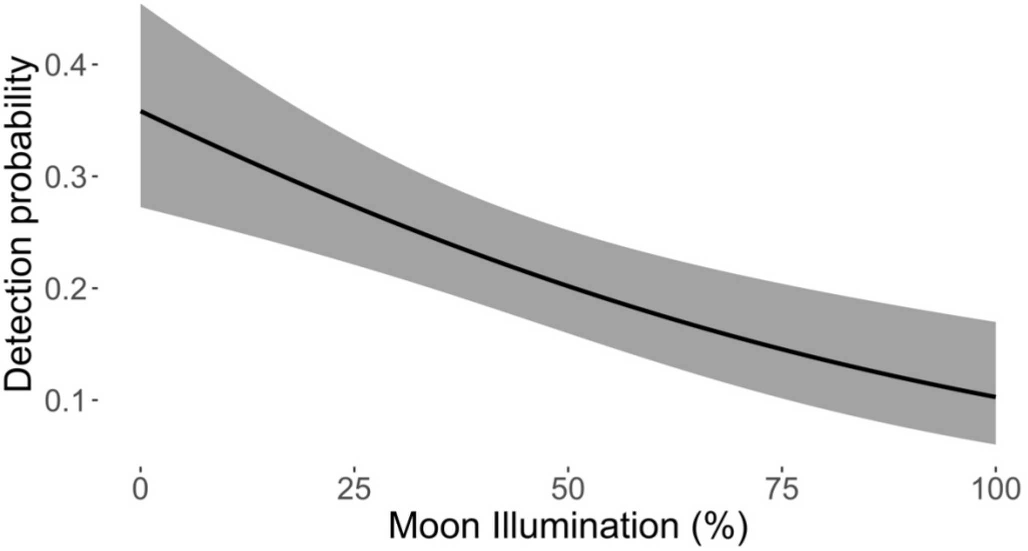


**Figure 2.16** Model predictions from the chosen single-season occupancy model showing the effect of moon illumination on detection probability.

## 2.4 Discussion

### 2.4.1 Surveying and capture methods

Carrying out transect surveys along riverbanks showed some potential as a method for surveying for reticulated pythons. This study found 159 individuals (plus 40 recapture events) over a 5-year period (from April 2016 to March 2021), making this the largest field study of reticulated pythons carried out to-date, outside of sampling python slaughterhouses. However, systematic surveying along riverbanks yielded only 83 individuals of this total (plus an additional 10 encountered that were not captured, and 27 recapture events), meaning that the overall mean encounter rate was 0.051 pythons per km, or that one python was detected for every 19.6km of survey effort on average. For capturing independent individuals only, this increases to one python for every 28.3km surveyed. Nevertheless, the relatively high proportion of individuals caught along riverbanks that were recaptured is initially suggestive of the potential efficacy of carrying out riverbank visual encounter surveys for this species and using mark-recapture to estimate population size, when in reality this is not the case.

The 40 total recapture events includes both individuals originally caught, or recaptured, outside of surveying times, and includes repeat recaptures, so considering survey efforts alone still leaves 17 individuals recaptured at least once of 83 individuals (27 recaptures total), or 20.5%. Auliya (2006) had a recapture rate of 15.8% (3/19), while Khadiejah et al. (2021) recorded only 2.3% (1/44). Mark-recapture models generally require a high capture probability, which can be problematic for many snake species, and low recapture rates often lead to large standard errors (Dorcas & Willson, 2009; 2013). While recapture bias (e.g., becoming trap-shy) can often be accounted for, it may still be problematic. In this study, most individuals encountered remained motionless after being spotlighted and approached by researchers, making capture easy. However, over the course of the study a small number of individuals began fleeing as soon as they were spotlighted. Many of these fleeing individuals were still captured (10 individuals were not), and they were almost invariably recaptures. At least one python behaved this way even two years post initial capture. The number of recaptures does not indicate a high level of avoidance of riverbanks post-capture (although this may still have been present), but these anecdotal observations of behavioural avoidance indicate further potential issues with VES methodology for accurate population estimates with mark-recapture studies.

If surveying were conducted only at times where python detectability is highest (e.g., around new moons), then the overall capture rate per unit effort could be much improved, and might make mark-recapture surveys for monitoring purposes more feasible in remote riparian areas. Despite the large amount of time required for carrying out monitoring surveys to obtain a large sample size, the use of a boat and spotlights would be advantageous for efficacy and repeatability compared with the use of attractant traps and nets. Regardless of what method is used to survey, there are inherent biases associated with it (Dorcas & Willson, 2009). This is only the third field study examining population-level traits in wild, free-living reticulated pythons, at the time of writing, and the first standardised attempt to utilise visual encounter surveys. The first study was carried out in West Kalimantan in 1996 (Auliya, 2006) over a six-month period. That study used live-baited traps to capture pythons, and recorded measurements of 19 individuals (plus 3 recaptures). The study by PERHILITAN (Khadiejah et al., 2021) took place across four years, involving funnel traps live-baited with ducks, as well as nets placed in rivers and drainage ditches, and captured 44 individuals (plus one recapture) from 7,679 trap days, meaning an average of 171 trap days were required to capture a single individual. Baiting traps with fowl is likely to bias towards larger animals that are actively hunting (when a sit-and-wait ambush hunting method is generally considered more common for the species – Reed & Rodda, 2009), and perhaps show a preference for avian rather than mammalian prey. Nets are similarly likely to bias against pythons that are small enough to fit through the mesh. Auliya (2006) caught one juvenile, but considered this to be accidental, while Khadiejah et al. (2021) did not capture any individuals below 140cm SVL.

Conversely, visual surveys of the type used here are biased towards animals that are visible to researchers, so may also bias towards larger individuals, but are also dependent upon hunting frequency (higher for younger individuals) and activity levels in different sexes or size classes. There may be demographic biases related to presence along riverbanks, as juveniles are thought to spend more time in trees than adults (O’Shea et al., 2004). Similarly, population-level inferences from slaughter houses (Shine et al., 1998a;b; 1999b Natusch et al., 2016a;b) are biased by activity levels in different size classes, as well as towards animals inhabiting anthropogenically-altered habitats, and individuals that have commercial value (i.e. excluding animals that are very small or heavily scarred, and some hunters do not capture gravid females). Clearly, at least in riparian habitats, no method can be considered “better”, and barring logistical constraints, a combination of methods would most likely be best for maximizing capture rates. Live-baiting traps was not considered for this study due to ethical concerns.

Reed et al. (2011) used a more ethical method of trapping Burmese pythons by having the live-bait in a separate compartment so they could not be consumed, but this approach would have still been difficult to attempt in this study while maintaining reasonable welfare standards over long time periods, especially as the Kinabatangan is prone to regular flooding, and Bornean elephants in the area regularly delight in destroying traps they come across (pers. obs.). Furthermore, that study only managed to catch three pythons over 6053 trap nights (Reed et al., 2011), which reflects an unreasonable amount of survey effort required to achieve a reasonable sample size. Nets placed in water are regularly used by hunters to capture reticulated pythons (Natusch et al., 2016b; Khadiejah et al., 2021), but this can have ethical concerns as well, as the nets can injure or drown pythons, and any other species indiscriminately caught. Auliya (2006) attempted netting in his riparian study area, but issues arose when fisherman dismantled them for river access, and the nets often washed away with rising water levels. The Kinabatangan river has the highest density of crocodiles in Sabah, which may attack wildlife caught in nets or, indeed, the researchers collecting them (Kntayya et al., 2021). For both practical and safety reasons, therefore, using nets may be a more effective method in the drainage ditches in plantations rather than in natural rivers.

Due to logistical considerations, transect surveying was not able to be carried out in a fully controlled and randomised fashion. This was due to the considerable time necessary to travel between transects, as well as a need to be as fuel-efficient as possible. The sequential surveying of transects also meant that pythons captured the previous night could usually be released at their capture point on the way to survey the next river section without spending an extended amount of time constrained inside their bag. Additionally, as surveys were carried out only when the river level was low enough to expose the banks below the vegetation line to allow pythons to be spotted, survey periods were often irregular. Transects were also not surveyed an equal number of times, nor were they of equal standardised length. Accurate population estimates from mark-recapture were never a goal of this study, as it was assumed that capture rates would be too low to provide reliable estimates given that mark-recapture is generally better when conducted in intense bursts, rather than continuous sampling (Dorcas & Willson, 2009). Even if estimating the population size had been an initial goal, and surveys had been planned and carried out in a manner more conducive to mark-recapture analysis, the sample sizes and recapture rates in this study were too low for this to have worked.

It is not known what the edge effects of capturing only pythons along the river edge might be. For example, pythons could be more likely to avoid these edges so as not to be exposed to potential predators, or conversely congregate at riverbank edges for ambush opportunities or for thermoregulation. The interplay between detectability and behavioural changes in different habitats would make it extremely hard to determine real differences in population density. This is a fundamental issue for any attempt to make reliable comparisons of population sizes in different areas. Detectability is modified at both the macro- and micro-habitat scale, and when detectability and catch rate is so low, any higher-level effects can be masked (Steen, 2010; Ward et al., 2017).

North and south banks along the river were surveyed equally, and as both the north and south bank of a river section were surveyed on any given survey night, the order in which they were surveyed was stratified. Pythons were far more likely to be found along the south bank than the north bank. When the comparisons are split into the 13 river sections, this effect is lost, however, presumably due to low capture rates in the majority of transects, or simply because of a very high skew resulting from captures within lot 6. If this north-south disparity is a real effect, what might cause this? South-facing slopes are often better for reptile thermoregulation in the northern hemisphere, but at 5˚N and with large meanders and changes of direction in the river this seems unlikely, and in any case pythons were found more on the north-facing side. Higher capture rates were observed on the south bank regardless of which side the nearest large forest fragment was located (i.e., adjacent to lot 5, which is on the north bank, more individuals were captured on the south bank). Avoidance of direct illumination from the moon is also unlikely, as the moon's tilt relative to earth means that any influence of the direction of illumination would average out over such a long time period. There may have been differences in logging history of the north and south banks of the river, before large scale clearing for oil palm, which has led to some differences in plant species composition within forest monitoring plots on either side of the river (N. DeVere, pers. Comms.), and this can in turn affect prey abundances or species richness. Brunke et al., (2020) found that tree shrews (*Tupaia longipes*) in the study area, which largely do not disperse across the river, were significantly more related overall along the southern side of the river than the northern, suggesting greater historical levels of connectivity, despite lower connectivity presently. They also found greater abundances of 16 out of 19 species (with the other three equal) on the southern bank, despite a higher number of trap sites on the northern side (Brunke et al., 2021). These studies were not concurrent with this study, but it is possible that there are more pythons on the south because there is a higher prey availability. Preliminary unpublished population genetic data also suggests that water monitors (*Varanus salvator*) in the study area move southwards across the river at roughly a 20-fold rate compared to northwards (P. Orozco-terWengel, pers. comms.).

One of the difficulties involved in surveying in this study was finding a reliable technique within plantations. VESs were initially carried out on foot, at times when river surveys could not be conducted due to the river being too high, and yielding no encounters. Only a few animals were collected thanks to help from local residents and plantation workers. VES in plantations was never standardised as varying methodologies were employed to improve effectiveness, such as slow, intense searching, fast walking to cover greater distance (Lardner et al., 2019), and systematically turning over vegetation. The plantations in the study area are easily accessible from the river, but not by car, as they are far from main roads. However, towards the end of the study a pickup truck was made available and parked in plantations close to the river to facilitate its use. Using spotlight surveying from the back of a pickup truck allowed greater distances to be covered similar to boat surveys, as well as a higher vantage point for improving detection, and proved more effective for capturing pythons in a short space of time. However, making robust comparisons of detectability rates using this method with surveys along riverbanks was not feasible, as there were too many confounding variables. As this was intended as a final effort to collect a more representative sample size of pythons in plantations for comparison purposes, and to find individuals to implant with radio transmitters (see chapters 4 & 5) before the end of the study, surveys in plantations were mainly carried out around the new moon to improve capture rates.

Anecdotally, then, spotlighting by car may have merit for sampling in oil palm plantations. Surveying was carried out in two large plantations for around 90 minutes at a time (or until all available snake bags had been filled), patrolling along roads between planting blocks. Encounters only occurred in one area of one of these plantations, suggesting density in this one area may be much higher than elsewhere. However, this was former peat forest, and the ground vegetation was different to other areas, which may have improved python detection rates in this area. 11 pythons were captured/encountered from eight surveying occasions in one plantation, while six surveys were conducted in the other and no pythons were encountered. With some back-of-the-envelope calculations this roughly equates to 0.6 pythons per hour (0.9 per hour for the single plantation alone). River transects were not time constrained, but given that it usually took about an hour to survey one river transect, then the modelled detectability rates focusing solely around new moon would yield somewhere in the region of 0.28-0.45 pythons per hour. If monitoring were conducted for a week at a time around each new moon, six hours per night, for an entire year (n = 84 days), these values could equate to as much as 300-450 pythons caught per year in plantation, and 140-230 pythons per year along riverbanks (but only if the river is low enough at every new moon). Considering that Natusch et al. (2019) sampled between 24 and 186 pythons per day at different python processing facilities, by similar crude extrapolation 84 days of effort per year in slaughterhouses could equate to 2,000-15,000 pythons being sampled. These numbers are highly optimistic, but they still illustrate a point; field surveys are not able to provide a competitive sample size and associated statistical power for assessing non-detriment findings, given limited time and resources.

### 2.4.2 Morphology

The morphological data presented here do not appear to overly differ from previous studies examining population size traits. The mean SVL of 222.7cm was less than the values reported by Shine et al. (1998a;b, 1999b) and Natusch et al. (2016a), which ranged between 245.5 and 305.9cm, in different slaughter house sites in North and South Sumatra. Natusch et al. (2019) surveyed slaughterhouses in the same areas of Sumatra in addition to Peninsular Malaysia and Kalimantan, and yielded a mean SVL of 279cm for males and 319cm for females. However, those studies did not include juveniles as they are not commercially viable. Auliya (2006), who conducted his field study in Kalimantan, recorded a mean SVL of 235.3cm, which is much closer to the values reported here, but again, his trapping method largely excluded juveniles. Khadiejah et al. (2021) reported mean SVL of 262cm for males, and 266cm for females in Peninsular Malaysia, and again this trapping methodology excluded smaller individuals below about 140cm SVL. In all cases, however, despite different biases, geographical variability, and environmental plasticity, the large majority of individuals sampled in every study appear to be within 200-350cm SVL, and very few individuals are found over 400cm (0.97% in Kalimantan and 3.6% in South Sumatra – Natusch et al., 2019). There was only one individual found in this study (including incidental captures) over 400cm SVL. In areas where there are heavy levels of python off-take for trade, average sizes are smaller, possibly due to a higher capture rate of large individuals (Natusch et al., 2019).

The survey methodology employed allowed for the capture of a number of juveniles, which could initially be interpreted to conclude that this methodology is better at assessing true population demographics compared to slaughterhouse studies. However, juveniles are still likely underrepresented, as they were only spotted when they were fully in the open on riverbanks, and likely exist at higher densities shortly after the breeding season. It is unlikely that the size distributions from this study are a fully accurate indicator of the true population characteristics because there is a complex interplay between recruitment rates, rapid initial growth rates, increasing survivorship probability with size, increasing detectability with size (easier to spot larger animals), and varying detectability due to behaviour at different life-stages (e.g., larger animals may be more sedentary) (Madsen et al., 2006). However, the fact that the distribution of individuals caught and measured from visual encounter surveys in this study ties relatively closely to the size distributions from other studies lends weight to previous assertions that assessing potential changes in morphological characteristics from pythons in slaughterhouses is a reasonable methodology for monitoring sustainability of trade dynamics (Natusch et al., 2016a;b). Juveniles are not commercially viable, so their inclusion in sustainability monitoring is largely inconsequential (juvenile recruitment varies seasonally, and they exhibit higher mortality rates. See below, section 2.4.5), and field surveys of wild populations (which require considerably more effort and expense) are unlikely to provide any additional benefit for detecting population-level traits in morphology.

Reticulated pythons have been reported in the past to exhibit high levels of sexual size dimorphism (SSD), with females attaining far larger sizes than males (Murphy & Henderson, 1997; Shine et al., 1998a). Shine et al. (1998a) stated this species has far more extreme SSD than most other snakes, except perhaps green anacondas (*Eunectes notaeus*), and females measured were more than a metre longer on average. However, later studies (Shine et al., 1999b; Natusch et al., 2016b; 2019; Khadiejah et al., 2021) all found the disparity to be far smaller (although statistical tests of these differences were only reported by Khadiejah et al., 2021). In this study, neither length nor mass were significantly different between the sexes. Females certainly can grow far larger than males, but larger individuals are likely rarer, and the switch to larger prey may change their hunting frequency, making them less detectable (Shine et al., 1998a).

High rates of off-take for trade do not occur in this study area. Therefore, the similar overall demographic distribution to previous studies in slaughterhouses suggests that, contrary to what might be expected, high-levels of off-take make little appreciable difference to reticulated python demographics. From this one can surmise that either: a) python breeding and growth rates are so high and rapid that they can quickly compensate for the loss of larger individuals within the population, b) pythons are so numerous that the high levels of off-take have little effect on their overall numbers, or c) a combination of the two. Natusch et al. (2016a) found that in the 20 years between their study (n = 2,361) and the ones by Shine et al. (1998a;b; 1999b) (n = 1,670) in Sumatra, pythons were still being harvested in largely the same areas (mostly oil palm plantations) as before, nearly a million individuals had been harvested for trade in that time, and the average sizes actually increased slightly. Regardless of how these results may be interpreted in terms of sustainability and allowable trade quotas, the available evidence points towards reticulated python abundance being considerably higher than might be assumed from encounter rates in the field.

### 2.4.3 Body Condition

The most common way to assign body condition in snakes (and many other species) is to take the residuals of from a linear model of mass and length (most often log-log transformed) (Green, 2001). This has the advantage of being able to assign scores to individuals, and potentially link individual body condition to other intrinsic factors, but here the aim was to perform comparisons (male:female and forest:plantation) so it makes more sense to model these together in a GLM rather than performing separate tests on means of residuals. The advantage of this approach is it allows for the inclusion of the interactions of these categories with SVL, thereby incorporating allometric changes, such as the increased amount of pythons' fat scores relative to their length as they get larger (Falk et al., 2017). This approach therefore removes some of the bias caused by differing lengths in the two groups being compared.

When controlling for length in a model of body condition, males caught in this study tended to be slightly heavier than females, albeit this divergence only starts at between 200 and 250cm SVL. This is the size at which reticulated pythons start to become sexually mature (although males mature at a smaller range; 130-290cm SVL vs. females 210-390cm SVL; Shine et al., 1998a; Natusch et al., 2016a), and the same trend of males having better body condition than females has been noted previously (Shine et al., 1998a). None of the females captured during surveys were clearly gravid (and there was only one incidental capture of a gravid female), so the survey technique used here likely biases against their capture as they are less likely to come to the riverbanks. Females post-parturition tend to be in poor body condition (Shine et al., 1998a), and it may take two or more years to recover enough body fat to breed again, meaning that only a portion will breed in any given year (Natusch et al., 2019). If females are less likely to be encountered when in full breeding condition, this will be a cause of bias in an array of survey methods. To provide an example, one large female that was radio-telemetered in this study (see chapter 4) weighed 17kg when the tracking tag unfortunately had to be removed while she was showing early signs of gravidity, but she was caught incidentally again seven months later weighing only 9.2kg. Lower detectability of gravid females would be likely beneficial for trade sustainability because it helps to sustain recruitment levels and population recovery. Natusch et al. (2019) calculated large differences in reproductive frequency of females (using the proportion of gravid females) at different sites, and suggested this might at least partially be due to biases in capture rates of gravid females, rather than a geographical difference in population traits *per se*.

The GLM found no significant difference in body condition between pythons caught in plantations, and those caught in forest fragments. The results suggested that body condition is higher in plantations, but the number of captures in plantations was much lower compared to forested areas, and did not occur over the same time periods, and the difference was not significant. Body condition would be expected to be higher due to the higher availability of prey, but growth rates will also increase with higher food availability, and as body condition is a function of size, this relationship might not be directly proportional (Murphy & Henderson, 1997). Comparing growth rates by regularly recapturing individual pythons (using telemetry) might therefore be a more reliable method of determining any differences between habitat types than simply comparing body condition, albeit that this would require a very large number of telemetered animals.

### 2.4.4 Growth Rates

Accurately measuring live large snakes is problematic. Firstly, it is difficult to orient them sufficiently straight to get an accurate length measurement, and they are also to some degree able to contract and extend their bodies, which can cause errors (Auliya, 2006). Since the same methods were used here as Auliya (2006), size measurements should be directly comparable, having similar levels of error (in comparison with measurements of dead pythons). However, for repeated measures of individuals, this becomes problematic. Just as for Auliya (2006) , it was found that in a few cases of recaptured individuals, SVL measurements taken a few months apart decreased slightly. However, head length measurements, taken from the base of the cranium to the tip of the snout, were subject to far less error, and did not show shrinkage. As HL and SVL were directly proportionate across all measured sizes, it appears that HL could be a more reliable way to compare sizes of individuals of all ages.

The sample size of 40 recapture events, from 24 individuals over a five year period, is still very small to draw population-level conclusions about growth rates. Like most reptiles, reticulated pythons will grow larger throughout their life, long after they reach sexual maturity (Shine et al., 1998a), rather than reaching an adult size and ceasing to grow further as in mammals and birds. However, growth rates of reptiles tend to slow with increasing size, resulting in logistic growth curves (Shine et al., 1998b). As this dataset does not contain multiple measures for most individuals, and they were not measured at standardised intervals, it is difficult to find a way to infer growth rates. Therefore, standardizing growth rate measurements by a daily growth rate, and plotting them by individual size seemed the best option. This is similar to that carried out by Shelton et al., (2018) on *Hoplocephalus bitorquatus*, where the underlying assumption is that relative change in growth rate is a fixed function of size/age. In this case, there was no significant relationship between size and growth rate, and there were also no discernible differences in growth rates for males and females. For individuals between 200 and 300cm, there were a number that showed very low or no growth compared to the model expectations. Growth rates and maximum attainable sizes in pythons are known to be correlated with feeding rate, and can be highly variable (Madsen & Shine, 2000), with reports from captive reticulated pythons suggesting exceptional growth rates if they are fed enough (Auliya, 2006; Reed & Rodda, 2009). Therefore, prey availability is one of the most likely confounding variables here, and this will vary across both time and space. Madsen & Shine (2000) showed a strong linear correlation between rat numbers and *Liasis fuscus* yearly growth rates. Females reach sexual maturity around 250cm SVL, and it is also possible that resources move away from growth and into improving breeding condition. Any attempt to control for these effects in the absence of concurrent prey availability data is not possible with such a small dataset, and without standardised sampling events. The low number of small and large individuals that were recaptured here makes estimating a generalisable trend quite difficult. Very young pythons that exhibit low growth rates are also likely to have reduced survivorship, as they would stay at a size that is vulnerable to predation for longer, or are more vulnerable to starvation.

This effect of prey availability is particularly interesting in the case of pythons that may be inhabiting oil palm plantations, as they will feed primarily on rats (Shine et al., 1998b), which can be extremely abundant in plantations (Puan et al., 2011). The implications of this trend are that pythons may be able to grow and reach sexual maturity faster within plantations, which could help to offset any potential negative impacts, such as lack of diet variability and human conflict. If growth and breeding rates are higher in plantations, and results in a net increase in population size, this could have negative consequences for endangered prey species inhabiting isolated forest fragments bordering plantations, such as the LKWS. This is especially true given that reticulated python diet shifts ontogenetically towards larger prey with increasing body size, so larger snakes may move from plantations into forests to seek larger prey items (Shine et al., 1998a; Natusch et al., 2016a). Unfortunately, however, sampling of pythons in plantations occurred over a shorter timeframe, and the number of recaptures within plantations was too low to be able to make any statistical comparisons.

### 2.4.5 Annual and seasonal trends in captures/encounters

A GAM showed no differences in capture rates between males and females in different months, when controlling for the effect of year and survey effort. With only 93 captures, and uneven sampling, assessing capture rates split by multiple categories in this way leaves little statistical power to detect changes, and the model that allowed spline terms to vary between males and females was a poor fit. Male snakes are generally more active in the breeding season as they move more to seek out females (e.g., Wilson et al., 2006), while females are assumed to be less active when gravid, and almost completely inactive when incubating (Reed & Rodda, 2009). While capture rates are not activity rates, it is a reasonable assumption that with more activity, a greater proportion of individuals will be visible at any given time, and so capture rates would correlate with activity. Such seasonal trends are not apparent here.

Capture rates were shown to be much lower in year 3 compared to year 1, but it would be unwise to conclude here that this indicates any change in population size. Instead, this likely reflects other confounding factors. If, for instance, prey availabilities are fluctuating, then this may change how much time pythons are spending using the riverbanks as ambush sites. It is difficult to predict whether increased prey abundance would improve detectability as more pythons take advantage of increased hunting opportunities along the riverbank, or whether they would be less detectable because they spend more time satiated. However, a telemetric study on *Bitis arietans* suggested that well-fed snakes moved shorter distances and spent less time foraging (Glaudas & Alexander, 2017). In a 17-year study of tropical pythons, *Liasis fuscus*, annual population shifts were caused by the number of rats available as prey, which greatly affected the proportion of breeding females and subsequent recruitment rates, so shifting proportions of sub-adults between years. This was visible as demographic shifts in population structure – when recruitment rates were high, the average sizes of pythons caught decreased. Further, there was very strong correlation between body condition and the number of rats (Madsen & Shine, 2006). An earlier paper from the same study showed consistent correlation between capture rates of both pythons and rats (Madsen & Shine, 1996).

The GLMM found differences in the lengths of pythons caught between years, with years 3 and 4 showing smaller sizes than others. Years 3 and 4 were the only two years when very young (<1m total length) pythons were located along the riverbanks. Rather than assuming capture of hatchlings in this case reflects anything related to prey availability and recruitment, it is likely just chance. In year 3 (2018/2019) only 17 pythons were caught (excluding recaptures) with one hatchling. In year 4

(2019/2020) six hatchlings were caught on a single night, with four grouped along a 100m stretch, and the other two in another area 1.2km away but 20m apart. Perhaps these reflect two separate nests that had recently hatched, and/or some form of climatic conditions that day caused them to venture into the open mudbanks. In any case, these are likely the source of bias. When controlling for the differences in annual capture sizes, the model also showed the differences in length between males and females to be significant, when previously all individuals together has shown no significant differences. Re-running the Wilcox rank sum test found the overall difference between male and female SVL to be significant when the hatchlings were removed (W=1590, p=0.029).

Body condition was also different in years 3 and 4. Due to body mass predictions varying by size, and different average sizes being caught in different years, comparing residuals from the original body condition model (although excluding plantation individuals here) would be biased. When examining predicted mass from the model at different size classes, it appears that there are some intriguing disparities, due to allowing slopes to vary between years. Variations in body mass appear relatively more stable between years for smaller pythons, while larger pythons show greater variability. An average 286cm SVL python was predicted to weigh about 6.9kg on average in year 2, while in year 3 it would be 9.3kg (a 35% increase). This might be related to different prey being consumed by different size classes, and their associated annual abundances, causing bountiful or lean years only within specific size classes. However, a larger sample size is likely needed to ensure that stochastic differences are not the cause.

The goal of assessing these various temporal trends is largely to reflect whether annual monitoring of a population in the field could allow for assessing changes over time related to population size or demographics. With much greater survey effort leading to larger sample sizes, and removal of some of the confounding factors (such as indiscrepancies in transect lengths and number of surveys along each transect), it might be theoretically possible. But for many of the potential effects that might indicate declines as a result of large-scale harvesting, the effect sizes would need to be extremely large to be detectable. Natusch et al (2016a) assessed potential effects of intensive harvesting such as size of maturity (assessing maturity requires dissection of gonads, so precluding this from the study of live animals), and estimated that detecting an annual change of 10% would require a sample size of 1,238 pythons. A 5% annual change would necessitate nearly 5,000 pythons to be measured. This is before any attempts to take environmental effects or survey biases into account. The effort required to do so in just a single site would be prohibitively demanding.

### 2.4.6 Environmental predictors of encounter rate

Pythons were less likely to be encountered with increasing brightness of the moon (figure 2.10). Moon luminosity is known to affect the behaviour of many different species, including other snakes (Lillywhite & Brischoux, 2012; Sperry et al., 2013). Based on their behaviour, it appears that the pythons encountered along the riverbanks in this study were primarily attempting to ambush prey, as they were typically found lying still at the edge of vegetation, with heads extended slightly into the open, pointing downslope. In brighter moonlight, python prey species may be less likely to venture into the open, ambushing may be less effective as pythons become more visible to prey, or pythons themselves may be more visible to their own predators and less willing to be more exposed (or a combination of these effects). The precise nature of the relationship between encounter probability and moon luminosity could be refined by taking direct measurements of light levels in the field, rather than the phases of the moon. Cloud cover and the elevation of the moon will alter the amount of moonlight reaching the ground in practice. The evidence shown here, however, clearly indicates that any future monitoring of the species should be carried out during periods around the new moon, in order to maximize the potential for encounters and improve sample sizes.

There is not yet sufficient information about python movements or how long they may typically spend at the riverbanks, but it is not unreasonable to think that, as ectotherms, weather patterns would play a role in their behavioural choices. Temperature is particularly important for snakes in temperate areas, but may be less so in hotter and more stable tropical regions (Asad et al., 2021). The GLMM included temperature here, but it was not significant. There may be a suggestion that hotter temperatures increase the likelihood of encountering pythons.

An important point to note, however, is that these data are entirely dependent on the ability of the researchers to spot pythons. Rain makes this considerably harder, and surveys were not carried out in very heavy rain, when it is also typically colder. Pythons lying along the riverbank are primarily distinguishable at a distance by torchlight by their colour and shape, which often makes it very difficult to distinguish them from woody debris, which tends to be common. The iridescence of their scales helps, but when logs, leaves and other debris are wet, it becomes far more difficult to distinguish pythons from the background. Therefore, observer biases in the survey methodology make it difficult to tell what, if any, effect rain has on python behaviour.

### 2.4.7 Occupancy and detectability

There were large differences in encounter rates between individual transects (figure 2.2), with seven out of 26 transects having no encounters, while at the other end of the spectrum, 40 encounters occurred along transect AS, giving an average rate of 0.27 pythons per km surveyed. For every river section surveyed where encounters occurred, there were more encounters along the south bank than the north bank. This was reflected in the occupancy model, as riverbank (north or south) was the only site-level covariate that showed significant correlation with the probability of occupancy. Reasons for this can only be speculated, as discussed above in section 2.4.1, and this pattern is probably only interesting in the context of the LKWS, rather than suggesting any general species trends that might occur elsewhere.

Assigning individual estimates of occupancy for each transect was not possible based on the covariates included within the global model. One of the likely reasons for this is the relatively low number of transects compared with what is typically used for occupancy models. This could have been mitigated by dividing surveyed transects into smaller independent sections *post hoc*, but particularly as the number of detections were so low, this would have excluded a significant portion of the dataset. Transect length typically shows a positive correlation with the probability of occupancy (e.g., Ward et al., 2017), but this was not reflected in the model. Similarly, the proportion of plantation within 250 and 500m buffers was not linked to occupancy rates.

Oil palm plantations have been suggested to cause an increase in reticulated python densities (Natusch et al., 2016a), and if this is the case, it might have been expected that riparian transects that are closer to plantations would experience higher abundances. The highest encounter rates were in river sections adjacent to large forest fragments (A, B, C & I), but this was not universal to all areas of forest. As mentioned above, there are likely edge effects involved with the encountering pythons along riverbanks, and so it is unknown whether encounter rates, occupancy, or detectability are in any way a fair reflection of underlying population density. For instance, if it was hypothesized that pythons might have a preference for seeking out water sources for ambush opportunities, then the number encountered would be reflective of the relative availability of alternative water sources. Namely, with fewer alternatives, pythons might seek out the main river from further away. Most of the plantations in the vicinity of the main river contain irrigation/drainage ditches, and the large fragments of forest where encounter rates were very low (lots 5 and 7, and Pin-Supu forest reserve) all contain either many oxbow lakes or large areas of swamp near to the river. The westernmost portion of lot 6, where there is an oxbow lake adjacent to the river, had very low encounter rates, but the rest of lot 6 had the highest encounter rates. Proving this relationship definitively is difficult, because in this floodplain environment, water availability is relatively fixed in some areas (e.g., oxbow lakes), while in others it is variable depending on rainfall and the level of the river, and therefore difficult to measure. Additionally, surveys could only be conducted when the river was low, as otherwise pythons were not detectable along the riverbanks, automatically biasing this effect if it existed. In short, the lack of an association between adjacency of oil palm and likelihood of detecting pythons along riverbanks does not disprove higher population densities in oil palm plantations.

Similar to the mixed model exploring encounter rates, the only covariate that appeared to correlate with detectability was moon illumination, and the effects are broadly similar. One other candidate model suggested the inclusion of humidity, but this was not significant. Higher humidity has been shown to have positive effects on detectability for some other snake species (e.g., Daltry et al., 1998; Asad et al., 2021), but the fact that this, and other climatological covariates were only recorded from a single station, means that any local microclimate variations may not have been well represented.

Detectability rates for snakes are usually extremely low, especially in tropical areas (Dorcas & Wilson, 2013). As already mentioned, edge effects may be playing a role along riverbanks, but in addition it is not possible to determine to what degree this is caused by detectability itself being easier along riverbanks, versus simply having a very high population density within the study site. With sufficient practice, pythons could be quite easily spotted when they were partially lying against the mud, or in certain vegetation such as elephant grass (see chapter 5). A recent study looking at snake detectability in another area of Sabah using VES found detectability values for the five most common species along stream transects to range between 0.05 and 0.14 (Asad et al., 2021). Reticulated python detections in that study were too low to analyse in the models they used, with only 5 detections over 295 surveys (S. Asad, pers. comms.). The results of this present study, with a null detectability of 0.22, are therefore perhaps surprisingly high at first glance. However, this value is per transect, and transects had a mean length of 4.9km, so if ignoring differences between transect survey frequency this translates to a rough encounter rate of 0.045 pythons per km. The study by Asad et al. covered 89.4km of transect in total, so their study detected five reticulated pythons at a rough rate of 0.17 pythons per km. Walking slowly greatly improves detection rates, but there is a trade-off between covering larger distances (and encountering more individuals per unit of time spent searching) and the ability to search more methodically (Lardner et al., 2019).

## 2.5 2.5 Conclusion

The results presented here provide useful data on an enigmatic species, but have not been able to fully achieve the intended comparison between pythons in plantations and forests. Differences in sample sizes, times and regimes, and a host of potential other biases preclude full comparisons. Body condition, however, did not differ significantly between animals caught in forests and those in plantations, but may have greater variability within plantations. Detection rates and site occupancy rates along riverbanks do not appear to be overly impacted by proximity to plantations, yet while any suggestion of greater abundances in plantations is still perhaps anecdotal at best, this does at least appear plausible based on a small number of surveys carried out there.

Visual encounter surveying resulted in very low encounter rates, but with considerable heterogeneity both along river transects and in oil palm plantations. Despite this low yield, the increased amount of survey effort compared to previous field survey attempts has generated some useful morphological data. However, far more survey effort would have been required in order to achieve a sample size that would allow estimation of population size, growth rates, or changes in capture rate or demographics over time. Ontological shifts in behaviour, diet, detectability, and environmental and habitat-mediated influences on these variables are fascinating from an ecological perspective, but complicate any inferences that can be made about population characteristics. Further research on the ecology of this species will be complex and extremely difficult, but can be immensely valuable, and focusing survey efforts around new moons could improve the amount of data generated relative to survey effort. However, any insistence by trade authorities for regular monitoring of wild populations to assess Non-Detriment Findings would be non-sensical based on current findings. Use of visual encounter surveying along riverbanks is far too labour intensive for the catch-per-unit effort, creates unaccountable edge effects, and regular repeated surveys are severely hampered by changing water levels. Standardised road surveys within plantations may still warrant further investigation, however. None of the data collected here present any strong evidence against continuing to monitor trade sustainability through direct examination of the trade itself.

# 3 Developing GPS telemetry for studying snake spatial ecology: considerations for prospective researchers, and a case study of methodological development on *Malayopython reticulatus*.

## 3.1 Introduction

### 3.1.1 Telemetry

Radio telemetry via the use of very high frequency (VHF) radio signals has been a vital tool in understanding the ecology and behaviour of animals for nearly 60 years (Craighead et al., 1963). By allowing researchers the ability to reliably locate and record information on species, much more information is able to be gathered than could be obtained by direct observation and opportunistic surveying. Often, one of the main applications of this technology is in understanding spatial ecology; namely how animals move and use space within their habitat, habitat preferences, and the sizes of the areas they might inhabit (or "home range") (Fieberg & Börger, 2012). For snakes, telemetry is a vital tool for answering ecological questions, as the majority of species are cryptic and difficult to observe reliably without the means to track their location (Shine & Bonnet, 2000; Boback et al., 2020; Crane et al., 2021).

### 3.1.2 VHF use in snakes

In a recent review of reptile home range (hereafter "range distribution") literature, Crane et al. (2021) found 135 studies published between 2000 and 2019 on snakes. Almost all of these involved the use of VHF telemetry. VHF transmitters have been successfully used in telemetry studies of snakes for more than 40 years. Snake body plans make attachment of radio transmitters more difficult than for many other well studied taxa, and techniques to achieve this have included ingestion (Madsen & Shine, 1994; Rivas, 2001), subcutaneous implants (Weatherhead & Anderka, 1984; Peterson, 1987), and external attachment using glue or tape (Gent & Spellerberg 1993; Tozetti & Martins, 2007; Riley et al., 2017) or subdermal stitching to the tail (Cioffi & Chelazzi, 1991; Riley et al., 2017). Intraperitoneal implants, however, have been the preferred methodology in the large majority of studies (e.g., Reinert & Cundall, 1982; Slip & Shine, 1988; Hyslop et al., 2009; Bryant et al., 2010; Croak et al., 2013; Sperry et al., 2013; Bauder & Barnhart, 2014; Lindström et al., 2015; Corey & Doody, 2016; Walters et al., 2016). Most reptile studies estimating range distributions still use minimum convex polygons (MCP) and kernel density estimation (KDE), rather than making use of more recently developed movement-based methods that are not limited by the assumption that successive positions are not autocorrelated (i.e., correlations between observed locations as a function of time or space) (Crane et al., 2021). These estimation methods have been developed in response to the burgeoning use of GPS in telemetry studies.

In an effort to reduce autocorrelation, or due to logistical constraints, many telemetry studies on snakes have low frequencies of locations, as little as one location per month. Crane et al. (2021) provided data sourced from 120 snake studies using manual VHF tracking over the last 20 years (where frequency of tracking was reported in the manuscript). While the mean location frequency for all these studies was very close to once per day, 82 had a maximum location frequency less than once per day, and 41 had a minimum location frequency of once per week or less. This is not a criticism, as some data is generally far preferable to no data at all. But higher frequency data, if it is achievable, is better, and the benefits this brings of better describing space use outweighs any statistical concerns regarding the potential for autocorrelation (De Solla et al., 1999; Fieberg, 2007; Fieberg & Börger, 2012). Another justification often used for low sampling frequency in the study of snakes and other reptiles is that they move infrequently, and exhibit high site fidelity, so this biases KDE estimates (Row & Blouin-Demers, 2006). However, for KDEs, removing non-relocations (i.e. where there are multiple positions in a single location due to the animal being sedentary) from a dataset worsens area estimates (Silva et al., 2020). Having a number of locations from the same place should therefore not be considered a negative outcome for home range estimates, and may also be useful information for answering questions about habitat choice and behaviour. Whether the often-low sampling frequency prevalent in snake telemetry studies is due to statistical or logistical concerns, the potential for high sampling frequency offered by GPS technology is surely an attractive prospect.

### 3.1.3 GPS use in telemetry studies

GPS (Global Positioning System) tracking technology has revolutionised the study of animal movement patterns, habitat utilisation, and behaviour (Hebblewhite & Haydon, 2010). The recent development of smaller, lightweight GPS collars coupled with improved battery efficiency and falling costs has enabled the deployment of GPS receivers on a wider range of species; previously, large mammals were the focus of GPS telemetry mediated studies (Craighead et al., 1972; Rodgers, 2001). GPS units weighing less than 20g are widely available (McMahon et al., 2017), while plans for satellite units as small as 1g are currently in development (ICARUS project – Curry, 2018). The high frequency and precision of location data from GPS devices has allowed for the study of fine scale movement and habitat preferences, enabling the development of more in-depth analyses and research questions than are possible with traditional VHF telemetry (Hebblewhite & Haydon, 2010; Rogers, 2010). Where a higher number of positions per animal is required, GPS is far superior (Smith et al., 2018). VHF transmitters are typically cheap, reliable and long lasting, but cost-per-datum is also often higher than that of GPS units, despite higher initial costs of equipment, due to the decreased need for intensive fieldwork that GPS affords (Wyckoff et al., 2007). However, it is important to recognise the trade-off in sample size; for a given budget outlay, the increased cost of GPS units compared to VHF transmitters tends to result in fewer animals tracked, reducing the potential for population-level inferences from independent individual animals (Hebblewhite & Haydon, 2010).

### 3.1.4 GPS use in snakes

Increasingly, studies on other taxa are choosing to use GPS technology for analysing movement and space use of wildlife, but this has not yet taken off in snakes. Unlike for many larger or more mobile taxa, VHF telemetry typically has a high level of accuracy when used on snakes, as it is often possible to home in much closer to take a manual positional reading, rather than relying on triangulation from a distance, although this varies by habitat type (Újvári & Korsós, 2000). While manual tracking is logistically expensive and time-consuming, for many snake species this not as much of a hindrance as for most mammals and birds, which would typically occupy much larger range distributions (Todd & Nowakowski, 2021). However, when manually tracking it is usually difficult to increase the frequency of positional readings to study fine-scale movements, as this incurs increased workloads, logistical problems, and costs. It also increases the likelihood of disturbing the study animals and interrupting their natural behaviour (e.g., Smith et al., 2021).

Snake telemetry studies, just as the wider reptile literature, continue largely to adhere to using traditional range estimation methods such as MCPs and KDEs (Crane et al., 2021). However, as demonstrated by Silva et al. (2020), movement-based models, which account for autocorrelation, are a viable improvement even on low location frequency reptile data, so long as a tracking schedule is reasonably regular and consistent through time. Even at a very low location frequency, reptile data is likely to still show autocorrelation, so if studies seek to reduce the frequency of locations *a priori*, this does not solve statistical issues, and merely reduces the inferences that can be made about the study species (Fieberg & Börger, 2012). If movement-based modelling such as dynamic Brownian bridge movement models (dBBMMs) (e.g., Marshall et al., 2020a; Silva et al., 2020; Smith et al., 2020) or autocorrelated kernel density estimation (AKDE) (e.g., Averill-Murray et al., 2020;

Montano et al., 2021; Silva et al., 2021) become more widely adopted, then high frequency data becomes increasingly advantageous. Similarly, for habitat or resource selection studies, many methods now exist that can account for autocorrelation in high frequency location data from GPS datasets (Martin et al., 2009; Fieberg et al., 2010; Fieberg et al., 2021), allowing the relaxation of assumptions of independence of data. One potential drawback that GPS brings is bias of fix rate and accuracy in different habitats (e.g., lower likelihood of fixes under dense forest canopy compared to open areas), but there are weighting methods that can partially account for this (Frair et al., 2004; Nielson et al., 2009; Frair et al., 2010), and this is not entirely dissimilar to the bias in location accuracy from triangulation with VHF (e.g., missing or inaccurate locations due to animals being in intraversable terrain) (Bauder & Barnhart, 2014).

