ECOLOGY AND HEALTH OF THE ASIAN WATER MONITOR LIZARD (*Varanus salvator*) IN THE FRAGMENTED LANDSCAPE OF THE KINABATANGAN FLOODPLAIN, SABAH, MALAYSIA

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A thesis submitted to Cardiff University in accordance with the requirements for the degree of Doctor of Philosophy in the School of Biosciences. Cardiff University
March 2019

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This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is being submitted concurrently in candidature for any degree or other award.

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List of publications and activities not related with this Thesis

Publications:

Evans M.N., **Guerrero-Sánchez S.**, Bakar M.S.A., Kille, P., Goossens, B. (2016). First known satellite collaring of a viverrid species: preliminary performance and implications of GPS tracking Malay civets (*Viverra tangalunga*). Ecological Research, 31(3), 475-481.

Najera F., Hearn A.J., Ross J., Ramirez Saldivar D.A., Evans M.N., **Guerrero-Sánchez S.**, Nathan S.K.S.S. De Gaspar-Simon I., MacDonald, D.W. Goossens, B.J., Revuelta L. (2017). Chemical immobilization of free-ranging and captive Sunda clouded leopard (*Neofelis diardi*) with two anesthetic protocols: medetomidine-ketamine and Tiletamine-Zolazepam. Journal of Veterinary Medical Science,79 (11), 1892-1898.

Supervised projects:

Anya Tober (2014). Impact of habitat fragmentation on the ecto and haemo- parasite fauna of the water monitor lizard (*Varanus salvator*) in Borneo. Professional Year Training dissertation. Cardiff University. UK.

Maëlle Fusillier (2013). Assessment of small mammals' ectoparasites in the fragmented forest of lower Kinabatangan. Bachelor dissertation. Ecole National Veterinaire de Toulouse. France.

Alexandre Schaal (2013). A preliminary comparison of monitor lizard, *Varanus salvator*, body condition, abundance and density between a secondary rainforest and an oil palm plantation, in Kinabatangan basin, Sabah, Malaysia. Master's report. Université Joseph Fourier. France.

Aimee Holborow (2015). The effect of habitat fragmentation on the gastrointestinal parasites within the water monitor (*Varanus salvator*) in Sabah, Borneo. Professional Year Training dissertation. Cardiff University. UK.

Charlie Cooper (2016). A preliminary survey for the richness and abundance of Squamata species within Lot 6 of Lower Kinabatangan Wildlife Sanctuary, Sabah and advisory notes for future surveys. Professional Year Training dissertation. Cardiff University. UK.

Toby Stock. (2017). Comparing the rate of growth of Asian water monitor lizards (*Varanus salvator*) in forest and agricultural habitats, within the Lower Kinabatangan Wildlife Sanctuary and surrounding areas. Professional Year Training dissertation. Cardiff University. UK.

Anya Tober (2017). Assessing the seroprevalence of *Toxoplasma gondii* and oocyst shedding in free ranging domestic cats and wild civets in the Lower Kinabatangan Floodplain in Sabah, Borneo. MSc. One Health Project Report. Royal Veterinary College / London School of Hygiene and Tropical Medicine. UK

Katherine Majevski (2017). Diversity of prey associated with *Varanus salvator*'s diet in the Lower Kinabatangan Wildlife Sanctuary, Malaysia. MRes. Thesis dissertation. Cardiff University. UK.

Other activities:

Collaborator as Field Veterinarian in different projects with Danau Girang Field Centre (2013- 2017):

- Landscape ecology of Sunda clouded leopard (*Neofelis diardi*)
- Kinabatangan Small Carnivore Project
- Landscape ecology of Sunda pangolin (*Manis javanica*)
- Ecology of reticulated python (*Malayopython reticulatus*)
- Landscape ecology of Wild boar (*Sus barbatus*)
- MonkeyBAR: Understanding the malaria transmission in the human-wildlife interface (Collaboration with the London School of Hygiene and Tropical Medicine)

Abstract

The Asian water monitor lizard (*Varanus salvator*) is well adapted to anthropogenic landscapes. Its abundance makes the species a good candidate to assess ecosystem health and the influence of human-modified habitats over adjacent forests. In order to understand how habitat fragmentation in the Kinabatangan Floodplain influences the dynamics of monitor lizard populations, 402 lizards were trapped, measured and sampled to obtain information regarding population size. From these, 14 individuals were tagged with Geographic Position System devices to estimate home range and habitat utilization. Additionally, a set of bio-markers were analysed from blood and a parasitological assessment was conducted. Results showed that a larger number of lizards inhabit forested areas ($\bar{x}$ = 1,492 ind.) than oil palm plantations ($\bar{x}$ = 280 ind.), while home ranges (Minimum Convex Polygon; MCP) were smaller in plantations ($\bar{x}$MCP = 1.54 km^2) than in forested areas ($\bar{x}$MCP = 3.920 km^2). In both habitats, water bodies and dense riparian understory were a more suitable habitat for monitor lizards. High levels of bio-markers such as low-density cholesterol, albumin and uric acid, as well as higher abundance of generalist parasites were associated with a rodent-dominated diet in plantations. *Amblyomma helvolum* was the only ixodid tick detected in the lizard population, with a higher abundance in plantations than in forested areas. Tick abundance was associated with body size, abundance, and the presence of grasslands and riparian understory. This study covers the most extensive ecological analysis of the Asian water monitor lizard to date and generated information that can be used to monitor habitat quality. Lastly, the data presented here support the idea that the Asian water monitor lizard population in the Kinabatangan Floodplain is stable and widely distributed across the landscape, with its diet indicating differences in availability through the landscape, and reflecting the condition of such a fragmented ecosystem.