While GPS technology is unlikely at present to be the superior option for every telemetry study on snakes, it still offers a tantalising number of advantages for certain applications, and this attractivity is likely to increase in the future as the technology improves, miniaturises, and reduces the disparity in costs. Some of the potential trade-offs between GPS and VHF on snakes are given in table 3.1. The use of GPS units still remains a relatively unexplored avenue for studies analysing snake space use. There are currently only five published studies from four research projects to-date, using GPS technology on snakes (Hart et al., 2015; Smith et al., 2018; Wolfe et al.,2018; Gerke et al., 2020; Smaniotto et al., 2020). These studies were all relatively small scale (max 13 units deployed), as might be expected where funding is a limiting factor. As is usually the case with early adoption of new technology, all of these studies met with challenges (Table 3.2), either involving the efficacy of the GPS units themselves, or with the attachment methods employed. Smaniotto et al. (2020) achieved so few GPS data points that their analysis only used the VHF locations they obtained. Wolfe et al. (2018) found that their study would have been more successful solely with VHF (GPS was around ten times the cost-per-datum for their study). Gerke et al. (2020) only tagged snakes for very short periods of up to 20 days, but still lost 22% of the tags deployed. Smith et al. (2018) were more successful, but still only recorded a fix rate of 18.1%, and half of the units deployed suffered some sort of failure. However, these widespread logistical issues highlight that future studies must consider carefully whether GPS is a feasible option worth pursuing.

*Table 3.1 A general comparison of GPS and VHF when carrying out telemetry studies on snakes on research costs and data quality likely to be gathered. This is a rough guideline only - use of these technologies for different applications may have different outcomes.*

| | Costs | | | | | Data | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Technology** | **Equipment** | **Logistics** | **Personnel** | **Risk of loss/ damage to assets** | **Cost-per-data point** | **Frequency of positions** | **Track regularity** | **Precision and Accuracy** | **Auto-correlation** | **Sample size** |
| **VHF** | Low | High | High | Low | High | Low | Dependent on logistical constraints/ study design | Dependent on ease of "homing in" | Medium | Med-high |
| **GPS** | High | Low-med | Low | Med-high | Low-high | High | Dependent on fix schedule or success rate | Dependent on habitat and behaviour | High | Low-med |

*Table 3.2 Some parameters of all published studies using GPS units on snakes to date.*

| Study | Species | Number of individuals | Attachment | Fix frequency (per day) | Expected GPS fixes* | Obtained GPS fixes | Number of units lost/failed/dropped early |
|---|---|---|---|---|---|---|---|
| **Smith et al., 2018 (and Hart et al., 2015)** | *Python bivittatus* | 13 | Subcutaneous implant | 24 | 20,344 | 1,269 | 5/2/2 |
| **Wolfe et al., 2018** | *Pseudonaja affinis* | 10 | External (subdermal stitch) | 5 | 3,140 | 110 | 0/0/3 |
| **Smaniotto et al., 2020** | *Eunectes notaeus* | 8 | Subcutaneous implant | 6 | 10,464 | 50 | 3/4/5 |
| **Gerke et al., 2020** | *Elaphe* spp. | 9 | External (tape) | Not reported | Not reported | Not reported | 0/0/2 |
| **This study** | *Malayopython reticulatus* | 4 | External (subdermal stitch)<br>• Large remote-download units | 6-12 | 15,330 | 186 | 0/2/1 |
| | | 5 | External (subdermal stitch)<br>• Rechargeable SOBs | 29 | 22,852 | 60 | 0/2/2 |

*** Expected fixes calculated based on 100% fix rate of units for the number of days they were deployed, although there is some discrepancy here when accounting for lost tags that were never recovered, or the date that a device failed.**

Previous reviews evaluating considerations for researchers before carrying out GPS telemetry studies (see for example; Cagnacci et al., 2010; Hebblewhite & Haydon, 2010; Thomas et al., 2011; Gutema, 2015; Latham et al., 2015; Hofman et al., 2019; Williams et al., 2019) primarily focus from the perspective of mammals and birds. For snakes, there are specific concerns that may not be applicable to other more commonly telemetered taxa.

## 3.2 General considerations for GPS studies on snakes

### 3.2.1 Introduction

The following segment discusses some of the issues that must be considered before using GPS devices for telemetry on snakes. This is not intended as a step-by-step guide to study design, nor to critically review the advantages or disadvantages of GPS over VHF. The relative merits of whether GPS might be a technological option worth exploring will vary considerably on a case-by-case basis. Instead, under the assumption that other researchers are intending to attempt to answer questions using this technology on snakes, the following highlights some of the challenges that must be overcome, and some of the options that may accomplish this. These challenges include how to attach GPS devices to snakes, how habitat and the peculiarities of snake behaviour (e.g., highly sedentary) affect data acquisition, and how to schedule data acquisition as a result. Considerations regarding the trade-off between device size/weight and battery life, the logistics of retrieving data, costs, and ethical concerns are typical for most GPS tracking studies, but the interplay between all the factors mentioned bears additional consideration for the special case of snakes. While this considers GPS units primarily in terms of positional data, it is worth noting that many commercially available units come with additional biotelemetry options, such as accelerometers, magnetometers, light readers, depth gauges, and thermometers, allowing for a wide range of ecological information to be gathered simultaneously (e.g., Hart & Fujisaki, 2010; Brown et al., 2012; Ericsson et al., 2015; Evans et al., 2016; McMahon et al., 2017; Williams et al., 2019; Munden et al., 2021).

While other forms of passive telemetry that can accomplish a higher fix frequency than manual VHF tracking are available, they are not considered here. Argos units use a Doppler-based approach to calculate their position relative to the Argos satellite network, and while they are typically smaller and cheaper than GPS satellite transmitters, the best positional accuracy they can achieve is 150m, and often exceeds 1000m (Argos user manual, www.argos-system.org/manual/), which is unlikely to prove useful in studies on snakes. Light-level Geolocation units rely on sunrise and sunset times to calculate latitude and longitude, and becomes inaccurate if an animal spends time in cover or under cloudy conditions, and have positioning errors that can be up to 100's of kilometres (Werfeli et al., 2021). Another alternative method is automated radio-telemetry, which can calculate positions based on triangulating radio signal strength and direction relative to fixed receiver towers (e.g., Kays et al., 2011; Sperry et al., 2013; Ward et al., 2013; DeGregorio et al., 2018; Gottwald et al., 2019). However, the cost of setting up a new tower network is prohibitively expensive, and becomes ineffective if study animals stray outside of the range of tower arrays. Acoustic telemetry is another option, where units emitting sound waves are picked up by hydrophone arrays (which are easier to move around than large receiver towers) that can pinpoint their location. This has been employed mostly for use on fish, but has also been successful in crocodiles, and some aquatic snakes (Franklin et al., 2009; Campbell et al., 2010; Campbell et al., 2012; Udyawer et al., 2016; Udyawer et al., 2017). However, as this is only effective underwater, it is not fully applicable to the vast majority of snake species.

### 3.2.2 Attachment

How to attach a GPS transmitter safely and effectively to a snake is one of the main difficulties that need to be overcome to improve efficacy of GPS technology. There are currently two main options that can be considered, namely implantation or external attachment.

Implantation is standard practice for snake VHF transmitters and other biotelemetric devices (Reinert & Cundall, 1982; Weatherhead & Anderka, 1984), but implanting devices that use GPS within the body cavity or subcutaneously in a similar manner to VHF transmitters is not as straight-forward, as GPS signal is attenuated by animal tissues and may cause unacceptable levels of signal loss (Smith et al., 2018; Wolfe et al., 2018). Signal loss would result in fix attempts taking longer (and therefore draining battery at a higher rate), failing more frequently, and reduced positional accuracy. Placing the GPS antenna to externally protrude through the skin is a partial remedy to this problem, but creates complications if the antenna becomes caught and pulls the tag out of the body, as was documented in the studies by Smith et al. (2018) and Smaniotto et al. (2020). For increased signal acquisition and accuracy, most GPS devices use patch antennas, but these are not typically streamlined in shape. An omni-directional whip antenna partially solves this issue, as it is able to receive GPS signals from a wider field of view, but at the potential expense of precision and/or accuracy of recorded positions (Telemetry Solutions, CA, USA, pers. comm.).

Another potential issue with implantation is that small GPS tags, often being relatively new and untested technology, can be unreliable, with failure rates of up to 50% (Gau et al., 2004; Hebblewhite & Haydon, 2010; Tomkiewicz et al., 2010; Hofman et al., 2019). This unreliability has to be considered in the context of implantation and associated ethics, as recovering and/or replacing faulty units becomes more difficult when it involves invasive surgery under anaesthesia, and will also lead to more frequent interruptions in data collection. This may be perhaps why the studies that have used this technique opted for subcutaneous implantation over intracoelomic implantation (Hart et al., 2015; Smith et al., 2018; Smaniotto et al., 2020), but subcutaneous implantation is less viable for smaller snake species.

Externally attached telemetry devices have been predominantly trialled with VHF transmitters, using either a sub-dermal stitch to attach the unit to the tail (Ciofi & Chelazzi, 1991; Riley et al., 2017) or by gluing/taping to the skin (Gent & Spellerberg, 1993; Cobb et al., 2005; Figueroa, 2006; Jellen & Kowalski 2007; Tozetti & Martins, 2007; Maritz & Alexander, 2012; Riley et al., 2017; Nash & Griffiths, 2018). Attaching directly to skin is rarely carried out as the unit will naturally be lost when undergoing sloughing, and so only permits data collection for short periods of time. This is in theory a more attractive method when used with GPS devices (as opposed to VHF telemetry) for certain applications, such as studying fine-scale space use with a very high fix frequency over short time periods up to several weeks. Gerke et al. (2020) used tape for attaching GPS units to *Elaphe* spp., as the units were simply to record locations over a short time period to help estimate radiation exposure in the vicinity of the Fukishima Daini power plant in Japan. It is also by far the least invasive method and attachment can be accomplished very quickly in the field. However, the increased chance of losing the units within burrows or aquatic habitats is a serious consideration with the more expensive GPS units.

For longer-term studies, attaching a device externally to a snake without impeding movement, feeding or sloughing and which does not lead to injury is a difficult task. Ciofi and Chelazzi (1991) successfully demonstrated a method involving a small VHF transmitter backpack attached to the tail of *Coluber viridiflavus* via small, subdermally-attached wires leading above the subcaudal scales. Despite apparent efficacy, it was not readily adopted, although Riley et al. (2017) also trialed this method on *Sistrurus catenatus,* finding it superior to glue and tape. The tail is preferred due to the wires, which would restrict feeding if placed around the mid-body, but the diameter of the unit and tail together must be smaller than the midbody, to allow it to fit through tight spaces. Wolfe et al. (2018) chose this method for attaching GPS units to *Pseudonaja affinis,* and despite the units being smaller than the midbody, found the GPS units to still be a hindrance to movement in tight spaces.

While GPS units are potentially interchangeable with the external VHF transmitters used in these studies, they are typically much larger and heavier, which limits them to use on larger species. Though small VHF units may cause few problems from devices becoming stuck, and the skin is able to withstand the forces applied through the subdermal stitch, this does not necessarily translate with bulkier units and stronger snakes, such as large constrictors. Being attached externally means the unit itself could be subjected to considerably more stress than an internally implanted unit, and this may cause a higher rate of failure in the more delicate electronics within a GPS unit.

Conversely to implants, externally attached units can be removed and replaced very easily in the field. Attaching them only requires local anaesthetic, rather than full anaesthesia and associated recovery times. Rechargeable GPS devices could be used with a system that allows the unit to be replaced quickly with minimal handling time, reducing the drawbacks of the larger single use batteries required by GPS units while still allowing for the collection of long-term data at a low cost-per-datum. For example, the method applied by Ciofi & Chelazzi (1991) would allow the nylon threads to be cut, the device removed, new nylon threads threaded through the attached silicon tubes, and a new fully-charged device tied back on in a matter of minutes. Alternatively, a custom-built permanently attached frame could also be conceived, that allows rechargeable devices (or their batteries) to be unclipped, recharged, and clipped back on. For shorter-term studies of movement or behaviour, being able to quickly remove a GPS device, recharge it, and then apply the same device to a new animal would be advantageous for improving sample sizes and increasing cost-effectiveness.

Both methods, then, have pros and cons (table 3.3). One of the main advantages that implants have is that they will typically be less limited in terms of size and shape than an external device, allowing for larger batteries (although still within weight constraints of being less than 3-5% body mass), and therefore longer periods of data collection. Being internal, they reduce the potential complications that external units would create from snagging on vegetation, albeit the external antennas may still pose a problem. External units have the potential to be more flexible in how they are used, and can potentially be at the same time both smaller and longer lasting (if used with rechargeable batteries – see section on battery life, below), but at the cost of more fieldwork and (semi) regular handling, and would necessitate more trial and error to determine efficacy for different species and environments.

*Table 3.3 Pros and cons of potential attachment methods of GPS devices on snakes.*

| | Pros | Cons |
|---|---|---|
| **Internal: coelomic cavity** | • Larger batteries possible<br>• Shape of unit less of a concern<br>• Unit least likely to cause issues to movement | • Signal attenuates under the skin<br>• With an external antenna, will cause greater injury if antenna becomes caught<br>• Invasive surgical procedure<br>• More difficult to retrieve/ replace in case of failure or expiry<br>• Rechargeable units difficult to recharge |
| **Internal: subcutaneous** | • Less impact on body profile than external units<br>• Lower harm to animal than coelomic units if unit expelled from body<br>• Easier implantation and retrieval than coelomic | • Signal attenuates under the skin<br>• Possibly more likely to be expelled through surgical incision than coelomic, especially with external antenna<br>• Size limited to fit under the skin and must be reasonably streamlined<br>• Rechargeable units difficult to recharge |
| **External: glue-on or tape** | • Easy to apply in the field – no anaesthesia necessary<br>• Easy to check on faulty units<br>• Better signal acquisition<br>• Easy to recharge/combine with solar | • Short term studies only – tag lost after shedding<br>• More likely to become entangled in vegetation, etc. This could lead to loss of dermis or even degloving in serious cases.<br>• Size limited and must have a streamlined profile |
| **External: subdermal stitch** | • Only requires local anaesthesia to attach<br>• Easy to check on faulty units<br>• Better signal acquisition<br>• Easy to recharge/combine with solar | • More likely to become entangled in vegetation. This could cause damage to the tail or the piercing location points.<br>• Maintaining open piercing creates more opportunity for infection<br>• May impede use of tail for some species<br>• Size limited and must have a streamlined profile |

### 3.2.3 Habitat

Topology, canopy cover, vegetation density, proximity of buildings and the presence of water all have the ability to negatively impact GPS signals, and therefore accuracy of positions (Frair et al., 2010; Hebblewhite & Haydon, 2010; Recio et al., 2011). Under ideal conditions in a flat landscape with clear view of the sky, the maximum accuracy attainable from typical GPS systems is around 3 metres, but under most conditions accuracy will be considerably less than this (Adams et al., 2013). Habitat related biases are a well-known problem in GPS telemetry (Frair et al., 2004), but are arguably an even bigger issue for non-arboreal snakes. A typical device might be set to attempt to retrieve a GPS signal for 1-2 minutes, after which it will record a failure to avoid depleting the battery. Actively moving animals will increase the chance that a signal is obtainable within this acquisition time by moving into an area with better signal (Graves & Waller, 2006; Heard et al., 2008), but this is less likely to occur for most species of snakes that move far less frequently, and smaller distances. This leads to a dataset that might falsely represent more open areas as more important than they are in reality. For studies that intend to analyse fine-scale resource selection or microhabitat, GPS alone may not be best suited under these conditions, but this can be overcome by maintaining course-scale VHF tracking alongside GPS tracking to overcome these biases (Wolfe et al., 2018; this study – see chapter 4).

Before beginning any study, it is imperative to perform stationary tests of the GPS tags to understand the typical attainable accuracies in different habitat types throughout the study area (Quaglietta et al., 2012; Evans et al., 2016; Fisher et al., 2018; Smith et al., 2018). Not all GPS capable devices are created equal, and may differ considerably in their performance in different environments (Adams et al., 2013; Forin-Wiart et al., 2015). In habitats with typically low signal strength, such as a densely canopied forest, there is typically a trade-off between signal acquisition and accuracy of recorded positions (Frair et al., 2004). Many devices can be set to only record fixes if certain conditions are met; such as the number of satellites in view and relative signal strength. If a device is set with loose parameters regarding fix acquisition, it may be able to record a successful fix under difficult conditions such as in dense forest but such data points might not be a reliable indication of the animal's true location. These errors may be unacceptably large and would need to be filtered from the dataset (most devices provide some level of estimation of dilution of precision) (Laver et al., 2015). Conversely, devices set with overly strict parameters for signal acquisition might never record a fix under these conditions. Some products allow researchers to toggle these parameters to fine-tune settings, while for others this will be hard-coded by the manufacturer and must be decided *a priori*. Several movement-based methods for modelling space use, such as dBBMMs (Kranstauber et al., 2012) or BRBs (Benhamou, 2011), can incorporate spatial uncertainty when creating utilisation distributions. This can be useful to obtain a habitat-dependent average, but it is still difficult to accurately account for microhabitat-related variations when snakes are resting in cover, or behaviour such as coiling, which may further impede signal.

### 3.2.4 Behaviour & Physiology

When it comes to GPS signal, snakes that are predominantly terrestrial have a disadvantage in terms of proximity to the ground. Study animal height has a strong positive correlation with fix success rate. Even being a short distance of a few centimetres above the ground can improve tag performance by increasing the number of satellites within line of sight and reducing interference from ground vegetation (Hofman et al., 2019). A tag setup or habitat that might work well for small terrestrial mammals might not work for snakes. This needs to be accounted for when assessing what devices to purchase, especially if settings that determine how fixes are obtained (e.g., minimum GPS signal required to obtain a fix) are hardcoded and cannot be manually changed by the researcher. Extremely lightweight devices, such as those used for birds, may use hardware that requires good signal, such as very tiny antennas. For primarily arboreal species of snakes, this limitation may be less of a concern, but may still bias locations to when the animal is above ground level. Snakes that exhibit aquatic behaviour pose a problem as GPS signal does not penetrate water (Thomas et al., 2011). While many studies have successfully overcome this on aquatic and semi-aquatic species (Ryan et al., 2004; Mate et al., 2011; Quaglietta et al., 2012; Owen et al., 2016; Dewar et al., 2018; Cochrane et al., 2019; Hart et al., 2021), the unit antenna must be above the water level to record the position, and it may be difficult to attach a GPS in such a way that this occurs with regularity. Many units for aquatic species come with a water switch, turning devices off while they are underwater to save on wasted battery, or on to only record movements when out at sea (at the water surface) (Mattern et al., 2007).

Activity levels of different species of snakes can vary widely between long-ranging active hunters to sit-and-wait, ambush foraging species. Yet all snakes typically exhibit highly sedentary periods, particularly after feeding, undergoing sloughing, in unfavourable weather conditions, or when hibernating, and it is not unusual for an individual to spend a week or more laid up in cover (Brown et al., 2005; George et al., 2015; Lindström et al., 2015; DeGregorio et al., 2018; Smith et al., 2020). If these periods of inactivity occur within a burrow, hollow, or dense vegetation, GPS devices that are set on a regular schedule will continuously waste battery attempting to obtain a fix that is unobtainable due to a persistent lack of GPS signal. Primarily fossorial species are unlikely to be viable candidates for fitting with GPS devices. It should be expected as a general rule for snakes that the percentage of successful fixes will be drastically lower than what is achievable for most other commonly tagged taxa (see table 3.2). If, on the other hand, snakes are sedentary for long periods of time in areas that are able to record fixes, then this biases space-use and habitat selection estimates heavily in their favour, compared to the relatively short periods of time that may be spent moving. Cohen et al., (2018) found this problem for nesting turkeys, and suggested that simply removing these fixes is generally preferable to using a lower fix rate and missing important ecological information despite the waste of precious battery life. The optimal approach would therefore be to configure devices to record fixes at a high rate while the animal is moving, and switch off during sedentary periods (e.g., Brown et al., 2012).

*Table 3.4 Pros and cons of behavioural/physiological traits of snakes.*

| | Pros | Cons |
|---|---|---|
| **Large body size** | • Able to accommodate larger sized tags and therefore longer durations | • More liable to cause self-injury if external tags become stuck/entangled, due to increased animal strength |
| **High activity** | • Easier to obtain regular GPS fixes<br>• Fewer failed fixes and wasted battery life | • Higher activity levels may lead to increased chances of external tags becoming entangled in vegetation<br>• Greater trade-off between need for high fix rate when active, and low fix rate when inactive |
| **Hibernation** | • GPS needed to last for shorter length of time to cover entire season | • Colder climates suffer lower battery capacity<br>• Devices attempting regular fixes while snakes are inactive are liable to waste battery quickly |
| **Terrestrial** | • Less subject to some types of fix bias compared to arboreal/aquatic species | • GPS signal at ground level is typically poor unless in very flat open terrain |
| **Arboreal** | • Better GPS signal acquisition in forest canopy<br>• Fewer failed fixes | • Possibly greater chance of external tags causing issues with movement or becoming entangled<br>• GPS systems are typically poor at calculating vertical height<br>• Locations may be biased towards positions higher in canopy |
| **Aquatic/semi-aquatic** | • Many devices designed for diving mammals and birds can be equipped with a water switch and depth readers.<br>• Options available for obtaining very fast fixes when GPS breaks the surface | • GPS signal penetration of water is very poor<br>• Locations may be biased towards dry land<br>• Long periods of time attempting fixes while in water will drain battery |

### 3.2.5 Device settings and schedules

Most modern GPS devices can be scheduled at a desired fix frequency, ranging between seconds to hours, depending on the behaviour of the research animal and the outcomes required by the researcher. A higher fix frequency will require more battery power, and therefore the higher the fix frequency, the larger the batteries needed in order to last for a given experimental time period (Latham et al., 2015). However, another consideration is what is typically referred to as “time-to-fix” or “time-to-first-fix” (TTF or TTFF), which is the period of time the GPS device takes before calculating its position. With shorter times between fixes, the TTF is also typically shorter, as the device knows roughly where satellites should be. This is referred to as a “hot start”. With fix intervals of roughly three hours or greater, devices have to undergo a “cold start”, where they take longer to locate the satellites and therefore obtain a fix. This can also result in less accurate positions (Moriarty & Epps, 2015). So, while a higher number of fixes will typically require more battery, this does not necessarily scale linearly; doubling the fix rate might not necessarily double the battery consumption if TTF is reduced drastically (Tomkiewicz et al., 2010; Recio et al., 2011; Moriarty & Epps, 2015).

As discussed above, the percentage of successful fixes would be expected to be quite low for snakes. The simplest way to overcome this problem is to increase the fix frequency to ensure that a reasonable number of locations are still achievable, but this will increase battery consumption and reduce the amount of time the tag will last. Ideally, a tag should be optimised to record at a high frequency while the animal is moving, and shut off while it is sedentary and out of signal, in order to maximise the ratio of battery consumption to successful fixes. The most common way this is achieved for most species is to schedule the device to only record (or at higher frequency) during periods when the animal is expected to be active, i.e., duty-cycling (Tomkiewicz et al., 2010; Williams et al., 2019; Price-Rees et al., 2012; 2013). So, for a nocturnal animal, the device is turned off during the middle of the day. However, as the devices available are becoming more sophisticated, it is increasingly common for GPS tags to come with accelerometers as standard. As well as providing valuable behavioural information such as when the study animals are most active, this can be used to optimise the GPS schedule, if periods of activity show some regularity. It is also possible to use the accelerometers to set the schedule so that the GPS only turns on when the animal is moving, and switches off during sedentary periods (Brown et al., 2012). While care and prior experimentation needs to be carried out to determine the threshold values for turning the GPS on, this is likely the best method currently available for optimising fix rates and battery usage. While accelerometers will draw additional power, this is much lower than that required for fixing GPS positions. Accelerometer data depicting activity levels can be extremely useful for troubleshooting to ensure the GPS devices are working as intended, but they also offer a tantalising wealth of information about snake activity, movement, behaviour and energy budgets that cannot be gleaned from positional data alone (Halsey et al., 2011; Williams et al., 2019; Whitney et al., 2021).

Devices are now also available that offer some form of “smart GPS”, which causes devices to switch off very quickly if out of signal, such as when in a burrow. A device with this capability may spend only ~20 seconds searching for satellites before shutting off, rather than continuing to waste battery for the entire fix acquisition time (often two minutes or more) (TechnoSmart, Italy, Pers. Comms). This can also be accomplished using accelerometers that detect if the animal has moved since the previous fix (Telemetry Solutions, CA, USA, Pers. Comms.). Another technology that can help to reduce battery usage was originally designed for use with marine animals, to obtain a position in the brief periods devices break the water surface. Snapshot or Fastloc technology simply records the raw data signals of satellites, without using battery power to compute the tag position, which is calculated in downstream data processing instead. This means tags only need to be switched on for less than a second for each fix, instead of tens or hundreds of seconds. The drawback is that this tends to result in higher location errors (Tomkiwicz et al., 2010; McMahon et al., 2017).

It is likely that for GPS to work effectively on snakes, a lot of effort should be put into analysing device capabilities and the settings that can minimise wasted battery and so make them last longer and/or allow smaller sizes. There are trade-offs in this approach, however (Table 2.5), and so it is important to consider how this might influence the research questions being asked.

*Table 3.5 Pros and cons of different device settings and schedules.*

| | Pros | Cons |
|---|---|---|
| **Long Duration study** | - Lower cost per position obtained<br>- Better representation of animal space use over time | - Larger tags required or frequent recharge/replacement needed<br>- Greater potential for complications arising from external attachment |
| **Low fix rate** | - Batteries last longer | - Individual fixes take longer (cold start) and can be less accurate<br>- Low data resolution<br>- Greater potential for data gaps<br>- Misses important movement behaviour |
| **Duty cycling for active/inactive periods (e.g., day/night cycle)** | - Reduce battery consumption when animal is inactive | - Fails to capture unexpected behaviour (e.g., if escaping from a predator)<br>- Still results in a lot of missed fixes and wasted battery if snake is sedentary for long periods |
| **Accelerometer-informed GPS** | - Only records data when snake is moving | - Careful testing required to set correct threshold and ensure accelerometer performs as required<br>- Autocorrelation of data changes with activity level |
| **Smart GPS** | - Saves battery when snake is out of signal (e.g., in burrow) | - Does not differentiate between sedentary behaviour and moving within dense cover/ out of signal |
| **Snapshot technology** | - Saves battery when recording fixes | - Higher location error<br>- Larger data storage/transfer required |

### 3.2.6 Battery life

For studies on all but the largest animals, battery life is one of the primary considerations before deploying GPS devices in the field (Table 3.6). While efficiency (in terms of power draw) is continuously improving, a study aiming to use GPS instead of VHF will have to contend with the simple fact that battery draw is considerably higher, and therefore will not last as long as a similarly-sized VHF implant (Hebblewhite & Haydon, 2010). As GPS electronics continue to miniaturise, batteries become the limiting factor in study design (Williams et al., 2019). This is particularly critical for small species where VHF tags are already at the threshold of acceptable weight limit (Recio et al., 2011). The type of battery used can dramatically alter the duration and weight required. For example, the minimum voltage required for a GPS unit to function is typically around 1.8 V, and a lithium battery would need to be at least 8g to achieve this, while a rechargeable lithium polymer battery only needs to be ~0.3g. However, a lithium battery has around a 4-fold capacity per gram, so lasts considerably longer for a given weight/size (Toledo, 2015; Holton et al., 2021).

Most GPS devices for other species are single-use, non-rechargeable, and so there is a trade-off between study duration, location frequency, and the size of animal that can be studied (Brown et al., 2012). Very small devices therefore become less cost-effective. While for most studies weight is the primary concern (typically aiming for the device to below 3-5% of the tagged animal's body mass – Latham et al., 2015), just as important a consideration for snakes will be the size and shape of the unit, especially if implanted subcutaneously or attached externally. For example, a large-bodied constrictor that might typically weigh over 5kg at maturity could theoretically comfortably accommodate a 150g transmitter. The reality is that this is likely too bulky, and so a smaller unit is probably necessary than what a GPS tag manufacturer may typically quote. Whether size or weight is the biggest issue for much smaller snakes remains to be seen, but one of the limiting factors may simply be based around what configuration is achievable by tag manufacturers (Holton et al., 2021).

Increasingly, rechargeable GPS units are being utilised, particularly for smaller species such as birds and bats (Thomas et al., 2011; Holton et al., 2021). This ensures units can be redeployed multiple times, either on the same animal or on new animals, increasing cost-effectiveness and sample size (Guthrie et al., 2011). For studies where it is preferable to record data for long periods, such as across seasons, this presents logistical problems for most species, as it requires regularly recapturing study animals in order to recharge or replace the units. Calculating how often this would be required is a function of battery capacity and size, fix schedule, animal behaviour, and the environment it inhabits, so may vary widely depending on study requirements and species. Not only can this be challenging or dangerous in many cases, this also has the potential to impact behaviour. If this option is considered, minimising handling times and performing replacement or recharging of units quickly in the field should be prioritised. For snakes, this option would be more difficult to accomplish with implanted devices, unless it could be demonstrated that having a charging port protruding externally is possible. However, the potential for Lithium polymer batteries to expand or combust when damaged is a serious ethical concern if they are implanted.

Many units, particularly those used for studies on birds, can be outfitted with solar chargers, meaning they can last for extended periods of time (Thomas et al., 2011; Holton et al., 2021). Of course, this is only really feasible with units that are externally attached, and limited to species that can be expected to spend reasonable amounts of time in sunlight (so preventing its use on nocturnal, tropical species that are unlikely to spend long periods of time basking fully in the open). Temperate species that bask in the open regularly are therefore particularly suited to this, but these areas typically experience lower levels of direct sunlight. Preliminary trials using units fitted with light sensors could be a useful way to determine the potential feasibility of solar panels for a particular study species. A reasonable buffer of battery storage would still likely be required to ensure the units can operate between infrequent charges while snakes are remaining sedentary.

A further consideration for the future that might be useful for many snakes is trickle-charging the batteries with a thermo-electric generator. This is not particularly in use with commercial devices at this time, but offers a lot of promise (Lund et al., 2020; Holton et al., 2021). As these devices require temperature changes to operate, this has more potential for implantation in ectotherms than endotherms, but would likely still operate better on external devices (Holton et al., 2021). In temperate climates where snakes are changing temperature due to basking behaviour, this could be extremely useful for extending GPS durations. Similarly, In urban environments, trickle-charging by capturing radio waves could be possible, but would provide limited additional power at present (Song et al., 2016; Holton et al., 2021). Mechano-harvesters are another future option, generating power from kinetic energy, but require vigorous movement, and/or lots of continuous movement to function well (Niroomand & Foroughi, 2016; Holton et al., 2021), which would probably exclude its usefulness in snakes.

*Table 3.6 Pros and cons of different options for batteries in GPS devices.*

| | Pros | Cons |
|---|---|---|
| **Non-rechargeable batteries** | • High capacity<br>• Allows units to be completely sealed | • Units must be larger for long term studies<br>• Units are single use (but can sometimes be refurbished) |
| **Rechargeable batteries** | • Smaller and more lightweight tags possible<br>• Re-deployable to improve study sample size/duration | • Charge does not last as long as equivalent-sized non-rechargeable batteries; shorter study timeframes on a single use<br>• Regular recapture required for recharging in order to study a single animal for a long period |
| **Rechargeable batteries with solar** | • Allow for extremely small sizes of tags<br>• Re-deployable<br>• Can in theory last longer than any other option under optimal conditions | • Not suitable for species that do not spend a considerable amount of time in the open during daytime<br>• Must be placed externally<br>• Rendered ineffective if solar panel becomes dirty |

### 3.2.7 Logistics and data collection

If carrying out GPS telemetry, one of the important questions to ask is how to go about retrieving the data. For very large, wide ranging mammals, the solution is to have the unit transmit the data at regular intervals via satellite, thus essentially removing the need to spend large amounts of time manually tracking in the field. One of the many criticisms of GPS telemetry compared with VHF is that this divorces biologists from the field (Hebblewhite & Haydon, 2010), removing important qualitative understanding of the habitat and behaviour of the study species. This is particularly important for studies wishing to understand microhabitat usage and resource use. This type of satellite-based data relay is not currently widely available for very small units less than around 40g, because the amount of power required is far too high to transmit the data. Additionally, animals that spend large amounts of time out of GPS signal will waste large amounts of power attempting and failing to transmit the data (as well as for acquiring the data). There are additional costs associated with sending and receiving data via satellite. Costs vary, but for example, sending data via Iridium satellite may be around $7.50 per month per unit (Telonics, AZ, USA - https://www.telonics.com/products/gps4/gps-iridium.php).

A lower-power alternative is GPS-GSM (Global System for Mobile communication), transmitting location data at regular intervals via the GSM network. This is only viable in areas where the study animal can be expected to be regularly within GSM coverage, which may be poor in remote areas, and particularly poor close to the ground. Some of these devices are also able to supplement positional readings using triangulation from mobile phone towers (e.g., Pheasey et al., 2020). Costs for data transmission are typically similar to rates for sending SMS messages (Thomas et al., 2011). This can become expensive for wide ranging species such as birds crossing international boundaries, but this drawback is unlikely to be an issue for most studies on snakes.

For smaller units, another common method of data collection is to transmit the data over short range via VHF or UHF (Ultra High Frequency) signals, which can be picked up from a base station placed within range. Transmission can be scheduled to periods when researchers expect to be able to track and locate the animal, in order to reduce battery usage (Thomas et al., 2011). This also allows for the simultaneous collecting of microhabitat data and manual locations for validation of the GPS positions (Hebblewhite & Haydon, 2010). While units with this capability require considerably less power than satellite transmission, it still increases the size/weight due to additional electronics and increased battery requirements.

For optimal battery usage, some studies opt for simple “store-on-board” (SOB) GPS loggers, which have no ability to transmit the data, merely storing the information until it can be retrieved manually upon recapture or after the unit has dropped off (Thomas et al., 2011). This is certainly a realistic option for most snake species, where approaching to within close proximity of a few metres during telemetry work is fairly typical, allowing easy recapture. While many devices for other species come with automatic drop-off, either programmed for after a set interval, or through a segment of material designed to degrade over time, this is unlikely to be relevant in most cases for studies on snakes (although only really viable for external attachments), and often creates further problems from devices failing to drop-off or dropping off too early (e.g., Wyckoff et al., 2007). The main drawback of SOB units is that there is no easy way of checking that the device is functioning as intended until after it is collected. It can become extremely costly to deploy a unit for several months and then discover that no data has been collected (Smaniotto et al., 2020), either because the unit stopped working, or settings were not configured correctly (Holton et al., 2021). This could be offset to a degree if researchers were to choose to use small rechargeable SOB devices that required recharging/changing at regular intervals, as data can be collected simultaneously, reducing the potential for lost data. This mode of operation was very successful on bluetongue skinks (Price-Rees & Shine, 2011; Price-Rees et al., 2013). However, this necessitates regular handling, which may affect any behavioural parameters under study.

While some of the major commercially available data retrieval methods are discussed here (Table 3.7), it is likely that SOB units will generally be the only option available for most snake researchers, due to lower costs and smaller sizes. Other options may only be viable for very large species (e.g., Smith et al., 2018), but new technologies may close the gap. For example, the ICARUS project (Curry, 2018) is designing solar-powered devices as small as 1g that can automatically transmit data to a receiver on board the International Space Station, and these devices could be an excellent option for small diurnal snakes.

*Table 3.7 Pros and cons of different options for collecting GPS data.*

| | **Pros** | **Cons** |
|---|---|---|
| **Satellite transmission (e.g., iridium, globalstar, argos)** | • Data collection and changing settings without required fieldwork | • Large and heavy<br>• Use greater battery power<br>• Require direct satellite communication to send data (habitat/behaviour limited)<br>• Additional costs to send data |
| **GSM** | • Data collection and changing settings without required fieldwork<br>• Lightweight | • Require GSM signal to send data (location and habitat/behaviour limited)<br>• Additional costs to send data |
| **VHF/UHF wireless download** | • Data collection without disturbing study animal | • Manual tracking still required to get to a downloadable distance<br>• Antenna must be external to allow data transfer<br>• Additional equipment costs to download data |
| **Store on board (SOB)** | • Very small and lightweight configurations possible (lowest energy consumption)<br>• Fewer variables for tag electronic failure | • Manual tracking still required to keep track of location<br>• Unit must be physically recovered to retrieve data or perform checks of unit functionality |

### 3.2.8 Costs

GPS devices are typically expensive compared to VHF transmitters. While GPS devices generally reduce the cost-per-datum compared with VHF telemetry, this usually comes at the expense of the number of sampled individuals (Hebblewhite & Haydon, 2010). Failure rates can be quite high for some smaller units, increasing research costs further. For example, Hofman et al. (2019) conducted a survey of researchers using GPS tracking and found that 38% of 123 studies reported a unit failure rate over 50%. While many manufacturers may offer to replace faulty units (if they can be recovered), this still costs valuable research time. To facilitate this, it may be a good option to include a backup VHF implant to improve the recoverability of faulty units (as per Smith et al., 2018), but this increases initial costs further, and would not be possible for smaller species that are already hindered at their weight limit. Options that include remote download of data require additional outlays for base station equipment, while passive transmitters such as GSM or satellite options incur additional costs to send and receive the data.

Most manufacturers of GPS tags for wildlife provide a limited number of standard tag options at various sizes, and development of a new system or housing that encompasses all the requirements for adopting their use on snakes will likely require custom design and manufacture. This will often make the costs of tags especially high, and may only be an option if purchasing a minimum number of units (which may have no guarantee of performing as intended until after testing) (Holton et al., 2021). Many larger manufacturers may consider tag designs for snakes to lack commercial viability at small scales of production. The use of 3-D printed housing, however, does improve the potential for quick and easy customisation and design modifications.

There are cheaper alternatives than custom built-in collars from wildlife telemetry specialists. For example, cheap devices intended for use for personal use, tracking pets or commercial fleets are increasingly available, and may be customised to fit potential needs for use on snakes. Some of these devices are certainly able to achieve similar performance levels as commercial wildlife devices (e.g., Allan et al., 2013; Freeman et al., 2013; Forin-Wiart et al., 2015; Fischer et al., 2018). It is also possible to custom build and program devices from scratch, such as with a Raspberry pi or Arduino, at low cost, but it may be more difficult to achieve extremely small sizes/weights of devices (e.g., Quaglietta, 2012; Foley et al., 2020).

***Table 3.8:*** *relative initial costs of GPS tag types*

| Tag type | Cost |
|---|---|
| GPS- satellite | Decreasing<br>↓ |
| GPS/GSM | |
| VHF/UHF remote download | |
| SOB | |
| Low-cost pet tags | |

### 3.2.9 Ethics

In any study deploying devices onto wild animals, there are potential ethical concerns resulting from the stress of handling, anaesthesia, and the potential for devices themselves to reduce fitness and alter animal behaviour (Bodey et al., 2017). While the many ways this can manifest will not be reviewed here, it is worth considering that many of these concerns are perhaps currently greater for snakes, as this technology has still not been widely applied, or demonstrated to be highly effective for a range of different species. The limitations of attachment options mean that there are many possibilities for complications to arise with external devices or protruding antennas (Smith et al., 2018; Wolfe et al., 2018). It is highly recommended that any study attempting to trial the use of GPS devices in this way ensure that the study animals are regularly checked to ensure there are no unintended negative consequences. There may not be a single solution that is applicable to all species, and until this is reached, it is just as important to document failures as successes, to avoid other researchers repeating the same processes. Bodey et al., (2017) provide recommendations on the type of information that should be included in all biologging studies to be able to evaluate impacts of devices, as this is still sorely missing from a large proportion of studies on all species.

### 3.2.10 Recommendations for best practice

- Perform stationary field tests in various habitat types to determine efficacy of devices and allow familiarity with equipment/software before deploying on snakes, similar to that demonstrated by Smith et al. (2018).

- Similar to the study by Riley et al. (2017), if possible, trial devices on captive animals and observe how the animals move through debris and other obstacles they might encounter in the wild to reduce the possibility of devices causing impediment to movement. Buying a large number of devices at the start of a project would be a risk, as tweaks may be needed to improve attachment or performance.

- Regularly check the study animals in the field to ensure there are no unintended negative consequences resulting from the chosen attachment method, and devices work as intended. Until efficacy can be demonstrated, attaching GPS devices and leaving animals out in the field to passively collect data, as is done for many other studies, may result in unacceptable data losses and ethical concerns regarding animal welfare (e.g., Smaniotto et al., 2020).

- If possible to implement (depending on weight/size of snake), implanted VHF backups (as in Smith et al., 2018) are a good idea to allow the improved monitoring of outcomes in the event of device failure or detachment.

- If purchased devices come integrated with VHF transmitters as standard, ensure these operate on a separate battery circuit from the GPS device, and that they last longer than the GPS, so that units are still able to be tracked and recovered in the event of a device failure.

- Ensure that failures in early prototypes are properly described and published, in order to avoid other researchers repeating similar methods. Making every effort to try to uncover why devices failed is extremely useful for future developments of this technology on snakes.

### 3.2.11 Summary

As costs and device weights fall, the efficiency of GPS devices increases as new options become available. Therefore, GPS technologies will become increasingly feasible for use on snakes and the number of potential use-cases will expand. While the ability to generate more frequent positional data would generally improve studies of movement and behaviour, this must be balanced against acknowledging the limitations inherent in the study of snakes compared with many other taxa. The information presented here is a list of some of the key considerations before undertaking a study on snakes using GPS technology. At present, there is no single “silver bullet” methodology that would be able to address the large majority of cases, and researchers will have to carefully weigh the costs and benefits of different options, and make compromises, in order to determine what might work best within their study system, if at all.

In finding ways to develop this technology to a point that it can have widespread potential for different snake species for long term tracking, it seems prudent to first consider larger species for trialing GPS transmitters, as they can accommodate larger devices (Smith et al., 2018; Smaniotto et al., 2020). More demonstrated successes here would then allow adoption of miniaturised systems for smaller species. Studies that require only short-term positional data may particularly benefit from adoption of GPS technology, and this may also be a route into further pioneering its use. Development of a GPS device and attachment system that can reach an acceptable compromise between maximising the amount of locational data while minimising ethical concerns and equipment costs is therefore imperative to allow the advantages of using GPS technology to be fully embraced by snake biologists.

## *3.3* Case study: Trialing the use of GPS tags on *Malayopython reticulatus*

### 3.3.1 Aims and Objectives

At the outset of the project, the intention was to test and implement low-cost, externally mounted GPS units that could provide long-term fine-scale spatial data for between 6 months to a year in dense tropical forest, where signal acquisition is considerably more difficult. The attachment methods, device settings, and tag types were modified over time to overcome shortcomings of previous iterations. The aims of this study were to evaluate tag retention and any damage occurring to the animals in the process. The nature of trialling single units meant that evaluations had to be carried out subjectively, and units were removed immediately if they appeared to cause discomfort or damage to the animals.

### 3.3.2 Methods and Results

I describe here the methodological development of using external GPS tags on reticulated pythons (*Malayopython reticulatus*), adopting the “sub-dermal stitch” method employed in a small number of other snake studies (Ciofi & Chelazzi, 1991; Riley et al., 2017; Wolfe et al., 2018), and shown to be a relatively successful method of attachment, with no evidence of causing long term harm. I considered that implantation was too risky, especially given the difficulties of performing invasive surgery under anaesthetic in a remote field station (Anderson & Talcott, 2006), and the difficulty for removing faulty units. A secondary consideration was that quotes from various Wildlife Telemetry companies for implantable tags were generally considerably higher (up to US$7,000 per unit) than for external units

(US$100-1200 per unit). Most of the units used within this study were custom-made to specification, and the added cost of this was compounded by the need to test efficacy of single units before making bulk purchases.