To Sergio, Yadira, Enedina and Liesbeth:
With my love

To Alicia:
You will always be in my heart, Mum, and
I will always honour your name

Acknowledgments

This thesis is the product of four years of work, and one of the greatest experiences in my life. It would have not been possible without the support and trust of my main supervisor, Benoit Goossens. I will always be grateful for his friendship and company during all these years in Sabah. I would also like to thank Milena and Naollin, who as well as Benoit, have been part of my family in this marvellous island. Thanks to Pablo and Mike, for their great support, advice and inspiration. I would also like to thank my family and friends in Mexico, especially my parents, my sister and my grandma, for being there despite of the distance, and for accepting my absence during all these years. My heart is always with you all. To Liesbeth Frias, for the help and advice during the writing up, but more importantly, for the complicity and inspiration. Let's keep walking together for more adventures!

This experience would not have been the same without the Danau Girang Field Centre's family. Thanks to Koko, Alut, Lee, Samsir, Yusri, for walking with me in the field and for teaching me how to handle dragons. To Hasna, Kila, Ryeca, for the amazing food. To Peter, for the logistics. But most importantly, thank you all for your friendship. To the Kota Kinabalu team: Lucy, Tini, Alwani, Cyrleen, and one of the pillars of this great team, Audrey, for your help and friendship. You all have made my life in DG just great.

Success is contagious, and I am blessed to be surrounded by successful people that inspire me to do my best: Danica, Farina, Penny, Meaghan, Luke, Elisa, Rich, Timothy, Leona, and Kerisha, for being part of this team. To all the PTYs, volunteers and interns that have walked through DG and joined me in this project, especially Paco, Alexandre, Anya, Aimee, Charlie, Toby, Noemi, Hannah and Kasia. Special thanks to Rudi Delvaux for the great pictures he shared with me. Two of them are part of the front page of this thesis. Noemi Naszarkowsky drew the *Biawak Projek* logo.

My scholarship was granted by the Mexican Council for Science and Technology, and my research permit was granted by the Sabah Biodiversity Council and supported by Sabah Wildlife Department through a collaboration with Mr. Silvester Saimin under the direction of Mr. Augustine Tuuga.

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*Dragons have always fascinated me since I met Falkor, the lucky dragon. Then I learnt about the legend of the first mountain climbers who wanted to kill an evil dragon. One of them, the one that succeeded, realized that there were no dragons on the top of the mountain, they had been always inside his heart, and he did not kill them. Instead, he learnt to embrace them, to accept them, while climbing the mountain. Then, almost 20 years later, I read the very first sentence written by Erik R. Pianka in the foreword of the book "Komodo dragons, biology and conservation" that "Ancient cartographers marked the Lesser Sunda Islands on their maps of South eastern Asia with an ominous warning: "**Here be Dragons**". And then, here I am, dreaming, playing, running with Dragons, while embracing the ones inside me.*

SGS

March 2019

Chapter 1

General Introduction

1.1. *Varanus salvator*

Among the 53 species of varanids (Pianka and King, 2004), the Asian water monitor lizard (*Varanus salvator*) is the second biggest varanid in Southeast Asia after the Komodo dragon (*V. komodensis)* (Gaulke and Horn, 2004), and has the largest distribution range extending from Sri Lanka and the east coast of India, Bangladesh, Myanmar, Thailand, Cambodia, Vietnam, China, across Malaysia and Indonesia (Sunda Islands) (Gaulke and Horn, 2004). Recent studies suggest that in Myanmar, Thailand and Cambodia, the species is restricted to the coast, and may be absent in Laos (Fig.1.1) (Cota et al., 2009).

Fig 1.1 Distribution map of *Varanus salvator*. Source: IUCN, Red List of Threatened Species v. 2019-1.

The taxonomic status at the subspecies level is not yet a settled issue with between six and eight subspecies recognised (Gaulke and Horn, 2004). *V. salvator macromacolatus* is the most largely-spread subspecies occurring in almost the whole species' distribution range and the only one found in Borneo (Gaulke and Horn, 2004; Koch et al., 2013). This semi-aquatic lizard prefers lowlands; however, it has occasionally been found at altitudes near 1100 m. asl. (Erdelen, 1991). It is a generalist species occurring in both primary and secondary forests, swamps, mangroves, riparian forest, as well as human dominated habitats (Erdelen, 1991; Shine et al., 1996; Traeholt, 1998; Gaulke and Horn, 2004; Uyeda, 2009).

The Asian water monitor lizard is also considered one of the biggest predators in the Asian wetlands (Traeholt, 1998); it usually feeds on live small mammals, insects, fish, crabs, turtles, small crocodiles and lizards (Das, 2002), but it has also been found that scavenging is an important part of its feeding behaviour. As a generalist, the species has an extraordinary adaptation to anthropogenic habitats (Traeholt, 1998). Nevertheless, it remains unknown how its populations are affected by human environmental disturbance. This gap largely derives from an important lack of knowledge about this species' ecology, behaviour and health condition in fragmented landscapes (Inger, 1996). The plasticity that enables *V. salvator* to inhabit the variety of ecosystems throughout its range has been an important factor for the species to remain stable despite being one of the most hunted varanids in the World (Das, 2002; Koch et al., 2013).

The species has a high demand in the international market, predominantly for the pet and skin trade. Additionally, it is also used in traditional medicine and its meat is consumed by humans, although the latter impact is considerably lower since it corresponds to local consumption (King and Green, 1999; Das, 2002; Pernetta, 2009; Koch et al., 2013). The IUCN Red List (IUCN, Jan – 2019) reported that ~168,000 individuals were extracted from the wild in Malaysia alone (~3,000 from Sabah), while ~427,838 were collected from the Indonesian forest. International trade is considered the main reason why some local populations have gone extinct (Herrmann, 1999). The species is listed in Appendix II of the CITES, and it is categorised as "Least Concern" in the IUCN Red List (Bennett et al., 2010; Koch et al., 2013). The species is listed within Schedule 2 within Sabah (protected species of animals and plants; limited hunting and collection under license; Wildlife Conservation Enactment, 1997). It is possible that other anthropogenic factors, such as road traffic, intensive farming and timber, play an important role in the decreasing numbers of lizards in some areas.

1.2. The second largest but most neglected varanid

There are around 53 different species of varanids in the world (Pianka and King, 2004), which occupy different kind of habitats, from deserts to tropical forests and wetlands, from specialist frugivores (*V. olivaceus*) to venomous carnivores (*V. komodensis*). Several show a large range of dietary preferences, and they dramatically vary in size and weight ranging from 0.2 m and 9-10g in weight (*V. brevicauda*) up to a total length of ~3m and weights of ~150Kg (the largest lizard in the world, *V. komodensis)*. The genus is distributed within the southern hemisphere, from Africa (4 *spp.*) to Australia (with the largest number of species of varanids - 27 *spp.*). Asia and the Arabian Peninsula present 14 species and one of them, *V. indicus*, can also be found in Australia (Table 1 of Appendix I; Pianka and King, 2004).

The systematics of the genus *Varanus* has been described as complex with several changes in the composition of the taxonomic groups since its first description in 1766 by Linné (Koch, 2013). Since then, the number of species and subspecies have increased from 1 to 73 species and subspecies around the World (Koch et al., 2010; Koch et al., 2013). *V. salvator* is the most complex species with five currently accepted subspecies (Koch et al., 2010; Karunarathna et al., 2017). Nevertheless, regardless of being the second largest varanid, a top predator in the Asian wetlands and the monitor lizard with the largest distribution range, the Asian water monitor lizard is one of the most understudied varanids as it is represented in only ~8% of the scientific literature on Varanids over the past 50 years (Fig 1.2a). A search in Scopus showed that between 1999 and 2018, 36% of the studies on varanids focused on systematics, biogeography and morphometry, while human-animal interactions studies accounted for 20% and habitat utilisation covered just 4% (Fig 1.2b).

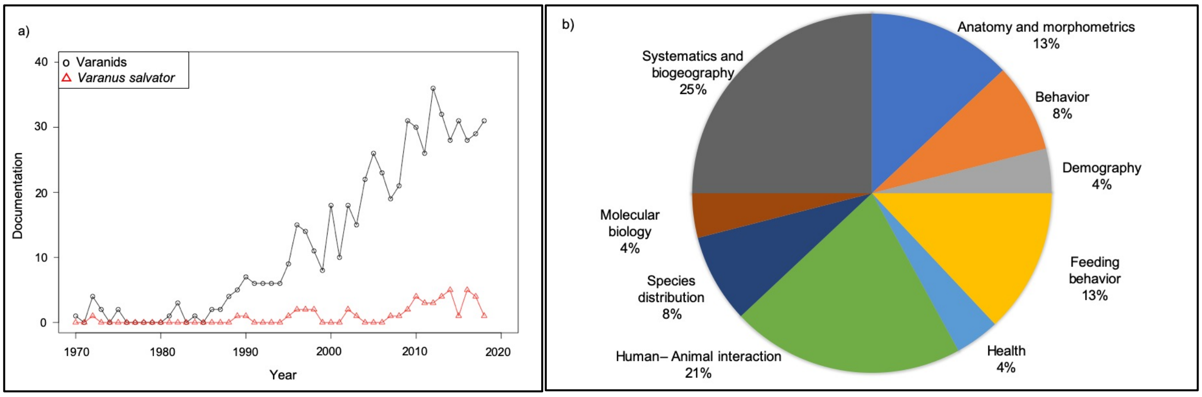

Fig 1.2. Published studies on varanids. Plot (a) shows the number of studies carried out between 1970 and 2018 in the whole family Varanidae (in black; N = 598) and just in *V. salvator* (in red; N = 47). Plot (b) shows the distribution of the topics studied on *V. salvator* between 1999 and 2018 (N = 25). Source: Scopus (Jan, 2019).