The study species appeared a good choice for trialing GPS tags, owing to their large size, leaving fewer restrictions on tag size and weight, and allowing collection of long-term data for a previously little studied species in its natural habitat. As Hart et al. (2015) had reported range distribution sizes of Burmese pythons in Florida to average 22.5km$^2$, necessitating the use of helicopters to aid tracking, manual VHF tracking seemed likely to fail when carried out on foot. GPS data would allow for continuous location data even if animals were missing for long periods of time. Further, successful deployment on a species so difficult to study, in dense tropical habitat, would lead to much wider demonstrated applicability for the use of GPS on other species of snakes in a wide variety of situations.

Five distinct phases of GPS tag design and implementation were used, hereafter referred to as phases 1-5 (Table 3.8). Phase 1 consisted of development and testing of tags that met the original specifications (above), without *a priori* knowledge of python behaviour, nor of some of the considerations of what was feasible in the field. This was, in essence, using relatively large units that could last for up to a year, with remote download of location data. Phase 2 encompassed the development of a system that would allow smaller, lighter tags with rechargeable batteries, and without remote download (SOB – Store-on-board), to be deployed and easily swapped non-invasively in the field, within a more flexible package, to allow it to move more naturally with the animal's tail. Phase 2 was a result of better understanding of the feasibility of python telemetry, GPS capability in the field, and, predominantly, ethical considerations. Phase 3 continued in the use of these smaller removable and rechargeable units, but attempting to find an improved, novel way of attaching external units. Phase 4 involved improved material design and durability of external tags using 3D printed shells, as well as continuing to try to improve attachment and a quick replacement system. Phase 5 involved the use of SOB micro-GPS loggers, coupled with accelerometers. A detachable system was abandoned in favour of recharging units directly on the animal in the field at regular intervals.

*Table 3.9 Specifications of the different tagging options that were used during this study.*

| Tag | Telenax | AWT 1 | AWT 2 & 3 | Neoprene pouch 1 & 2 | Piercing 1 | Piercing 2 | Piercing 3 | 3D-printed casing | Technosmart |
|---|---|---|---|---|---|---|---|---|---|
| **Phase** | 1 | 1 | 1 | 2 | 3 | 3 | 3 | 4 | 5 |
| **Tag Manufacturer** | Telenax | AWT | AWT | Perdix | Perthold & Perdix | Perthold & Perdix | Perthold & Perdix | Perthold & Perdix | Technosmart |
| **Model Number** | TGB-327/311B (custom) | Custom | Custom | Custom | Cat-Log-S | Cat-Log-S | Cat-Log-S | Cat-Log-S | Axytrek |
| **Dimensions (mm) (LxWxH)** | 62x53x36 | 91x42x33 | 73x52x23 | 110x28x15 | 130x35x18 | 150x35x20 | 170x35x20 | 133x38x20 | 50x20x15 |
| **Mass (g)** | 145 | 120 | 120 | **** | 58 | 85 | 100 | 65 | 15 |
| **Length of external antennas (mm)** | 113 | 153 | 220 | N/A | N/A | N/A | N/A | 215 | N/A |
| **Batteries for GPS tag circuit** | 2 x AA | 2 x AA | 2 x AA | 2 x 1100mAh LiPo | 750mAh LiPo | 750mAh LiPo | 750mAh LiPo | 750mAh LiPo | 300mAh LiPo |
| **Satellite positioning system** | GPS and GLONASS | GPS | GPS | N/A | GPS | GPS | GPS | GPS | GPS |
| **GPS antenna type** | Omni-directional whip antenna | Patch antenna | Patch antenna | Chip antenna | Patch antenna | Patch antenna | Patch antenna | Patch antenna | Patch antenna |
| **Positional schedule** | Every 3 hours | Every hour | Every hour | N/A | Every 30 minutes (9:00UTC – 23:00UTC) | Every 30 minutes (9:00UTC – 23:00UTC) | Every 30 minutes (9:00UTC – 23:00UTC) | Every 30 minutes (9:00UTC – 23:00UTC) | Every 30 minutes (9:00UTC – 23:00UTC) |
| **Fix attempt duration (secs)** | 90 | 120 | 120 | N/A | 120 | 120 | 120 | 120 | 120 |
| **VHF type** | Built-in | Built-in | Built-in | Separate | Separate | Separate | Separate | Separate | Separate |
| **VHF duration** | 20-25 months | ≥12 months | ≥12 months | ~12 months | ~12 months | ~12 months | ~12 months | ~12 months | ~12 months |
| **Remote download** | Bluetooth™ | UHF | UHF | GSM | N/A | N/A | N/A | N/A | N/A |

#### 3.3.2.1 Phase 1: Non-rechargeable remote download tags

***Methods***

In collaboration with wildlife telemetry companies, I designed custom GPS satellite tags that were attached externally to the tails of adult *M. reticulatus*, adapting the VHF attachment protocols of Ciofi and Chelazzi (1991). Tags were designed so that the height and width of the unit, when attached to the tail, was narrower than the diameter of the snake's midbody, in order to prevent units becoming caught in vegetation. Tag mass was below 150g. Conservative recommendations that tag mass should be no more than 3% of a reptile's mass meant that this allowed tags to be used on animals above 5kg (Weatherhead & Blouin-Demers, 2004). Tags were designed to last one year with hourly fixes (24 spatial fixes per day). Tags allowed for remote download of data in the field, as sending data remotely via satellite required too much added weight from additional batteries, and using the global system for mobile communications (GSM) was not considered due to low network coverage in the study area. To aid with tracking and remote downloading of data, VHF radio transmitters were also included within the units on separate electronic circuits, which also enabled units to be recovered if the main tag circuits should fail. Tags were purchased from two different companies, Telenax (Mexico) and Africa Wildlife Tracking (AWT) (South Africa). The differences between these units are shown in Table 3.8.

Before deploying units attached to animals, stationary tests were conducted under different habitat conditions to ensure efficacy at ground level within typical habitat found in the study area, and ensure devices were functioning effectively, similar to that described by Evans et al. (2016). Tags were placed in reference locations for a period of 24 hours to test efficacy under semi closed canopy, closed canopy, within a hollow log, and under dead leaves and vegetation. 'True' positions of the reference locations were taken by averaging 30 positional readings from a handheld GPS. Accuracy of locations was determined by Euclidean distances of GPS tag readings to this position. While positional error was typically less than 30m under semi-closed canopy, readings were less accurate under closed canopy and vegetation, while no fixes were successful inside the hollow log.

There were two slightly different protocols for attachment of the first tag (Telenax) and for the three subsequent tags from AWT. For the first tag, a sterile 18G hypodermic needle was used to create two small transverse punctures through the tissue of the tail, located ventrally so as to avoid the spinal column and the caudal vein. The anterior-most piercing was located 22 caudal scales posterior to the cloaca, so as to avoid possible damage to sexual organs and associated musculature (Ciofi & Chelazzi, 1991). An 18G cannula was passed through the puncture holes, with carbon-coated steel fishing wire (minimum breakage strength 50kg) passed through the lumen. 2mm diameter silicon tubing was then threaded onto the wires, and this was superglued to the cannulae, to create a seal protecting the skin from the wire. The wires were then passed through pre-drilled holes in the tag, and tied on top of the tag, with a metal crimp sleeve. The python was kept in captivity for three days for monitoring, and Gentamycin cream (0.3% - Noripharma SDN. BHD.) was applied daily to prevent infection. Subsequent tags were attached in a similar manner, except that 2mm silicon tubing was passed all the way through each of the two puncture wounds, and medical cerclage wire (0.7mm diameter for two of the tags, and 0.5mm diameter for one) instead of steel wire was passed through the tubing. Instead of predrilled holes, these tags had protruding metal loops built in. After fastening the wires on top of the tag, they were sealed with fast drying epoxy resin to reduce the chance of them getting caught in vegetation. These animals were kept in captivity for between seven and nine days before being released, to allow the puncture wounds to completely heal, observe any potential negative effects caused by tag attachment, and allow acclimation to the devices.

*Figure 3.1 Phase 1 tags after attachment to python tails. The Telenax unit is top left, while the other three were manufactured by AWT.*

### ***Results***

Telenax

The bulky shape of the device contributed to it becoming regularly stuck in vegetation, and over time this caused damage to the tail at the attachment points, causing minor tears in the skin and muscle. The tag was removed immediately, wounds were treated and the animal released. Further modifications to improve streamlining in subsequent models were not made, due to the GPS failing to properly record data, even in open habitat, and the Bluetooth download not functioning as advertised.

AWT 1

The GPS tag initially appeared to perform well, and was a much-improved shape, with little sign of the attachment method causing issues, but experienced some programming malfunctions, and was set to be replaced after 3 months. However, upon capture, it was clear that the tag had become stuck in vegetation one or two days prior, and caused some minor tears in the skin and muscle. The wounds were treated and the animal released. The design was modified to reduce the height of the tag, in an effort to reduce the likelihood of the tag becoming caught.

AWT 2

The GPS tag stopped working before the animal was released from captivity. A replacement was ordered, and the decision was made to continue to track the animal in the field using solely VHF until the unit could be replaced, as the VHF operated on a separate circuit. However, the tag was found unattached after the first day post-release. The 0.5mm wires were both snapped, and clearly not strong enough to handle the stresses placed upon the tag.

AWT 3

After initial success, the tag developed a fault that prevented remote download of data. I captured the animal to attempt to manually reset the tag, but found on close inspection that the tag had started to rub considerably around the pierced holes, so it was removed. The wounds were treated and the animal released. I decided to switch companies, and use tags that were lighter, with a lower profile, and able to flex with tail movements.

#### *3.3.2.2 Phase 2: Neoprene backpack with SOB tags*

***Methods***

For phase 2, I intended to use smaller, rechargeable GPS loggers, with more limited capabilities, and separately purchase small VHF transmitters, and place them together within a hand-made package that would remain attached to the python, but allow the loggers to be easily removed, swapped, and then recharged and the data downloaded manually. Dimensions were to be limited to a width of 35mm, and a height of 15mm, in order to minimise the profile, but length was less restrictive. Based on the results from phase 1, these tags were intended to record positions at 30-minute intervals throughout the night, to better record short-term movements between cover, for 29 fix locations per day, and to last on a single charge for a minimum of 30 days (assuming a maximum 120 second fix time for every fix attempt), so that pythons would only have to be captured monthly to change tags, in order to minimise disturbance as best as possible. I purchased a single unit from Movetech (British Trust for Ornithology, UK). This unit was intended for use on seabirds, and was unpotted, consisting solely of a printed circuit board and Lithium polymer batteries. To make the unit waterproof, it had to be placed within heat-shrinkable tubing, and the ends sealed. Application of heat would then unseal the ends, allowing the data to be downloaded and the batteries recharged. Additional GPS loggers were also ordered from Perthold Engineering (Germany), but manufacture and shipping for both tags was considerably delayed. Therefore, before deploying the GPS loggers, I tested the efficacy of a lightweight flexible pouch, within which the tag and separate VHF transmitter (US$117, Perdix Wildlife Supplies, UK) would eventually be placed.

This pouch was constructed from two pieces of 2mm breathable neoprene foam, which were shaped and stitched together to create a cylinder, with the anterior end formed into a cone, and the posterior end open to allow placement of transmitters. The anterior end was then sealed through the addition of glued and stitched strips of Velcro™. Anterior and posterior holes were made to allow wires to be threaded through, and these were reinforced with metal eyelets. The stitched edges and anterior end of the pouch were sealed and reinforced with clear epoxy. As there was the possibility of the neoprene becoming wet and blocking GPS signals to the unit, a rectangular hole was cut into the dorsal piece of neoprene, and this was covered with a shaped piece of clear epoxy 2mm thick, to create a “window” that also provided some structural strength and dorsal protection to units placed inside.

For testing purposes, the VHF transmitter was placed in the anterior portion of the neoprene pouch, and the presence of a GPS logger was simulated using wood and cardboard of the same dimensions and weight sealed within heat-shrink tubing. The same method of attachment and animal recovery was used as in phase 1, but with carbon coated steel fishing wire instead of cerclage wire, which was passed through the holes, and tied together and sealed with metal crimp sleeves. The knots and crimp sleeves were then rotated so that they sat inside the pouch, rather than externally. Two of these pouches were tested simultaneously on two different pythons, which were tracked and located every other day in order to see how well the pouches were able to withstand field conditions, and to ensure that they caused the animals no problems.

*Figure 3.2 Prototype flexible neoprene pouch design used in phase 2. The top and front can be seen to be reinforced with epoxy resin.*

### ***Results***

#### Neoprene pouch 1

The pouch showed considerable signs of wear after one month attached in the field. The wires had not torn the skin and muscle as with the larger tags, but there was evidence of considerable rubbing on the outside of the skin and loss of some scales, due to the increased flexibility the tag allowed.

Neoprene pouch 2

Results were similar to pouch 1, but additionally the dummy GPS tag had become lost, indicating that the Velcro used would not be strong enough to contain the device. Usage of flexible pouches appeared to mostly solve the problem of having the wires pulling through the skin, but created the new problem of rubbing away the scales from the continuous movement of the wires. I decided to look for an alternative attachment method to the wires; creating a solid attachment point to the skin, but without rubbing, and spreading pressure more effectively to the outside of the tail, rather than internal tissues.

#### *3.3.2.3 Phase 3: Metal piercing attachment points with SOB tags*

***Methods***

Phase 2 was relatively unsuccessful, as the increased flexibility created alternative attachment issues by increasing the potential for wires rubbing the skin, and so I instead focused on a way to prevent tags that catch on vegetation from applying force to the suture openings. Large solid tags pulled the wires dorsally and posteriorly, while flexible tags rubbed the skin and opened up the suture holes. The potential solution was to find a way to have any force resulting from the tags applied externally, rather than pulling on internal musculature and connective tissue, and having the pressure spread more evenly across the entire circumference of the tail, rather than focused on the suture holes when wire was used. I settled on adapting commercially available body modification piercings to achieve this, as they could be ordered to a desired shape and size, and the material (surgical stainless steel) was already specifically designed to be pierced through skin and to be body-safe.

I purchased “circular barbells” made of 2mm diameter surgical stainless steel, with 6mm diameter threaded ball ends, of various sizes between 16mm and 26mm internal ring diameter from two different online companies (Wildcat.EU, Germany; Bodyjewelleryshop.com, UK). The ball ends prevented the piercings from falling out, and also provided anchor points to attach tags to. The piercing rings were attached to pythons by creating transverse subdermal piercings laterally on each side of the tail, and when the rings were passed through, the balls ends were located dorsally and exterior, while the ventral portion of the rings were also exterior, resting lightly against the subcaudal scales. The ring size was carefully selected beforehand, to ensure that it fitted closely to the subcaudal scales, but without constricting blood flow to the tail. To prevent the ball ends from unscrewing, a drop of cyanoacrylate glue was used inside the threads, prior to attachment of the tag. Pythons were monitored in captivity for several days after the piercings were attached, and iodine solution and gentamycin cream applied topically to prevent infection. Once it was clear that the piercings were not causing any undue problems, such as inflammation or infection, and had been allowed to heal, the tags were attached.

I used different GPS loggers (Perthold Engineering, Germany), which cost only US$80 each, and were already shown to be comparable in performance to the more expensive commercially built-in GPS collars available from other commonly used wildlife telemetry companies (Forin-Wiart et al., 2015). Initially, these were packaged with VHF transmitters, within heat shrink tubing, to both improve water resistance, and allow them to be attached. After the ends were sealed, two holes were drilled through the sealed portion of tubing front and rear, and strengthened with metal eyelets. Nylon fishing wire was then used to tie the tags onto the piercing rings, behind the ball ends. A drop of cyanoacrylate glue was then applied to the knots to prevent them from coming undone. I subsequently modified this considerably, as the heat shrink tubing, despite a high tensile strength, was prone to tearing where the holes were drilled. I glued the sealed package to a length of woven synthetic belting, 30mm wide by 140mm long, using epoxy, and then encased the entire package in epoxy, shaping it to be streamlined. The rear portion of the heat shrink tubing was not encased, so as to allow the seals to be accessed to place a charging/download cable. Instead of front and rear piercings, I opted to attach the tag only anteriorly, but use two piercings at the front, spaced 15mm apart to spread any potential strain. Four holes were therefore cut in the synthetic belting, and reinforced with metal eyelets. The synthetic belting would therefore allow a degree of flexibility between where the tag was glued and the attachment holes, to allow the tag to move out of the way if encountering an obstacle (Knapp & Owens, 2005), and give the tail greater freedom of movement. The epoxy was found to not adhere properly to the synthetic belting, however, and so a further improvement was made by attaching the unit to the belting using a strip of stainless steel and steel rivets, prior to encasing in epoxy resin. Improvements were also made in the attachment of the belting to the metal piercings, using commercial brass fishing swivels (allowing flexible movement) and small nuts and bolts, which would facilitate quick removal and replacement of the units. An angled metal sheathing was also included at the front in order to help prevent the screws from becoming caught on vegetation.

During this phase, a large 3m x 3m outdoor enclosure was constructed and equipped with refugia and a number of branches, in order that units could be tested and animals observed prior to release, particularly when manoeuvring around obstacles. It was hoped that this would also allow for acclimatisation to the unit before hard release.

***Figure 3.3*** *Showing how the steel piercings were placed under the skin for phase 3. The ventral portions of the rings were kept on the exterior of the tail, to allow any pressure to be applied to the outside of the skin, rather than inside. Top right: A GPS logger and VHF transmitter sealed in heat shrink tubing attached to the piercings.*

***Figure 3.4*** *A later development during phase 3, placing two piercings frontally, and securing them to the unit using screws and fishing swivels, rather than wire. The VHF and GPS logger have been placed within a far stronger housing, attached to flexible belting.*

## ***Results***

### Piercing 1

I was unable to effectively test how the piercing method works. The animal was only tracked for two days, and the tag was found detached from the animal on the second day. The issues appeared to be with the materials used to encase the tag, rather than the piercings themselves. It appeared that the front set of wires attached to the piercing had managed to be removed over the ball bearings, leaving only the rear attached. The tag had then become caught, and while the heat shrink housing had been tested for tensile strength, it was found to have relatively low shear strength, and ripped off. I therefore set out to create a tag that was far more resilient, and would prevent the possibility of the wires slipping over the ball bearings. I decided that based on recent successful efforts at tagging Sunda pangolins (E. Panjang et al., Cardiff University, unpublished data), and a paper on external attachment methods on iguanas (Knapp & Owens, 2005), I could modify the piercings to create redundancy at the anterior end, in case of a wire failure, while also allowing for greater flexibility of tail movement, and allow the tag to move around obstacles with more ease.

### Piercing 2

The tag again did not stay attached long enough to adequately test the efficacy of the piercings. The first day of tracking post-release, the tag was found detached. The epoxy-coated logger and VHF housing had peeled completely away from the synthetic belting that was attached to the piercings. I had tested a prototype to see how likely it was to fail, and could not peel the epoxy away from the belting without the use of a hammer and pliers. While the tag was built in the exact same manner as this prototype, the epoxy clearly did not fuse with the belting as adequately for the tag itself.

### Piercing 3

This tag was first tested attached to a python in the external enclosure described above for a week. The tag itself was engineered well enough this time that it did not fall apart, so the metal piercings could be evaluated properly on this occasion. However, by using metal components to strengthen the tag, the weight (~100g) was considerably close to the original units from phase 1. The decision to allow the unit more freedom to move resulted in considerable twisting, which rotated the piercings. These were therefore removed and the animal released. While it was possible that an additional piercing at the rear of the unit may have been one way to solve this problem, the potential problems associated with this attachment in the case of units falling off meant that it was abandoned, as wire had proven considerably more effective previously.

#### 3.3.2.4 Phase 4: 3D printed casing with SOB tag

***Methods***

Stainless steel piercings proved ineffective, and this was abandoned as a method of attachment. Instead, I sought to attempt to modify the original wire and silicone tubing used in phases 1 and 2 so as to spread wire tension. As forces applied to previous tags appeared to be primarily in the anterior-posterior direction, a 'harness' design was created anterior to the tag position. The wire was inserted vertically on lateral sides of the tail, joined externally on the ventral side, in a similar manner to the steel piercings. The wires were then passed under the skin again dorsally in the posterior direction, before being tied to the front of the unit. In order to reduce pressure being applied to entry/exit locations, shaped and drilled pieces of custom-made clear epoxy-coated neoprene were using as spacers both dorsally and ventrally. This was intended to convert the direction of pressure applied to the wires so that they clamped externally onto the tail on the dorsal and ventral surface, thereby considerably spreading pressure over a greater surface area. A further incision was made midway along the tag with similar wire and spacers applied, to reduce lateral movements and twisting. A final wire was placed at the rear of the tag casing, threaded through another spacer, but not passed beneath the skin, only looped around the tail to further ensure the tag remained snugly fitted.

A new prototype tag casing was designed using CAD software and 3D printed using PLA plastic. The VHF transmitter was placed at the front, with the antenna running through to the rear, and this was sealed with epoxy putty. The antenna was placed into silicone tubing and sealed using silicone sealant to reduce water ingression and to strengthen the antenna integrity. The GPS was housed within the casing, with a lid attached and removed with four metal screws. Holes were placed into the tag for wire attachment to the tail, with lateral grooves to reduce protrusion.

Subcutaneously implanted VHF transmitters (AI-2, Holohil Systems Ltd, Canada) were also employed at this point as a backup, in order that spatial data could still be collected for the project under the assumption that an effective GPS tag design would not be found, and so as to ensure recapture was still possible if the tag became detached.

An alternative configuration was also designed, with the VHF transmitter and GPS logger within separate housings, jointed together to allow increased flexibility, but this was never implemented.

*Figure 3.5 Highlighting Phase 4 tag casing design and attachment. The anterior attachment consisted of a "saddle" intended to spread any forces created by the tag being caught on vegetation. Epoxy spacers were used ventrally with the wires to further reduce any force on a single location. GPS loggers could be quickly replaced within the casing by unscrewing the lid.*

***Results***

3D printed casing

The use of a 3D printed casing ensured a strong, lightweight, resilient, standardised, and easily modifiable method of keeping both GPS logger and VHF transmitter secure. At the same time, I wanted to try to test a way to improve upon the attachment methods from phase 1. As previously, this was first tested in the outdoor enclosure for one week, during which it became clear that the rear-most wire (which was not attached to the skin) provided little benefit, as the animal was able to unhook its tail, so this was removed. There were no concerns at this stage, so the animal was released into the field. However, after less than two weeks in the field, it was clear that the new method of attachment was considerably worse than previous attempts; the saddle became loose and had started to rub away at the scales beneath. The unit was removed, the piercing points disinfected, and the animal was released. Additionally, the datalogger had stopped working and no data was recoverable.

#### *3.3.2.5 Phase 5: SOB Micro-GPS tags with accelerometers*

***Methods***

Various attempts at creating a system for quick detachment and exchange of SOB loggers inevitably led to packages that were still fairly large. As the attachment protocols of the tags in phase 1 had been effective for between 2-3 months, I considered that similar attachment but with considerably smaller and lighter units might be a more effective solution. Technosmart (Italy) make very small and efficient tags, predominantly for use on seabirds, which come equipped with “smart GPS” to prevent battery drainage while animals are in burrows, and can record accelerometer data, in order to trigger the GPS only when the animal is moving. The drawback of using a rechargeable tag attached as in Phase 1 is that the unit must be recharged while remaining on the animal, but this was felt to be relatively achievable with a short recharge time if the python is kept calm within a snake bag while the charging cable was attached.

Tags came with small metal loops for attachment, and strong nylon (rated to 50kg) thread was threaded through silicon tubes and attached at the top of the tag, and sealed with quick drying epoxy. Two 15g tags were ordered, with the intention of trialing one with and one without a plastic spacer, similar to those used in phase 4, but made of much thinner, clear PET plastic. However, only one with the spacer was able to be trialed, owing to logistical constraints resulting from the 2020 pandemic. The tag had no inbuilt VHF transmitter, and tracking was accomplished with the use of a subcutaneously-implanted VHF (Holohil SI-2). This was the trade-off in terms of being able to collect the GPS if it became detached, versus the increase in size and weight resulting from the addition of an external VHF transmitter. The tag was set to the same schedule as the previous SOB phases, with 29 fixes between dusk and dawn. The accelerometer was set at 1Hz. After a trial period to establish the baseline data, it was intended to be set to only record positions when movement parameters exceeded a threshold value (i.e., only when the animal was moving), thus improving battery usage, but it was still able to record around 900 fix attempts on a single charge.

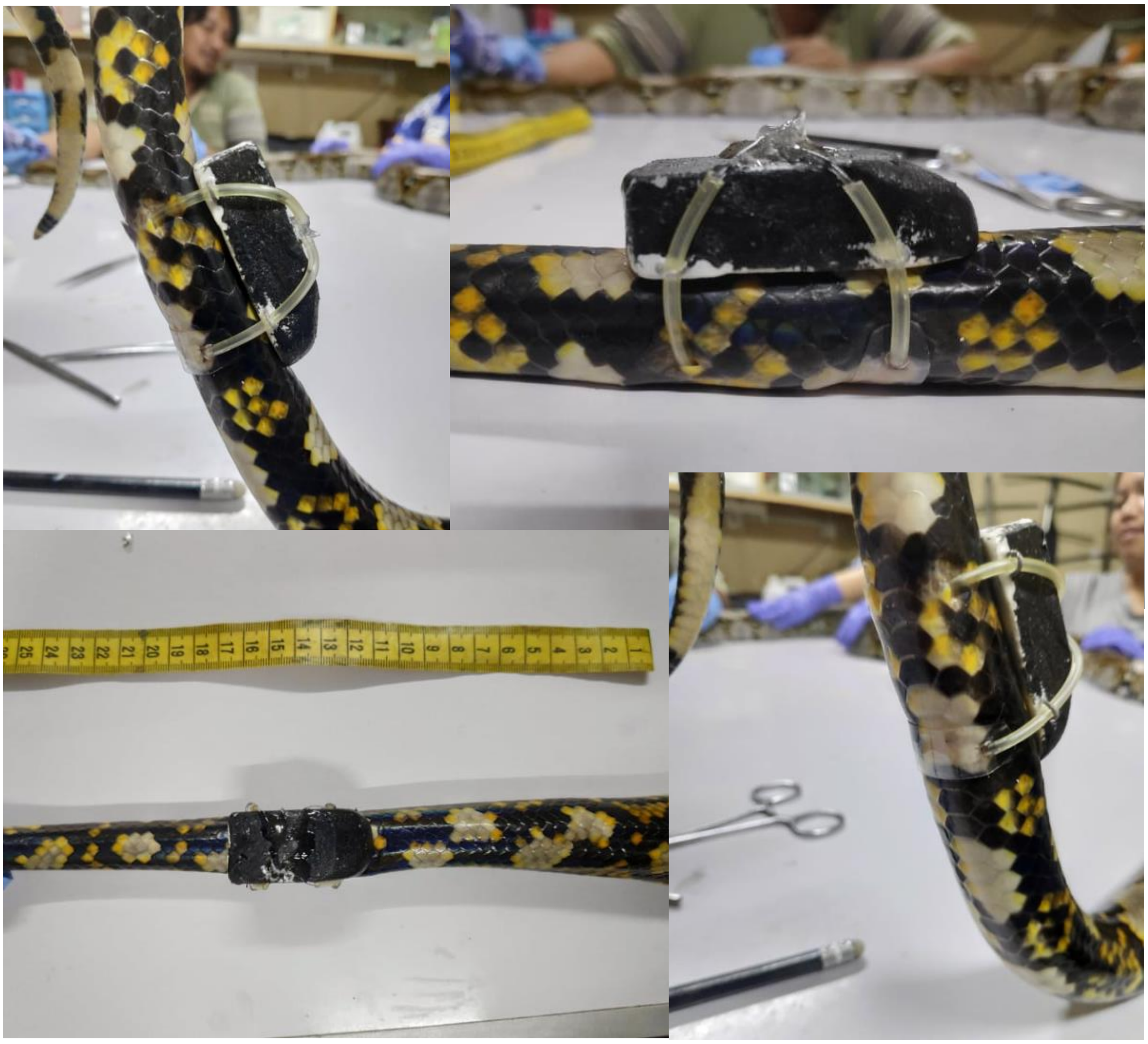


***Figure 3.6*** *Technosmart SOB GPS tag used in phase 5. The tag was considerably smaller than previous designs. The clear plastic spacer can be seen fitted snugly to the ventral side, to prevent too much tension occurring at the suture site.*

***Results***

Technosmart GPS logger and accelerometer

One of the GPS tags was attached to a python that had previously been tracked with VHF for around 8 months. This meant that it would be possible to see if the additional external tag caused any changes in behaviour. After the first check-up around 3 weeks post-release, it was found that the plastic spacer, intended to reduce pressure around the incision site, was itself catching on the ground and rubbing the skin. It was thus removed, and tracking continued with just the implanted VHF transmitter. The python had spent the majority of the tracking period in underground burrows, and the tag had apparently not recorded any fixes during movements in the open between these locations. The “Smart GPS” turns the tag off quickly when there is no signal, but eventually turns it off completely for long periods if this lack of signal continues, rather than continuing wasted attempts at the designated fix schedule. Attempts to attach the units to other tracked animals were hampered by cessations in tracking resulting from severe flooding and the 2020 pandemic, so the device was never fully tested with an accelerometer switch, nor without the plastic spacer to see if this was an improvement for attachment.

#### *3.3.2.6 Ethics Statement*

Permission for this study was granted by the Sabah Biodiversity Centre. All procedures for attaching of external tags and post-attachment monitoring were carried out with the assistance and supervision of qualified veterinarians. Local anaesthetic (Lidocaine) was injected prior to insertion of sutures for tag attachment, and prophylactic doses of intramuscular anti-inflammatories were provided to all research animals post-procedure. Utmost care was taken to ensure animal welfare was a priority, and tags were immediately removed if deemed to be causing injury or undue irritation. In these cases, animals were kept temporarily in captivity for assessment, and any wounds resulting were treated topically with disinfectant (iodine and gentamycin cream), and given intramuscular anti-inflammatories and/or antibiotics as necessary. The animals were then re-released at their original capture location once the veterinarian was satisfied that no further complications would occur.

### 3.3.3 Discussion

In any study that seeks to involve the manipulation of live animals, it is just as important to document failures as successes. Publishing bias is still prevalent in many areas of science, including conservation (Knight, 2009), with successful studies considerably more likely to be published than failures. Due to the difficulties associated with successfully attaching GPS devices to snakes, thorough reporting of failed attempts is vital to ensure that future researchers have all the available information required to make informed decisions. While many studies may report new methods for attaching devices to animals in novel ways, they may often fail to adequately document the processes that led to the development and testing of these methods, and it may therefore be assumed from a majority of the literature that experimental methods are often immediately successful. As an anecdotal example, I have been told of researchers gluing GPS devices to the mid-body of large constrictors, and abandoning the research, due to causing serious injury to the study animals (Telemetry Solutions, pers. comm.). Another study in the US attempted gluing GPS loggers to the rattles of rattlesnakes, and the rattles came off after a few days to a few weeks. While not so serious to animal welfare, the research was abandoned after running out of funding (A. Bentley, pers. Comms.). At the time of writing, these studies remain unpublished, and it is therefore conceivable that others may attempt similar methods, particularly as simply gluing devices has been shown to be a viable method in other reptile species, especially turtles (e.g., Hart & Fujisaki, 2010). Luckily, a separate study (Riley et al., 2017), while not experiencing negative consequences quite so severe, reported how they were forced to abandon their planned use of glue as an attachment method in their study due to the negative impact it had, and try other methods. Compiling these kinds of data together would be extremely beneficial in moving towards more viable methods that can bring the study of snake spatial ecology in line with the exciting advances being made in other taxa.

External tag attachment methods using a subdermal stitch have been shown to be successful (at least in terms of showing minimal negative consequences for study animals) in smaller species than *M. reticulatus* (*Hierophis viridiflavus* - Ciofi & Chelazzi, 1991; *Sistrurus catenatus* & *Pantherophis guttatus* - Riley et al., 2017; *Pseudonaja affinis* - Wolfe et al., 2018). Based on this information when this project began, scaling up to larger snakes seemed a conceivable prospect that would allow for the collection of novel high frequency location data of an understudied species. However, it is clear that in *M. reticulatus*, at least, and probably also in similarly–sized constrictors, this is not the case. The forces exerted by these animals are considerably higher than in smaller species of snakes, while the strength of skin and muscle tissue in the tail does not scale in the same manner. Rattlesnakes fitted with tags were shown to stop and carefully move their tails around obstacles if they became caught (Riley et al., 2017), but from limited observations of *M. reticulatus* in which I observed tags snagging on vegetation, the animals appeared to simply continue to pull away, ignoring any apparent discomfort this might cause. I did not carry out controlled tests of animal’s responses to the tagging in a controlled semi-natural environment, because the purchasing of multiple tags simultaneously and locating multiple study animals in a short period of time was not feasible. I opted instead to closely monitor the animals in their natural environment, and remove the tags at the first sign of them causing complications, with the aid of monitoring from qualified veterinarians. For later phases of tagging, I constructed a small outdoor enclosure to monitor the tag attachments and python responses to them. This allowed the cessation of one design before deployment in the field. However, adequately representing the variety of microhabitats that these animals experience in the study area, such as grasses, plantations, dense vines and swamps, within a contained enclosure, would have been difficult to accomplish in a limited field setting. In addition, pythons may not exhibit the same range of behaviours in a captive setting as in their natural environment, and tags that appeared to cause no hindrance in the enclosure were nonetheless unsuccessful in the field.

I do not advocate the use of the sub-dermal stitch method in large constrictors with similarly-sized tags as those used in this study (during phase 1), although with smaller devices with lower profiles it may still be viable. As GPS tags become smaller, more efficient, and batteries with increased efficiency are developed, this potential only increases. I have found, at least in the case for these very large and strong snakes, that shape and cross-sectional area of external tags are a far more important consideration than weight, which is the primary limiting factor in many studies using GPS devices on small animals (Tomkiewicz et al., 2010).

In seeking a viable long-term attachment method and tag design for these animals, considerable compromises had to be made, including costs, logistics, and the type of data to be collected. Cost is extremely important as funding was limited for this study, but also developing a relatively low-cost solution would have the additional benefit to highlight the technology as an economically viable method, as well as technically feasible, for a wider number of studies that may have limited budgets. Expensive custom-designed implanted tags were therefore not considered, and it was also felt this would introduce too many issues, including performing surgery under anaesthetic in a field setting, and potential complications if the tags had a potential to be ripped out and leave large wounds in the mid-body (Smith et al., 2018). The primary costs of GPS tags are the hardware (and associated software development), so testing tags with smaller batteries increases the cost-per-datum considerably, as costs do not scale with tag size. Tags that use solar panels to overcome the battery weight issue are widely available, particularly for use on birds, but as *M. reticulatus* are primarily nocturnal, this was not an option in this case, but may be for diurnal species, especially ones that exhibit basking behaviour in temperate habitats.

The battery requirements in this study shifted throughout the development of different tags, partly due to the different hardware capabilities, and upon gaining more understanding of python behaviour, realising the type of data that was possible. Without any prior similar studies on the species, it was initially impossible to say how easy it would be to use simple GPS loggers, and replace or recharge them regularly, and not be able to remotely download the data, so I initially opted for tags that would potentially last an entire year. While in hindsight this was the wrong option, valuable information was gathered during tracking, and it became clear that smaller loggers were a reasonable option, and that recapturing pythons regularly was not too difficult. As the cost of these SOB loggers is considerably less, if an animal is lost or a tag breaks, losing the data stored on board is offset by the fact that a much larger number of tags are affordable. However, the associated cost of this to the animal is that it must be regularly restrained in the field to change the tags, potentially modifying behaviour and causing additional stress. Due to the fact that any future tagging efforts would require regular capture to inspect the tag attachment sites, it was deemed acceptable, as long as a system was designed that would allow tag replacement to be accomplished very quickly in the field, without the need for transporting back to the field centre. These commercial SOB loggers (CatLog – Forin-Wiart et al., 2015) were less than US$100 each (although separate VHF units also had to be purchased) and performed well in stationary tests, making them a very attractive option. But as they came with no holes or hooks to attach them, designing a housing or attachment system with the limited materials available proved challenging. Eventually, the housing had to be made so robust that it largely negated the size and weight advantages these smaller tags afforded.

Seeking telemetry companies that were willing to develop custom housing designs at a reasonable cost for testing in small numbers was difficult, as this has reduced profit margins, and limited the options available for this study. This had a knock-on effect that it often took considerable time waiting for tags to be designed and manufactured. Additionally, not all GPS tags are made equally, and some tags failed to adequately record positions in dense tropical habitat, or to survive the stresses of the hot and humid environment, despite having proven reliability in other studies. In changing manufacturer several times, this induced further time constraints on developing a viable attachment method. Two of the tags from AWT provided some data (see chapter 4), even though the attachment method did not last as long as hoped, and all three AWT tags developed faults very early on. The tags provided by TechnoSmart (Italy) might have proved more successful, especially if applied to pythons inhabiting oil palm plantation, as there is less structurally complex vegetation. However, only a short field trial was able to be carried out before disruptions from flooding, and denied access to the plantation due to COVID-19 pandemic protocols before my field work ended meant that this was not fully tested. These tags were US$750 each, and the decision not to attach a VHF to them was a risk if the tags became detached. However, as this allowed them to be smaller, it likely reduced the risk of becoming detached in the first place. Using plastic spacers to reduce pressure and rubbing of the wires on the incision sites seemed reasonable, but did not work as intended. This may still be a way to make long-lasting external GPS tags more viable on other species, but it is very difficult to get them to the exact size required, as they must be tight enough to provide support and prevent catching on vegetation, but not so tight that they prevent sloughing of skin.

In the end, I was not able to fulfil the aims of this study, as none of the devices tested functioned or remained attached as intended. Nevertheless, this serves as a valuable lesson highlighting the difficulties associated with adapting GPS technology for use on snakes. External attachment likely is best employed for shorter duration studies, and this also allows more freedom for very high frequency positional data. In essence, a tag design that works in one study or for one species will most likely not be the best option in another, and various factors must be considered properly and tested thoroughly before large numbers of devices are deployed in the field. Given sufficient time and resources, it should be possible to build on the work carried out here and in the few other studies that have attempted to use GPS, perform larger scale initial experiments into attachment options, and develop a system that is able to offer novel insights and improve our understanding of the behaviour and space use of snakes.

# 4 Slithering Through Time and Space: Movement and Space Use of the Reticulated Python, *Malayopython reticulatus*, in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Borneo.

## 4.1 Introduction

For any animal species, movement is a complex process, arising from a need to find food, shelter, mates, and to avoid predators (Nathan et al., 2008). Understanding what drives these processes, and their associations with habitat characteristics and other parameters, is an important part of understanding a species' ecology (Demšar et al., 2015). Telemetry is increasingly being used as a tool to accomplish this goal, as it allows for the study of individuals, their spatial and habitat requirements, and their behaviour across spatio-temporal scales (Hebblewhite & Haydon, 2010; Tao et al., 2016). This information is crucial for species conservation, with habitat use playing a major role in population management (Cooke, 2008). Often one of the primary aims of telemetry research is to define a species' home range, or utilisation distribution (Buchin et al., 2015). Although the former term is often used synonymously for both, a home range is often defined as the area traversed by an animal during its normal activities (Tao et al., 2016), while a utilisation distribution extends this with the probability of finding an animal in any given area (Buchin et al., 2015). In an attempt to standardise the nomenclature, it has recently been suggested that studies differentiate between a *range distribution* and an *occurrence distribution* (Fieberg & Börger, 2012; Fleming et al., 2016; Horne et al., 2020; Signer & Fieberg, 2021). A range distribution is synonymous with the traditional concept of home range, being the full extent of an area that an animal is expected to inhabit, while an occurrence distribution describes the space use and movement path of an animal within a specific window of time. Occurrence distributions can allow for comparison of areas traversed over time (e.g., between seasons), but the distinction between the two terms also ensures that studies do not refer to home ranges when animals have not been tracked for long enough to reach a stable estimate (or asymptote), which would lead to under-estimates of area size.

Very High Frequency (VHF) radio-transmitters have been one of the principal methods for understanding snake ecology over the last 40 years, as snakes are usually cryptic and secretive, and can in some cases be dangerous to handle (Shine & Bonnet, 2000). While this allows for studies examining aspects of ecology including microhabitat use, thermoregulation, breeding ecology, neonatal dispersal and mortality, studies on home range and movement are more common. Snakes occupy a diverse range of niches, and so inferring generalisations regarding snake movement and home ranges as a whole are difficult. Macartney et al., (1988) failed to find any general trends among snake home ranges, but a more recent review inferred a positive correlation between body size and home range sizes, which was more apparent among active predators than ambushers (Todd & Nowakowski, 2021). Males usually tend to move more than females, owing to behavioural differences during the breeding season (Macartney et al., 1988; Fiedler et al., 2021) when males travel larger distances to seek out females. This disparity tends to be greater in warmer regions such as the tropics (Fiedler et al., 2021; Todd & Nowakowski, 2021). However, large disparities can exist within the same or closely related species (Fiedler et al., 2021) (see Table 4.1 for a summary of home range studies on Pythonidae), meaning that studies seeking to apply data from single studies to other areas within a species' range may not be appropriate.

There are currently very few studies on snakes involving the use of GPS technology to study snake movements and habitat requirements at very fine spatio-temporal scales (but see Hart et al., 2015; Smith et al., 2018; Wolfe et al., 2018; Smaniotto et al., 2020; Gerke et al., 2021; chapter 3). Some studies have demonstrated the use of finer scale data with novel methods, such as automated radio tracking systems (Sperry et al., 2013; Ward et al., 2013; DeGregorio et al., 2018), but this does not yet have wide applicability. Possible reasons for the lack of studies involving GPS devices include: difficulty of attachment, high costs, and low levels of activity in many species (chapter 3 provides a more in-depth discussion of these issues). For large, relatively active snakes such as the reticulated python, *Malayopython reticulatus*, there may be considerable benefit to utilising GPS technology as a telemetry tool to better understand animal movement (discussed in chapter 3). One limitation of VHF transmitters is that considerable amounts of field work are required for obtaining a relatively low number of data points; for example, many studies on snakes only collect positions at a rate as low as one or two locations per week (e.g., Pearson et al., 2005; Croak et al., 2015; Crane et al., 2021). For elucidating long term range distributions, or as a tool for measuring other aspects of snake biology (e.g., thermoregulation or breeding ecology: Stahlschmidt et al., 2012a; Stahlschmidt et al., 2012b), this may be sufficient, but generally precludes analysis of fine-scale movement and behaviour. GPS technology may be advantageous for answering research questions of this nature, but owing to the limited demonstrated usage on snakes, studies systematically assessing the benefit relative to traditional VHF telemetry techniques have not yet been carried out.