As generalist, the Asian water monitor lizard is well adapted to different types of habitat as long as they exist nearby water bodies (Cota, 2009; Karunarathna et al., 2017;).

The species is also well adapted to human-modified habitats (Shine et al., 1996; Traeholt, 1997; Lauprasert, 2001; Uyeda, 2009; Koch et al., 2010; Kulabtong & Mahaprom, 2015). Individuals have been seen in great numbers inhabiting urban and sub-urban areas, including human settlements, farms and industrial crops (Shine et al., 1996; Koch, 1997; Uyeda, 2009; Koch, 2010; Karunarathna et al. 2017).

The Asian water monitor lizard's diet preferences are very broad, including fish, invertebrates, small mammals, birds and other reptiles and their eggs (Cota & Sommerlad 2013, Fitzsimons & Thomas 2016;). It is also a well-known scavenger that feeds on carcasses, human food waste as well as on rodents, which are commonly perceived as pest in farms and crops (Uyeda, 2009; Karunarathna et al. 2017). Some individuals have been observed also searching for prey into other animals borrows and nests (Karunarathna et al. 2017).

Although essentially a terrestrial and semi-aquatic species, juvenile individuals like to display semi-arboreal behaviour as a protective measure, as has also been observed in the Komodo dragon (Purwandana et al., 2014; Karunarathna et al. 2017). Therefore, the habitat preferences for the species rely not just on the abundance of prey but also on the features of their environment.

1.3. Threats to the Asian water monitor lizard

International pet and skin trades, as well as local consumption for meat or traditional medicine are the main threats for the species (Lauprasert, 2001; Koch et al., 2013). However, the current status of the population and the impact of these human activities on the species remain unknown (Koch et al., 2013; Karunarathna et al., 2017) and the IUCN lists the species as of Least Concern (Bennett et al., 2010).

Anthropogenic habitats seem to be highly utilised by such a well-adapted species that has been seen in high numbers roaming near adjacent farms, households, and even urbanized areas (Uyeda, 2009; Karunarathna et al., 2017). Nevertheless, there is no information on how this behavioural adaptation may affect the species in the long-term.

Human activities could promote a sedentary behaviour in scavengers due to the abundance of food, such as food waste and small mammals, which could translate into a reduction of the home range and an increase in population size (Smith and Griffith, 2009; Jessop et al., 2012). These changes represent a potential risk in disease transmission dynamics by increasing the contact rates between pathogen carriers and susceptible individuals.

Although reptiles have not been reported as carriers of important zoonotic diseases, the interactions between *V. salvator* and humans as well as domestic and wild animals may represent a risk of transmission for endo and ectoparasites. Additionally, feeding behaviour changes and abundance of food sources could reflect changes of the body condition and physiology by the accumulation of blood metabolites, such as lipids, uric acid and protein derivate (Jessop et al., 2012; Smyth et al., 2014). In highly fragmented landscapes, small animal populations could decline in forested areas adjacent to human-modified habitats due to the increase in population of generalist predators.

1.4. The Kinabatangan Floodplain: A highly fragmented landscape

The Kinabatangan Floodplain is located on the eastern side of the Malaysian state of Sabah, Northern Borneo (between 5°10’ to 5°50’N and 117°40’ to 118°30’E) (Fig 1.3). Humidity and rainfall from Central Sabah’s mountainous region drain into the Kinabatangan river, the longest in Sabah, and runs through the floodplain after about 560 km (Ancrenaz et al., 2004; Estes et al., 2012). The amount of water drained into the floodplain, an annual rainfall of 3,000mm and temperatures between 21–34°C (Ancrenaz et al., 2004) provide a landscape with a unique matrix of habitats such as riparian forest, swamps, dry dipterocarp, estuarine nipa palm and mangrove forests (Estes et al., 2012). The Kinabatangan Floodplain is considered as one of the most productive wetlands in Sabah (Davison, 2006).

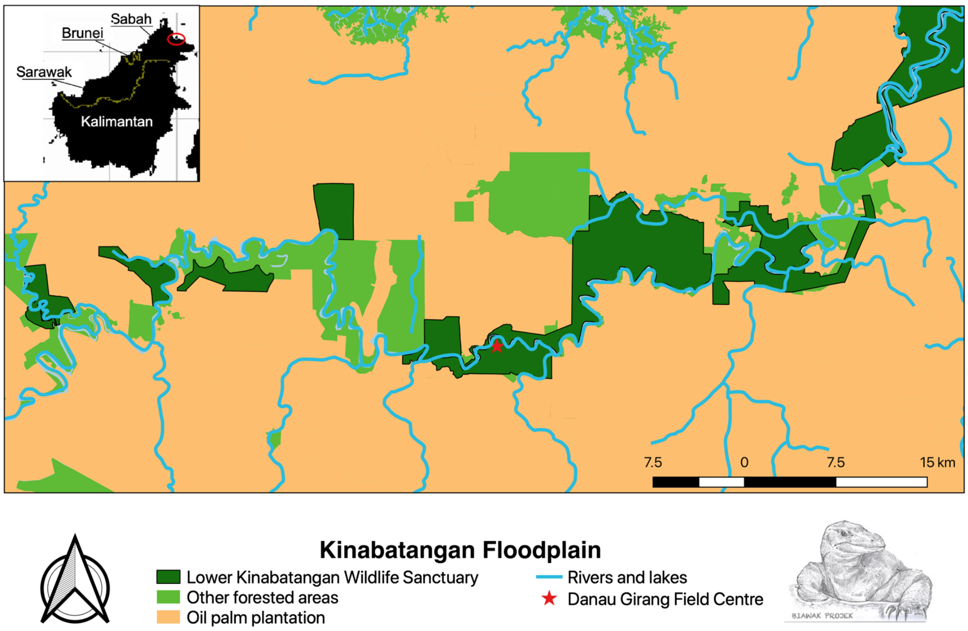

Fig 1.3. Geographical location of the Kinabatangan Floodplain and distribution of the 10 blocks belonging to the Lower Kinabatangan Wildlife Sanctuary.

The floodplain is an important biodiversity hotspot and is home to at least 129 species of mammals, 314 species of birds, 101 species of reptiles and 33 known species of amphibians. Iconic species such as the Bornean elephant (*Elephas maximus borneensis*), Bornean orangutan (*Pongo pygmaeus*), Sunda clouded leopard (*Neofelis diardi*), proboscis monkey (*Nasalis larvatus*), Malayan sun bear (*Helarctos malayanus*), storm's stork (*Ciconia stormi*) and rhinoceros hornbill (*Buceros rhinoceros*) are just few of the IUCN Red List species that inhabit the floodplain.

Since the 1950's, the Kinabatangan Floodplain has experienced a huge rate of forest loss due to large-scale commercial logging and land use change as a result of industrial oil palm plantations (Hai et al., 2001; Lackman-Ancrenaz et al., 2001). It is estimated that almost half of the Kinabatangan Floodplain has been converted into commercial oil palm plantations (Abram et al., 2014). The riparian corridor extant between the Kinabatangan river and its tributaries and the oil palm crops, by law have to be at least 50m wide, nevertheless, this distance is highly variable along the river course, and sometimes, totally absent.

The Lower Kinabatangan Wildlife Sanctuary (LKWS) was established in 2002, by the State Government in order to protect the remaining forests threatened by agriculture expansion. The LKWS comprises a total of 27,000 ha of protected forest divided into 10 blocks of forest (hereafter “lots”) distributed along the Kinabatangan river. These lots are interconnected by small narrow corridors and are linked to 10,000 ha of state and private forests with different stages of degradation and 15,000 ha of protected forests (Virgin Jungle Forest Reserves) (Ancrenaz et al., 2004). Nevertheless, the connectivity between the LKWS patches and between them and the other forested areas is still deficient with narrow strips of highly degraded forest and, in the worst cases, connectivity is totally absent (Abram et al., 2014).

The highly fragmented landscape in the Kinabatangan Floodplain offers the opportunity to develop an understanding of how habitat loss and fragmentation impact the wildlife community, and how species have adapted to survive within a severely degraded landscape. Simultaneously, the development of such knowledge facilitates influencing state policies on wildlife conservation (*i.e.* action plans) with on-the-ground information to improve the forest connectivity and decrease oil palm expansion (i.e. Ancrenaz et al., 2004; Estes et al., 2012; Abram et al., 2014; Goossens et al., 2016; Thiry et al., 2016; Stark et al., 2017; Hearn et al., 2018; Frias, 2019).

1.5. Study overview

Specialist species are widely studied and considered indicators of changes in their respective ecosystem. Nevertheless, due to their low abundance and limited distribution range, these species fail in representing ecosystem complexity (Landres et al., 1988; Menge, 1995; Rice, 2003; Huges, 2017). This complexity could be better explained by species that are highly abundant and widely distributed within the landscape (Landres et al. 1988; Rice, 2003). The plasticity of *Varanus salvator*, its tolerance to human-modified landscapes and widespread distribution in different kinds of habitats can help explain how anthropogenic habitats impact the animal community in terms of diversity, distribution and health.

This study aims to provide ecological information regarding the status of the Asian water monitor lizard populations in the Kinabatangan Floodplain, as well as to understand how the species has adapted to such fragmented landscapes and what the consequences are of this adaptation. As it has been suggested, it is expected that the number of individuals is higher within oil palm plantations than within forested areas and that their home ranges are smaller in anthropogenic habitats (Traehold, 1994; Uyeda, 2009; Twining et al., 2017). These differences may also have an impact on the health of the population and on the ecology of the parasites associated with the species. Ecological and health-related aspects of this study are explained in five chapters in this thesis.