Alongside developments in tagging technologies, recent years have seen an increase in the number of movement modelling methods designed for high temporal frequency GPS-driven datasets, in order to understand movement decisions, habitat preferences and behaviour at finer and more accurate levels (e.g., Brownian Bridge Movement Models (BBMM) – Bullard, 1999; Biased Random Bridges (BRB) – Benhamou 2011; Dynamic BBMMs (dBBMM) – Kranstauber et al., 2012; Time Local Convex Hulls (T-

LoCoH) – Lyons et al., 2013; Autocorrelated Kernel Density Estimators (AKDE) – Fleming et al., 2015). However, these methods have not yet been widely adopted by herpetologists, despite clear evidence that Minimum Convex Polygons (MCP) and density-based kernel (KUD) methods are often unsuitable, e.g., including areas not traversed by the animals in home range estimates (Row & Blouin-

*Table 4.1 An overview of range distribution sizes of different Pythonidae species from radiotelemetry studies. Where daily movement rates were also given, these are included as well. Most studies used 95% MCP (Minimum Convex Polygon). If means were only calculated individually by sex, this is denoted in the table as F (Female) and M (Male). Studies that only refer to movement rates or other aspects of spatial ecology, and not home range sizes, are not included here.*

| Species | Number of radio-tracked animals | Mean home range estimate from MCP (ha) | Mean daily movement (m) | Study |
|---|---|---|---|---|
| **Diamond python (*Morelia spilota spilota*)** | 15 | F = 17.35<br>M = 43.03 | - | Slip & Shine, 1988 |
| **Carpet python (*Morelia spilota variegata*)** | 19 | 22.5 | 15 | Shine & Fitzgerald, 1996 |
| **South-western carpet python (*Morelia imbricata*)** | 91 | 17.6 | 14-21 | Pearson et al., 2005 |
| **Green python (*Morelia viridis*)** | 27 | F = 6.21 | - | Wilson et al., 2006 |
| **Carpet python (*Morelia spilota*)** | 17 | 4.6 | 4-30 | Corey & Doody, 2010 |
| **Diamond python** | 12 | F = 23.3<br>M = 41.3 | - | Michael et al., 2013 |
| **Burmese python (*Python bivittatus*)** | 4 | 95.7 | - | Rahmen et al., 2014 |
| **Burmese python** | 16 | 2,250 | 40-180 | Hart et al., 2015* |
| **Burmese python** | 7 | F = 99<br>(from dBBMM) | - | Smith et al., 2021 |
| **Burmese python** | 25 | F = 282<br>M= 675 | 20-140 | Bartoszek et al., 2021* |
| **Scrub python (*Simalia amethistina*)** | 27 | 38 | 9.8 | Natusch et al., 2022 |

*Study was in non-native range.

Demers, 2006; Bauder et al., 2015; Walter et al., 2015; Stark et al., 2017; Noonan et al., 2019; Silva et al., 2020; Crane et al., 2021; and see chapter 3). dBBMMs appear particularly promising for use with reptiles, as they are more robust to irregular data than some other methods and can cope with the long sedentary periods typical of many species, which often bias kernel smoothing parameters (Fieberg, 2007). Despite being intended for use with high-frequency telemetry data associated with GPS collars, Silva et al. (2020) showed that this estimation method is still viable for reptiles at the coarse temporal scales typically associated with VHF telemetry and outperformed all other methods at all temporal scales analysed, minimising both omission and commission rates. Omission errors occur where location points fall outside of the estimated area (Type II error), while commission errors refer to the inclusion of large areas where no locations have been recorded (Type I error). Several recent studies have also demonstrated use of dBBMMs for snakes, on king cobras and Burmese pythons, in the same field site in Thailand (Silva et al., 2018; Marshall et al., 2020a, Smith et al., 2021; Jones et al., 2022). However, highly irregular times between locations, or rapidly altering frequencies of locations may still lead to them failing to perform adequately (e.g., Natusch et al., 2022).

Studies of anthropogenic effects on the spatial ecology of snakes have come increasingly into focus. While habitat change threatens a large number of reptile taxa (Cox et al., 2022), there are many species of snake that can adapt to urban or agricultural areas, and even provide benefits to humans as predators of pests, although this proximity may also increase conflict. Species that regularly inhabit agricultural, fragmented, or urban landscapes often move less or have smaller occurrence distributions (Blouin-Demers & Weatherhead, 2001; Mitrovich et al., 2009; Corey & Doody, 2010; Carrasco-Harris et al., 2020; Bauder et al., 2020; Marshall et al., 2020a). Where snakes generally avoid active agriculture, this can distort range shapes due to moving along field boundaries (Reading & Jofré, 2009; Nordberg et al., 2021). However, for species with very small home ranges, levels of fragmentation and urbanisation may have little effect on range size (Anguiano & Diffendorfer, 2015). Understanding how these species are able to persist or disperse between populations in the face of anthropogenic change is important both for conservation and management efforts.

As ectotherms, snake behaviour is often dependent on ambient weather conditions, particularly considering the effects of temperature on thermoregulation and metabolism (Peterson, 1987; Brown et al., 2002; Bryant et al., 2012; Crowell et al., 2021). In warmer climes, range sizes are typically larger (Todd & Nowakowski, 2021), possibly due to cold temperatures being less common and allowing more frequent movement, as well as less seasonality. A review of snake literature in temperate areas (Eskew & Todd, 2017) found that temperature tends to be positively correlated with snake movement and activity, while precipitation tends to be negatively correlated. The level of moon illumination is also often negatively correlated with snake activity, but this is more variable between species.

Understanding how weather and other environmental variables may impact movement of snakes can be important for considering survey methods for population estimates due to changes in detectability (e.g., Asad et al., 2021). They may also play a role in understanding how anthropogenic climate change and disruption to weather patterns may alter species ecology (Huey et al., 2012; Crowell et al., 2021).

The reticulated python is a widespread species, found throughout tropical Southeast Asia, from Eastern India to Indonesia and the Philippines (Kasterine et al., 1991; Stuart et al., 2018). This region as a whole is experiencing very high levels of deforestation and fragmentation, particularly in the pursuit of palm oil (e.g., Koh & Wilcove, 2008; Gibbs et al., 2015; Gaveau et al., 2016; Vijay et al., 2016) (see chapter 1). As the species is highly adaptable and found in a variety of habitats, it is highly influential with the potentially large majority of vertebrate species found in the region as a whole (both as a predator and as prey), many of whom are highly threatened (Shine et al., 1998a,b). Obtaining baseline information about movements, activity patterns and space requirements using telemetry is therefore vital to indirectly benefit the understanding and conservation of other species, as well as for reticulated pythons themselves (Natusch. et al., 2016a,b). Reticulated python individuals are regularly found in oil palm plantations; they appear to be able to survive, and possibly even thrive, in rapidly changing landscapes (Kasterine et al., 1991; Natusch et al., 2016a). However, the effects and outcomes of living in plantations on their ecology are essentially unstudied, and thus poorly understood. Comparing population and density patterns within forests and plantations is hindered by exceptionally low detection rates (see chapter 2), but telemetry techniques could allow the comparison of behaviour and habitat requirements between these two contrasting landscapes (Anguiano & Diffendorfer, 2015). It may also be possible to elucidate factors required for successful plantation management to encourage pythons (Doherty & Driscoll, 2017), as reticulated pythons appear to primarily feed on rodents (Shine et al., 1998b), and so have considerable potential as natural pest control, which in turn could reduce the needs for rodenticides. The Lower Kinabatangan Wildlife Sanctuary (LKWS) (figure 1.3), consisting of degraded and fragmented forest lots, joined by riparian forest corridors and surrounded by commercial palm oil plantations, all easily accessed and surveyed by river, is therefore an ideal model study site to begin to explore these complex relationships.

This study aimed to estimate the occurrence and range distributions for *M. reticulatus,* and to test for differences in space use between individuals inhabiting forests and those in forest corridors or plantations. The original intention of developing suitable methods for using GPS telemetry to achieve these aims was relatively unsuccessful (see chapter 3), and so this study instead relied on VHF radio telemetry. The specific aims were to: i) estimate occurrence distributions from VHF telemetry data using dBBMMs, and contrast the results between plantations and forest, including ii) modelling occurrence distributions to estimate mean range distributions at asymptote, iii) model how environmental variables correlate with movement, including potential differences in response between plantations and forests, and iv) provide a small case study examining the potential for GPS tracking data to alter estimates of occurrence distributions and movement.

## 4.2 Methods

### 4.2.1 Capturing pythons and transmitter attachment

For detailed survey methods and study area description, see chapter 2. In tandem with these surveys, GPS (n=9) and VHF (n=17) tags were attached to pythons either found in the study area, or that were rescued by the Sabah Wildlife Rescue Unit (WRU) and translocated to the study area. Details of GPS tag design and attachment, as well as surgical protocols are given in detail in chapter 3. VHF tags were implanted subcutaneously.

Initially this was carried out with AI-2 (Holohil, ON, Canada) models with tapered ends, designed to last a minimum of 18 months. However, these proved too large for subcutaneous implantation, and so smaller SI-2 units, lasting a minimum of 12 months, were used instead. Initially these were implanted following the methods outlined by Smith et al. (2018), where a transverse incision was made on the side of the body around a third of the way anterior to the cloaca. A pocket was created posterior to this incision for the transmitter, while the antenna was fed subcutaneously anterior to the incision. The transmitter was attached in place by anchoring to a rib with non-dissolvable suture.

Subsequently, this method was improved upon by creating the incision laterally on the side towards the dorsum, so that the transmitter and antenna were both placed beneath the incision. This ensured less mud and other debris was able to enter the incision wound during healing. It also reduced the potential for the antenna and transmitter to place pressure directly on the incision site as the animal moved. To prevent the antenna coiling up around the transmitter, two additional small incisions were made along the length of the antenna, and the antenna was anchored loosely to ribs, which kept it roughly in place while allowing movement back and forth beneath the skin during sinuous movement.

After implantation, pythons were kept under observation for 1-3 days within before being released back at their initial capture location. The intention was to have all individuals tracked for a minimum of one year, with external GPS tags or implanted VHF tags removed before batteries failed. Any animals that exhibited signs of tags causing discomfort or irritation had the tags removed (under anaesthesia in the case of implants) (see chapter 3).

### 4.2.2 Telemetry

Daily radiotracking of the GPS-tagged pythons (which also contained VHF transmitters) was carried out usually between 08:00 and 11:00, or between 14:00 and 16:00 by a team of at least two researchers, between November 2016 and July 2019. For pythons implanted with VHF tags alone, tracking was carried out on alternate days between 07:00 and 12:00, or between 13:00 and 17:00, between February 2018 and August 2021.

As pythons are predominantly nocturnal, all positions recorded were of daytime resting locations, in an effort to minimise disturbance. A directional VHF "H" antenna (Model number RA-23 - Telonics, Inc.) and VHF transceiver (Model number R1000 – Communications Specialists, Inc.) were used to locate the animal, and its position was recorded using a handheld GPS. It was usually possible to fully home in on the animal; however, in cases where it was not possible to gain access (usually due to flooding or deep swamps), the location was recorded by triangulation from three different locations. Wherever possible, positions were recorded at or below 5m accuracy (as given by the handheld device precision), remaining stationary close to the animal until this positional accuracy was achieved, which was necessarily longer in dense, closed canopy areas. Descriptions of microhabitat were recorded, and an attempt was made to get a visual confirmation of the animal without disturbing its resting location. Locations were marked with biodegradable flagging tape, and to further reduce disturbance, if an animal remained in the same location as the previous day, a recording was not taken, and the previous positional reading was used.

The distance at which it was possible to identify signal in dense forest varied widely, but typically only exceeded 200m if the animal was sheltering in a tree. While an attempt was made to keep all telemetry as close to a regular schedule as possible, this was not always possible. In some cases, tracking was interrupted due to inclement weather, inaccessibility of forest due to flooding or the presence of elephants, inaccessibility of plantation due to protocols during the 2020 Covid-19 pandemic, or temporarily losing the animals if they had moved an unexpected distance and could not be relocated the same day near to their previous position. The tracking regime of 48-hour intervals was thus designed to allow the simultaneous and standardised tracking of multiple animals, and on days where an individual(s) could not be located within a reasonable timeframe, the days in-between allowing for searching for them more thoroughly while minimising disruption to the schedule.

### 4.2.3 Statistical Analyses

Data analysis was carried out in R (v. 4.0.2; R core team, 2020), using RStudio (v. 1.1.456; RStudio team, 2020) while maps were created using QGIS (v.3.4). For all linear and additive models used, checks on residuals were carried out with the R package *DHARMa* (Hartig, 2020), assessing uniformity of distribution, dispersion, presence of outliers, autocorrelation, and distribution across individual quantiles. Continuous variables were assessed for multiple collinearity prior to inclusion in models by checking the variance inflation factor (VIF) using the *olsrr* package (Hebbali, 2020), and a VIF of greater than 4 was used as the cut-off. Significance of individual variables were assessed with likelihood ratio tests by comparing models with and without the variable of interest. Model estimates were calculated with the package *ggeffects* (Lüdecke, 2018), and visualised with *ggplot2* (Wickham, 2016).

*Movement distances*

Average daily distances moved were calculated by summing Euclidean distances between all points and dividing by the number of tracking days. Step lengths, i.e., the distance between successive locations, were calculated using the R package *amt* (Signer et al., 2011), and then filtered to remove instances where individuals had remained stationary. Tracks (defined as a series of steps) were regularised to provide values for every 48 hours (± a tolerance of 12 hours), to ensure that different sampling regimes did not bias these values. This separates tracks into “bursts”, which identifies time gaps above or below the nominated threshold, and divides an individual’s track into subsections, thereby ensuring that large time gaps do not bias movement metrics by being treated the same as the standard time gaps (as a longer time between positions allows for a greater distance to have been travelled).

A generalised linear mixed model (GLMM) examining step length, with gamma errors and log link was fitted with sex, habitat, and translocation status as fixed categorical effects, and individual as a random intercept. While the model fitted by *lme4* (Bates et al., 2015) returned a warning of singular fit, this was also true of a null model with just random effects, so appeared to be due to 0 difference in intercept estimates between two or more individuals.

*Occurrence distributions*

Dynamic Brownian bridge movement models (dBBMMs) were used to assess space use of all telemetered pythons tracked continuously for at least 21 days (n = 16, excluding nine individuals that were fitted with GPS or VHF tags. See Table 4.5). For preparation and generation of data, the packages *readr* (Wickham et al., 2020b), *data.table* (Dowle & Srinivasan, 2020), *dplyr* (Wickham et al., 2020a), *lubridate* (Grolemund & Wickham, 2011), *sp* (Pebesma & Bivand, 2005), *rgdal* (Bivand et al., 2020), *rgeos* (Bivand & Rundel, 2020), *adehabitatHR* (Calenge, 2006), *amt* (Signer et al., 2011) and *move* (Kranstauber et al., 2020) were used. The packages *ggplot2* (Wickham, 2016), *ggspatial* (Dunnington, 2020), *ggthemes* (Arnold, 2019), *scico* (Pedersen & Crameri, 2020), and *scales* (Wickham & Seidel, 2020) were used for creating necessary figures. The analysis pipeline was adapted from code originally provided by Smith et al. (2021) and Marshall et al. (2020a;b). As dBBMMs model GPS error in the estimation, all positions recorded by VHF were set at 5m, unless points were recorded by triangulation, in which case the error was increased and estimated appropriately based on the distance between triangulation points. dBBMMs modify estimations of spatial uncertainty at each location (similar to a smoothing parameter for kernel estimation) by estimating Brownian motion variance ($\sigma^2$m) to correspond to underlying movement behaviour. While a BBMM takes an average for an entire dataset, dBBMMs modify the value for each data point by identifying changes in movement/behavioural state (Kranstauber et al., 2012). The calculation requires setting a sliding window size, corresponding to the maximum number of locations over which a single behavioural mode might be expected to remain the same. A 'margin' is also required, and estimates within the margin are compared to the entire window to identify sudden changes in behaviour, as a sliding window alone would lead to smoothed out $\sigma^2$m estimates. The values for the window and margin must be odd numbered, since model likelihood is calculated via a leave-one-out validation approach to provide the best estimate of $\sigma^2$m at each location. As the data used here showed that reticulated pythons can remain stationary in one location for up to three weeks, the window size was adjusted to reflect this based on tracking frequency for each animal. For a tracking regime of every other day, window size was set at 11, corresponding to 22 days, while for those tracked daily, window size was increased to 21. A margin of 3 was used in order to detect movement changes over two successive data points. Rasters of utilisation distributions were converted to polygons at the 50, 95 and 99th percentile contours, for ease of plotting and extent calculations.

As dBBMMs cannot calculate a distribution or $\sigma^2$m for the first and last set of unique points within the margin, the first three and last three points (i.e., the margin size) are generally not included, but this extends to many more positions if the animal was stationary over multiple days (Kranstauber et al., 2012). To account for this and reduce the loss of data, three pseudolocations were added in hourly steps before the first location and after the final location for all individuals, i.e., the first and last location was repeated three times in the dataset. To make these positions unique, a random amount of noise was added to simulate a small degree of positional inaccuracy, corresponding to only a few centimetres. This meant that spatial distribution estimation areas could cover the entirety of the real, observed data. While a dBBMM is robust to missing datapoints or irregular data (Kranstauber et al., 2012), the area that could have been traversed between two successive locations becomes very large if the time between them is too great, essentially oversmoothing the distribution area and leading to large commission errors. During data collection between January 16th and February 26th, 2020, an unusually large flooding event occurred in the study area, preventing access to interior forest and plantations to track tagged animals. Therefore, for individuals tracked after this date (n=4), utilisation distributions had to be calculated separately before and after. Where there was overlap between distributions before and after, rasters were combined and the area size recalculated for the individual, and where overlap did not occur, the area sizes were added together.

For comparison with other range distribution studies, 95% and 50% kernel utilisation distributions (KUD) and 95% minimum convex polygons (MCPs) were calculated using the package *adehabitatHR* (Calenge, 2006). Least-squares cross-validation for bandwidth (h) values in KUDs was only minimised for 6 of the 16 individuals, so the standard reference bandwidth method was used ($h = \sigma \times n^{-1/6}$, where $\sigma = 0.5 \times$ the standard deviations of the x and y coordinates). Additionally, KUDs were also calculated using the mean of these reference values, to provide a standardised bandwidth across all individuals.

### *Model validation*

Bootstrapped MCPs were used to assess whether occurrence distributions had reached asymptote, calculated within the package *move* (Kranstauber et al., 2020). Repeat locations (e.g., from spending multiple tracking days in a single location) were filtered from the dataset, and the MCP was calculated at logarithmic stepwise increases in the number of locations, which were randomly sampled from the full dataset. This is repeated 100 times, and provides the mean estimated MCP from all 100 repeats (with quartiles). For example, this provides 100 MCP estimations from 5 random locations, 100 from 8 locations, and so on. If the resulting curve flattens out (reaches asymptote) then this provides reasonable plausibility that the full range distribution of the individual has been traversed. Not all individuals were tracked for sufficient periods of time to be able to reach this asymptote, which is required to give unbiased comparisons of range distribution size between different groups. Rather than remove all individuals that did not reach asymptote, estimates of 99% dBBMMs were analysed with general additive models (GAMs) with gamma errors and log link, and the number of days of tracking was incuded as a spline term, with habitat type (forest/plantation) and sex as categorical explanatory variables. These were assessed separately owing to the low number of data points. The GAMs were modelled using the package *mgcv* (Wood, 2017). As there were only two individuals that utilised a mixture of the two habitats (and only for short periods), they were removed from the dataset. The two translocated individuals were also removed from the dataset to prevent the bias they may cause due to having a significantly higher rate of movement than resident pythons. Significance of explanatory variables was calculated with *emmeans* (Lenth, 2022).

Bootstrapped MCPs were also used in a similar manner to the dBBMM estimates. The mean bootstrapped MCP values were used as the dependent variable in a general additive mixed model (GAMM) with gaussian errors and an identity link. A thin-plate spline term for the number of locations was used, and a random intercept for individual (as each individual had repeat estimates), with habitat and sex as explantory categorical variables. As MCPs had to be calculated without repeat locations, and are point-based rather than time-based estimators, the number of unique locations was used as the main explanatory variable rather than number of days. Significance of terms was calculated with likelihood ratio tests.

### *Motion variance*

dBBMMs provide a measure of motion intensity (motion variance; $\sigma^2$m) for each location. These values were extracted and plotted as a time series to visualise movement rates; these values can provide insight into behavioural changes (Smith et al., 2021). To assess potential correlations in motion variance between individuals, the four forest pythons that were tracked simultaneously between 25-April-20 and 15-December-20 were assessed for synchronicity in motion variance values. Locations for all four were almost always carried out on the same day, but any days missing for a single individual were removed for all four. Two-tailed Pearson correlation was carried out using the R package *synchrony*. This uses Monte Carlo randomisations of the data to provide a test of significance, and 1000 randomisations were carried out in two different manners. Type 1 randomly shuffles the values for each individual, destroying the autocorrelation structure and cross-correlation between individuals, while type 2 shifts the values along by a random amount, which keeps the autocorrelation within each individual intact.

### *Case study of GPS-tracked pythons*

Two pythons (Nicknamed Cahaya and Juling) were fitted with external GPS devices that produced a useable number of GPS positions. Both of these pythons were rescues that were translocated to the study area. The device attached to Cahaya recorded 71 GPS fixes, while the device attached to Juling recorded 112. Other devices that were trialled (see chapter 3) either failed to record any fixes due to tag failure (except one that only recorded 4 positions in 30 days) or were not kept attached for long enough to achieve a space-use estimate (n = 2, one and two days of data collection, respectively). Both devices were set to record positions every hour, but due to an early malfunction, Cahaya’s unit attempted fixes every 131 minutes. The number of days between day of release to the day each device stopped recording fixes was 67 for Cahaya and 34 for Juling. Therefore fix success rate was roughly 4.4% (71/1608) for Cahaya (or 9.6% if taking the 131 minute malfunction into account), and 13.7% (112/816) for Juling. dBBMMs were fitted for fixed GPS positions alone, and then combined with the positions gathered from daily VHF telemetry, as well as the original values using solely VHF positions (above).

Initial stationary testing of both units under semi-closed canopy suggested a typical location error that did not exceed 30m. dBBMMs were therefore calculated with a conservative location error of 40m for all GPS points. However, validation with VHF to give true locations showed that there were a few positions that gave errors in excess of 80m while the pythons were resting during the day. As there was no way to evaluate erroneous locations while the pythons were moving between resting locations, and to allow direct comparison of the combined VHF/GPS data with naïve unvalidated GPS locations, these were not filtered from the dataset. At the onset of the study, the intention had been to perform additional stationary tests in a sample of areas after they had been visited by the pythons (as the necessary habitat types and areas could not be known *a priori*), to provide better values of GPS uncertainty. However, because both the units malfunctioned, and additional units from the same company were not ordered (due to switching to alternative options), this was ultimately not possible.

Due to the large difference in average time between GPS fixes for the two individuals (see table 4.4), the window size for calculating motion variance was increased for Juling (from 21 to 31) to give a more balanced period of time over which changes in behaviour were estimated. The window size was set at 15 for both individuals when calculating for the full GPS and VHF dataset.

Area estimates for each python with the three sets of data (VHF, VHF & GPS, and GPS) and motion variance were calculated. Statistical tests comparing significance of these data were not possible due to the sample size.

### *Environmental predictors of movement rates*

In order to evaluate the effect of weather patterns on movement rates, remotely sensed weather data were obtained from the Giovanni online data system, developed and maintained by the NASA GES DISC (Acker & Leptoukh, 2007). These use multiple satellite-based multispectral radiometers to provide research-ready global estimates of weather variables at a spatial resolution of 0.1˚. A bounding box around the study site (N 5.38˚ E117.9˚ to N5.5˚ E118.3˚) was drawn, and the daily mean values (averaged within the bounding area) were extracted. Variables used were mean precipitation (Huffman et al., 2019), mean atmospheric pressure (Platnick et al., 2015), mean cloud cover (Platnick et al., 2015) and mean air temperature at 2m (GMAO, 2015). Other variables (e.g., relative humidity, level of flooding) were considered, but did not meet the criteria of having daily recordings with few missing data points within the study time period and area. Moon phase (as the percentage illumination of the moon surface relative to the study time and location) was also used as a predictor variable, and the values were obtained using the R package *suncalc* (Thieurmel & Elmarhraoui, 2019) at midnight, i.e. the night before a python location was determined. While the angle of the moon relative to the location, and the amount of cloud cover are important determinants of the amount of moonlight illuminating the ground, this nevertheless serves for determining the effects of the lunar cycle on behaviour.

In chapter 2, python capture rates and detectability along riverbanks were shown to be strongly associated with the level of moon illumination. To initially explore whether this same association was shown to affect movement intensity for telemetered pythons, motion variance ($\sigma^2$m) estimates derived from dBBMMs were used as the dependent variable in generalized linear mixed models (GLMMs) using the *lme4* package (Bates et al., 2015). Initial exploration of the data suggested that the distribution of $\sigma^2$m values were highly skewed, and there were no models that could be fitted well to this continuous distribution. Instead, the response variable was simplified into binary data, representing no movement vs movement, and binomial logistic mixed models were fitted. As this aimed to test whether movement responses to weather and moonlight variables (described above) differed between habitat types, habitat was included as an interaction term with each fixed variable (with python ID as a random effect) to allow for different slope parameters. This was included because it was hypothesised that pythons might react differently to these variables in the more open vegetation structure exhibited in plantations. The habitat variable was divided into plantation, forest, or mixed (time spent in both habitats), but the mixed category only included two individuals tracked for short periods of time, so results for this are more suspect. However, the model would not converge with all these included variables and interactions.

To provide an approximate estimate for the moon light level (ignoring effects of moon angle), the complement of cloud cover fraction was taken (1 - cloud cover) and multiplied by the fraction of moon phase. During a full moon this results in low values when cloud cover is high, and high values when cloud cover is low, while during a new moon this results in low values regardless of cloud cover. This was compared with the original moon phase to assess whether it might be a better predictor than moon phase alone, and simultaneously to allow fewer variables to be included in the GLMM. Moonlight and moon phase were within <1AIC, so moonlight was chosen in the global model to allow the model to converge, as all other fixed variables interacted with habitat showed significance. The dredge function in the R package *MuMIn* (Bartón et al., 2020) was used to examine all possible variable combinations from the global model, and to select any that fell within <2AICc of the top performing model.

## 4.3 Results

A total of 24 reticulated pythons were fitted with a tracking device (either experimental GPS unit with built-in VHF unit, a lone VHF implant, or both) (see Table 4.2). Results herein are from pythons that were tracked continuously for at least 21 days, leaving a total of 16 individuals. Of these, the mean number of unique positions recorded for each animal was 78 (±SD 53), with a range between 12 and 173.

### 4.3.1 Movement distances

Average daily distance moved was 45.8m (±SD 112.2), although all animals had multiple instances in which they had not moved between successive relocations. The mean step length for all individuals was 167m (±SD 172). Step lengths did not differ significantly with habitat or sex (Habitat: $X^2 = 0.125$, $p = 0.939$. Sex: $X^2 = 0.671$, $p = 0.413$), while the two translocated individuals moved greater distances than resident individuals ($X^2 = 8.748$, $p = 0.0031$; Figure 4.1). Mean step length for translocated individuals was 284m (±SD 300), while for resident individuals this was 160m (±SD 159).

*Table 4.2* Details of all Individuals tagged in this study, and how long (if) they were tracked. Tags were either GPS (with associated VHF) or VHF implants alone. Where GPS tags were used, the number of fixes achieved are given.

| *Python ID* | *Nickname* | *Tag type* | *Sex* | *Mass (kg)* | *SVL (cm)* | *Habitat used* | *GPS fixes* | *Tracking duration (days)* |
|---|---|---|---|---|---|---|---|---|
| *RP20* | Pilat | GPS | F | 11.4 | 318 | Mixed | 4 | 30 |
| *RP22†* | Cahaya | GPS | F | 18.8 | 365 | Forest | 71 | 81 |
| *RP36* | Akar | GPS | M | 15.7 | 350 | Forest | 0 | 1 |
| *RP43†* | Juling | GPS | M | 11.9 | 292 | Forest | 112 | 53 |
| *RP69* | Terung | VHF | F | 7.5 | 313 | Forest | | 21 |
| *RP71* | Jurang | VHF | M | 9.5 | 287 | Forest | | 32 |
| *RP13* | Anting | GPS | M | 8.4 | 299 | Forest | 31 | 2 |
| *RP90* | Labu | GPS | M | 6.8 | 265 | Forest | 29 | 1 |
| *RP92* | - | GPS | F | 14.7 | 326 | Forest | - | ¥ |
| *RP102* | Manis (1)¤ | VHF | F | 4.0 | 236 | Forest | | 14 |
| *RP104†* | Gigit | GPS | M | 10.0 | 322 | Mixed | 0 | 18 |
| *RP105†* | Pandekar | VHF | M | 8.9 | 324 | Forest | | 17 |
| *RP70* | Jantung | VHF | M | 7.8 | 277 | Mixed | | 43 |
| *RP82* | Penagih | VHF | M | 4.3 | 249 | Forest | | 296 |
| *RP102* | Manis (2)¤ | VHF<br>(+GPS)§ | F | 5.2 | 274 | Forest | - | 267 |
| *RP50* | Nantuk | VHF | F | 4.1 | 261 | Forest | | 267 |
| *RP68* | Diam | VHF | F | 4.4 | 244 | Forest | | 87 |
| *RP133* | Banjir | VHF | F | 3.7 | 219 | Forest | | 266 |
| *RP148* | Montel | VHF | F | 11.7 | 326 | Plantation | | 242* |
| *RP149* | Kertas | VHF | M | 9.9 | 332 | Plantation | | 164* |
| *RP150* | Gelung | VHF | F | 7.1 | 349 | Plantation | | 28 |
| *RP152* | Houdini | VHF | M | 16.7 | 330 | Plantation | | # |
| *RP154* | Tangki | VHF | F | 17.3 | 335 | Plantation | | 176* |
| *RP155* | Bangsat | VHF | M | 13.5 | 332 | Plantation | | # |
| *RP158* | Lebar | VHF | F | 18.9 | 374 | Plantation | | 134* |

** Tracking period was interrupted by a 6-week flooding event (not included in total duration)*
*† Pythons were rescued from Sandakan and translocated to LKWS*
*¤ Individual expelled initial VHF tag, and was later recaptured and had a second tag implanted*
*§ GPS was attached towards end of VHF tracking period*
*¥ Tag removed before release*
*# Escaped from holding pen and lost before tracking commenced*

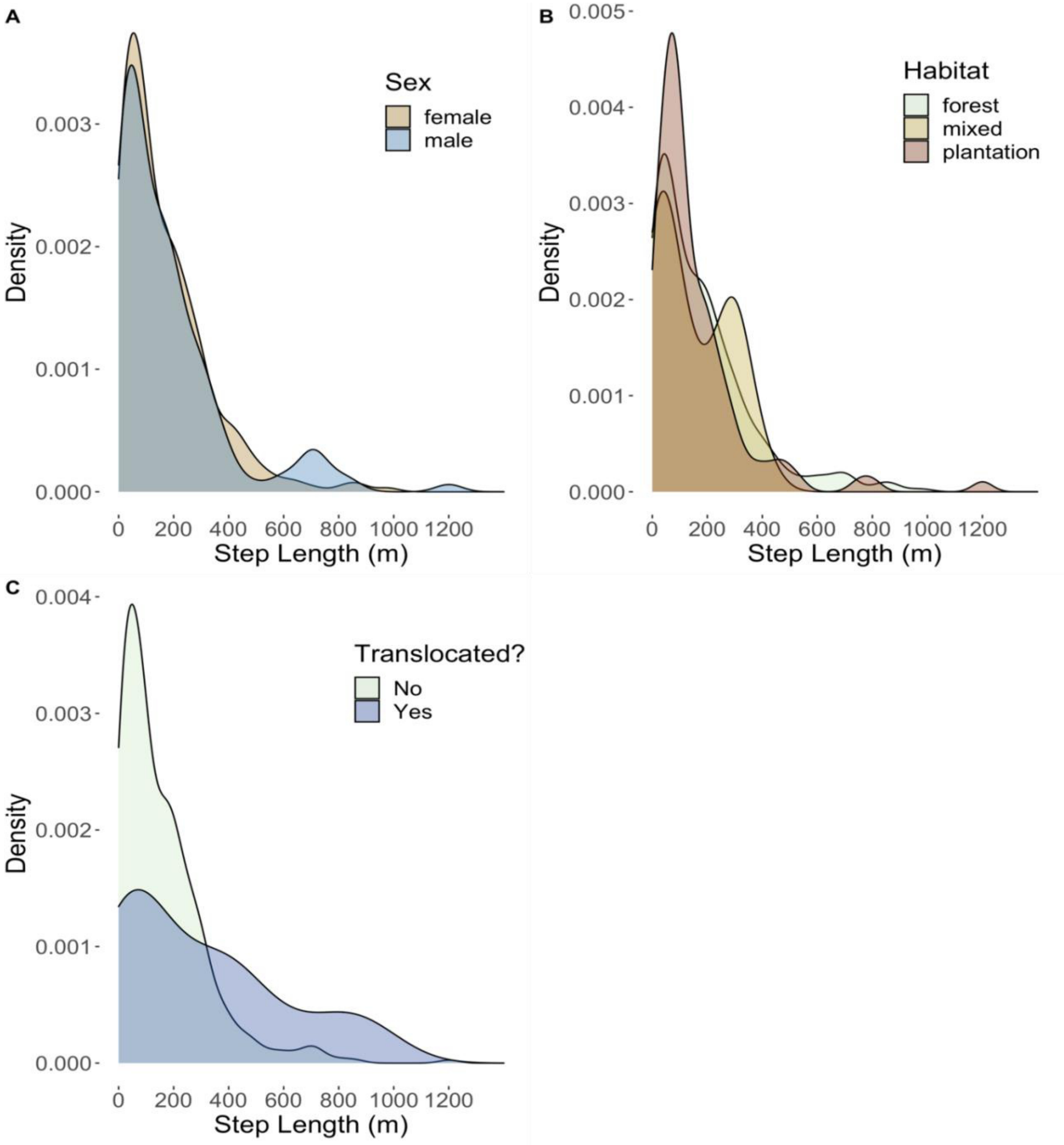


*Figure 4.1 Density plots of step lengths (straight-line distances) when pythons moved to a new location, separated by A: sex, B: Habitat type, C: Translocated and non-translocated individuals. Note that these are not daily values as locations were recorded every 48 hours.*

### 4.3.2 Occurrence distributions

dBBMMs were run for all 16 animals, and contours were extracted for 50, 95 and 99% confidence levels from the occurrence distribution rasters (Table 4.3 and Figure 4.2). The mean 99% confidence areas for all snakes was 52.2 ±SD 37.5 ha. However, as some individuals were only tracked for a short period of time, this is not indicative of the full range distribution, as many did not reach asymptote. As expected, both methods of calculating KUDs gave values that mostly exceeded dBBMM estimates, with the href parameter an average of 58.2ha (SD 79.1) and mean h 43.3ha (SD 23.0) larger than 99% dBBMMs. MCPs were more variable, either under or over estimating space use in comparison to dBBMMs. Maps of the locations of these distributions are shown in figures 4.4-4.7, and highlight the large discrepancies in area estimation and overlap between individuals.

***Table 4.3*** *Showing confidence areas of occurrence distributions from a dBBMM for all individual pythons, and comparison values calculated using minimum convex polygons (MCP) and kernel utilization distributions. Units are in hectares.*

| ***Name*** | ***50% dBBMM*** | ***95% dBBMM*** | ***99% dBBMM*** | ***95% MCP*** | ***50% Kernel UD (href)*** | ***95% Kernel UD (href)*** | ***50% Kernel UD (mean h)*** | ***95% Kernel UD (mean h)*** |
|---|---|---|---|---|---|---|---|---|
| *Banjir* | 2.78 | 49.75 | 76.60 | 36.81 | 16.39 | 79.81 | 21.67 | 99.52 |
| *Cahaya* | 4.91 | 77.77 | 125.21 | 100.46 | 121.64 | 407.51 | 55.60 | 186.67 |
| *Diam* | 1.01 | 18.00 | 30.35 | 21.58 | 21.33 | 84.96 | 21.36 | 85.06 |
| *Gelung* | 0.38 | 2.18 | 3.13 | 1.90 | 6.20 | 22.57 | 13.04 | 50.13 |
| *Jantung* | 0.06 | 6.00 | 10.66 | 11.48 | 20.46 | 75.62 | 20.72 | 76.84 |
| *Juling* | 0.32 | 34.53 | 73.24 | 33.30 | 42.71 | 257.13 | 17.99 | 122.07 |
| *Jurang* | 0.44 | 9.16 | 15.59 | 19.44 | 29.54 | 112.43 | 22.21 | 88.83 |
| *Kertas* | 4.34 | 46.06 | 90.34 | 32.46 | 18.40 | 91.37 | 20.09 | 100.36 |
| *Lebar* | 5.19 | 26.43 | 39.79 | 17.68 | 19.18 | 67.98 | 22.03 | 81.15 |
| *Manis* | 1.73 | 42.22 | 65.35 | 44.27 | 26.66 | 92.78 | 29.63 | 104.70 |
| *Montel* | 5.12 | 50.00 | 96.58 | 33.33 | 18.51 | 72.43 | 22.48 | 95.70 |
| *Nantuk* | 2.25 | 44.12 | 69.15 | 29.16 | 15.84 | 60.11 | 21.37 | 84.95 |
| *Penagih* | 4.80 | 64.68 | 94.75 | 51.92 | 33.51 | 121.09 | 34.61 | 125.19 |
| *Pilat* | 0.54 | 11.89 | 18.17 | 12.23 | 18.59 | 72.10 | 19.66 | 75.97 |
| *Tangki* | 1.05 | 11.07 | 22.82 | 31.18 | 34.54 | 130.06 | 26.48 | 102.88 |
| *Terung* | 0.52 | 2.54 | 3.86 | 0.74 | 4.49 | 18.74 | 11.50 | 49.02 |
| ***Mean*** | **2.21** | **31.02** | **52.22** | **29.87** | **23.78** | **95.56** | **28.00** | **110.42** |
| ***Standard deviation*** | 1.93 | 22.73 | 37.52 | 22.86 | 9.79 | 31.12 | 26.01 | 92.58 |

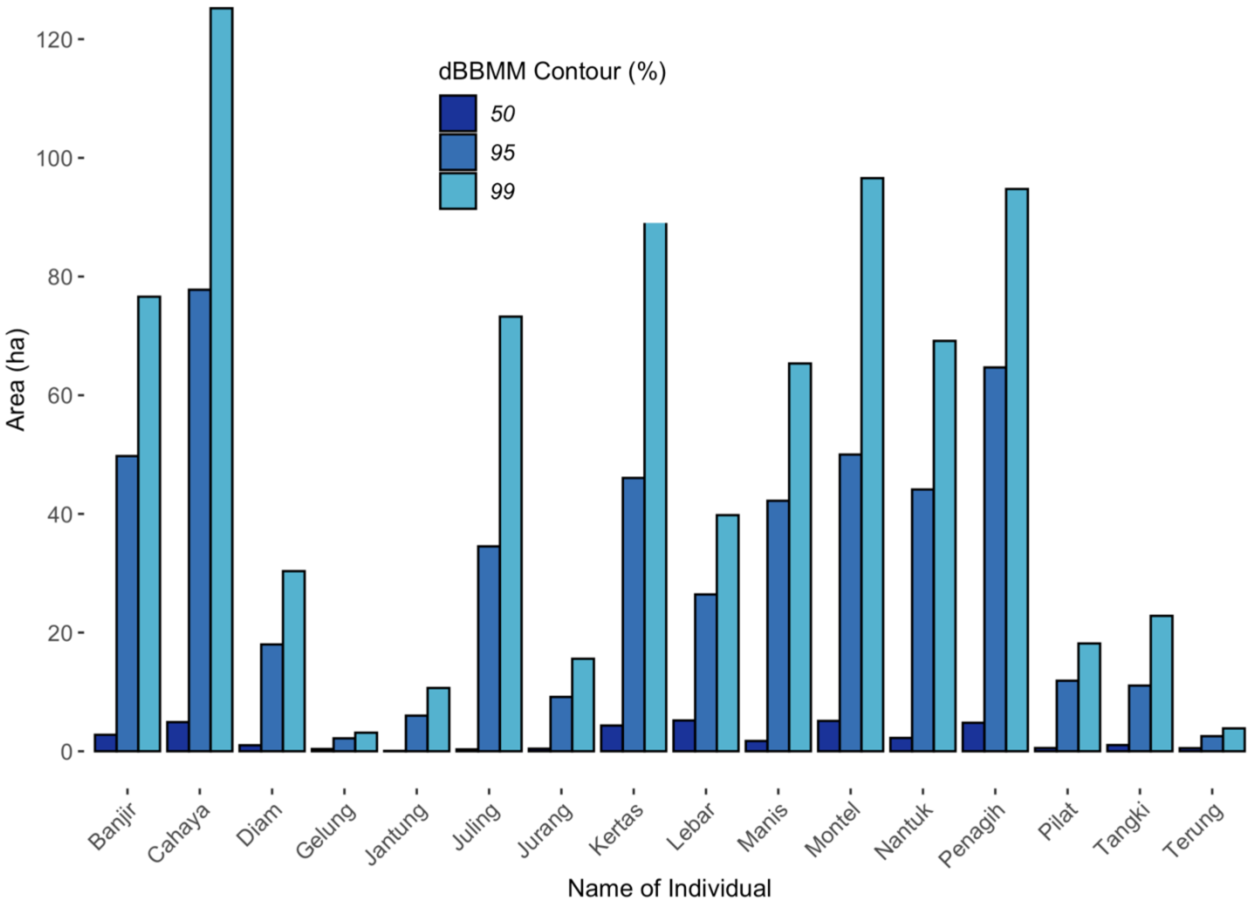


***Figure 4.2*** *Bar plot showing the size of occurrence distribution areas enclosed by the contours drawn at defined confidence levels, calculated from dBBMMs.*

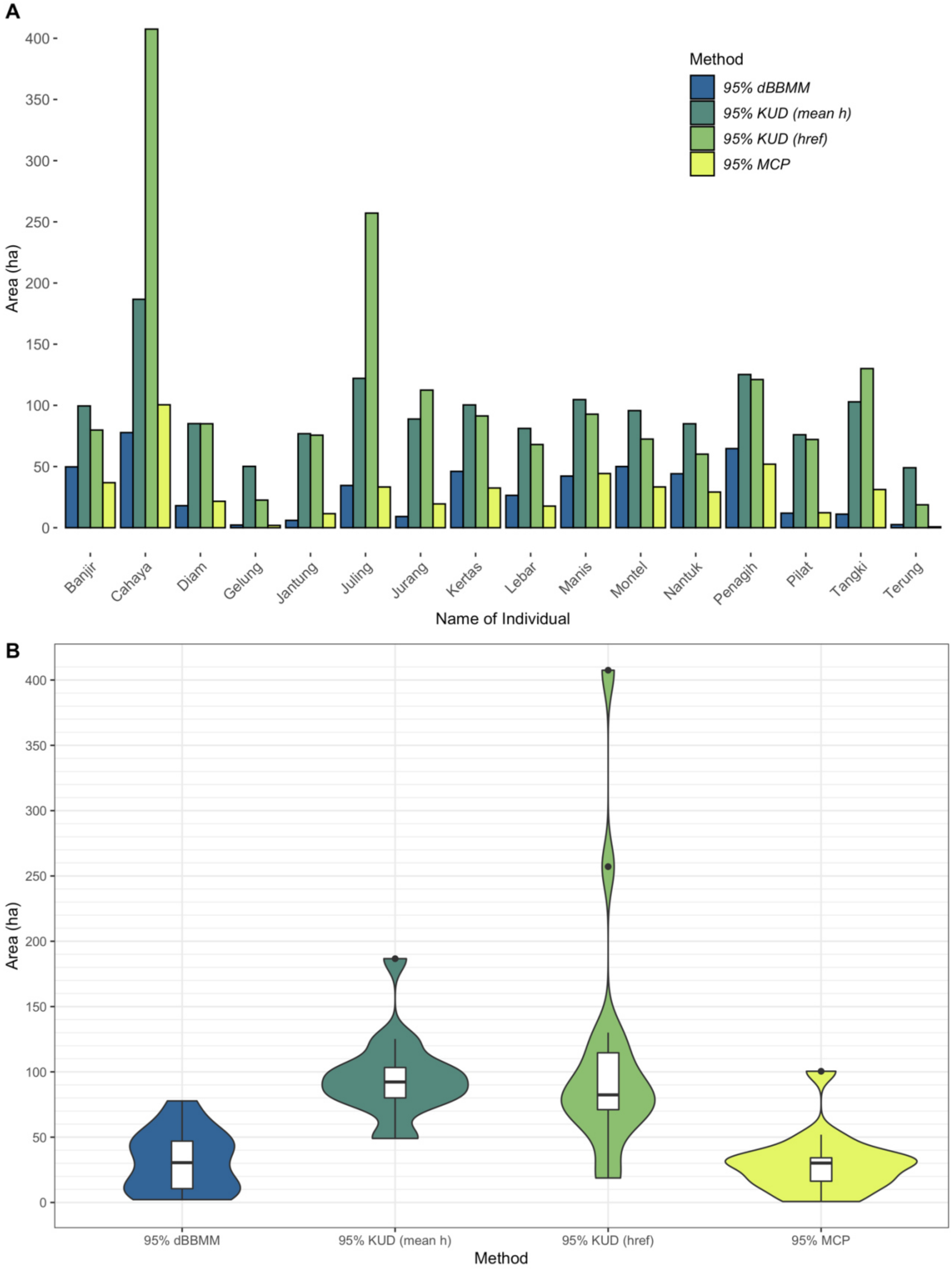


*Figure 4.3 Plots of comparisons for four different range estimators. A – bar plots of range distribution for each individual. B – box and violin plots comparing area estimates of each method.*