Chapter 2 aims to understand the dynamics of the population inhabiting the Kinabatangan Floodplain. Using Mark and Recapture (MR) methods, population size, survival, growth rate and body size were evaluated and compared between two different types of habitat. Distance surveys have been the most common method to estimate the population size of different species of varanids (Uyeda, 2009; Jessop et al., 2012; Ghimire and Phuyal, 2013; Chatterjee and Bhattacharyya, 2014) and just three studies reported results on abundance using MR methods on *V. komodensis* (Ariefiandy et al., 2014; Purwandana et al., 2014;) and *V. exanthemicus* (Bennet, 2000). The results of this study show more concordance with previous MR methods compared with those that used distance surveys.

Chapter 3 presents the results of the first home range and habitat selection assessment for the species using Geographical Positioning System (GPS) tracking technology. GPS technology has been helpful to understand how animals behave within the different landscapes. Nonetheless, this technology has not been widely used on varanids. While most of the studies on home ranging of varanids have relied on VHF radio-tracking systems (i.e. Ciofi et al.,2007; Doody et al., 2009; Smith and Griffiths, 2009; Purwandana et al., 2016), some research on *V. varius* (Flesh et al., 2009; Lei and Booth., 2017; Lei and Booth, 2018) and *V. panoptes* (Lei et al., 2017) used GPS technology. This chapter compares the home ranges of 14 individuals tagged with GPS devices for a period of at least two months. GPS data were also used to describe habitat preferences using high definition images provided by Light Detection And Ranging (LiDAR).

Chapter 4 suggests a *fast food effect* by evaluating the health of the Asian water monitor lizard population associated with the feeding habits and the prey that they consume in both forested areas or plantations. Oil palm plantations are recognized as areas with low biodiversity (Edwards et al., 2010, Azhar et al., 2011; Edwards et al., 2014a, 2014b), dominated by generalist species that find abundant food (McClure et al., 1995; Beasley et al., 2007; Morey et al., 2007; Abbas et al., 2011; Bastille-Rousseau et al., 2016). This low prey diversity may bring changes in diet composition with impact on the animal's physiology (Artacho et al., 2007; Stenhouse et al., 2008; Snoody et al, 2009; Smyth et al., 2014; Lloyd et al., 2016). After describing the ecology of *V. salvator* within the Kinabatangan Floodplain, this chapter aims to describe how the homogeneous prey community in plantations may have an impact on the physiology of this population.

A different aspect of the *fast food effect* is analysed in **Chapter 5**. Feeding behaviour is commonly associated to host-parasite interactions (Dunne et al., 2013; Wells et al., 2018; Leung and Koprivnikar, 2018). Parasite transmission through diet may represent an advantage to those generalist parasites able to infect different species (Leung and Koprivnikar, 2018), but also can represent a threat for those that are not able to infect the new host and survive (Laferty et al., 2006, Frias and MacIntosh, 2019). Furthermore, increased parasite infection may be reflected in a lower survival rate for hosts by affecting their ability to mate or making them vulnerable to other predators or competitors (Lafferty et al., 2006). The study aims to describe the diversity of parasites associated to the Asian water monitor lizard and understand how this community structure may be of risk to both the lizard's populations and other carnivores in the area.

Chapter 6 follows the parasite trend and aims to describe how habitat fragmentation and composition influence on the prevalence and intensity of a quasi-specialist ixodid tick associated to *V. salvator*. *Amblyomma helvolum* is considered the most common tick found in monitor lizards, and this host-parasite association is likely to be favourable for the ticks' survival due to host abundance and habitat preferences (Arneberg, 1998; Daszak et al., 2000; Diuk-Waser et al., 2006; Stein et al., 2008). Using LiDAR analysis and demographic information, this chapter aims to explain how both Asian water monitor lizards' abundance and a degraded habitat influence the ticks' abundance within their landscape.

Finally**, Chapter 7** draws on all of the information generated in the previous chapters to explain the status of the population of *V. salvator* within the Kinabatangan Floodplain, including the effects of oil palm plantations on its dynamic, as well as the consequences of shifts on diet and potential parasite dispersion. The chapter remarks the importance of long-term studies with a holistic perspective to understand how human-modified landscapes impact the ecology of both the species within the anthropogenic habitats as well as within the adjacent forest.

Chapter 2

Population assessment of the Asian water monitor lizard in a highly fragmented landscape

2.1. Introduction

Asian water monitor lizards (*Varanus salvator*), as well as most varanids, are commonly linked to human-modified habitats (Traeholt, 1993; Traeholt, 1994; Uyeda, 2009; Jessop, 2012). They have been reported in high numbers in locations where intensive human activities occur (*e.g.* settlements, farms, industrial crops), and places where food, such as small rodents, food leftovers, poultry, etc., may be abundant (Traeholt, 1993; Traeholt, 1994; Uyeda, 2009). The abundance of varanids has been welcomed in some anthropogenic habitats due to their role as pest control (BooLiat, 1999). As meso-predators, their abundance represents a potential impact on animal communities living in adjacent forests (Jessop et al., 2012).

As a generalist species and one of the largest predators in the Asian wetlands, the Asian water monitor lizard has been considered as one of the most successful species despite facing intense fragmentation throughout its distribution range (Shine et al., 1996; Traeholt, 1998, Uyeda, 2009). In Borneo, the Asian water monitor lizard is a top predator, just after the estuarine crocodile (*Crocodylus porosus*) and the Sunda clouded leopard (*Neofelis diardi*), with humans likely representing their main threat due to hunting and the leather trade (Traeholt, 1998; Koch et al., 2013). However, regardless of the high demand in the international market, the populations of *V. salvator* seem to be stable (Koch et al., 2013).

Few studies have been conducted to understand how human activities influence the population dynamics of different varanid species, and most of them have been based on distance surveys (Uyeda, 2009; Jessop, 2012). The largest study reported using mark and recapture techniques (MR) on any varanid was performed on Komodo dragons (*V. komodensis*) during a 10-year observational study (Purwandana et al., 2014). Additionally, these techniques were used to estimate the population density of *V. exanthemicus* in Ghana (Bennett, 2000). The use of MR methods can aid the understanding of the different aspects of an animal's population dynamics, in addition to providing information about the number of individuals, population growth, survival, and catchability (Pradel, 1996; Sibly and Hone, 2002). Although distance surveys are efficient methods that offer an idea of habitat occupancy and habitat selection of the target species within an ecosystem, they are not suitable to accurately estimate the number of individuals in a population (Williams et al., 2002; McClintock et al., 2010; Miller et al., 2011).

The use of MR in reptile occupancy studies can be expensive and sometimes restricted to a limited area depending on time and resources available (Karanth et al., 2011). Three different methods have been compared to estimate the size of Komodo dragon populations in Indonesia, where it has been suggested that both camera traps and cage trapping methods are considerably more efficient than distance surveys, with the camera trap method being even cheaper than cage trapping methods (Ariefiandy et al., 2014). However, the use of camera traps to detect animals and estimate occupancy has limitations as small poikilothermic individuals may go undetected, and identification of individuals based on skin patterns is unreliable in monitor lizards.

This study aims to describe the demography of the Asian water monitor lizard in the highly fragmented Kinabatangan Floodplain by estimating their population size in plantations and forested areas, as well as assessing their survival and growth rates in order to understand how the landscape may influence the distribution and demography of the species.

2.2. Methods

2.2.1. *Study area*

GPS data generated by 14 successfully tagged individuals contributed to establishing the limits of the study area, which corresponds to ~82.568 km^2. The defined area comprised three forest lots: Lot 5 and 7 on the northern side of the Kinabatangan river and Lot 6 on the southern side, and three oil palm plantation estates: Hillco, located on the North bank and Kuril and KKL, located on the south bank (Fig. 2.1). Although Asian water monitor lizards are good swimmers and able to cross the main river (as shown by satellite data), no lizard was spotted or trapped on both sides of the river, and only a few of the GPS tagged individuals crossed to the edge of the river for short periods of time. Therefore, for the purpose of this study, the main river was used as a boundary between the southern and northern sites.