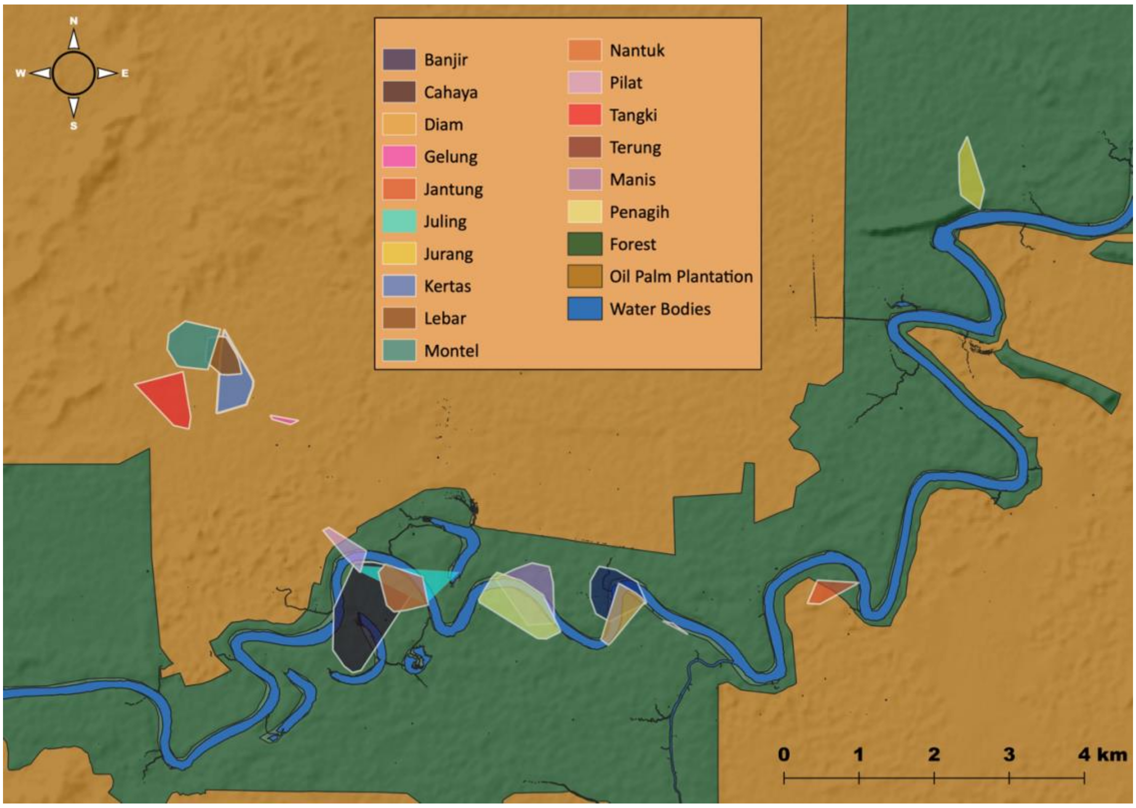


*Figure 4.4* *Map of the study area, showing locations of 95% Minimum Convex Polygons (MCP) for all tracked pythons analysed.*

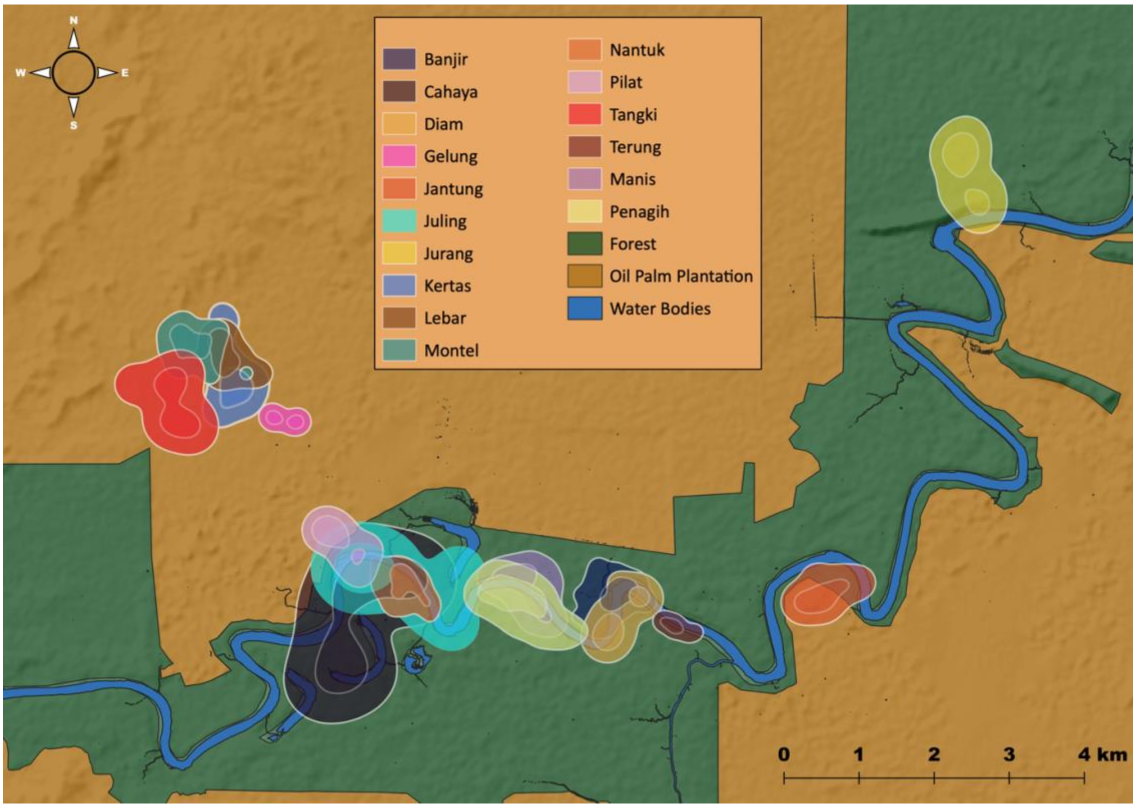


*Figure 4.5* *Map of the study area, showing locations of 95% and 50% kernel utilization distributions (UD) for all tracked pythons analysed. KUDs are estimated with a reference bandwidth.*

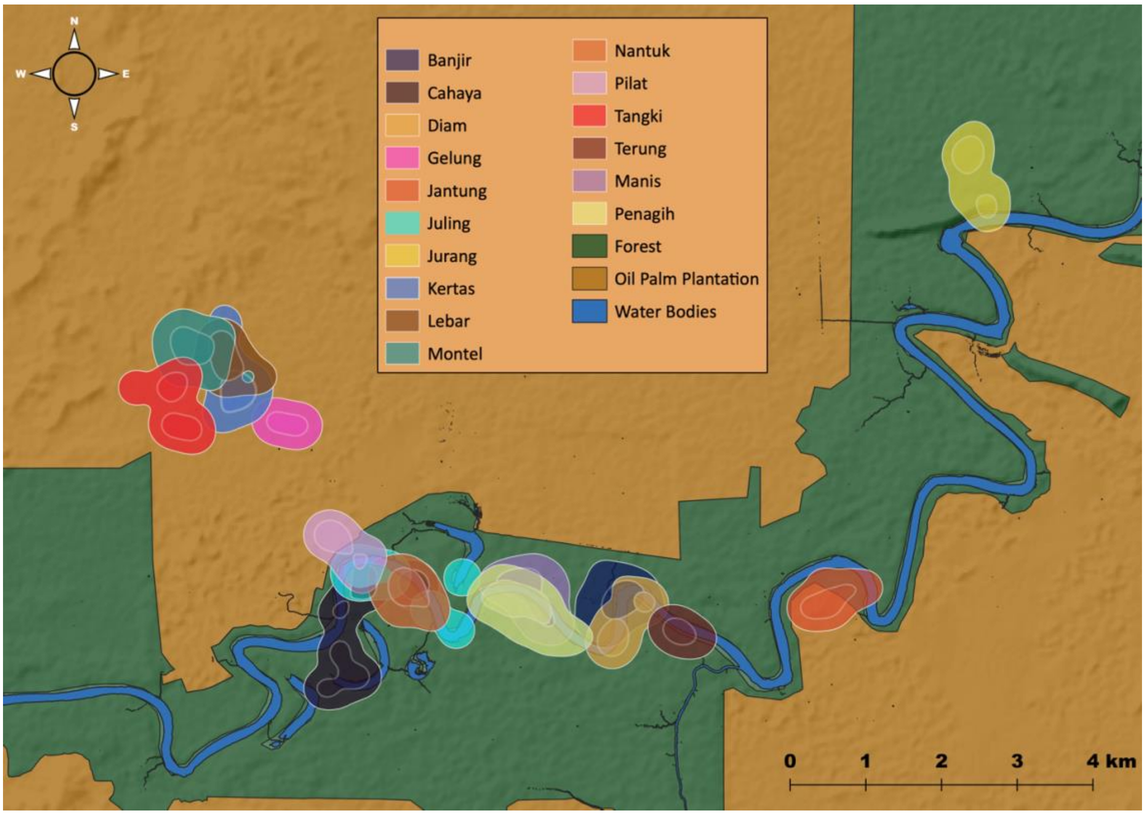


*Figure 4.6 Map of the study area, showing locations of 95% and 50% kernel utilization distributions (UD) for all tracked pythons analysed. KUDs are estimated with the same mean bandwidth for all individuals.*

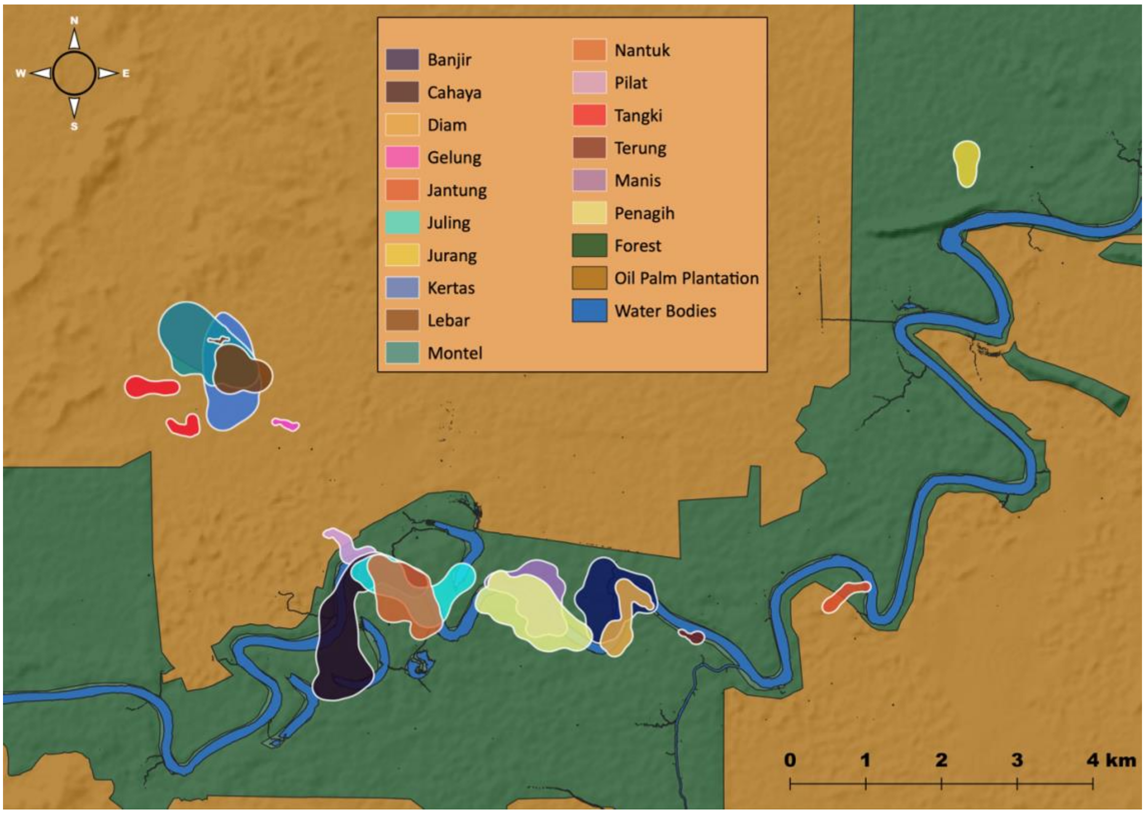


*Figure 4.7 Map of the study area, showing locations of 99% confidence occurrence distributions for all tracked pythons analysed, calculated using dBBMMs.*

*Occurrence distribution validation*

The GAM including habitat as an explanatory variable was a good fit (76.8% of deviance explained), but showed that habitat was not significant (t-ratio = 0.486, p = 0.640), with forest estimated at 88.8 ha (95% CI's between 43.2 and 183.2 ha) and plantation at 73.6 ha (95% CI's between 24.7 and 219.2 ha). The model including sex was slightly improved (84.9% of deviance explained) but sex was close to non-significance (t-ratio = 2.310, p = 0.049). Males were estimated at a peak of 131.2 ha (95% CI's between 78.2 and 220.2 ha) and females at a peak of 68.6 (95% CI's between 49.1 and 96.0 ha) after 246 days of tracking (figure 4.8). The overall mean estimate levelled off at 89.3 ha (95% CI's between 41.1 and 194.0 ha) after 304 days.

For the GAMM using means from bootstrapped MCPs, both habitat and sex were significant in a likelihood ratio test (habitat: F = 153.01, p = <0.001. Sex: F = 20.69, p = <0.001), with forest individuals having higher area estimates than plantation, and males having higher area estimates than females. The model suggests that at least 60 unique locations are likely to be required for achieving a full range occurrence estimate (figure 4.9). The effect sizes for the dependent variable from this model are not indicative of true range area values, due to the method of calculation.

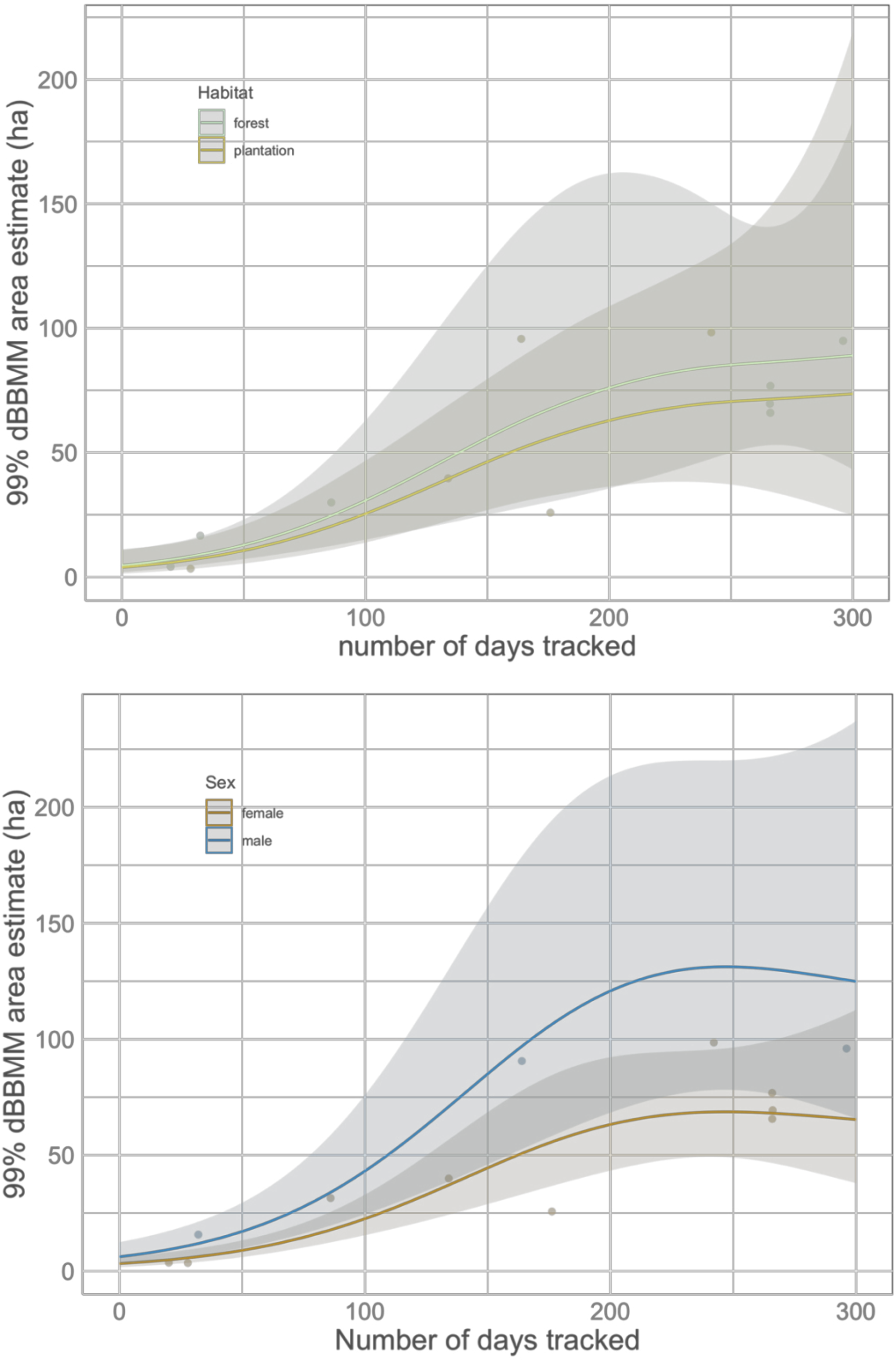


*Figure 4.8 Mean estimates from GAMs, showing 99% dBBMM contour area estimates against the number of days individuals were tracked. Separate models were used to evaluate the differences for habitat (above) and sex (below). The models suggest slightly larger area estimates in forest than plantations, as well as larger areas occupied by males.*

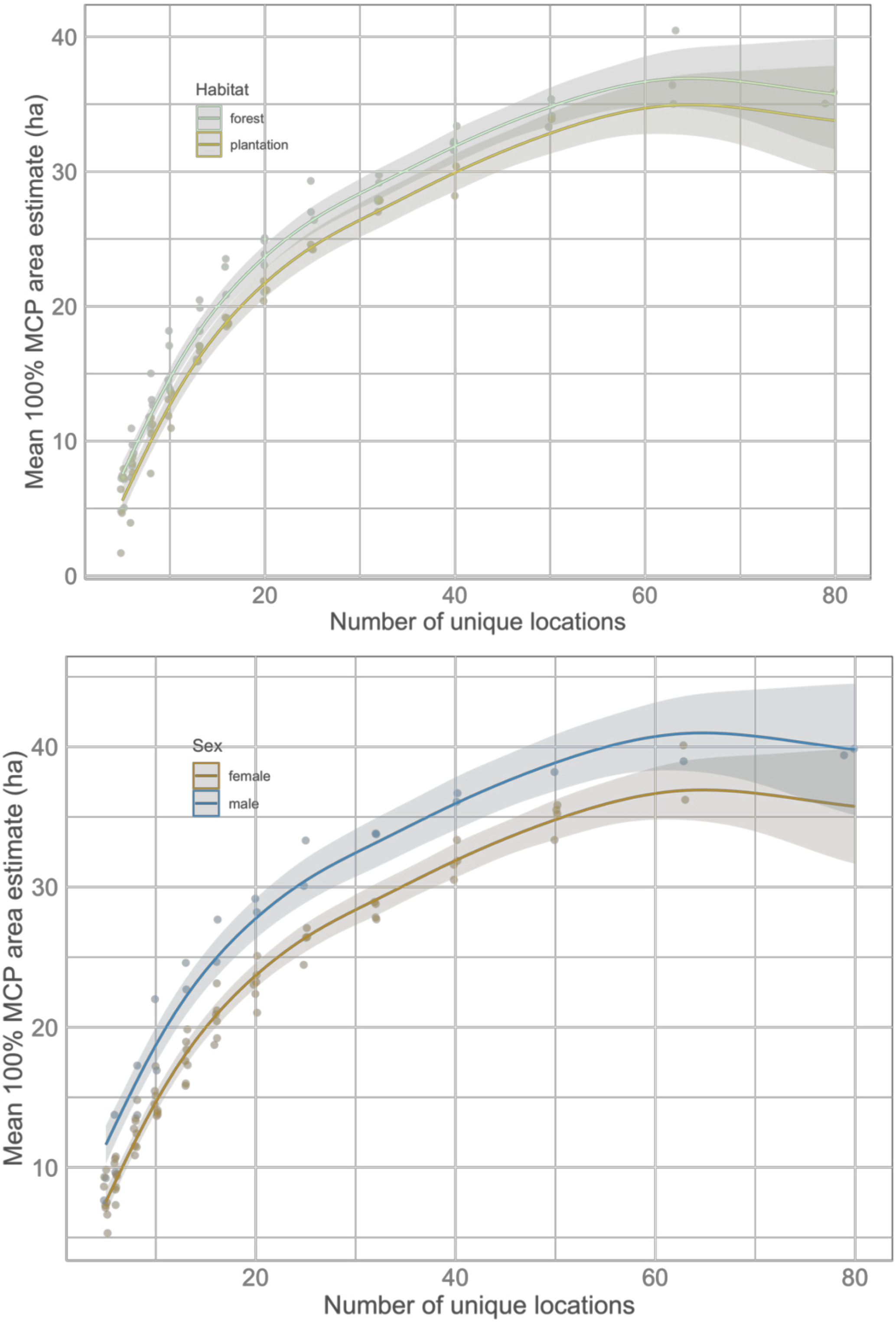


*Figure 4.9 Mean estimates from a GAMM, showing how calculation of 100% MCPs increases with the number of unique locations averaged across all individuals. The model suggests that at least 60 unique locations may be required for a reasonable estimate of a python's full range distribution. As these are mean values from 100 randomisations, the MCP range size estimates along the y-axis are below the "true" values.*

### 4.3.3 Motion Variance

Plots of motion variance, calculated from dBBMMs are shown in figure 4.10. These show how movement rates change over time. For individuals tracked over a longer period of time, a clear cyclic pattern can be observed, corresponding to periods of time where pythons are regularly relocating their position, and periods of resting in a single location. For individuals that were tracked concurrently, there is a suggestion that these active and sedentary periods often align in time, showing a level of synchrony. Mean correlation in motion variance values between the four forest pythons tested was 0.167 and this was significant for both type 1 ($p = 0.002$) and type 2 ($p = 0.039$) methods of data randomisation.

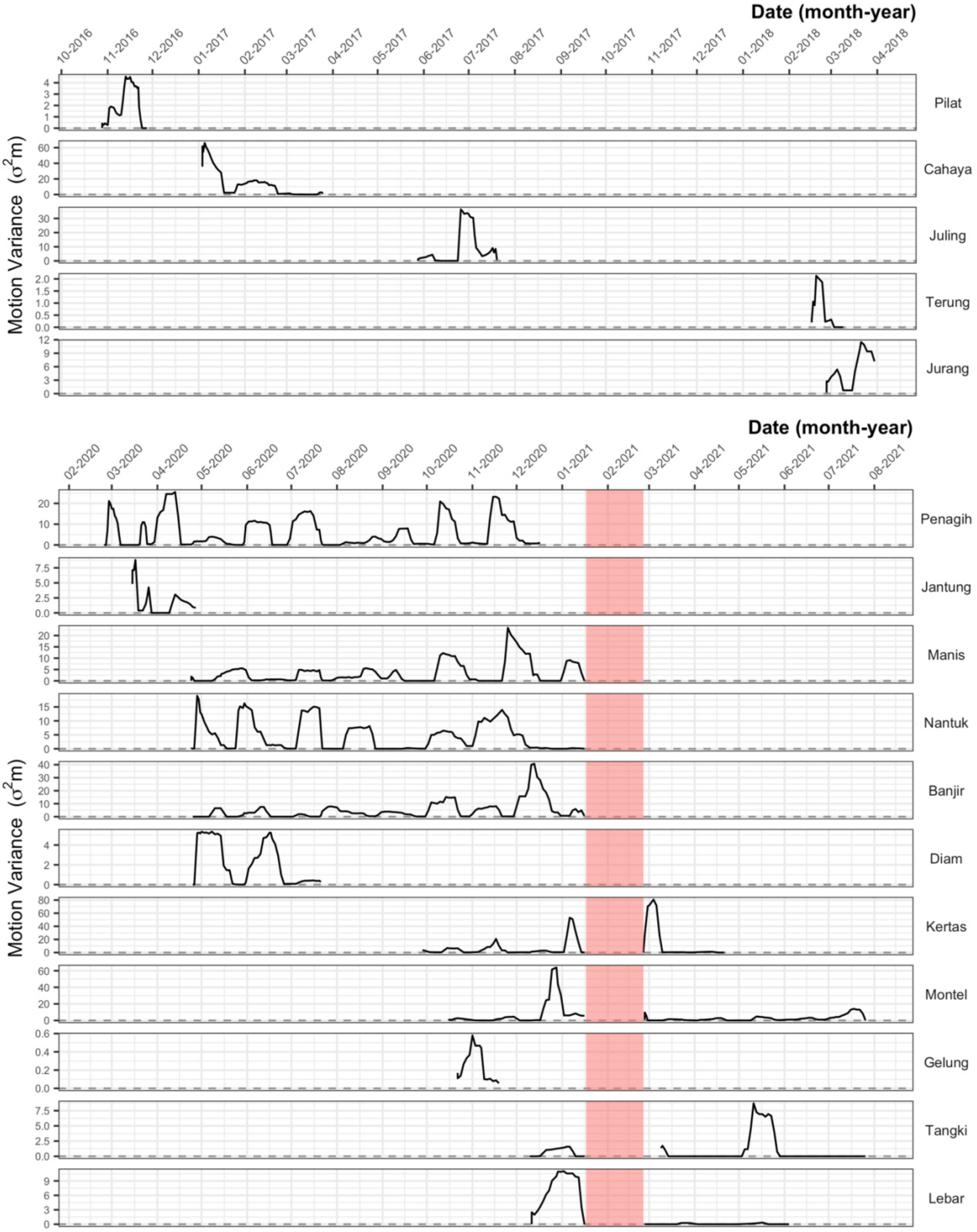


*Figure 4.10* *Changes in Motion Variance estimates from dBBMMs for each individual. Note that y axes are not on the same scales. The red boxes indicate where tracking was not possible due to a large flooding event in the study area. The lower 5 individuals (Kertas – Lebar) were tracked solely within a palm oil plantation.*

### 4.3.4 GPS vs VHF

The GPS fixes were patchy, with the largest gaps between fixes being 9 days for Cahaya and 9.5 days for Juling. The highly irregular times between fixes made choosing an appropriate window size (indicating the time period over which changes in behavioural state might be expected to occur) for dBBMM difficult, because the period of time being analysed in the window changed depending on how many fixes the GPS devices achieved.

Motion variances estimated from dBBMMs (figure 4.11) suggest that the GPS fixes allow for estimating quicker transitions between behavioural states than VHF fixes. While the time periods over which pythons are either in motion or resting are broadly in congruence between all three methods, including GPS fixes potentially allows for much finer-scale delimitation of when those changes in state occur, with the caveat that a degree of this variation is due to GPS positional error rather than true movement.

**Table 4.4** *Time between locations when considering VHF positions, GPS positions, or both together. Note that for both devices, the GPS stopped working and tracking continued using just VHF, hence a larger average time between locations for GPS & VHF compared to GPS alone for Juling.*

| **Name** | **Average time between locations (±SD) (mins)** | | |
|---|---|---|---|
| | ***VHF*** | ***GPS*** | ***GPS & VHF*** |
| *Cahaya* | *1473 (282)* | *1367 (3494)* | *762 (616)* |
| *Juling* | *1438 (116)* | *393 (1367)* | *448 (547)* |

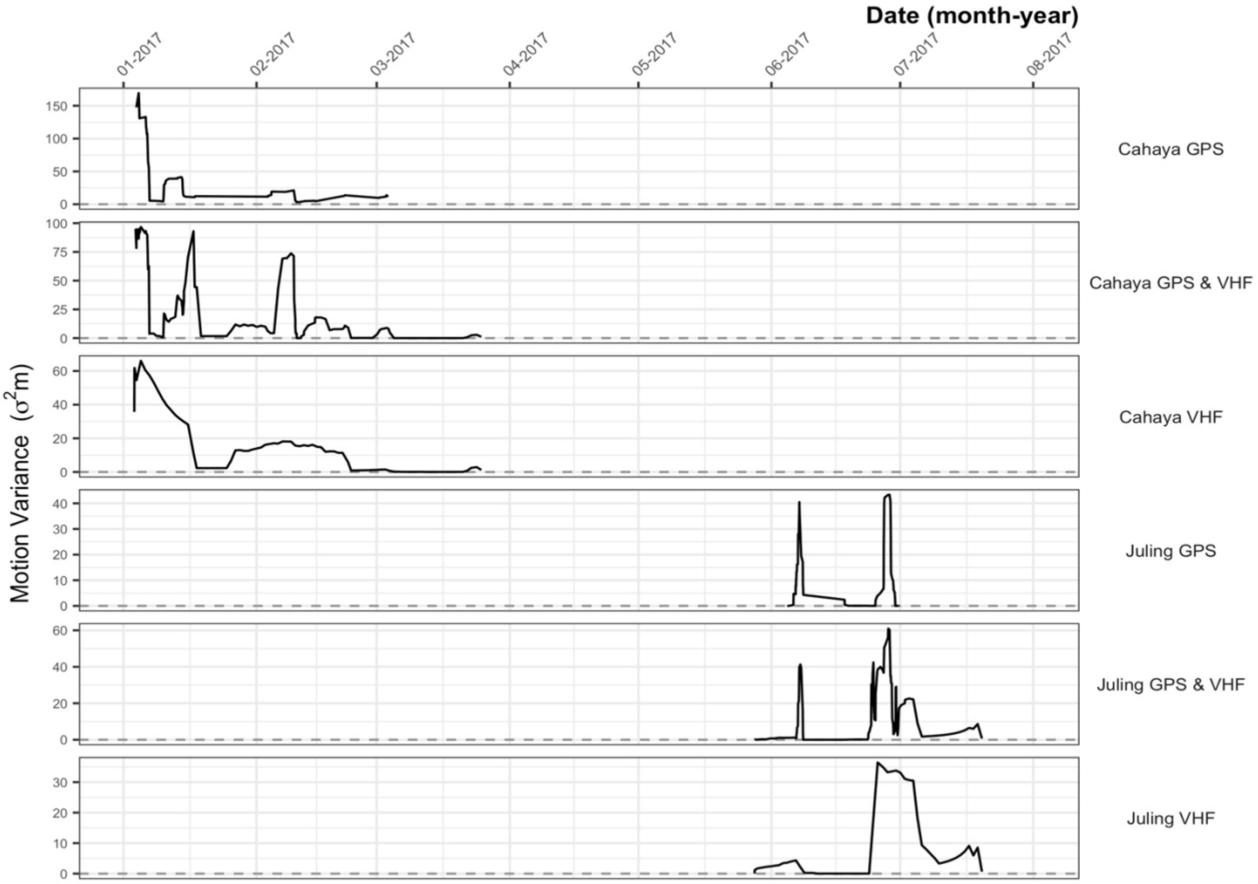
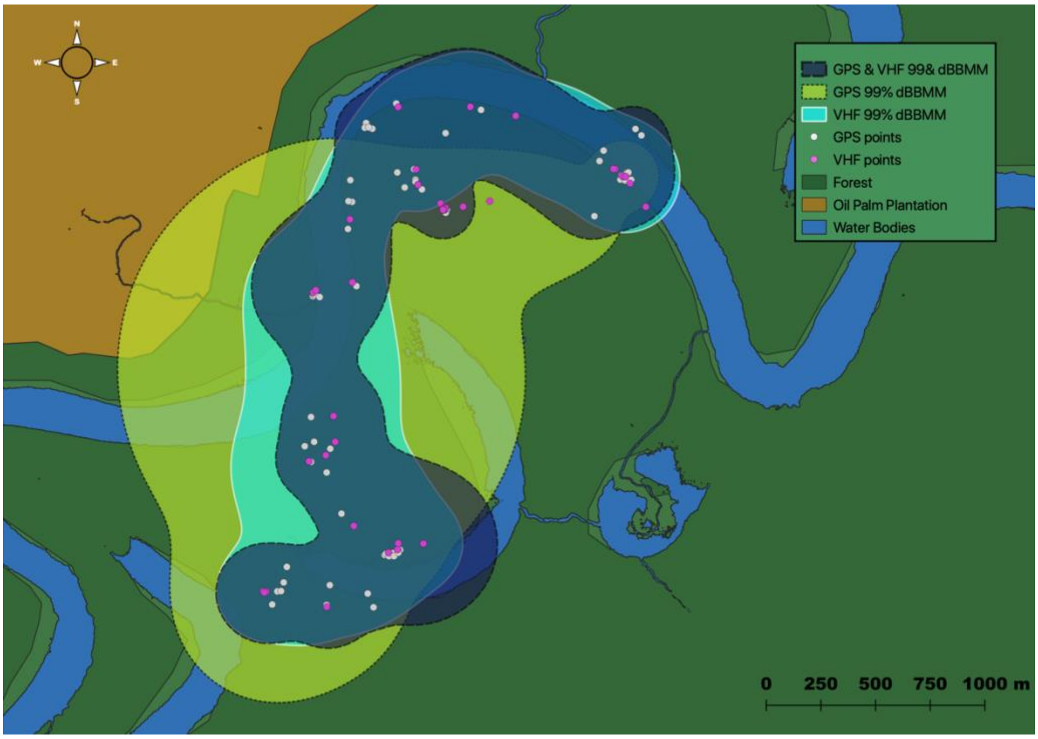


*Figure 4.11* *Changes in Motion Variance estimates over time for the two GPS-tagged pythons, comparing the three tracking methods.*



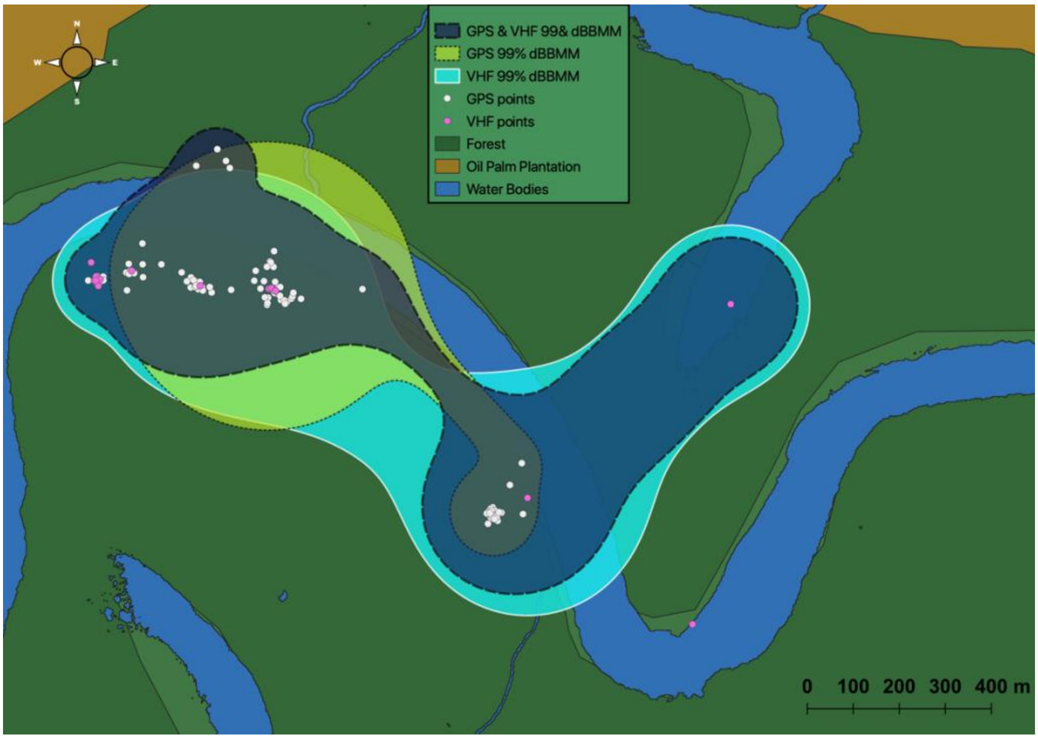


*Figure 4.12 Maps showing the areas encompassed by 99% dBBMM contours for Cahaya (above) and Juling (below), when calculated using VHF positions, GPS positions, and VHF and GPS combined.*

When comparing the areas encompassed within the 99th percentile contours for all three estimation methods visually, it appears that combining VHF positions with GPS generally improves area estimation when compared with VHF alone, by reducing commission errors and fitting more tightly to the locations. GPS without VHF telemetry appears to increase both omission and commision errors. Relative sizes of the 50, 95 and 99th percentile contours are shown in figures 4.11 and 4.12. Relying on GPS alone appears to lead to inflated area estimates, although the reduced total area sizes for Juling are a result of the GPS malfunctioning before tracking was completed.

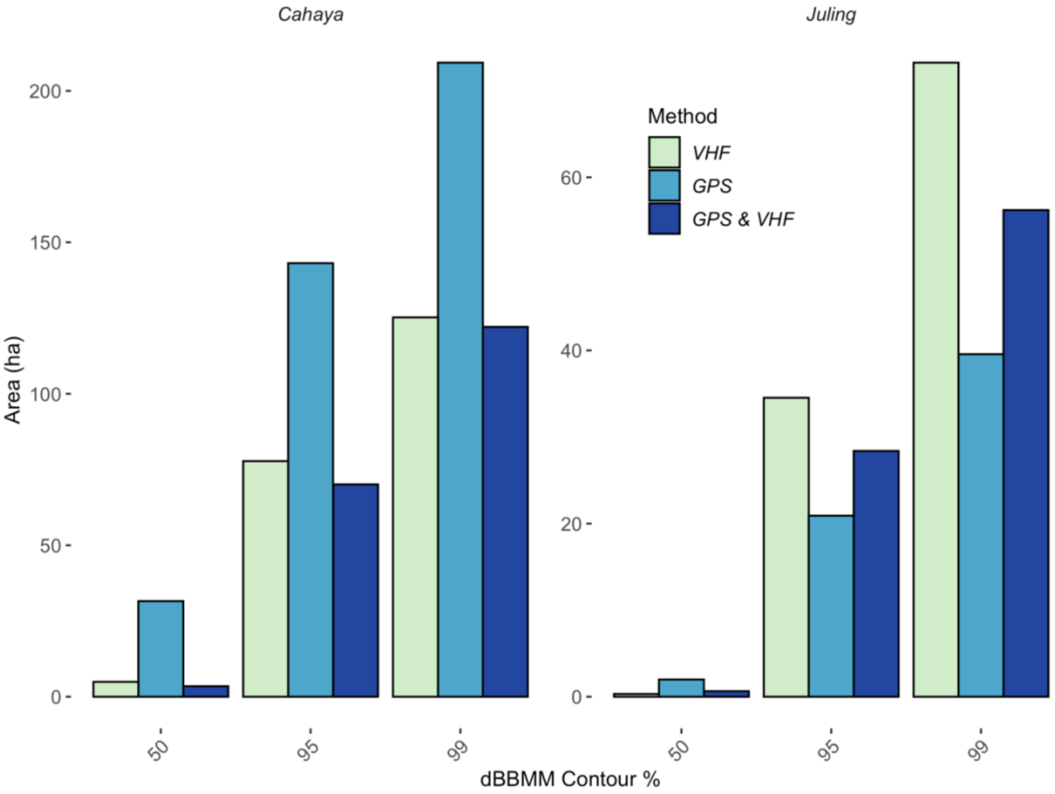


*Figure 4.13 Comparisons of occurrence distribution area sizes at 50, 95 and 99 percentile contours from dBBMMs for the two GPS-tagged pythons, when calculated using VHF, GPS or combined VHF and GPS positions.*

### *Environmental predictors of movement rates*

After examining potential models from the global starting model, three candidate models were within 2 AICc of each other (table 4.5). The model chosen had the best balance between AICc, log-likelihood and number of parameters, and included pressure, moonlight and precipitation all interacted with habitat type. While the interaction term habitat by pressure was not significant at alpha = 0.05, it was only slightly above this threshold (table 4.6), and its exclusion substantially decreased the log likelihood of the model. Movement probability differed significantly between the habitats (likelihood ratio test: $X^2 = 13.38$, $p = 0.0012$), with forest pythons moving more often on average than plantation pythons (figure 4.14). On average, when covariates were set to their means, forest pythons had a much higher probability of moving (50.2% ± 21.9) than plantation pythons (22.7% ± 31.3), indicating they move more often and spend less time remaining stationary. Post-hoc tests carried out with the R package *emmeans* showed that differences were significant only between the categories of forest and plantation, for both moonlight and precipitation (Table 4.7). The probability of moving increased with increasing levels of moonlight for forest pythons but decreased for plantation pythons. A full moon increased probability of movement of ~13% over a new moon for forest pythons. Plantation pythons showed a negative relationship, decreasing from 30% probability at new moon to 17% at full moon (figure 4.15).

*Table 4.5 Model comparisons for a binomial GLMM determining the effects of weather and moonlight on movement of telemetered reticulated pythons. Models within <2AICc of the top model are shown in the top box, while separate models fitted for each interaction term are given in the middle box for comparison. Fixed variables that were significant at alpha=0.05 in a likelihood ratio test are underlined. Final single model chosen is highlighted in bold.*

| Model specifications | k | LL | AICc | ΔAICc | $w_i$ | $R^2m$ | $R^2c$ |
|---|---|---|---|---|---|---|---|
| **Habitat * pressure + Habitat * Moonlight + Habitat * Precipitation + (1\|id)** | **13** | **-782.10** | **1590.49** | **0.00** | **0.373** | **0.114** | **0.198** |
| Temperature + Habitat * pressure + Habitat * Moonlight + Habitat * Precipitation + (1\|id) | 14 | -781.70 | 1591.75 | 1.26 | 0.199 | 0.114 | 0.195 |
| Pressure + Habitat * Moonlight + Habitat * Precipitation + (1\|id) | 11 | -784.84 | 1591.90 | 1.41 | 0.184 | 0.107 | 0.197 |
| Habitat * Cloud cover + (1\|id) | 7 | -789.17 | 1592.44 | 1.95 | 0.141 | 0.101 | 0.189 |
| Habitat * Moon phase + (1\|id) | 7 | -790.35 | 1594.78 | 4.29 | 0.044 | 0.089 | 0.189 |
| Habitat * Moonlight + (1\|id) | 7 | -790.46 | 1595.02 | 4.52 | 0.039 | 0.096 | 0.188 |
| Habitat * Pressure + (1\|id) | 7 | -791.80 | 1597.69 | 7.20 | 0.010 | 0.092 | 0.179 |
| Habitat * Precipitation + (1\|id) | 7 | -792.03 | 1598.15 | 7.66 | 0.008 | 0.088 | 0.180 |
| Habitat * temperature + (1\|id) | 7 | -793.12 | 1600.33 | 9.84 | 0.003 | 0.087 | 0.177 |
| Null + (1\|individual) | 2 | -801.58 | 1607.17 | 16.68 | 0.000 | 0.000 | 0.179 |

*k: number of parameters*
*LL: Log-Likelihood*
*AICc: Model fit corrected for sample size*
*ΔAICc: Change in AICc from the best model*
*$w_i$: Akaike weight – strength of model in relation to other models*
*$R^2m$: marginal R-squared value – proportional of variance explained by fixed effects alone*
*$R^2c$: conditional R-squared value – proportion of variance explained by fixed and random effects combined*

*Table 4.6 Individual likelihood ratio results for each fixed effect in the chosen final mixed model to examine weather and moonlight on telemetered python movement probability.*

| Variable | X² | P-value |
|---|---|---|
| *Habitat * Pressure* | 5.496 | 0.0640 |
| *Habitat * Moonlight* | 7.898 | **0.0193 *** |
| *Habitat * Precipitation* | 9.350 | **0.0093 *** |

*Table 4.7 Post-hoc tests for pairwise contrasts in slope coefficients derived using R package emmeans. For both moonlight and precipitation, significant differences were only observed between forest and plantation.*

| *Categorical pairs* | *Continuous variable* | *Slope coefficient estimate* | *z-ratio* | *p-value* |
|---|---|---|---|---|
| *Mixed- forest* | Moonlight | -0.243 | -0.133 | 0.990 |
| | Precipitation | 0.021 | 0.888 | 0.648 |
| *Mixed – plantation* | Moonlight | 3.664 | 1.710 | 0.201 |
| | Precipitation | -0.013 | -0.557 | 0.843 |
| ***Forest - plantation*** | **Moonlight** | **3.907** | **2.668** | **0.021** |
| | **Precipitation** | **-0.034** | **-3.012** | **0.007** |

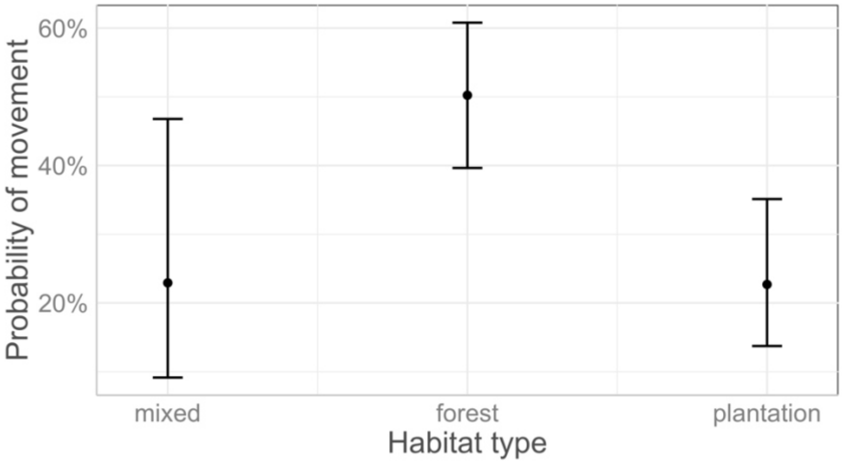


*Figure 4.14 Predicted differences in probability of movement for pythons within the three habitat categories, averaged across individuals and with model parameters set to their means. On average, pythons in forest are more likely to move than pythons in plantations.*

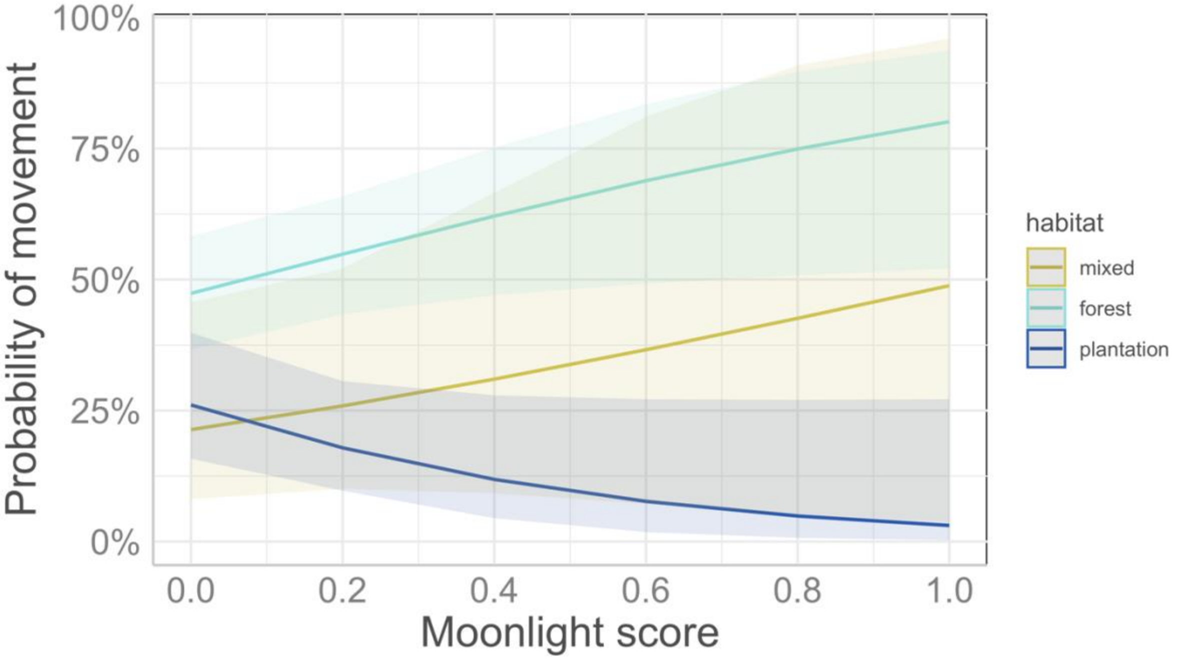


*Figure 4.15* Modelled estimates of how the amount of moonlight affects the probability of python movement, separated by habitat type. A moonlight score of 1 would indicate a full moon with no cloud cover, while a score of 0 would indicate either a new moon, full cloud cover, or a combination of these. Pythons in plantations are less likely to move with increasing levels of moonlight, while pythons in forest are more likely to move.

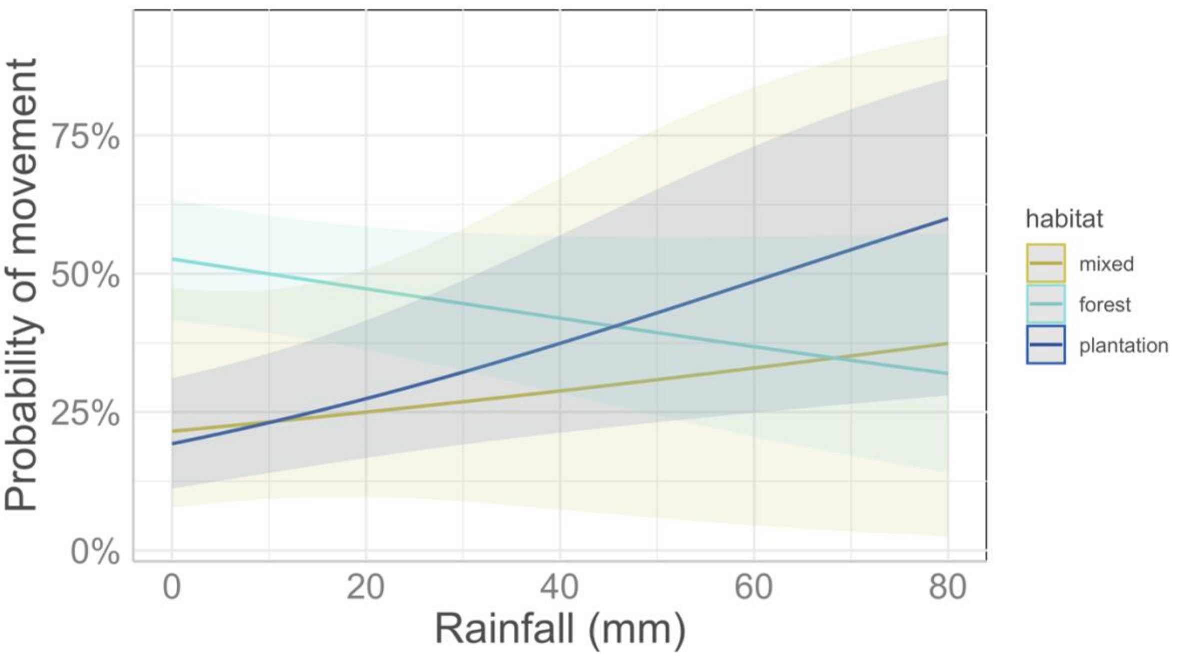


*Figure 4.16* Modelled estimates of how rainfall affects the probability of python movement, separated by habitat type. Pythons in plantation are more likely to move with higher levels of rainfall, while the opposite trend is observed for pythons in forests.

## 4.4 Discussion

This study is the first to produce publicly available results assessing space use and movements of reticulated pythons (see Low et al., 2018). The statistical methods employed here (e.g., dBBMMs) further demonstrate the potential to improve upon much of the previously-published snake home range literature (Crane et al., 2021). The results have demonstrated the potential applicability of the use of telemetry on reticulated pythons, which is an important component of the ability to study the ecology of such an enigmatic species.

### 4.4.1 Occurrence distributions

The results of this study indicate that reticulated pythons use larger areas than many of their smaller Australian relatives, but generally smaller than those of Burmese pythons (see table 4.1). It was hypothesised prior to the commencement of this study that reticulated pythons might be more active than Burmese pythons; the reported range distributions for Burmese pythons in Florida averaged up to 2,250 ha (Hart et al., 2015). Early work in this project employed experimental GPS devices (see chapter 3), and one of the reasons for this was the potential for these animals to be traversing extremely large, inaccessible areas. After using the VHF transmitters incorporated into the GPS tags to track several individuals this way, it became apparent that while still challenging, VHF telemetry within the Kinabatangan on multiple reticulated pythons simultaneously was a feasible endeavour.

Silva et al. (2020) showed that for reptiles at least, dBBMMs are robust to data at a temporal resolution as low as one position per month, and still generally outperform MCPs and KUDs at this level. For reptiles that move infrequently, interpolating between individual points separated by a considerable amount of time is more permissible than it would be for more active taxa, such as birds and mammals. With irregular locations, dBBMMs are more robust than many other time-based methods (Kranstauber et al., 2012). However, they start to suffer when interspersed with very large gaps, such as if an animal is unable to be located for a period of time, and they will fill this in by smoothing over very large areas. There were four individuals in this study that were tracked after a 6-week gap due to a flooding event, but this did not preclude the ability to use dBBMMs, as these sequences could be treated separately. As noted by Crane et al. (2020), there is now little reason for herpetologists to continue to ignore the potential of movement-based models to improve our understanding of reptile spatial ecology.

At the 99% dBBMM contours, the mean occurrence distribution was 52.2ha (±SD 37.5). Removing the translocated individuals, as well as the two that utilised a mix of both forest and plantation habitat, the mean increased to 88.8ha (±SD 56.7). Of these, individuals from plantation averaged an area size of 76.4ha (±SD 39.6) and those from forested areas 97.6 (±SD 68.0). Many home range studies will simply report these mean figures without taking into account whether each individual has been tracked for long enough to achieve a full range distribution, or if they do, it is by the removal of individuals without asymptotes or the inclusion of caveat statements (Crane et al., 2020; and see Fleming et al., 2016; Horne et al., 2020). This could be potentially misleading if the aim is to determine absolute space requirements for a species. While dBBMMs could be generally considered 'better' estimators of reptile space use than the traditional MCPs and KUDs (Silva et al., 2018, 2020; Crane et al., 2020; Smith et al., 2021), the fact that space use is estimated along the movement track precludes the possibility of randomisation and bootstrapping to fully assess whether the occurrence distribution estimate has reached an asymptote (= range distribution). While it is possible to divide a movement path into segments and re-calculate at intervals (Carlisle et al., 2019), this is computationally intensive, and recursive movements back to core-use areas may give the false impression that an asymptote has been reached early. Additionally, due to the way motion variance estimates are calculated, space-use estimates may differ at the ends of tracks if they are segmented, which complicates this procedure.

As there was a reasonable spread in the lengths of time that different pythons were tracked in this study, it was possible to fit GAMs to the dBBMM estimates for each individual, to provide an estimate for the mean occurrence distributions should all individuals be tracked for a similar length of time, and give an indication of a minimum amount of time required to provide a full range distribution estimate. This also allowed for testing for a significant difference between the two habitat types whilst taking into account the length of time individuals had been tracked. This reduced mean estimates slightly, giving values of 73.6ha for plantation and 88.8ha for forest, albeit with large confidence intervals. While this was not significant, the model is essentially operating under the assumption that the parameters of space use are generalisable across all individuals based on the amount of time they were tracked for, and it uses a low number of individuals to do this. Despite this very low sample size for fitting a GAM ($n=12$), males were estimated to have range distributions almost double the size of females, although barely significant ($p = 0.049$). As there was little difference in the distances that males and females moved between locations (figure 4.1), this likely is a result of females exhibiting greater site fidelity, which is quite common in snakes (Todd & Nowakowski, 2021).

This study has already shown that movement rates are dependent on external environmental variables, which demonstrates a degree of bias. Without data that looks at how stable the ranges are across longer periods of time, over multiple years, and in a greater range of habitat types, these should perhaps be considered lower end estimates. Similarly, a greater sample size might allow for more complex modelling, such as including an interaction term to allow different slope parameters for the two categories. It could also better quantify the degree of inter-individual variation, which is likely to be much larger than the results here might suggest (e.g., Hart et al., 2015).

While MCPs are often unreliable at providing realistic values of space use, bootstrapping random samples of locations can nevertheless give a reasonable estimate of when an asymptote has been reached. Modelling the accumulation curves of each individual allows for considerable improvement in accounting for individual variation. Using this method in GAMMS yielded similar overall results to the GAM models using dBBMM area estimates, with pythons from plantations appearing to require less space than those that live in forest. This is perhaps counter-intuitive, as it could be expected that fewer available sources of shelter and lower habitat heterogeneity would lead to a requirement for more space, as was found for Malay civets (*Viverra tangalunga*) within the same study area (Evans et al., 2021). However, this is similar to the pattern observed in the Asian water monitor (*Varanus salvator*) (Guerrero-Sanchez et al., 2022), and also for other studies on snake home ranges in other human-modified habitats (Blouin-Demers & Weatherhead, 2001; Mitrovich et al., 2009; Corey & Doody, 2010; Carrasco-Harris et al., 2020; Bauder et al., 2020; Marshall et al., 2020). Long range movement for species such as reticulated pythons is primarily driven by either mating or searching for suitable areas to catch prey. Higher feeding rate has been shown to correlate with smaller range distributions in snakes (Glaudas & Alexander, 2017). Therefore, the high density of rodents in oil palm plantations may explain why pythons move less and occupy smaller ranges, as suggested for water monitors (Guerrero-Sanchez et al., 2022).

### 4.4.2 GPS vs VHF

An original aim of this study was to develop GPS devices that provide improved estimation of space use and a better understanding of behaviour. While this was largely unsuccessful, and the study instead relied on traditional VHF radio-telemetry, the two GPS-tagged individuals provided some key insights into the effectiveness of GPS data for understanding space use in snakes.

VHF locations in this study were obtained during the day when pythons were resting, which means that any movements between locations are assumed to follow a roughly straight path, simulated with Brownian motion. Inclusion of additional GPS points, then, gives a better indication of where and how much an animal has moved by filling in these gaps. However, in this case, GPS points were recorded throughout the diel, including daytime locations when pythons were not moving. Due to a much higher positional error than VHF, GPS has the potential to increase uncertainty around resting locations. Neither GPS device was particularly effective, with fix rates between 4.4 and 13.7%, often with large gaps between fixes. This meant that analysing fine-scale behaviour in more detail, such as nocturnal activity rates, was not possible.

The maps of 99th percentile dBBMM contours (Figure 4.12) suggest that inclusion of the additional GPS fixes improves the area of estimation over VHF alone, reduces commission errors, and reduces the overall estimates of occurrence distribution size, although this was more marked for Juling than for Cahaya. However, the shapes of the distributions are broadly in agreement, suggesting that VHF alone may be adequate as a reasonable estimate of space use and habitat selection with dBBMMs. There were few indications from GPS data of pythons traversing large distances outside of the area estimated by VHF, despite these two individuals being translocated, and therefore probably making more exploratory movements than resident individuals would (Pittman et al., 2014; Nash & Griffiths, 2018; Wolfe et al., 2018). Both individuals, however, were found on one occasion to have crossed the Kinabatangan River during a single night before returning to a position closer to their previous locations.

Any future study seeking to employ GPS devices on snakes should be wary of the low fix rates that are likely to occur for most species (Smith et al., 2018; Wolfe et al., 2018; Smaniotto et al., 2020, and see chapter 3), particularly large gaps in the data while animals are sheltering for long periods of time. Relying on releasing animals with GPS devices and allowing them to passively collect data often works well for birds and mammals and can work for more active reptiles (e.g., Guerrero-Sanchez et al., 2022), but may not produce reliable estimates of space use when used with movement-based estimators. dBBMMs are particularly robust to gaps and irregularities compared with many other methods (Kranstauber et al., 2012), but they still performed poorly on the GPS data alone presented here. While tracks can be “bursted” to account for these gaps, within the *move* package this currently requires manually annotating the data, which would be time consuming for very large GPS datasets. Combining manual VHF radio tracking with GPS units appears to be the best way to improve data collection, allowing for both calibration and to fill in gaps (Smith et al., 2018; Wolfe et al., 2018). However, this removes one of the primary advantages that GPS tracking has over VHF telemetry, in terms of effort and cost-per-datum (Hebblewhite & Haydon, 2010). The advantage of doing this for early adopters of GPS technology on snakes, however, is that if GPS units fail to provide data (as for Smaniotto et al., 2020), there is still the possibility of achieving a reasonable dataset. Further, it allows direct comparison of the methods, to determine whether there are any advantages of GPS when it comes to snakes. That was certainly a goal here, but unfortunately the level of depth of conclusions are limited by only having two individuals.

### 4.4.3 Environmental predictors of movement rates

Chapter 2 demonstrated that capture rates along the Kinabatangan River correlated with weather and moon phase. Patterns of motion variance, extracted from the dBBMM estimates, seemed to follow a cyclical pattern, with periods of several days of activity followed by periods of inactivity (figure 4.10). Pearson correlation of the four forest pythons showed that the level of correlation between motion variance estimates for all four was significantly different from random. This is a striking result that provides further suggestion that reticulated python behaviour is strongly influenced by external factors. Burmese pythons in Thailand did not appear to exhibit this same trend (Smith et al., 2021), albeit there were fewer individuals in that study that were tracked concurrently over a long time period. Unfortunately, surveying efforts (chapter 2) were considerably reduced during the final year of this study, in order to focus more on telemetry work, but it would have been interesting to look at the correlation between capture rates and the cycles of movement exhibited by the telemetered pythons. Nevertheless, the synchronicity is surprising given the inter-individual variation that would be expected in whether and how much pythons are moving.

The cyclical pattern of several days of movement, followed by several days in a single location may be expected to correspond with periods of prey (or mate) searching, followed by digestion or ecdysis. However, while attempts were made to sight tracked individuals, determining the presence of a recent meal was generally not possible without overly disturbing the animals. For pythons tracked solely within plantation, these periods of inactivity appeared to persist for longer than for pythons solely within forest, and this contributes to the overall lower movement rates observed. Figure 4.1 highlights that the actual distances moved between steps follow a very similar distribution. The motion variance graphs (figure 4.10) indicate a degree of synchronicity in movement patterns between individuals, hinting at the possibility of external cues that may drive movement decisions at the population level (Lindström et al., 2015). Some of the potential cues for this were examined to explore any correlation between weather and moonlight levels with python movement (or lack of movement).

Telemetered pythons showed that their probability of moving was correlated with both the amount of moonlight and the amount of rainfall. However, the response to both variables is starkly contrasted for pythons that were living in plantations than those inhabiting forested areas. Under the assumption that encounter rates are intrinsically linked to whether pythons are more active, in chapter 2 the results showed that pythons along riverbanks were more likely to be spotted in low moonlight. In contrast, the results here suggest that forest pythons actually move less in low moonlight. Plantation-inhabiting pythons suggest a similar trend to that found for captures along riverbanks. The model used here did not account for whether the forest-dwelling pythons were located along riverbanks or forest interior at different points in time, and this spatial bias may be important. But this difference can perhaps be explained by the fact that both riverbanks and plantations generally are far more open and exposed, and therefore pythons there exhibit a greater response to the level of light.

Previous literature examining the effects of moonlight levels on snakes is surprisingly sparse, but most studies found significant trends in activity or movement characteristics (Yamagishi, 1974 (cited in Kronfeld-Schor et al., 2013); Madsen & Osterkamp, 1982; Clark et al., 1996; Campbell et al., 2008; Weaver, 2011; Lillywhite & Brischoux, 2012; Eskew & Todd, 2017), and one study found no effect (Sperry et al., 2013). The general conclusion from controlled lab experiments appears to be that prey density/activity levels are generally a more important factor for snakes than the increased predation risk afforded by high levels of moonlight. However, rodent activity in response to moonlight is highly variable (Maestri & Marinho, 2014), so without examining prey responses to moonlight in the study area (and there are many different potential prey) this is difficult to confirm.

Weather should be expected to play a major role in the activity levels of ectotherms, but most studies on snakes have explored longer-term seasonal effects rather than daily fluctuations in weather (George et al., 2015). While the present study did not isolate temporal effects for examination (e.g., George et al., 2015), this was not deemed necessary due to the lack of serial autocorrelation in the data as is often typical for models examining weather effects (Lindström et al., 2015). Rainfall was not found to impact the likelihood of capturing pythons (chapter 2), but it nevertheless appears to correlate with their likelihood of movement. This can partly be explained by the fact that surveying for pythons was not carried out during heavy rain, as it made spotting them extremely difficult. As to reasons why pythons in plantations respond positively to rainfall, while pythons in forest respond negatively, this is difficult to determine. It may be due to differential responses of rodent prey, which have been hypothesised to be forced to relocate more often to seek shelter in heavy rain (Maestri & Marinho, 2014), and this effect would likely be more pronounced without the protection of dense canopy forest. Alternatively, the pythons that were followed in the plantation were all located in an area that was formerly peat forest, with soft ground and with a very high water table that was prone to flooding. It may be that the pythons themselves seek alternative shelter; as they were often found resting partially or entirely underwater in drainage ditches or flooded burrows, this seems a less likely explanation.

While motion variance derived from dBBMMs provides a numerical measure of the amount of movement occurring, fitting a model with a continuous outcome was not possible, which necessitated the use of a more simplistic binary outcome. The distance a python moves once that decision has been made could perhaps be determined more by the available habitat than by environmental variables. Similarly, there are certainly other intrinsic factors that impact a python's decision to remain in one spot over multiple days, which were not possible to include as covariates here. Particularly whether the animal has recently fed, or is undergoing ecdysis, could be expected to take precedence over favourable/unfavourable weather conditions. Setting movement as a binary variable in a logistic regression therefore removes some of this potential noise.

The weather variables that were used for fitting the model were derived as daily (24 hour) means across the study area, from satellite remote sensing data. While this makes sense due to the coarse scale of tracking every two days, it inevitably glosses over the potential for elucidating finer-scale effects. For example, the majority of movements are likely to occur at night, so it may be that weather patterns during daylight hours have less of an impact on whether a python chooses to move. Rainfall can often occur at quite a localised scale, so averaging out rainfall across the study area inevitably weakens any perceived relationship, despite its significance in the model. Responses may be more nuanced. For example, what if rain during the afternoon makes pythons less likely to move (perhaps because it is colder while they are resting), but a sunny afternoon with rain during the night makes less of an impact? GPS or accelerometer data would be able to answer more refined questions than the generalisations presented here, and combining this data with temperature loggers would be advantageous.

Temperatures from the field centre weather station indicated a slight (but insignificant) relationship with capture rates (chapter 2), and responses of ectotherm behaviour and activity to temperatures is well-documented. This weather station was unfortunately not functional throughout the period in which the pythons were tracked, necessitating use of remotely-sensed data. Remotely-sensed temperature values for the study area (without large chunks of missing data) were only available at a 2m height. This was averaged across the study area in both space and time to provide an indication of how hot it was on average on a given day. Remotely sensed-data were at a scale too coarse to look at differences between habitats (e.g., oil palm plantations are generally far hotter than surrounding forest - Hardwick et al., 2015). However, a single weather station in forest (if it had been working) would possibly have been more biased.

### 4.4.4 Drawbacks

While a sample size of 16 individuals is not unusual for snake telemetry studies, it is still small in comparison to many studies on other taxa, especially considering many individuals were only tracked for short periods of time. This is compounded by the nature of comparison between habitat types, as well as the decision to place tags on individuals of both sexes. While some telemetry studies purposefully avoid this by only tagging study animals of a single sex (e.g., Brito, 2003; Evans et al., 2021; Smith et al., 2021), there is the potential for large discrepancies between male and female movement (e.g., Pearson et al., 2005; Wilson et al., 2006; Smith et al., 2009; Anguiano & Diffendorfer, 2015; but cf. Diffendorfer et al., 2005; Carfagno & Weatherhead, 2008) which meant that sex was decided to be an important variable to include. Further, there is the potential for differences in movement rates at different sizes; it is hypothesised that larger individuals will move less frequently, as they feed less frequently but on larger prey that take longer to digest (Shine et al., 1998b). Snake movement rates will also vary with season, either because of weather patterns or because of mate or nest searching (Madsen & Shine, 1996; Brown & Weatherhead, 1999; Brito, 2003; Diffendorfer et al., 2005; Smith et al., 2021), but too few animals were followed concurrently over long enough time periods to investigate these trends here. Previous studies have already demonstrated strong differences in seasonal breeding patterns of reticulated pythons north and south of the equator (e.g., Natusch et al., 2019) and so movement responses to weather patterns may well differ by locality as well. Drawing species-level inferences from the data presented here is therefore strongly cautioned against, but the demonstration here that such studies are feasible on such an elusive species may hopefully trigger similar studies in other parts of their geographical range.

## 4.5 Conclusion

Overall, this study provides some initial evidence that suggests inhabiting oil palm plantations leads to changes in space use and movement behaviour. In plantations, range distributions appear to be smaller, movements less frequent, and movement responses to moonlight and rainfall differ markedly. Decreased space requirements in plantations may be indicative of increased densities, and there have been suggestions that population densities may increase for this species in oil palm plantations (Natusch et al., 2016a), but determining this empirically is extremely difficult (see chapter 2). While this may be good news for long term population viability of reticulated pythons in response to habitat alteration, the outcome for more vulnerable, isolated forest prey species in places such as the Lower Kinabatangan Wildlife Sanctuary may be a negative one. While not explored here, the fact that three of five tracked pythons in plantations died (strongly suspected from human conflict in all three cases) during tracking also points to the potential trade-offs involved in adapting to anthropogenic habitats.

Studies seeking to determine the effects of short-term weather patterns on snake behaviour are important, but still remain sparse (Crowell et al., 2021). Changes in temperature and rainfall patterns as a result of anthropological climate change will inevitably play a role in snake survival rates, and predator-prey dynamics (Bickford et al., 2010; Böhm et al., 2016; Cox et al., 2022). While that goes beyond the remit of the present study, the influence of reticulated pythons in trophic dynamics as a top predator warrants further investigation into these effects.

# 5 Snakes and LiDARs: Habitat selection by reticulated pythons in the lower Kinabatangan Wildlife Sanctuary, Sabah, Borneo

## 5.1 Introduction

Habitat (or resource) selection occurs at different scales, with a conceptual framework first described by Johnson (1980), where: 1st order selection is the selection of habitat variables encompassed within a species' geographic range; 2nd order is the selection of home ranges within the habitat of the landscape; 3rd order is selection of habitat patches within the home range; and 4th order is selection of specific resources within a habitat patch. Considering habitat selection at multiple scales is highly beneficial for a thorough understanding of a species' ecology; just as habitat and environmental variables differ across different scales of space and time, so too do the ways in which a species responds to them (McGarigal et al., 2016). Telemetry data are often employed for studying habitat selection at more local scales (i.e, 2nd order and above), and particularly so for snakes, where low detectability rates and habitat-related detectability biases often make it difficult to determine species presence accurately.

The term "selection" implies the use of a resource or habitat at a higher rate than its availability in the environment. How availability is defined is therefore key to determining whether selection for a particular resource is occurring. For 3rd order selection, it is common to define availability as being an individual's home range (i.e., range distribution, see chapter 4), or with a reasonable buffer around it, and comparing the availability within this to the actual recorded locations. However, as discussed in chapter 4, the choice of home range estimator may play a considerable role in defining how much of the habitat is designated as 'available', as sizes may vary considerably between methods, and may therefore impact any inferences that can be made. Furthermore, reptile movement data tend to be highly autocorrelated (Silva et al., 2018), and the assumption that an animal has selected a particular location in comparison to the entirety of its range distribution is not reasonable for less mobile species. With the rise in popularity of GPS data, with associated spatial and temporal autocorrelation due to smaller time steps between locations, has come the development of Step Selection Functions (SSFs) (Fortin et al., 2005; Thurfjell et al., 2014). This characterises resource availability at each specific time point, comparing the movement decision of an animal with the potential moves that could have been made in the same timeframe.

A commonly-applied approach for population inference from SSFs is a two-step process, where conditional logistic regression models are fitted to each of the individual animals in a dataset, and then models are fitted to the response parameters (i.e., selection coefficients) (Craiu et al., 2011). This has the advantage of being easier to fit and interpret compared to a mixed regression model, and is equivalent to fitting a random slope that may be computationally difficult in a mixed regression approach. The two-step process also does not require any assumptions of normality in the random slope coefficients. Random slopes are required in order to consider the functional response of an animal; namely, that resource selection coefficients are dependent on the availability for each animal (Fieberg et al., 2021). However, for the two-step approach to work it requires considerable variability in the locations of individuals, and fails when not all levels of a categorical covariate (e.g., habitat type) are found in all individuals. Muff et al. (2019) instead proposed the use of a Bayesian approach as an effective way of incorporating random slopes that can overcome these limitations.

When making management decisions about a species, it is often useful to be able to predict and map areas that might be suitable for a species, or where it is more likely to occur. Habitat suitability modelling is part of a broad and diverse area of related ecological research, but fundamentally involves the use of presence (and usually absence or pseudoabsence) data to identify a species' multidimensional environmental niche, and interpolate or extrapolate this across space (and/or time) to identify areas that meet similar conditions. However, depending on the variables chosen, it generally requires all model variables to be mapped across the landscape of interest, which usually requires remotely-sensed data, such as satellite or drone images. Alternatively (or additionally), a newer approach is the use of LiDAR (light detection and ranging) data to perform laser scans of the habitat to create 3-dimensional models of the landscape (Asner et al., 2012).

Snakes are not well-represented among studies of vertebrate habitat selection due to the difficulties associated with studying them in the field (Dorcas & Willson, 2009; see chapter 1). Within tropical ecosystems, and amongst large-bodied constrictors, this discrepancy is even more apparent (Natusch et al., 2022). Understanding habitat associations is critically important for conservation and management of populations within protected areas. For reticulated pythons, which are not currently under threat, and can exist in modified habitats (Stuart et al., 2020), habitat selection is nevertheless important for maintaining sustainability of trade and further understanding of the species' ecology may improve the ability to carry out reliable monitoring (Natush et al., 2016a). Focusing surveys on areas that may have greater relative abundances could help to improve study sample sizes by increasing relative capture rates. As top predators, the maintenance of ecosystems services provided by reticulated pythons is vital, and this has the potential to be exploited within oil palm plantations to provide biological control of rodents (Lim, 1999). Additionally, there could be benefits in identifying areas where python abundance and predation pressure might be less intense, for example to improve outcomes for translocations of endangered prey species.

The aims of this study were to: i) assess habitat selection of reticulated pythons where they were caught along riverbanks, to determine microhabitat variables that may be important (4th order habitat selection); ii) Use integrated step selection functions to determine functional response to habitat variables that may be important at the movement scale (3rd order habitat selection); ii) model habitat suitability for reticulated pythons at the landscape scale within the LKWS based on telemetry data, and determine relative suitability of plantations and forests (2nd order habitat selection); and iv) assess the predictive ability of habitat suitability models using data from standardised surveys along the riverbanks.

## 5.2 Methods

### 5.2.1 Riverbank transect surveying and captures

For full details of how transect surveys were carried out, see chapter 2.

### 5.2.2 Riverbank microhabitat surveys

As part of this wider project, a professional training year (PTY) student, Alex Rose, collected data on the habitat characteristics of reticulated python capture sites along the riverbanks between February and June 2018. Five random background locations within each of the 26 transects were chosen, to provide a stratified random sample of available river bank habitat. During periods where the river level was low, a 5m-wide grid of variable length was set up at each location, with one side at the bottom of the vegetation line (where pythons are spotted during surveys), and another side placed 1m behind the crest of the riverbank. The distance from top to bottom was measured with a tape measure. To standardise all plots, percentage ground cover of vegetation up to 1m in height was estimated, to the nearest 5%, and the density of trees and woody saplings over 1m was counted.

Canopy cover was measured at the crest of the riverbank, by taking vertical photos (using a Canon EOS 1300D, set at 24mm zoom) from 1.5m height at the corners and centre of the top edge of the plot, and percentage cover estimated using ImageJ software, and averaged for each plot.

Measurements of vegetation density were taken behind the riverbank (as the amount of cover pythons would have when travelling to the riverbank) by placing a vegetation density stick (180cm pole divided with 44 white and 44 black bands approximately 2cm wide) vertically 8m away from each point, and taking photos at a height of 120cm and 180cm. Photos were later analysed and the number of visible white bands were counted and averaged for each plot. Finally, the slope incline for each plot was estimated as an ordinal score between 0 and 4, where 0 is flat and 4 is a sheer cliff face.

### 5.2.3 Telemetry

For full details of the collection of telemetry location data, see chapter 4.

### 5.2.4 Habitat Covariates

The study area was mapped by LiDAR (Light Detection And Ranging) in 2016 using the Global Airborne Observatory (Formerly Carnegie Airborne Observatory; Asner et al., 2012), producing high resolution (2m) 3-dimensional maps of the landscape, including digital surface models (DSM) and local digital terrain models of elevation (DTM). Top of Canopy Height (TCH) was calculated by subtracting the difference between the DSM and the DTM. Aboveground Carbon Density (ACD) was calculated based on ground-truthed data, with allometric equations based on TCH and canopy cover (Asner & Mascaro, 2014; Asner et al., 2018; Jucker et al., 2018). Data from flights covering around 29% of the state were upscaled to 30m resolution across the entirety of Sabah, using a suite of environmental variables from satellite data. Further details about the methodology of how these data were collected and calculated are available in Asner et al. (2018). For analyses in this study, maps of TCH, ACD, and elevation at a spatial resolution of 30m were used, as the area covered at high resolution did not include all areas where pythons were located.

TCH and ACD are generally quite closely correlated variables within forests (Jucker et al., 2018), as the height of trees can provide a reasonable estimation of the amount of carbon they contain. However, using TCH alone does not provide enough distinction between forests and plantations, especially as most of the forest in the study area is highly degraded. As the values were averaged at a course scale of 30m, the maximum values of TCH (which are therefore averaged over 30m$^2$) within the study bounds were 32m, while the maximum values at this same scale in parts of Sabah's primary forests reaches up to 74m. The height of oil palm trees reaches up to 20m (Yue et al., 2015), and so this overlaps considerably with large areas of degraded forest. Oil palm trees, however, are far less dense, and contain relatively little carbon. Therefore, despite a correlation coefficient within the bounds of the study area between TCH and ACD of 0.88, it was deemed necessary to include both within models of habitat selection (figure 5.1). The areas where these two variables interact non-linearly are likely important for distinguishing between different habitat types. Both variables therefore provide an index of habitat quality, and this is particularly important in the LKWS as past selective logging and fires have created many highly disturbed areas within the protected forests (Abram et al., 2016). Animals exhibiting selection or preference for these variables are likely to prefer older-growth forest, and larger trees, or associated hidden variables. Selection against these variables indicates a preference for younger forest, smaller trees, and potentially higher levels of disturbance.

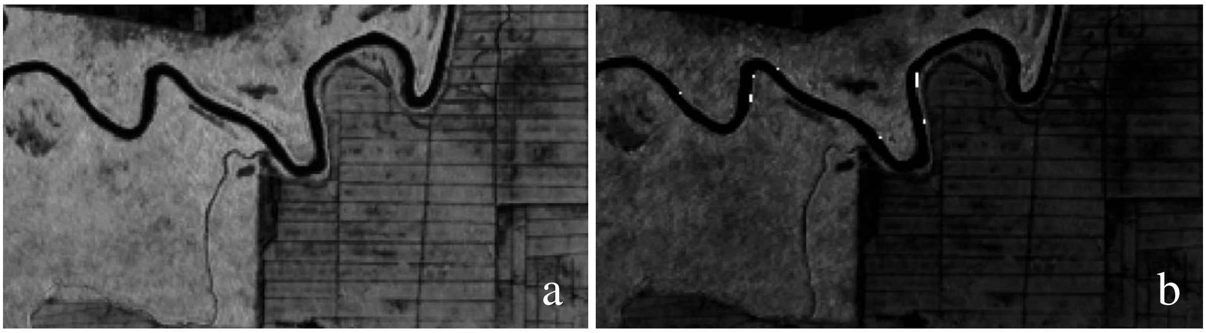


***Figure 5.1*** *Raster images derived from LiDAR data, showcasing a) Top of Canopy Height (TCH) and b) Above-ground Carbon Density (ACD) at the interface between a forest fragment and oil palm plantation (rectangular roads between planting blocks are clearly visible). ACD generally provides a greater level of contrast between these habitats than TCH, despite the high level of overall correlation between these variables.*

A land cover map was created using satellite imagery from Google Earth, broadly classifying together areas of forest, oil palm plantation, and water bodies. Rasters of distance to these features at 5m resolution were calculated in QGIS, with grid cells aligned to the LiDAR rasters. The LiDAR rasters were then reclassified to 5m resolution to allow the covariates to be stacked together. This meant that 30x30m grid cells were converted to 36 separate 5x5m grid cells, but their values were unchanged. All habitat covariates used for this study, along with justifications for their use, are provided in table 5.1.

*Table 5.1 Explanation of habitat covariates used for evaluating habitat selection.*

| Covariate | Definition | Justification |
|---|---|---|
| **Distance to oil palm plantation** | Euclidean distance to nearest oil palm plantation edge (m) | Edge effects within forests may alter resource availability, habitat structure, and some species may not venture near to disturbed or anthropogenic areas |
| **Distance to forest** | Euclidean distance to nearest forest edge (m) | Edge effects within plantations may alter resource availability, and some species may not venture far into plantation away from forest edges |
| **Distance to water** | Euclidean distance to nearest waterway (main river, semi-permanent tributaries or oxbow lakes) (m) | Identifies potential preferences for proximity to water sources or riparian vegetation |
| **Top of Canopy Height (TCH)** | Mean height of canopy within 30m resolution (m) measured | Indicates forest structure and quality, and resources associated with this. Within plantations it indicates age of palms. |
| **Aboveground Carbon Density (ACD)** | Estimation of the amount of carbon (Mg C $ha^{-1}$) stored within aboveground vegetation, derived from allometric measurements of canopy height and canopy cover. 30m resolution. | Correlated with TCH, but deviations may be important in characterising habitat type. Commonly used as a metric for assessing forest quality, particularly in the context of climate change mitigation. |
| **Elevation** | Height of ground, relative to local water table (m). 30m resolution | Within the floodplain landscape lower elevations are more flood-prone. This in turn modifies vegetation composition and associated available resources. |

### 5.2.5 Statistical analyses

*Riverbank habitat associations*

A binomial generalised linear model (GLM) was used to identify riverbank habitat variables associated with locations where pythons were captured, compared with randomly sampled background sites along riverbank transects. Five random locations were chosen along each riverbank transect in order to stratify random locations across the entire survey area, giving 130 background locations, while 51 capture locations were used in the analysis. No recapture locations were used, to avoid any pseudoreplication. Explanatory variables were examined with principal component analysis and checked for variance inflation factors (VIF), to avoid multicollinearity, and variables with a VIF over 4 were discarded. A global model was created with the explanatory variables of slope score (modelled as a continuous variable), percentage cover of elephant grass (or Napier grass, *Cenchrus purpureus*), percentage cover of other grasses, percentage cover of leaf litter, and percentage vine cover. The dredge function in the R package *MuMIn* (Bartón, 2022) was used to examine all combinations of explanatory variables, and return all models within <2 AICc of the top performing model. Model checks were performed with the R package *DHARMa* (Hartig, 2022). A single model was chosen based on the highest value of area under the ROC (receiver operating characteristic) curve (AUC). Explanatory variables were tested for significance with likelihood ratio tests. McFadden's pseudo $R^2$ (McFadden, 1974) was calculated as:

$$1 - \frac{LogLik\ (model)}{LogLik\ (null\ model)}$$

*Integrated Step selection Functions*

Telemetry locations of all 16 pythons described in chapter 4 were analysed. Using the *amt* package (Signer et al., 2011), location data were converted into 'steps', where each row of data has a start and end location, representing a single movement. The successional series of steps for each individual, termed tracks, were 'bursted' into multiple sets of tracks to only use steps that fell within a period of 2 days (plus or minus 28 hours). This filtered out steps between locations over longer time periods. Bursting separates the movement path of an individual into one or more separate tracks, which ensures that time gaps above or below the proscribed threshold are not counted as steps. This ensures there is less bias resulting from irregularities in the frequency of locations over time. For each step, 200 random steps were used to provide a sample of available habitat with which to compare the observed movement. The *amt* package will calculate random steps by default by sampling step lengths from a gamma distribution, as well as turning angles from a von Mises distribution, both parameterised based on the step lengths and turning angles of the observed data. However, this led to some random step lengths that were an order of magnitude larger than the observed data, with some observations up to 2–3km away from the start location. Turning angles could not be computed for most steps because the turning angle function requires three steps in sequence, which were typically not available when pythons spent multiple days in a single location. All step lengths were therefore sampled from a gamma distribution with a shape of four and scale of 40, which was chosen by trial and error to best approximate the distribution of real step lengths in the dataset. Turning angles were sampled from a uniform distribution, so that they did not contain any directional bias. An example of the distributions of step lengths and turning angles are shown in figure 5.2.

Models were fitted separately for each habitat covariate: aboveground carbon density, top of canopy height, elevation, and distance to water, using a mixed conditional Poisson regression, estimated by integrated nested Laplace approximation (INLA) within the R package *inla* (Lindgren & Rue, 2015; Bakka et al., 2018). Each model also included fixed effects of the covariate in interactions with both step length and turning angle. The interaction terms allow selection coefficients to differ based on the distance the individual moved and the turning angle. Habitat might be selected differently within a long-distance movement versus a short distance movement, for instance. The distance to water raster was inverted to prevent zero-inflation, and provide a more meaningful interpretation of coefficients (i.e., positive coefficients indicate selection towards water) (Smith et al., 2021).

Code was adapted from open-source code from Smith et al. (2021), itself based on code provided by Muff et al. (2020). Models were fitted with stratum-specific effects for each step (i.e., each individual step treated as a separate stratum), and with individuals as random intercepts and slopes. Both step and individual were modelled as Gaussian processes. Steps were given a fixed prior precision of 0.0001, while individuals were given a penalised complexity prior, PC (1,0.05). Fixed effects were given uninformative normal priors, Normal (0,10). Marginal posterior probability coefficient mean estimates were used to assess functional responses to fixed effects, with credible intervals crossing a value of 0 being considered ambiguous.

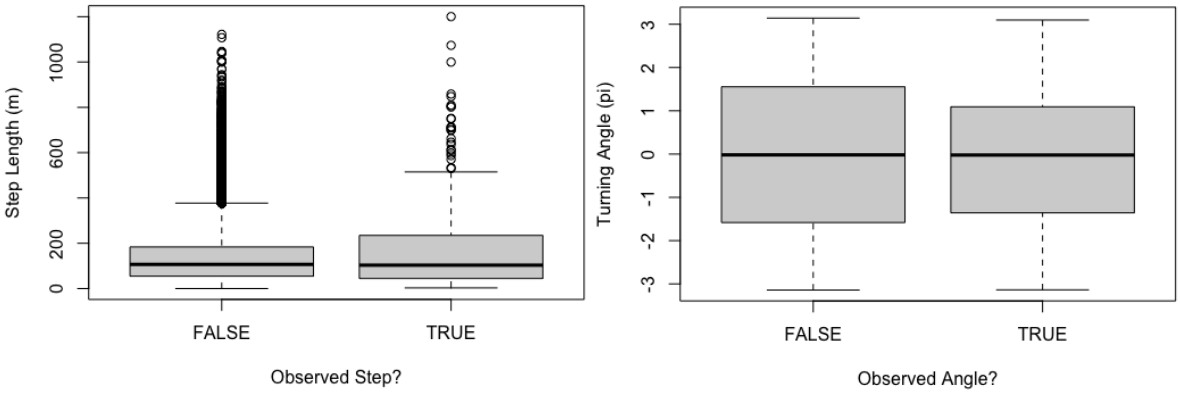


***Figure 5.2*** *Boxplots of the distributions of step lengths and turning angles used in the Step Selection Function. 'True' indicates values from the observed data, while 'False' indicates values from the random points generated to characterise available habitat.*

### *Habitat Suitability Modelling*

Habitat suitability modelling was carried out with the use of a Support Vector Machine (SVM) (Guo et al., 2005), using the R packages *kernlab* (Karatzoglou et al., 2022) and *dismo* (Hijmans et al., 2021). SVMs are non-parametric machine-learning methods that have no underlying assumptions of data distribution, do not require data points to be independent, are easy to implement, and have been shown to perform well even with limited training data (Drake et al., 2006; Mountrakis et al., 2011). They generally are able to balance well between overfitting and over-generalisation (Mountrakis et al., 2011). To fit linear trends to non-linear overlapping data requires higher dimensional space (e.g., in parametric terms through the use of quadratic or cubic functions), and SVMs use "slack variables" to achieve a higher dimensional feature space while reducing computational complexity (Mountrakis et al., 2011; Karatzoglou et al., 2022). The SVM here was modelled using a Gaussian radial basis kernel function ("rbfdot") to achieve this. Habitat covariates used in the model were top of canopy height (TCH), aboveground carbon density (ACD), elevation, and distances to water, plantation, and forest. 1000 random background points were generated within the area of interest, and k-fold partitioning of the data (k=5) was applied, using random subsets of the telemetry data to train and test the model. Evaluation was carried out with a Receiver Operating Characteristic (ROC), using Area Under the Curve (AUC), where a value of 0.5 is no different from random, and a value of 1 indicates perfect characterisation. An overall model was built from the five k-fold models, by averaging them together, weighted by AUC. This model was then used to predict the habitat suitability, using the raster images of the covariates within the study area.

To test the accuracy of the SVM model, riverbank survey capture data were used (n = 84), and compared to the randomised locations along the riverbank transects (described above) that were used for assessing riverbank microhabitat. The mean predicted suitability scores of all grid cells within a 10m radius of each location were used for comparisons, extracted using the *Zonal Statistics* function in QGIS. ANOVA was used to compare SVM estimates between capture locations and background, while evaluation using the *dismo* package was also carried out, by treating the locations as model test data in the same way as previously for model evaluation. Additionally, capture rates along each transect (pythons caught per km of surveying – described in more detail in chapter 2) were analysed in a linear regression model with the mean SVM model predictions within a 150m buffer, to further assess whether model predictions may be indicative of python abundance within the study area.

Habitat suitability modelling predictions involve extrapolating suitability values into areas that were not traversed by telemetered pythons. This can create a degree of bias, whereby areas that pythons were not telemetered can be predicted to have low suitability, when that may not be the case in reality, as the dataset is not representative of the entire area population (Vaughan & Ormerod, 2005; Rocchini et al., 2011). Estimates of model uncertainty can be derived by cross-validation of the k-fold predictions and mapped, but this does not provide a means to fully account for potential unknown error resulting from spatial bias in the predictions. If all k-folds of the model predict equally low suitability for these unrepresented areas, then this can appear as though the model has performed well there. Distance measures will therefore bias suitability scores to within the observed ranges, i.e., predicting low suitability for areas that are far from water, forest, or plantation. Elevation was intended to account for flooding potential and changes in vegetation that result, but the study area also contains several outcrops of limestone hills, and the true suitability of these limestone outcrops is largely unknown. An effort was made to partially account for this spatial and habitat bias by removing areas of the map judged to fall too far outside of the predictive ability of the model. By examining the predicted values assigned for each of the covariates (figure 5.6), it was possible to estimate the covariate values beyond which model predictions converged to 0. Cut-off values were selected and the map was clipped to remove areas where the distance to water was above 500m, distance to forest above 600m, distance to plantation above 400m, and elevation above 50m. Within this more conservative prediction map, mean habitat suitability scores were derived for forests and plantations as a whole.

## 5.3 Results

### 5.3.1 Riverbank microhabitat

The final model indicated that steeper slope angles and higher percentages of vine cover and elephant grass were all significantly associated with sites where pythons were caught (Table 5.2). Leaf litter cover was also included in the final model as this improved fit and predictive ability, but the effect was not significant at alpha = 0.05 (Table 5.3). Model predictions are shown for each explanatory variable in figure 5.3, where other model variables are set at their mean (elephant grass, leaf litter and vine) or median (slope score) values. The area under the receiver operator curve (AUC) value of 0.737 indicates that the model has an acceptable level of discriminatory ability (Mandrekar, 2010).

*Table 5.2 Model comparisons for a binomial logistic GLM determining the effect of riverbank habitat characteristics on the probability of a location being a capture site vs random background. Fixed variables that were significant in a likelihood ration test are underlined in the model specifications. The single model chosen is chosen in bold.*

| ***Model specifications*** | ***k*** | ***LL*** | ***AICc*** | ***ΔAICc*** | ***$w_i$*** | ***$R^2$*** | ***AUC*** |
|---|---|---|---|---|---|---|---|
| *Slope + vine + elephant grass* | 4 | -95.25 | 198.74 | 0.00 | 0.42 | 0.11 | 0.721 |
| ***Slope + vine + elephant grass + leaf litter*** | **5** | **-94.26** | **198.86** | **0.12** | **0.40** | **0.12** | **0.737** |
| *Slope + vine + elephant grass + grass* | 5 | -95.06 | 200.46 | 1.72 | 0.18 | 0.11 | 0.725 |
| *Null model* | 1 | -106.96 | 215.94 | 17.20 | 0.00 | 0.00 | 0.5 |

*k: number of parameters*
*LL: Log-Likelihood*
*AICc: Model fit corrected for sample size*
*ΔAICc: Change in AICc from the best model*
*$w_i$: Akaike weight – strength of model in relation to other models*
*$R^2$: McFadden's pseudo $R^2$ as a measure of variance explained*
*AUC: Area under the ROC curve – model discriminatory ability*

*Table 5.3 Individual likelihood ratio test results for each explanatory variable in the chosen model in table 1.*

| **Variable** | **$X^2$** | **P-value** |
|---|---|---|
| *Slope score* | 6.863 | **0.0088 *** |
| *Percent leaf litter* | 1.997 | 0.1576 |
| *Percent elephant grass* | 10.882 | **0.0010 *** |
| *Percent vine cover* | 9.876 | **0.0017 *** |

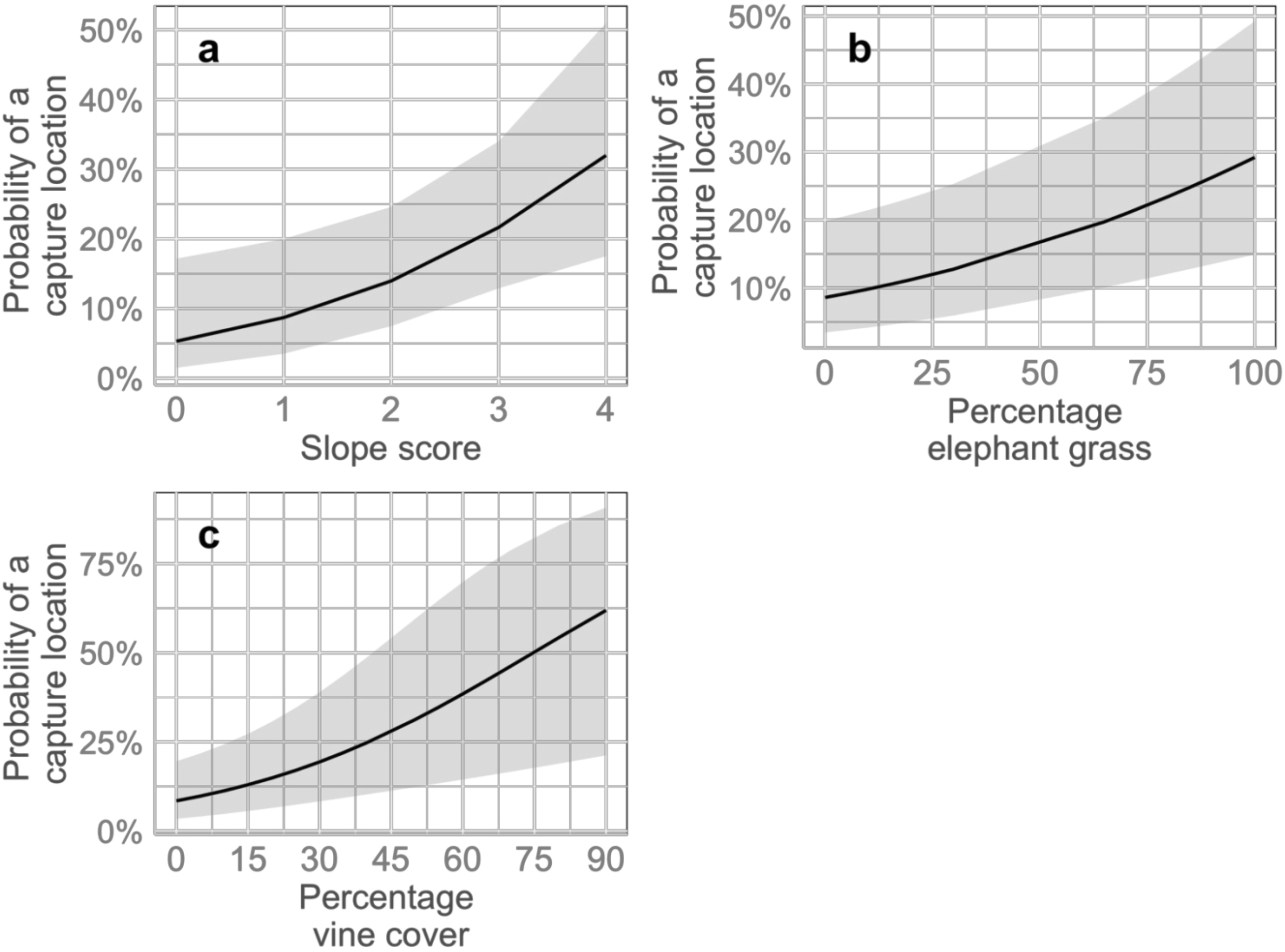


***Figure 5.3*** *Model predictions for significant explanatory habitat variables in a binomial GLM assessing python capture locations against random background locations. a-c: Slope score (0 = flat, 4 = steep – modelled linearly), percentage elephant grass cover, and percentage vine cover.*

### 5.3.2 Integrated Step Selection Functions

Population-level estimates of habitat selection indicate that pythons were slightly positively associated with water and negatively associated with elevation (figure 5.4). Pythons therefore tended to be more likely to move towards areas closer to water and with lower elevations. They did not appear to prefer to move towards or away from areas with higher canopies or aboveground carbon density. There was no indication of any positive or negative interactions between step length and any of the variables tested (figure 5.5), suggesting that the telemetered pythons did not alter their distances moved in accordance with the availability of these variables in their vicinity.

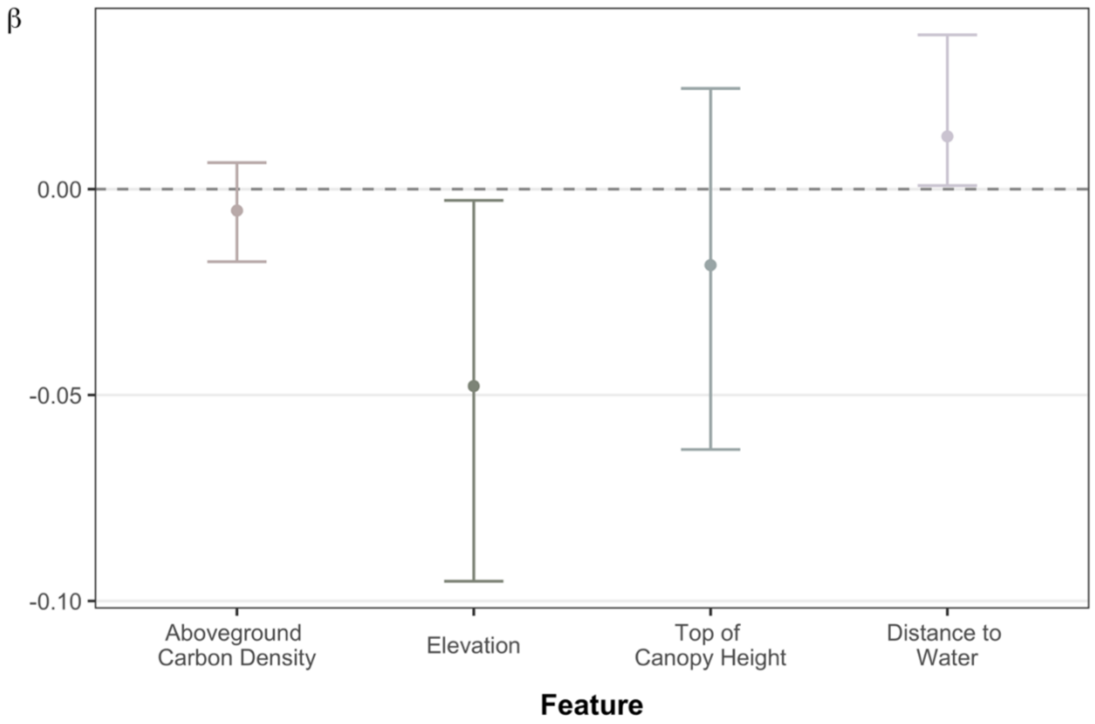


*Figure 5.4 Habitat selection coefficients of telemetered reticulated pythons, from posterior distributions of a mixed conditional Poisson regression model. Error bars represent coefficient credible intervals, with positive estimates indicating selection and negative estimates indicating avoidance. Error bars that do not overlap 0 are treated as non-ambiguous.*

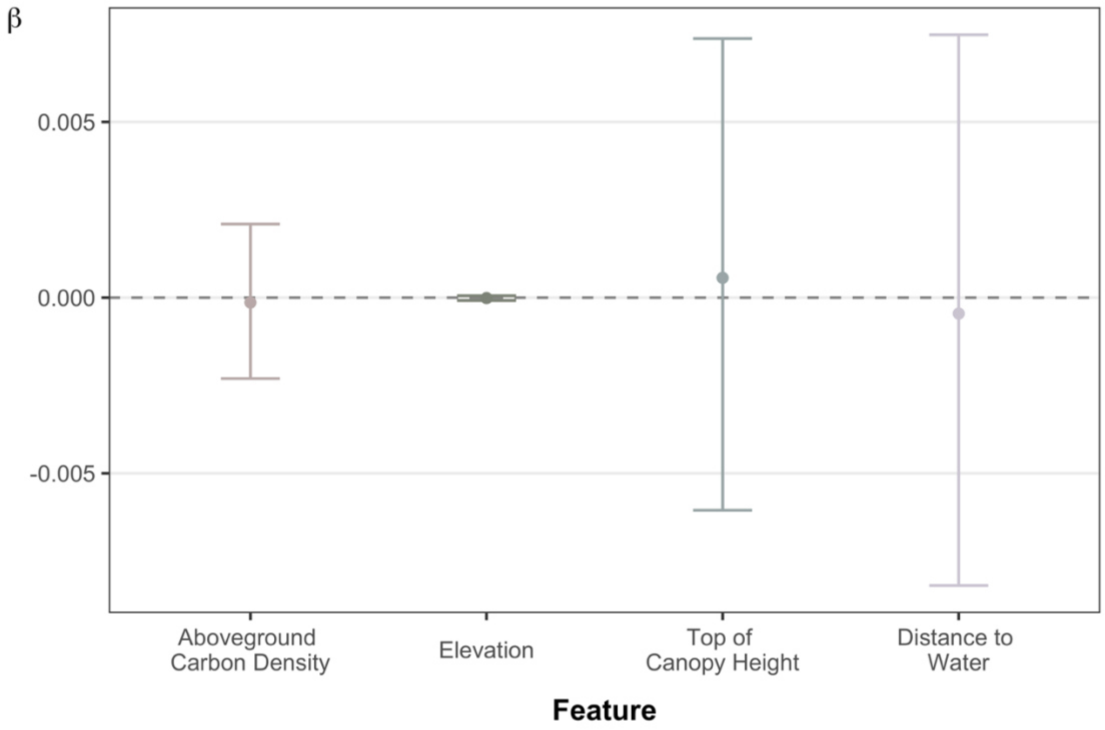


*Figure 5.5 Habitat selection coefficients of telemetered reticulated pythons, when covariates are interacted with step length, from posterior distributions of a mixed conditional Poisson regression model. Error bars represent coefficient credible intervals, with positive estimates indicating selection and negative estimates indicating avoidance. Error bars that do not overlap 0 are treated as non-ambiguous.*

*Table 5.4 Values for the mean beta coefficients of posterior distributions from a mixed conditional Poisson regression model, and variance estimates for individual random effects.*

| ***Model name*** | ***Model formula fixed effects*** | ***Mean $\beta$ coefficient for feature*** | ***Mean $\beta$ coefficient for feature interacted with step length*** | ***Individual Variance*** |
|---|---|---|---|---|
| ***Aboveground Carbon Density*** | Step ID + acd + acd:sl + acd:ta | -0.005216 | -0.000139 | 0.000015 |
| ***Elevation*** | Step ID + ele + ele:sl + ele:ta | 0.047824 | -0.000562 | 0.001012 |
| ***Top of Canopy Height*** | Step ID + tch + tch:sl + tch:ta | -0.018460 | -0.000454 | 0.000627 |
| ***Distance to Water*** | Step ID + dtw + dtw:sl + dtw:ta | 0.012793 | -0.000014 | 0.000302 |

*Step ID: each step, with both observed and random locations, as a stratum-specific random effect*
*acd: aboveground carbon density*
*ele: elevation*
*tch: top of canopy height*
*dtw: distance to water*
*sl: step length (i.e., distance between location points)*
*ta: turning angle (relative to previous step)*

### *5.3.3 Habitat suitability modelling*

The habitat suitability model showed a clear ability to differentiate the habitat into areas that may be more or less suitable for pythons. K-fold cross-validation of training and testing data gave a mean AUC value of 0.961 ± SD 0.008, indicating excellent discriminatory ability (Mandrekar, 2010), and a mean correlation coefficient of 0.845 ± SD 0.016 (p = <0.0001).

*Table 5.5 Mean evaluation statistics of the 5 SVM models resulting from the 5 k-folds of training and testing data.*

| | ***AUC*** | ***Correlation coefficient*** | ***Correct classification rate*** | ***Sensitivity*** | ***Specificity*** | ***True skill statistic*** |
|---|---|---|---|---|---|---|
| ***Mean*** | 0.961 | 0.833 | 0.728 | 0.738 | 0.716 | 0.455 |
| ***Standard deviation*** | 0.008 | 0.014 | 0.006 | 0.012 | 0.004 | 0.011 |

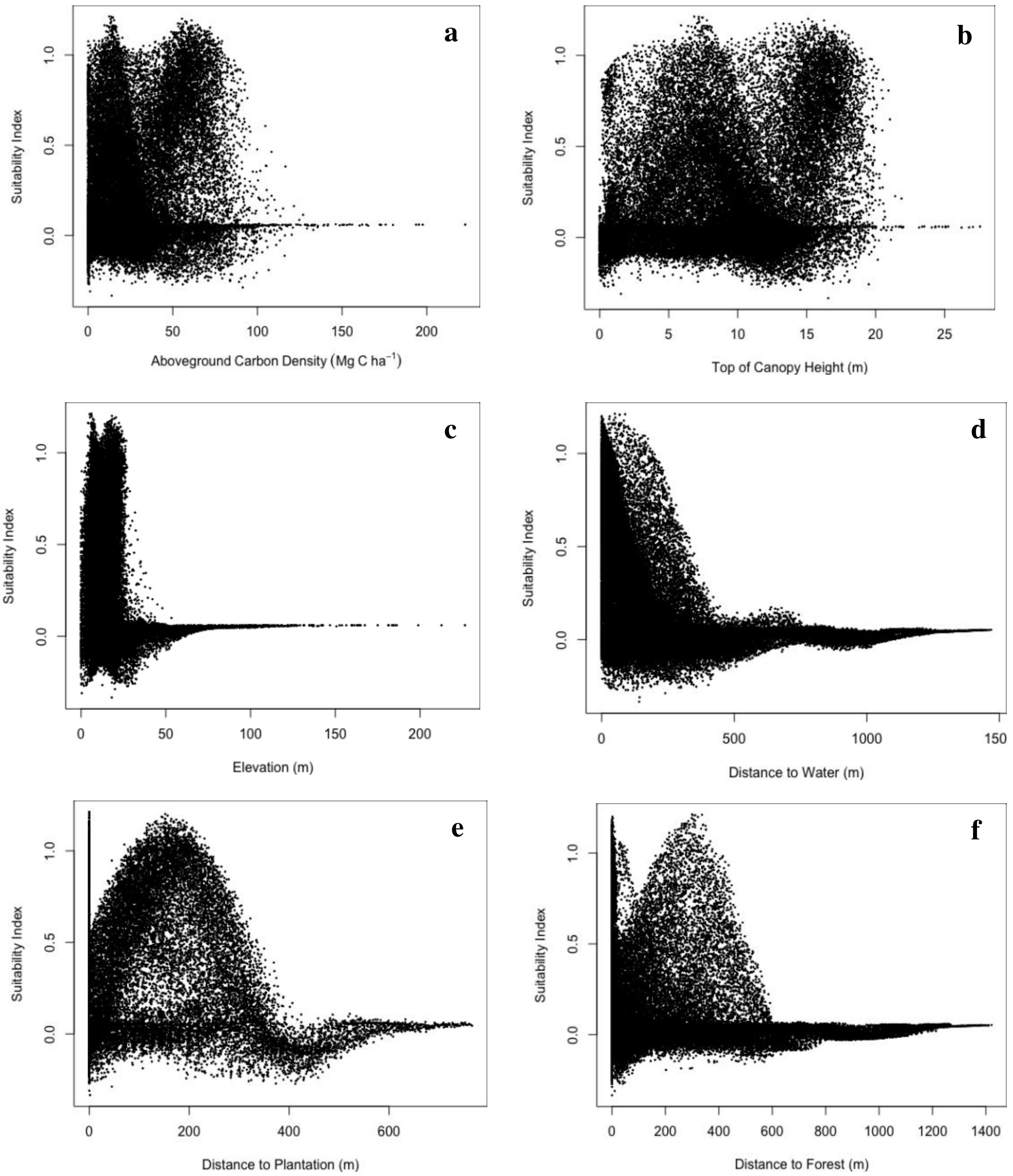


*Figure 5.6 Scatterplots of habitat suitability index values for each predictor variable used for SVM modelling. Each point in the scatterplot represents the values for a cell within the predictor variable raster image of the study region. Each plot shows a random sample of 50,000 cells. a-f: Aboveground carbon density, Top of Canopy Height, Elevation, Distance to Water, Distance to Plantation, Distance to Forest.*

Suitability scores were significantly higher for capture locations (mean = 0.80 ±SD 0.15) than for the random background locations (mean = 0.61 ±SD 0.26) (ANOVA: $F_{1,178} = 24.8$, $p = <0.0001$). The AUC value for these locations was 0.731, indicating a modest ability to discriminate capture locations from randomly selected locations along riverbanks.

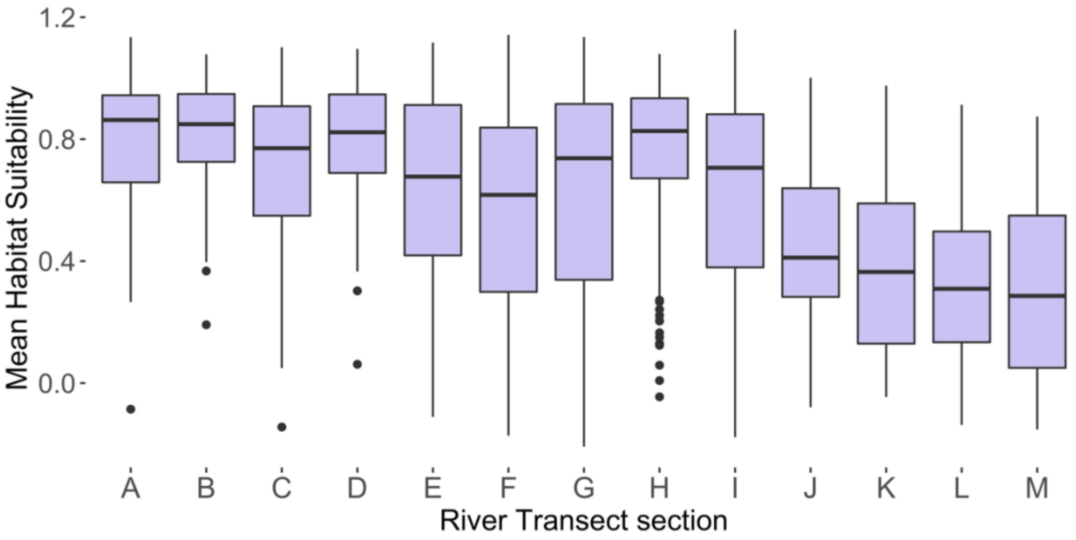


***Figure 5.7*** *Boxplots of Habitat suitability scores within a 150m buffer around each survey transect section. Transect section locations are depicted in Chapter 2, figure 2.1.*

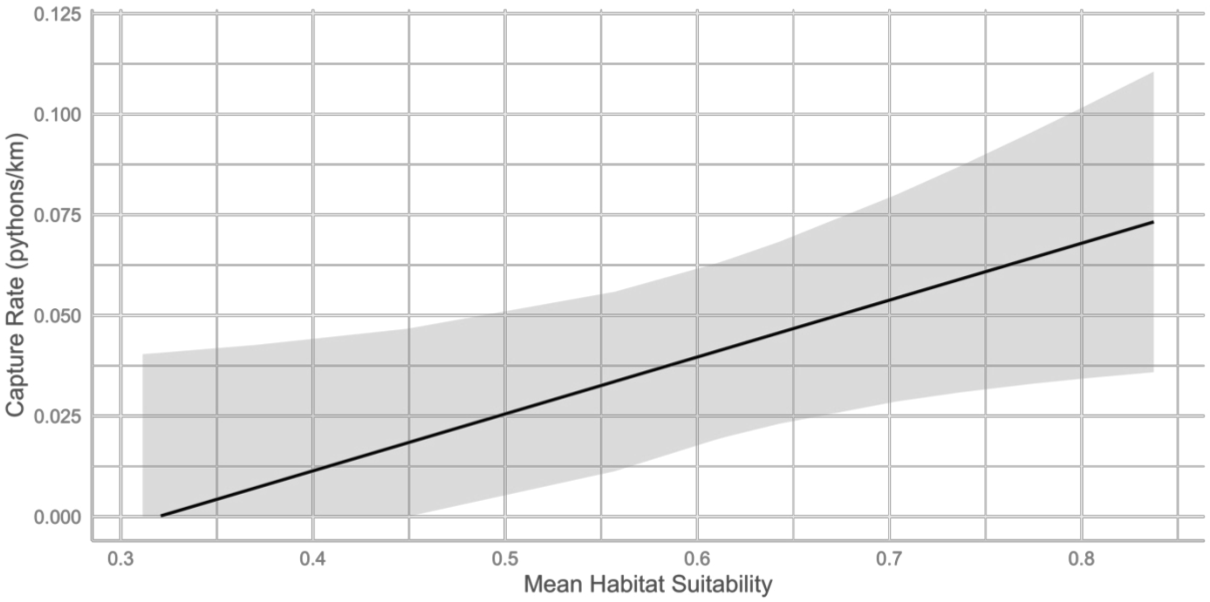


***Figure 5.8*** *Fitted predictions from a GLM exploring the relationship between habitat suitability score and capture rate.*

A linear model exploring the relationship between capture rates within each river transect section (n=13) and the mean habitat suitability scores within a 150m buffer area indicated that there was a positive relationship between the rate at which pythons were captured and the predicted suitability (Likelihood ratio test: $X^2 = 4.81$, $p = 0.028$). While model checks indicated good fit, the adjusted $R^2$ value was only 0.247, indicating relatively poor predictive ability.

In general, most of the riverbanks had higher suitability scores than the immediate area behind them (figure 5.9). Forested areas close to the river and tributaries also tended to have high scores, although there were large areas within lots 6 and 7 with lower predicted suitability. Within plantations, roads between planting blocks were clearly defined, as the low-lying vegetation and drainage ditches along them seemed to be far more suitable habitat than within the blocks of palms themselves. Suitability scores within large plantations showed a high level of variability, with some areas highly suitable and others highly unsuitable.

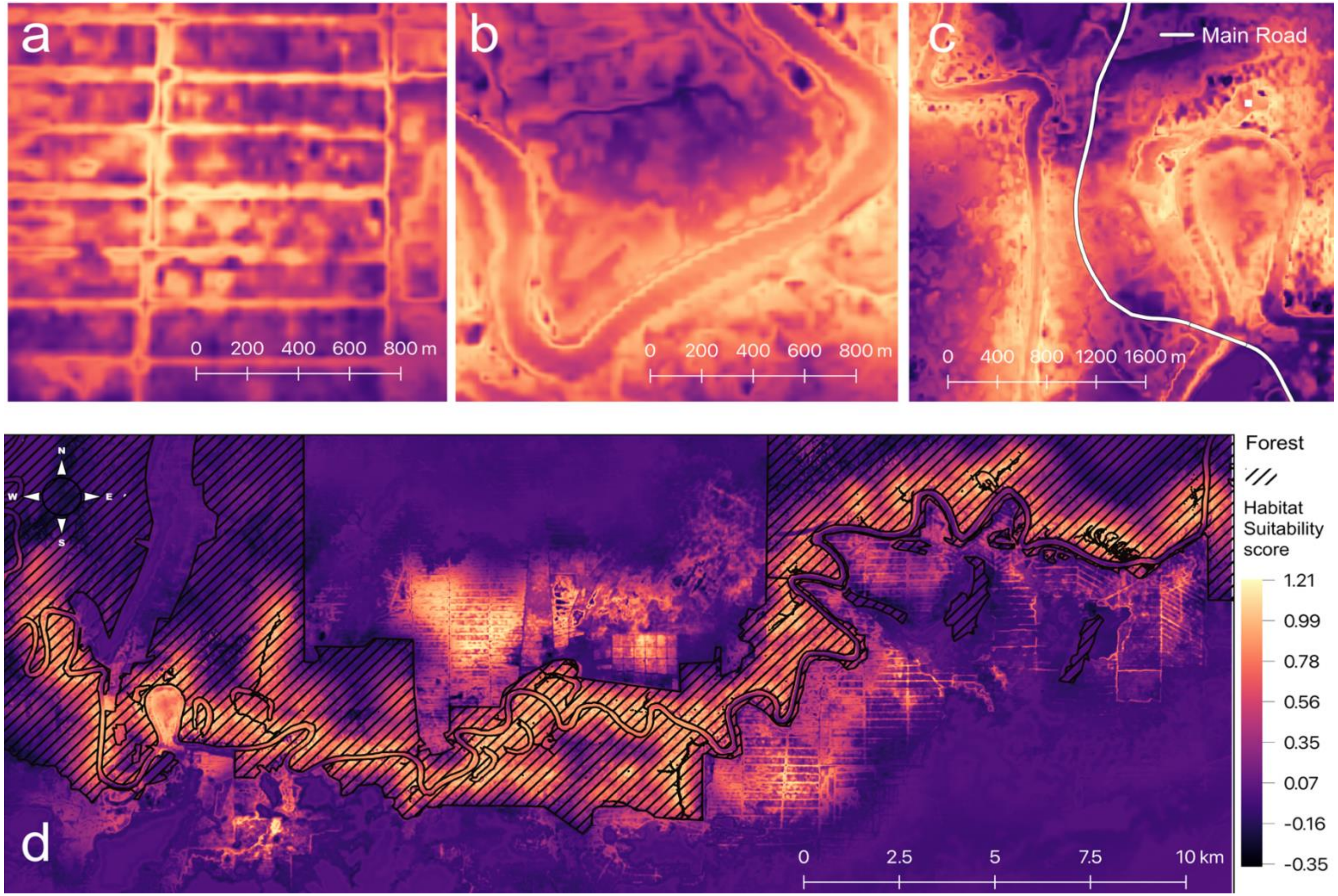


***Figure 5.9*** *Maps of habitat suitability predictions in the study area from a SVM model of telemetered python locations. a) close up of a region of oil palm plantation, highlighting how road verges between planting blocks tend to show a higher level of suitability than much of the block interiors. b) close up of the Kinabatangan river, highlighting how many of the riverbanks tend to be highlighted as particularly suitable locations. c) showing where the main road and bridge crosses the Kinabatangan. d) Overview of the entire study area. Forested areas are show with cross-hatching to better delineate the interplay of suitability scores between forest patches and plantation.*

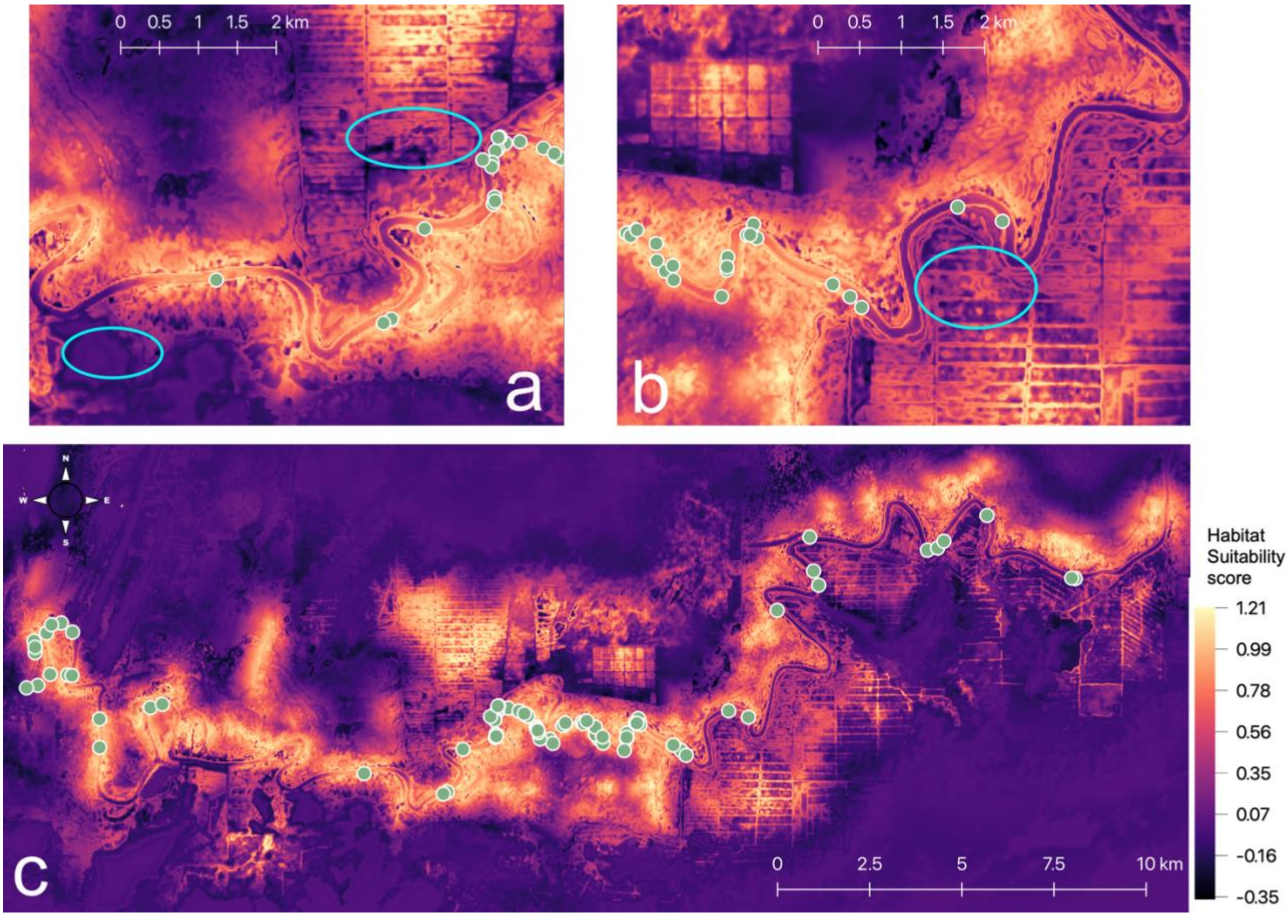


***Figure 5.10*** *Maps of habitat suitability predictions in the study area from a SVM model of telemetered python locations. a) & b) circles highlight the three areas of oil palm plantation where searches were carried out on foot at the beginning of the study, yielding no python captures. C) an overview of the study area where boat transect surveys were carried out. Points in green indicate where captures (not including recaptures) along riverbanks occurred during standardised surveys.*

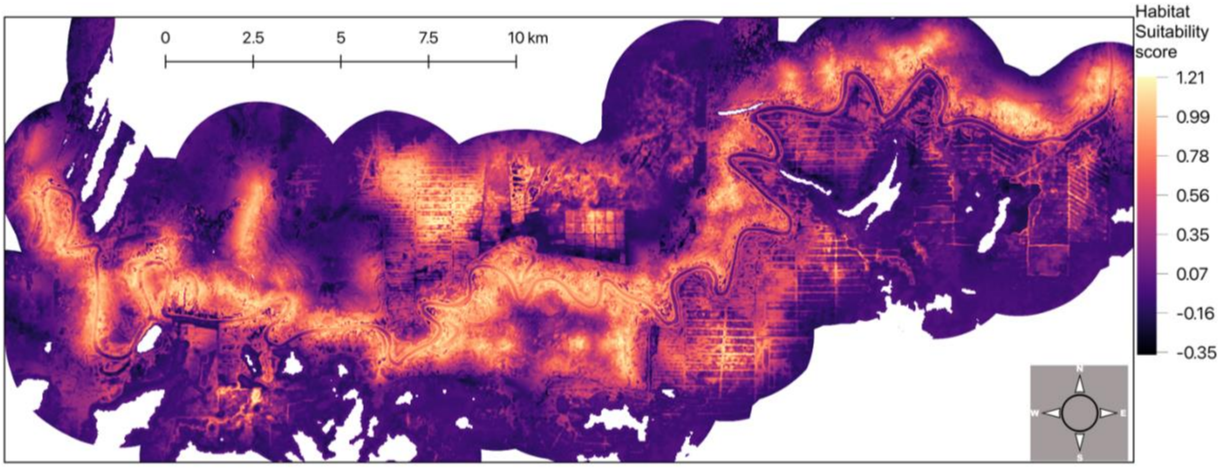


***Figure 5.11*** *Habitat suitability predictions for the study area from an SVM, when areas with distance thresholds and elevations beyond reasonable observed values are removed.*

Within the clipped prediction map (figure 5.11), mean suitability for forests was 0.397 ±SD 0.353, while for plantations the mean suitability was 0.159 ±SD 0.261.

## 5.4 Discussion

This study is the first to investigate habitat selection of reticulated pythons and showed evidence of selection occurring at different spatial scales (2nd, 3rd & 4th order). Along riverbanks, areas with high amounts of elephant grass, vine cover, and steep slopes appear to be positively correlated with finding pythons, and may indicate that pythons are selecting for these microhabitats. Python movement decisions appear to favour areas with lower elevations that are closer to large water bodies. At a broader scale across the study area, it appears that there is considerable heterogeneity in habitat suitability both within forested areas and plantations. While reticulated pythons are clearly able to thrive in plantations, within the study area it appears that plantations are less likely on average to contain suitable habitat than forests.

### 5.4.1 Riverbank microhabitats

The GLM provided some evidence that pythons are potentially not being caught at random, and selecting locations that have, on average, steeper slopes, and higher percentages of elephant grass and vine cover. The chosen model was only able to correctly distinguish a capture site against background in 73.9% of cases, but as sites were chosen at random, it can be expected that a proportion of those sites might be locations that could conceivably be favourable for pythons (Barbet-Massin et al., 2012). As all the variables that were kept in the model were estimated by eye, there is likely to be a degree of human error in the variation.

The detection probability of snakes is generally extremely low (Steen, 2010; Durso et al., 2011; Lardner et al., 2019), and reticulated pythons are no exception to that. Nafus et al. (2020) attempted to evaluate Burmese python (*P. bivittatus*) detectability along a Florida canal using telemetered animals known to be along the transect during surveying. Their estimates of between 0.0001 and 0.0146 (i.e., that for every python detected up to 10,000 go undetected) are probably much lower than that exhibited by reticulated pythons along the Kinabatangan, however, based on recapture rates in this study (see chapter 2). Nevertheless, very low detection rates hamper any attempt to separate differences in detectability in different habitats with true selection/avoidance exhibited by these animals.

Pythons appeared to show a preference for steeper riverbank slopes. Shallower riverbank slopes tend to occur on the inside of a river meander, and this both decreases the angle of view of the vegetation edge, and often means the boat is unable to be driven as close to the riverbank, due to shallow water. However, as the insides of meanders tend to be depositional (Horton et al., 2017), there is often less established tree growth and vegetation complexity, which may make pythons less likely to venture out to the vegetation edge along the riverbank. No pythons were detected in areas with a slope score of 0 (flat). Elephant grass may well be important habitat along riverbanks for pythons, as it both provides excellent cover and is simultaneously relatively easy for pythons to move through quickly (Pers. Obs.). Pythons tracked in the area during the day with VHF were often found resting within stands of elephant grass close to the river. However, due to the fairly uniform clumping and vertical structure, it is often also possible to detect a larger proportion of the animals' bodies at night than in many other vegetation types. There also tends to be a lower amount of leaves, branches, and other detritus within elephant grass stands that could reduce detectability, meaning that pythons within these areas stand out more to an experienced observer. Potential selection for vine-covered areas is interesting, as due to the serpentiform nature of vines, it can make it potentially harder to distinguish the presence of pythons, so this seems less likely to have any potential for detection bias. Like elephant grass, dense clumps of vines have also been found to represent a common choice for resting pythons during the day within the forest tracked with VHF (Pers. Obs.).

### 5.4.2 Integrated Step Selection Functions

The ISSFs showed that python movements appeared to be directed towards water bodies, and away from higher elevations. There was little evidence that they prefer areas with higher canopies or aboveground carbon density, which would be indicative of older, mature areas of forest. As the locations were all collected during the day, this actually represents selection of resting locations. Selection of resting locations that are closer to water and at lower elevations further highlights the fact that occupancy modelling in chapter 2 showed that the detectability rates of reticulated pythons along riverbanks appear to be much higher than expected when compared to detectability rates of Burmese pythons (Durso et al., 2011; Nafus et al., 2020). However, there is the potential for bias among the pythons telemetered in forests, as they were all caught along riverbanks, so may not be fully representative. A preference for areas close to water is something that has been previously noted for the species (Auliya, 2006), but not empirically investigated.

This dataset includes a mix of pythons utilising either forest or plantation, and two individuals that utilised both. ISSFs compare the functional response to habitat parameters of locations in comparison to what is immediately around them, i.e., it is relative to availability (Fieberg et al., 2021). There are vast differences in resource availability and habitat composition between the two habitats, with relatively few commonalities. During tracking the animals, pythons in forest were regularly resting in elephant grass and burrows along riverbanks, and when deeper into the forest, amongst clumps of vines, branches or buttress roots of large trees, and occasionally high up in the trees. In plantations, rodent burrows beneath oil palm trees, and drainage and irrigation ditches (or the vegetation bordering them) were more typical. The question being addressed in this analysis is therefore to identify whether there are commonalities in habitat selection despite inhabiting very different landscapes. Including an additional categorical variable in these models to separate results by habitat type, or separately sampling the responses of forest and plantation pythons from the posterior using Markov Chain Monte Carlo (MCMC) methods does not provide different results.

To improve this analysis in order to separate functional responses between pythons in plantations and forests would therefore necessitate fitting the models separately for each habitat type. To address the question of whether pythons actually prefer forest or plantation would require a dataset that involves mostly or exclusively individuals that utilise both habitats, similar to the study conducted by Evans et al. (2021) on Malay civets in the same study area. However, this would ignore the fact that reticulated pythons are able to live exclusively within plantations, which may not be the case for civets (Evans et al., 2021). The results suggest, however, that regardless of habitat type, pythons are showing preference for lower elevations (i.e., more flood-prone areas) and water sources. Across the study landscape, these two variables did not exhibit multicollinearity, and the correlation between these two variables is only 0.182. Correlation between them is likely to be stronger or more frequent at smaller spatial scales close to water.

The results here suggest that pythons are not exhibiting preferences for higher quality habitat. In both forest and plantation this would indicate areas with older mature trees. Diversity and composition of species in larger and older oil palm trees is often higher (Kurz et al., 2016). To fully investigate whether pythons prefer mature palms is difficult with the current data, as the age of palms is not heterogeneous; blocks of trees are planted simultaneously. Tracking pythons in areas of oil palm where a greater variety of palm ages exist in close proximity to each other would better allow this specific question to be addressed. It should not be altogether surprising, however, to find the same result as was demonstrated here; preference for tall or carbon dense trees is not exhibited by reticulated pythons. They are a remarkably adaptable species (Natusch et al., 2016a), and preferences for mature forest areas would run counter to the narrative that large-scale deforestation has likely benefitted them, at least in terms of abundance.

Step lengths, or the Euclidean distance between successive locations, were modelled in interactions with the covariates. This allowed identifying whether movement behaviour differed in response to these variables. This could be important, as it would indicate potential behavioural changes in response to different habitat types. For example, longer step lengths might indicate either a greater intention to search out more favourable habitat, or to move away from the habitat where the animal was previously located. GPS data would allow for a better understanding of this, as much of these complex movement patterns and decisions are lost when only taking single locations every 48 hours. There does not appear to be any indication that the habitat variables included for analysis influenced the distance that pythons will travel between resting sites. The same result was found for Burmese pythons in response to different categorical habitat types (Smith et al., 2021). It is difficult to fully determine from these data, but could be suggested that selection of resting locations is not a determinant of how far pythons are willing to travel. Perhaps choosing a location is more of an immediate decision, selecting the best source of cover within the vicinity after movements have ceased. Anecdotally, choosing to rest within the canopy was relatively rare, but did appear to coincide with areas where there was little ground vegetation in the immediate area, or if the forest floor was flooded. Studying these resting microhabitats in more detail was initiated by a collaborating student, but interrupted as a result of COVID-19. However, initial results suggested that resting locations within forests had lower canopy cover, higher vegetation density and greater amounts of fallen deadwood than randomly-selected nearby locations (Fitzpatrick, 2020). While understorey characteristics were not able to be included as covariates for the present study, it was thought there might be a degree of correlation with the forest structure, e.g., shorter or less dense trees would allow more light, encouraging understorey growth (Montgomery & Chazdon, 2001).

While ISSFs carried out in the manner presented here are useful for identifying the importance of individual variables, including each covariate within separate models removes the potential for assessing any complex interactions between them. The LiDAR data of ACD, TCH and elevation on their own may be poor metrics to elucidate specific habitats that pythons may be selecting or avoiding. This is not to say that LiDAR data is poor for addressing habitat selection. Rather, these variables likely interact non-linearly within different habitat types. A low elevation with low canopy height might indicate an open, swampy former oxbow lake, or a recently planted area of oil palm in a flood-prone area, and carbon density might be able to delineate the differences between them. Attempting to examine covariate interactions within a global model and carry out model selection using INLA proved difficult, and failed to converge, which led to using the simpler multi-model approach used by Smith et al. (2020) and Jones et al. (2022). Interpreting complex interactive effects as single coefficients can be difficult (Fieberg et al., 2021). It would probably be more useful to first classify both forests and plantations using the LiDAR data and satellite imagery into a number of categories, similar to how this was accomplished for the region by Abram et al. (2016). Using ISSFs to analyse distances to each of these habitat classes might provide a more biologically meaningful interpretation of habitat patch importance for reticulated pythons than the raw single metrics from LiDAR data. This would, of course, require considerable amounts of ground-truthing to ensure any machine-learning tool used for this purpose is classifying the region correctly. In the absence of this possibility, it is easier to carry out habitat suitability modelling, as this does not require *a priori* assumptions about class thresholds, and can interpolate the habitat characteristics linearly (e.g., Evans et al., 2018).

### 5.4.3 Habitat suitability modelling

While reticulated pythons are well-documented as habitat generalists (Shine et al., 1998a; Reed & Rodda 2009; Natusch et al., 2016a), habitat suitability modelling suggested considerable heterogeneity within the LKWS. While their ability to live within oil palm plantations is unquestionable, this study found that forested areas tend, on average, to have a higher proportion of suitable habitat than plantations. This is perhaps not surprising, given the degraded forests in the LKWS more closely match the species' original, natural habitat prior to human modification. But previous suggestions that the species may actually do better in plantations (e.g., higher density), might not be universally true. It is interesting to note that the habitat suitability predictions show a high level of heterogeneity within oil palm plantations. While a first impression when visiting these areas of monoculture might be one of a single homogenous habitat, differences both due to elevation and individual management practices can create a diversity of environments. For example, many areas surrounding the Kinabatangan are extremely low-lying and flood-prone, resulting in the need for drainage ditches between rows of palms and alongside road verges. If these are not intensively managed with chemical herbicides, then it results in a lot of low-lying vegetation, which are excellent microhabitats for pythons to rest in. Conversely, hillier areas of oil palm tend to be more barren (pers. obs.), and may therefore be less suitable areas for pythons to inhabit. Figure 5.9-a shows a close-up view of an area of oil palm plantation with relatively high suitability indices. The distinction of the roads between planting blocks is quite clear. These drainage ditches and roadside vegetation were commonly used as resting sites by the pythons that were tracked in the plantation. In a few instances where pythons were only moving short distances between successive locations, their path followed straight lines along these verges, indicating that they may act as corridors facilitating movement across the landscape. These are indeed areas that python hunters often set traps for pythons in plantations (Khadiejah et al., 2021).

During the first few years of this study, regular attempts were made to search for pythons on foot within three of the plantations around the study area, but none were encountered. Pythons were only encountered in plantations towards the end of the study, once the use of a vehicle was made possible (see chapter 2). However, even then, the areas previously covered on foot yielded no sightings, while deeper into the plantation away from the riparian zone, on new moons, it was possible to find multiple pythons in under an hour. Figures 5.10-a and 5.10-b show that the areas that were searched on foot all have relatively low predicted suitability. While there may be a degree of bias due to the fact that all the pythons used to build the model came from this one area of plantation, the fact that pythons were only encountered there lends some credence to the model predictions. However, the caveat is similar to that discussed in chapter 2; detectability bias in different habitats is a particular issue when it comes to the study of these animals.

Figure 5.9-c shows where the main road crosses the Kinabatangan river. For many snakes, roads can act as attractants as basking locations since roads heat up quickly and retain heat at night. While this is often useful for providing an easy way to carry out surveys for snakes by car (Madsen & Shine, 2000; Brown et al., 2002; Dorcas & Willson, 2009; Hart et al., 2015), it also often results in high levels of mortality from passing traffic (Jochimson et al., 2004; Hartmann et al., 2011). While nocturnal snakes are typically less vulnerable to road mortality than diurnal species (Hartmann et al., 2011), dispersing neonates tend to be particularly vulnerable (Enge & Wood, 2002). Conversely, many species may avoid roads due to a lack of enclosing vegetation, and disturbance from traffic (Andrews & Gibbons, 2005; Paterson et al., 2019; Jones et al., 2022). Roads were not a feature included in building the habitat suitability model, because none of the telemetered pythons were near a metalled road, and distinguishing between the small dirt roads between oil palm plantation blocks and other small or medium public roads in the area seems arbitrary, and difficult to achieve accurately at a 30m resolution. Roads, or at least the verges along them, between planting blocks in plantations appear to be generally attractive habitat, but the opposite may be true for small roads within built-up areas. The large intra-state highway that crosses the river is mostly within areas of

low predicted suitability for pythons. However, the small area shown in figure 5.9-c shows potentially higher suitability, which may be an area where higher numbers of roadkills could be expected to occur, as it represents a possible crossing point. This is the only stretch of the road with a reasonable level of forestation and in the vicinity of the river on both sides. Although anecdotal, this is where a recent roadkill of a hairy-nosed otter (*Lutra sumatrana*) was discovered (only the second record in the LKWS; the first was encountered during the course of this study while attempting to locate telemetered pythons – Wai et al., 2021), so this could be an area of the LKWS that is important from a conservation perspective for other species, such as endangered mammals. This is particularly relevant because this highway will be upgraded to a dual carriageway as part of the proposed Pan-Borneo Highway (Sloan et al., 2019). If pythons were to be telemetered within this area or other areas close to the highway, then it would provide an improved picture of how pythons respond to human modifications to the landscape. If they exhibited strong avoidance of roads, then it might suggest the possibility of restricted gene flow between populations on either side. Of course, this could also be tested by examining the landscape genomics of the samples that were collected during this study to see whether there is strong evidence of population structure between individuals caught east and west of the road (see figure 5.10-c).

The sample of individuals from which these data are drawn is relatively small for making large-scale extrapolations across the entire landscape. Both forest and plantation dwelling individuals were concentrated to relatively small areas, and so it is difficult to be sure of the accuracy of predictions within areas for which there are no data. While this is true to some extent for any species distribution model, care must always be taken when the pseudoabsences are derived from areas that are very different from the presence data (Vaughan & Ormerod, 2005). For example, initial attempts to model habitat suitability incorporated a low-resolution map of soil types, derived from data collected by Sabah Forestry Department. However, of 13 different categories within the study area, only 4 were within the vicinity of the telemetered pythons in forest, and only two in the plantation. Using this environmental layer resulted in a suitability map that only reflected these categories, with either a value of 1 or 0. For continuous environmental variables the same is true, but the results might not be as immediately obvious. In the absence of a reasonable method to map the size of confidence intervals in the generalisability of predictions for SVM models, areas where the model converged to 0 were removed (figure 5.11).

Distances to water were included in the suitability model to allow better delineation of water, and particularly riverbanks. Distances to plantations and forests were included to allow for an assessment of edge effects within both habitats and to allow LiDAR variables to be differentiated within each habitat, as they correspond to different habitat effects and resources in plantations and forests (table 5.1). Lower elevations were shown to be selected for at the scale of movement decisions in the ISSF, but the floodplain landscape from which the data were collected is largely flat and low-lying. Removing the elevation covariate, however, results in lower AUC scores, and leads to predictions of high suitability in areas where pythons were never encountered, and low suitability where they were frequently encountered. Within this floodplain landscape, elevation can be thought of in terms of flooding potential, and therefore helps to delineate between habitat types, such as between swamp and riparian forests (Guerrero-Sanchez et al., 2022). Despite the inclusion of elevation as a covariate in the model helping to improve predictive ability, it is probably not reasonable to conclude that the only suitable habitat is at low elevations; reticulated pythons have been recorded at elevations up to 1000m in other parts of their range (Stuart et al., 2018).

Despite these caveats in the modelling, the results show a reasonable congruence with reality. Further evaluation could be carried out by performing comparison abundance surveys in areas with high and low predicted suitabilities (but see chapter 2), but the model is in broad agreement with the analysis of riverbank microhabitat, and with the capture rates along the river transects. These results could be considered analogous to *a priori* ground-truthing of the model predictions. While there are undoubtedly microhabitat-level effects involved in selection of resting and ambush locations that are ignored here, the results indicate that even with LiDAR data collected at a relatively course resolution of 30m, it is still possible to provide meaningful assessment of python habitat preferences at the landscape-level. This 30m resolution map was derived by upscaling fine grain data across the entire state of Sabah, and this fine grain data digital surface model (DSM) included data collected over parts of the study area itself, with a resolution of 2m. However, all of the telemetered pythons in plantations and one in forest, as well as several of the riverbank transects, were located outside of this mapped area, limiting the ability to carry out the modelling in finer detail and make predictions for a larger area of the landscape. However, including distance covariates at a 5m resolution, and rescaling the cell sizes of the LiDAR rasters to the same resolution, allowed for creating predictions at this higher resolution, improving the depictions of edges, such as riverbanks.

Future work would undoubtedly benefit from a larger sample size, and carrying out telemetry over a larger spatial range, although this is logistically challenging to do on multiple individuals simultaneously without multiple research teams. Not only would this improve the overall models, it might allow for making inferences about how habitat selection changes with regards to body size, sex, or seasonality. If the habitat suitability map derived here is broadly in line with reality, then following individuals outside of currently predicted suitability areas would be difficult to achieve if pythons are not located in these areas, or only exist at very low densities. However, attempting to find and track pythons at higher elevations might be the most beneficial way to improve the modelling predictions. Further work could also be carried out to compare the habitat characteristics within areas of relatively high and low predicted suitability, particularly in plantations, to better assess what management strategies might be most beneficial to allow pythons to inhabit them. Improving habitat quality in plantations would likely see a beneficial effect, as this could lead to a reduction in rodent populations, improving crop yields and reducing the need for the use of pesticides. More work would need to be carried out to establish if this is true, however, and there might be more complex processes at play. A simple first step that could be informative would be to measure rodent densities in plantations in areas of high and low suitability for comparison.

## 5.5 Conclusion

This study provides important information on reticulated python habitat selection at multiple spatial scales, identifying several characteristics that may be important. By integrating the use of airborne LiDAR data with Bayesian step selection functions and machine learning methods, the study shows the possibility for determining habitat suitability for an understudied snake species in a manner that is relatively unprecedented. Further work is still needed to better characterise habitats that may be important for reticulated pythons both within forest fragments and in oil palm plantations, as this would allow for improved management and have important conservation implications.

# 6 Synthesis

## 6.1 Summary of aims

This research was intended as a largely exploratory comparison study to examine the ecological effects of oil palm plantations on the biology and behaviour of reticulated pythons, *Malayopython reticulatus* (Schneider, 1801), in relation to fragmented forest and riparian corridor habitats within the Lower Kinabatangan Wildlife Sanctuary (LKWS). Through the description of demographics, space use and habitat preferences, it aimed to use a model fragmented ecosystem to provide a picture of the changes that occur in a generalist species as a result of adapting to this anthropogenically-modified landscape.

Additionally, this study aimed to provide novel (for this taxon) methods for studying such a widely distributed, economically and ecologically important species that has nevertheless undergone relatively little study within natural field conditions. This includes long-term standardised visual encounter surveying, radio-telemetry and development of novel telemetry methods and analyses, and LiDAR remote sensing data for investigating habitat preferences. Most of the interest for studying reticulated pythons centres around trade dynamics and monitoring to assess sustainability, and there have been repeated calls to carry out monitoring within natural systems to alleviate any potential bias that might result from analysing the harvested trade directly. This study therefore, both explicitly and implicitly, aimed to provide a roadmap for carrying out and improving such studies, and simultaneously demonstrate and discuss the various problems and biases involved in attempting to do so.

## 6.2 Summary of findings

In **Chapter 1**, I provided background information about the study area and summarised much of the biological information that is currently known about the species (However, a more extensive and thorough report on their biology is found in Reed & Rodda, 2009). In doing so, I aimed to justify the need for this research, and argued that reticulated pythons are a far more integral species within their ecosystems than many people may realise.

In **Chapter 2**, I provided results from standardised visual encounter surveys along the Kinabatangan River, as well as unstandardised surveys and incidental captures to describe demographics of the study population, and explored how environmental variables may impact estimates of abundance from capture/encounter rates. Where possible, I looked at how these differ for pythons found in plantations with those found along riverbanks within the forest sanctuary. I also evaluated the potential for such studies to provide the relevant information needed to monitor population vital rates to assess trends resulting from intensive harvesting.

There is evidence to suggest that pythons in plantations may display better overall body condition than those found along the river, likely as a result of increased prey abundance in plantations. The implication of this is that pythons are not only able to exploit the resources within oil palm plantations, but (at least some) plantations may actually provide a better habitat for reticulated pythons than degraded riparian forests. Capture rates within these two habitats are not directly comparable due to methodological and detectability differences, but initial results suggest that in some areas of oil palm plantations, reticulated pythons may exist at higher densities than are typically found in more natural forest habitat.

I showed that some of the indices that might be used within the context of population monitoring (abundance, size and body condition) show significant differences between years, and capture rates can vary considerably between different times of year, even within a population that is not being harvested. These results suggest that any attempt to carry out monitoring in harvested populations will be fraught with stochasticity. In any case, achieving sample sizes sufficient to make robust conclusions about population declines from overharvesting in just a single site requires considerably more effort than is realistically achievable. However, the results demonstrate the potential feasibility of standardised surveying for answering other important scientific questions about the species.

By examining weather and moon phase during surveys, I showed that moonlight has a strong effect on the capture rates of pythons along riverbanks, and the probability of capturing pythons is highest during a new moon. If this is related to when pythons are most likely to be hunting for prey, then there are intriguing implications for how this would affect predation rates of various prey taxa (assuming they also show changes in activity in response to moonlight levels), and which species might be most vulnerable to any potential increases in python abundance.

Occupancy modelling was carried out to provide a more robust estimate of overall python detectability, and to assess whether proximity to oil palm plantations has any correlation to the occupancy rates of the riparian transects surveyed in this study. While there are many confounding variables, there is not a noticeably large effect. This does not rule out increased abundance in plantations, because potential spill-over from plantations into the forest fragments may have already occurred. Assessing the potential ecological consequences of changes in python abundance would require long term standardised data from forest areas both before and after deforestation and development of oil palm. The only detectable effect on occupancy rate was whether transects were located on the north or south bank of the river, and the reasons for this are unclear. If this is not a result of survey bias, then this may alter diversity and population dynamics of prey species isolated within forest fragments on either side of the river. Within an occupancy framework, detectability rates of pythons along transects were only noticeably affected by the moon, similar to the assessment of capture rates with weather. That this study was able to achieve a modest sample size larger than any previously conducted field studies is testament to an increased amount of effort and distance covered; detectability rates were low, and it required on average 19.6 km of standardised surveying per python encountered (2347.3km and 120 encounters, including repeat recaptures and pythons seen that evaded capture).

Overall, while surveying by river allows much greater distance to be covered in a given time and reduces physical effort (compared with visual surveys on foot in forest), it does not provide a highly efficient means to monitor populations. The results suggest that future survey efforts to study reticulated pythons or carry out regular monitoring should focus efforts towards times when moonlight levels are low to maximise encounter rates, as this is likely to be more important an effect than standardising monitoring to occur on the exact same dates each year to control for seasonal differences. However, the various biases and caveats involved, combined with low statistical power from low sample sizes, means that monitoring wild populations is unlikely to be useful for assessing changes in vital rates necessary to make conclusions regarding trade sustainability. The high costs of accurately doing so outweigh the potential modest benefits to improving on the methods that are already well-established.

In **Chapter 3**, I provided an overview of my iterative methodological developments of testing GPS tags on reticulated pythons. While I did not arrive at an effective solution to the question of how to accomplish GPS tagging of reticulated pythons, I nevertheless was able to use my experiences to provide valuable considerations and recommendations for other researchers seeking to accomplish something similar on other snakes. As the technology continues to improve and miniaturise, more researchers will doubtless seek to find a way to utilise the relative advantages of GPS telemetry in snake research. When this research began in 2016, one study (Hart et al., 2015) had published results using GPS in snakes, and there have been five studies published in the meantime (Smith et al., 2018; Wolfe et al., 2018; Gerke et al., 2020; 2021; Smaniotto et al., 2020), and all of them encountered problems to some extent. Snakes present a particular challenge to the use of this technology. Researchers need to consider carefully the trade-offs between the animals' physiology, behaviour and their habitat, as well as potential ways to save battery usage, improve fix rates and retrieve data. All while considering what is cost effective, best in terms of welfare, and how the technology can best answer specific study questions. The main barrier, however, remains in how to attach devices safely and effectively for long-term studies.

In **Chapter 4**, I detailed the results of VHF (Very High Frequency) telemetry work to provide estimates of movement and space use for reticulated pythons, and compared these between pythons in forest and plantation. Additionally, I provided a small case study of two pythons, comparing how these results differ when carrying out analysis using GPS telemetry data. Finally, I showed that reticulated pythons exhibit a degree of synchrony in their movement patterns, and linked these movements to moon phase and remotely-sensed weather patterns.

The distances that reticulated pythons move between observed locations does not differ between habitat types or between the sexes. However, pythons translocated into the study area moved greater distances than resident individuals, and pythons in forest move more often on average than plantation pythons. I provided evidence to suggest that male pythons have larger range distributions than females, and pythons in plantations may have smaller range distributions than those in forests. This last point provides indirect evidence that reticulated pythons may exist at higher densities in oil palm plantations, as has been previously suggested (e.g., Natusch et al., 2016a).

The case study using GPS telemetry demonstrated how additional GPS data can improve space-use estimates when using dBBMMs, but also highlighted several issues. If pythons had been left to passively collect GPS data without regularly collecting VHF positions simultaneously, occurrence distributions would have been biased and contained greater type I and type II errors. It also highlighted how GPS location error can create the appearance of movement while pythons remain stationary, and how a low and irregular fix success rate can bias estimates of movement. Estimates of space use from dBBMMs were larger using solely VHF than with VHF and GPS combined, but additional movements captured by GPS between resting VHF locations was well accounted for by dBBMMs, suggesting that they performed well at estimating space use for the other VHF-tracked pythons.

Finally, I demonstrated potential environmental covariates that are linked to the synchrony in movements exhibited by reticulated pythons. These effects were different for pythons in plantations and those in forests. In plantations, pythons were more likely to move to a new location during a new moon, while pythons in forest were more likely to move during a full moon. The amount of rainfall also showed a correlation, with pythons in forest more likely to move when there was no rain, and plantation pythons more likely to move in heavy rain. This may suggest that pythons in plantations are adapting their behaviour, or simply that pythons will naturally respond differently in open vs enclosed vegetation, and that the responses to moonlight in plantations ties to the results from surveying the open riverbanks may lead to the latter conclusion. It is certainly further testament to the difficulties associated with making unbiased survey comparisons between habitat types. Not only is detectability biased against denser habitats where it is more difficult to spot pythons, but differing activity responses to environmental conditions in different habitats will also further confuse attempts at population estimates. The results here point to the potential for surveying comparisons between habitats drawing completely different conclusions in occupancy rates or relative abundances depending on when the surveys are carried out.

In **Chapter 5**, I looked at habitat selection of reticulated pythons along riverbanks in relation to their movement and across the study area. A small study measuring habitat variables directly along riverbanks showed evidence that reticulated pythons appeared to be choosing specific habitat types, rather than being found at random. They appeared to be more likely to be spotted in areas with a greater proportion of elephant grass, steeper slopes, and a greater proportion of vine cover. Microhabitat differences therefore have the ability to influence conclusions surrounding population estimates, and these should ideally be incorporated into survey estimates of abundance or occupancy. For example, transects with large amounts of elephant grass and low capture rates should be considered as having a lower occupancy probability than transects with little or no elephant grass but similar capture rates.

Using telemetry data of resting locations and remote-sensing LiDAR data of the study area, I used integrated step selection functions to show that pythons exhibited no evidence of selection for forest characteristics that might indicate a preference for or avoidance of areas with mature forests. While the LiDAR variables of canopy height and aboveground carbon density may not be good predictors of habitat selection when used in isolation, this nevertheless highlights the adaptable nature of reticulated pythons. They did show a functional response to preferentially select areas that have lower elevations and are closer to water. This corroborates previous assertions that reticulated pythons are particularly associated with water and riparian habitats, and is also indicative of some of the potential edge effects associated with riverbank surveys.

Finally, using support vector machines and telemetry locations of resting locations, I estimated habitat suitability of the study area based on LiDAR data. I used capture rates along transects and the riverbank habitat locations to validate the model, and this showed a reasonable level of congruence. Habitat suitability estimates and transect capture rates are positively correlated, and capture locations showed higher levels of habitat suitability along riverbanks than randomly selected riverbank locations. Plantations were highly heterogeneous in suitability, and so determining the specific habitat variables that cause this will be important from a plantation management perspective. Improving plantation suitability for pythons could benefit the suppression of rodent pests, or help alleviate any existing concerns regarding harvesting levels in Peninsular Malaysia and Sumatra.

## 6.3 Limitations and future prospects

This is the most intensive and detailed field study that has yet been carried out on reticulated pythons. Despite numerous publications assessing large volumes of pythons in trade, and concluding that offtake is not (currently) detrimental to the survival of reticulated pythons, there remain calls to assess wild populations separately from the trade due to concerns over whether assessing animals in slaughterhouses introduce biases (e.g., European Union, 2021; Nijman, 2022). However, it remains the only feasible way to obtain large enough sample sizes to assess population changes over time (Natusch et al., 2016b; Natusch et al., 2019; Khadiejah et al., 2021). While numerous reptile species may be at risk by unregulated trade (Marshall et al., 2020c), reticulated pythons do not currently fall into this category. While there may be philosophical and ethical biases directing opinions on sustainability (Natusch et al., 2021), there may also simply be some misconceptions about their basic biology. Reticulated pythons are large predators, and for endothermic taxa particularly these traits are good predictors of large home range sizes, low densities and vulnerability to habitat fragmentation (e.g., Gehring & Swihart, 2003). This does not appear to be the case for reticulated pythons, but is difficult to prove empirically, because their habits and camouflage make detecting them extremely difficult. They do not trigger camera traps, they rarely leave noticeable signs of their presence (such as tracks or visible nests), cannot leave hair samples or make scratch marks, do not vocalise, and cannot be detected at a distance via eyeshine, all of which are methods that can allow detection of species that are otherwise difficult to observe and count. When hiding in undergrowth, they rely on camouflage and rarely flee, and if they are disturbed, they can often move away silently without detection (Pers. Obs.). Trapping similarly does not yield useful sample sizes (Abel, 1998; Auliya, 2006; Khadiejah et al., 2021). Anyone who spent time walking though tropical forest would be forgiven for thinking they are rare, especially given the relative encounter rates of many other snake species. Asad et al. (2021) carried out visual encounter surveys of snakes within forests on foot over three years, totalling 89.4km of transect, and detected five reticulated pythons (S. Asad, Pers. Coms), or one python for every 17.9km. To obtain a sample size similar to that carried out in slaughterhouses by Natusch et al. (2019), of ~7000 individuals, would therefore perhaps necessitate somewhere in the region of 125,000 km of walked nocturnal transects within tropical forests. My own study had slightly lower encounter rates, and depending on whether recaptured and uncaught pythons are included or not, this rises to nearly 200,000 km. The highest reported capture rate from interviewed python hunters (who operate largely in oil palm plantations and forest edges) of 20 pythons per month (Wardani, 2012), is likely supplemented with incidental encounters by other people, but if this capture rate were achievable by a single researcher, it would still take 29 years to achieve the sample size from slaughterhouses of Natusch et al. (2019).

Throughout this thesis I have highlighted various study limitations or ways in which biases may alter any interpretations made from the data. This was intended to highlight the various biases that inevitably come into play when attempting ecological research on a species such as the reticulated python. The most prominent biases include: edge effects along transects, variable detectability rates in different macro and microhabitats, larger animals being easier to detect at a distance, varying behavioural differences that might change detectability in different habitats (e.g. responses to weather and moonlight), males and females having different activity rates due to breeding (although not detectable in this study), ontological changes in behaviour and activity, and varying recruitment rates shifting demographic ratios throughout seasons and across years. Trying to account for some of these biases in order to get a true indication of population changes in response to harvesting rates would require much larger sample sizes than I was able to obtain. I had originally intended to compare encounter rates between plantations and forests. Until I was able to have access to a car to efficiently perform visual surveys in plantations, I was not able to find any pythons by surveying on foot. Numerous reports and anecdotal evidence from various researchers who have carried out short term surveys all suggest that reticulated pythons are more common in some oil palm plantations (D. Natusch, Pers. Coms.). Assessing this without bias is difficult because plantations typically have less complex vegetation, which likely makes detection easier. The telemetry work carried out in this study suggests that pythons move less often in plantations, and their movement decisions in response to rain and moonlight are the opposite to those tracked in forests. This would further make robust comparisons more difficult. While pythons appear to exist in large numbers in some plantations, it cannot be ruled out that this is actually similar to their abundances in forests, but they are just not as readily observable in these denser habitats. If, however, high densities of pythons in plantations results in spill-over into forests, this may partially explain the lack of differences in capture rates along transects bordering plantations and forests. The number of pythons in the degraded forests of the LKWS may have already increased a long time ago. Either way, the message is that the ecological impact that reticulated pythons have on trophic dynamics should not be underestimated. It is possible that very large pythons over 6m exist at very low densities, similar to large mammalian carnivores, but the majority of pythons are in the range of 2-4m, and so the impact they can have on suppressing numbers of small mammals and birds is a particularly important factor take into consideration.

When carrying out telemetry for studying space use and habitat preferences, the sample size made some of the inferences difficult to achieve when carrying out comparisons, and many of the individuals were not tracked for long enough to achieve their full range distribution. I attempted to account for this by modelling the potential mean asymptote against the duration that tracking was carried out. This is rarely carried out as a means to alleviate bias, despite its obvious merits (Haines et al., 2009). Home range studies on reptiles are often replete with poor reporting of methodology (Crane et al., 2021), but this is not unique to reptiles alone, and follows an ongoing trend within the wider literature (Laver et al., 2008). For studies on snakes, which are not typically as readily funded as those on mammals, birds, amphibians or some other select reptiles like turtles and crocodilians, small sample sizes are an understandable consequence. The GPS revolution has also not yet gathered pace in studies of snakes, and Chapter 3 details  the myriad reasons for this. In addition to large sample sizes being relatively rare, many studies experience the same issue that I had, which is that tags can fail, run out of batteries, or animals become lost or are killed before the intended tracking duration has been completed. If estimating home range size is a goal, then I believe that modelling methods similar to those I have carried out here to estimate range distribution based on duration or number of locations should be considered as standard. This allows the inclusion of individuals only tracked for short periods of time into estimates, preventing the need to discard valuable, hard-earned data.

My study mainly included forest individuals within a single area of forest (only caught along the river), and a single area of oil palm plantation. This was necessary to allow tracking multiple animals (up to 10) within the same day to be logistically feasible. VHF tracking was partially hampered by the use of subcutaneous implants, which is less common than intraperitoneal implants. I followed recommendations for how to carry this out, and found that the implants tended to get expelled through the incision site before it could heal. I switched to smaller units to counter this, which worked for some individuals, while for others it did not, and the antennas had a tendency to be able to protrude through the incision. After discussing solutions with the vet performing surgeries (M. Gonzalez), we decided upon changing where the incision was performed, and attached the antennas loosely to allow movement but prevent them from coiling around the tag. This approach was considerably more effective. This relatively simple adjustment could be applied to implanted GPS tags, and reduce the potential for them to be expelled, as was the case in previous studies on Burmese pythons and yellow Anacondas (Smith et al., 2018; Smaniotto et al., 2020).

The low sample size, concentrated within a relatively small area, has left the estimates of habitat selection to be somewhat biased. The extent to which the estimates are generalisable to all pythons within the study area is difficult to determine, but an important consideration in determining habitat selection and suitability (Vaughan & Ormerod, 2005). Further, tracking individuals only during the day means that it is only analysing the selection of resting sites. These probably correlate with where pythons are most likely to be found, as resting sites are where they appear to spend the majority of their time. One of the intentions of using GPS was to be able to see how habitat use differs between these resting locations and when making nocturnal movements, e.g., perhaps pythons hunt in areas away from where they rest, moving back and forth each night, as was found by Natusch et al. (2022) in scrub pythons (*Simalia amethistina*). Manually VHF tracking at night was not a realistically feasible option in this study, both due to the fact that I carried out surveys at night, and that there were safety concerns (e.g., no reliable form of communication, and crocodiles also hunt mainly at night).

Based on the available evidence, monitoring is not a realistically achievable target, but that does not mean that study of reticulated pythons should not be further attempted. My research has presented a number of intriguing findings that could allow for improvements in achieving this. The behavioural changes in response to moonlight are particularly useful. Searching for pythons could be made more fruitful by conducting surveys in plantations, and other open habitats such as wide riverbanks, at times around the new moon. Around the full moon, searches could be switched to interior forest. Rain also appears to play a role, but this is harder to schedule for. Within oil palm plantations, road surveys appear likely to be the best strategy; more distance can be covered by vehicle, and pythons may be using road verges preferentially to the interior blocks of palms. River edges appear to be generally good areas to find them as well, and this may extend to smaller streams and lakes where boats are not an option for carrying out searches.

Further telemetry work should be pursued in other parts of their range. The question of whether pythons exist at higher densities in oil palm might not be an easily answerable question from survey data, but inferences can be made from telemetry. The research by Nafus et al. (2020) offers an intriguing example of how radio-telemetry can be used to estimate detectability rates of pythons, by performing surveys in proximity to pythons whose locations are known *a priori*. These estimates could allow for controlling for biases and allow better inferences of abundances in different habitats. Smaller range distributions may imply higher densities, but to what extent is range overlap tolerated? Ranges overlapped considerably in this study, but there was not enough concurrent data to allow this to be properly estimated. Trapping for small mammals at the same time as python tracking (e.g., as in Madsen & Shine, 1996; 2006), would allow an assessment of whether/how prey density may cause shifts in movements, space use, and tolerance of conspecifics. Reticulated pythons shift their diet ontogenetically (Shine et al., 1998a;b), and this may be one way they reduce intraspecific competition and allow range overlap. Additionally, feeding on a variety of prey also probably reduces competition if one particular species is less abundant. But is this different in palm oil plantations, where diet mostly consists of rats? How do pythons respond to rodent poisoning regimes causing sudden collapses in prey density? Might this cause them to temporarily migrate to other areas, or move into forests? Higher densities usually lead to reduced body condition due to intra-specific competition, but this study found that body condition did not differ between plantations and forests. Perhaps rodent densities are not a limiting condition in these areas. Could pythons have an innate tolerance or limit for conspecific densities, and so there are relatively more prey available in palm oil plantations than in natural forest. Long-term studies could be used to discover if growth rates and survivorship differ for pythons living in plantations, as there are undoubtedly trade-offs to living there, especially in areas where they are intensively harvested, but more generally this may involve factors such as pollution and harsher temperatures.

Temperature was not found to play a major role in python activity in this study, but that does not mean that it is not an important factor in python behaviour. Mean study area air temperature was used in modelling, and the actual temperatures pythons experience may be altered by microhabitat level differences. Many studies employ either temperature-sensitive radio transmitters or can implant thermal loggers directly into snakes to monitor thermoregulatory behaviour (Williams et al., 2020). With the addition of accelerometers (e.g., Whitney et al., 2021), much could be learned about the relationship between temperature and activity. Temperature affects the metabolism of ectotherms, and this is an important consideration in plantations, where it is typically hotter than forest (Hardwick et al., 2015). Increased metabolic rates require increased food intake in order to grow to the same body size (Bickford et al., 2010). Thus, it is important to undertake more research to understand how future climate change may affect reticulated pythons, and the wider impacts they might have on the ecosystem and trophic dynamics (Böhm et al., 2016). Bickford et al. (2010) predicted that most herpetofauna in Southeast Asia will reach or exceed their limits to adapt to climate change in <40 years. Which way the pendulum will swing for reticulated pythons in the face of this impending ecological disaster would be quite interesting.

This thesis was originally intended to include a chapter involving experimental exclusion plots to assess how predation by pythons may limit rodent populations, and therefore damage to oil palm crops. Sadly, due to unavoidable circumstances resulting from the COVID-19 pandemic, this was not carried out to completion, despite a considerable effort made building large amounts of fencing. But exclusion plots on a larger scale could offer considerable insights into the ecological effects that pythons have within oil palm plantations. How much of an effect do they have as biological control agents suppressing rat numbers? What is the economic value of a python in terms of palm oil revenue, and reduction in need for rodenticides? Would additional forest need to be cleared to account for the gains that pythons provide by eating rats? The same questions could be asked for other reptiles such as water monitors (*Varanus salvator*), which also remain abundant in plantations despite intense harvesting (Khadiejah et al., 2019; Guerrero-Sanchez et al., 2022), or for short-tailed pythons (*Python curtus*, *P. brongersmai* & *P. breitensteini*), which are often abundant in plantations but may be less resilient to harvesting (Shine et al., 1999a; Natusch et al., 2020; Nijman 2022).

Another area that I had initially wanted to explore as part of this research was diet. Diet of reticulated pythons from dissections in slaughterhouses show a high proportion of commensal prey, predominantly rats and chickens (Shine et al., 1998a;b; 1999b; Natusch et al., 2019). However, most of those pythons came from around plantations and villages, and heavily-digested prey and remains in faeces are often non-identifiable to species level. I intended to explore dietary niche breadth, while simultaneously testing the efficacy of a DNA meta-barcoding approach to dietary analysis of faeces for large constrictors. This approach in many smaller snake species shows promise (e.g., Brown et al., 2014; Dixon, 2021; Swinehart, 2021; Durso et al., 2022; Scholtz, 2022), but a study on Burmese pythons (Falk & Reed, 2015) suggested it may be a poor method for large constrictors.

However, this latter study was carried out poorly, and did not follow established protocols (W. O. C. Symondson, pers. coms.).

I collected faecal samples from 25% of the pythons I captured, so the sample size (n=41) was not conducive to robust ecological inferences between habitat types, but I felt that testing the approach was still warranted. I used two different long-term storage methods to test DNA degradation rates, and extracted DNA from faeces at the Wildlife Health, Genetic and Forensic Laboratory (WHGFL) in Kota Kinabalu in small batches as they were collected, to reduce degradation over the years of study they were collected. I also conducted initial trials of targeted PCR of captive python DNA (from Lok Kawi Wildlife Park) and was able to amplify chicken DNA successfully, suggesting that sufficient amounts of prey DNA can indeed be obtained from python faeces. Due to COVID-19, funding of the project was diminished, and the costs of metabarcoding and high-throughput sequencing were ultimately too prohibitive, as well as lockdowns preventing the planned period of lab work. The samples are still available for future researchers to continue this work if they wish (n=166). I believe metabarcoding could be a useful approach for analysing the trophic interactions of reticulated pythons within their environment, especially for determining prey preferences and dietary diversity in forests. This could highlight small mammal or bird species that are particularly vulnerable to changes in python population density.

Reticulated pythons may be able to adapt well to living in oil palm plantations. But there are potential trade-offs including increased human conflict and the presence of pollutants. Natusch et al. (2018) found that tick loads on several species of snake in Australia varied by the type of refugia they utilise, while Guerrero-Sanchez (2019) found that tick loads on water monitors in the LKWS were higher in plantations than in forest. There are also links between ticks and transmission of haemogregarine parasites, such as *Hepatozoon* spp. (Mofokeng et al., 2021). I collected ticks from all captured pythons, and blood samples, the latter of which were screened by microscope for presence of blood parasites. The results of this have not yet been analysed, and are not included here. Partially this is due to biases involved with making ecological inferences, and parasite-host interactions are highly dependent on host density (which as chapter 1 has detailed, is not easy to determine for pythons). Partially this is also because a rat broke into the cabinet where the tick samples were stored, and ate the majority of them. However, a sub-sample of ticks recovered from pythons have been screened for Rickettsia, and tested positive (C. Jalius, pers. coms.). The potential for reticulated pythons (which can exist commensally with humans) as reservoirs of zoonotic diseases might be an interesting avenue of research. Previous research has already highlighted the potential for sarcosystosis infection in humans as a result of eating python meat (Esposito et al., 2014; Wassermann et al., 2017).

Finally, all of the pythons that I caught had blood and tissue samples taken (not described herein). While larger samples could be easily obtained from slaughterhouses, their origin is difficult to determine, and they may be collected from a relatively large area (Natusch et al., 2016a). Given that all of the genetic samples collected in this study can be traced back to a specific location, the hope from this study is that landscape genomics might be able to uncover more detail about how pythons within the study area disperse within plantations, between forest fragments, and whether the main road cutting across the sanctuary creates any barrier to geneflow. A technique such as ddRAD (double-digest Restriction-site Associated DNA)(e.g., Mahtani-Williams et al., 2020) could provide thousands of markers to investigate genetic diversity within sub-populations, relatedness of individuals, and identify adaptive markers. While pythons that were caught in the plantation were in close proximity to most of those caught within forested areas, it is not impossible that the differing conditions of inhabiting plantations would create selective pressure for different genetic traits. In the area of this present study, those pressures could involve genes relating to temperature and metabolism, digestion of fats, and enzymatic responses to the presence of herbicides and rodenticides (Evans et al., 2020; 2021b). Comparing this with areas of intense harvesting would certainly be interesting.

## 6.4 Conclusion

Previous research, in combination with some of the findings of this study, suggests that reticulated pythons are far more numerous than can be surmised from field studies. Despite over 100 years of being commercially utilized, and hundreds of thousands of individuals being removed from the wild each year, they still remain common in many areas. Boosted by the availability of rodents in oil palm plantations, indirect conclusions can be drawn that there now exist more reticulated pythons in many parts of Malaysia and Indonesia than there were prior to the wide-scale clearing of forests. The ecological consequences of this are that reticulated pythons likely contribute a significant proportion of top-down predation pressure upon populations of small and medium-sized mammals and birds within Southeast Asia. As deforestation and fragmentation continues, and large mammalian carnivore populations continue to decline, this proportion will increase. Reticulated pythons are deserving of far more research attention. The myriad ways that they, and other generalists, respond to habitat modification is a critical facet of a holistic approach to conservation biology. This thesis represents an important first step towards that goal.

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