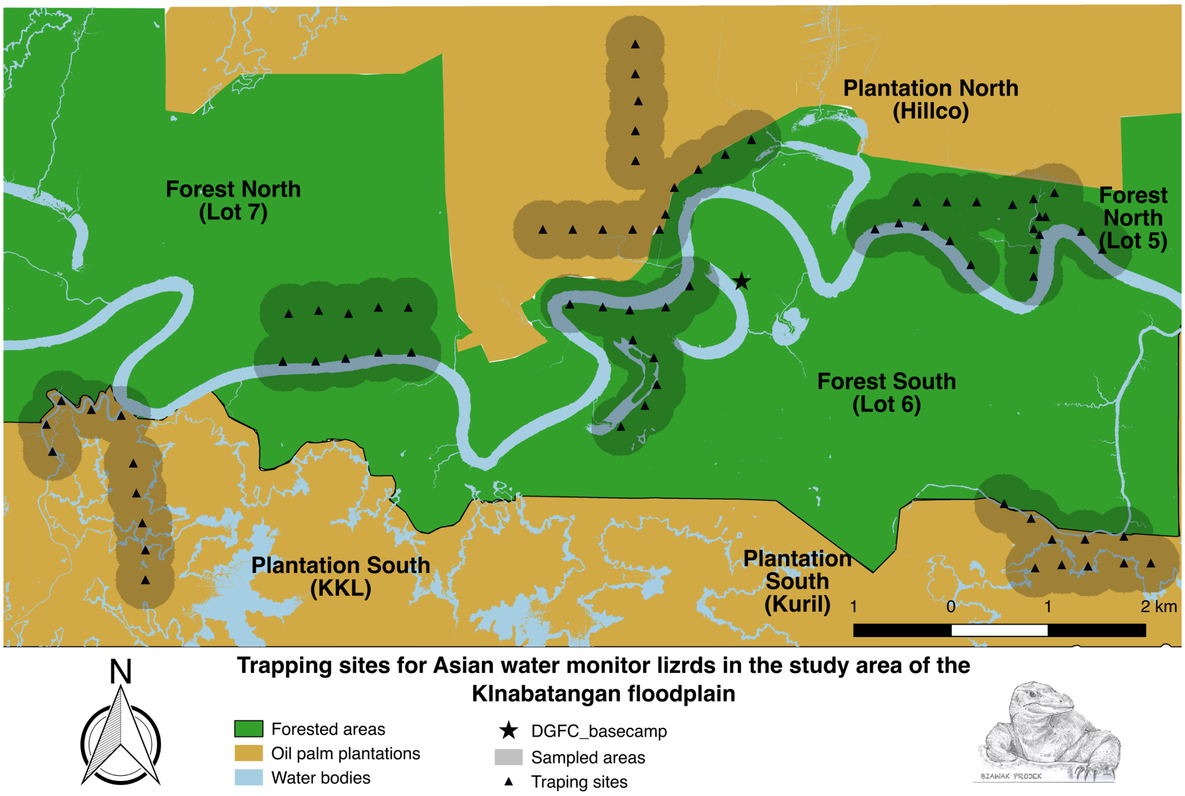

Fig. 2.1. Distribution of transects and areas of influence in the Lower Kinabatangan Wildlife Sanctuary and surrounding plantations.

2.2.2. *Trapping strategies*

Six different trapping sites were established within the Lower Kinabatangan Wildlife Sanctuary (LKWS) and surrounding oil palm plantations (OPP). Ten cage traps (90x40x40cm) were placed along the border (rivers and boundaries between plantations and forest), and in the interior (500 m from the border transects). Site selection used four different main criteria (1) to cover different habitat types (forest vs. oil palm plantation), (2) to include different vegetation types (riparian, grassland, swamp forest and seasonally flooded forest), (3) to minimize by-catch (avoiding dogs in the plantation sites) and (4) accessibility during the entire trapping period. To avoid pseudo-replication, traps were set at a distance of 400m from each other.

At the beginning of the study, different types of bait were tested, *e.g.* food remains, fish and shrimp, chicken meat and chicken entrails, which seemed to be the most successful bait and therefore, chosen to be used during this study. Every morning, between 7:30 and 9:00 am, the traps were visited and the chicken entrails were placed hanging in the back of them. The baited traps were revisited during the afternoon, between 3:00 and 5:00 pm, right after the peak of activities of varanids, and before their resting time (de Lisle, 2007; Jessop, 2012; Purwandana et al., 2014). Each trapped lizard was safely handled, measured, sampled and tagged with an intradermic transponder (Trovan ID-A100, Trovan Ltd., UK). Due to the presence of dogs and their inevitable disturbance, as well as flooding events, some traps had to be relocated within the same site while respecting the aforementioned criteria as closely as possible. Nonetheless, the few individuals trapped in this transect were included in the demographic analysis.

For the analysis, the estimated area covered by each trap (*i.e.* trap influence area) was calculated as half the radius of the mean distance between all recapture sites (Krebs, 1999; Ciofi et al., 2007; Uyeda, 2009; Jessop et al., 2012; Purwandana et al., 2014). Each transect study site was sampled once a year for 15 days during three consecutive years (Oct, 2013 - Set, 2016) (Purwandana et al., 2014).

2.2.3. <u>Population size and density</u>

Population size was estimated using the POPAN formulation for the Jolly-Seber (JS) method to estimate the abundance of open populations, (Lebreton et al., 1992; Schwartz and Amason, 1996; Mills, 2013). This formulation is able to estimate the population size (*N*) by considering apparent survival (Φ; the mean estimation of the probability that one individual trapped during *i* season will still alive in season *i* + 1, even if it is not seen anymore), recapture probability (*p*; the estimated probability of one individual trapped in season *i* will be trapped again in season *i* + 1) and probability of entry into the population at each occasion (*Pent*; the estimated probability of one individual trapped in season *i* + 1 was not in the population during season *i*). This method also considers variations between trapping seasons and between study groups and is appropriate for the analysis because its assumptions match the characteristics of the trapping method used in this project (*e.g.* variable rates of incomes and outcomes, marked individuals easy to identify, and homogeneous survival and catchability) (Schwartz and Amason, 1996). The analysis was run using the program MARK v. 7.2 (Colorado State University; USA) considering a 95% of confidence interval. A total of 93 models were run considering no time variations (·), and variations between trapping seasons (*t*), group (*g*) and season/group (*t* * *g*) for Φ and *p*. *Pent* was estimated with both variations (*t*) and no variations (·) between seasons and variation among groups (*g*). N was assessed considering no variations between seasons (·) and variations between groups (*g*). The best model was selected by the lowest Akaike Information Criterion (AIC).

Water bodies such as streams, lakes and drains, as well as the surrounding dense understory was identified as the most suitable habitat for the Asian water monitor lizards within the landscape (Fig. 2.2). The population size estimated by the model was adjusted to reflect the size of suitable area within each study site to estimate the actual population size. Density was calculated by dividing the number of lizards by the whole area (individuals / Km^2).

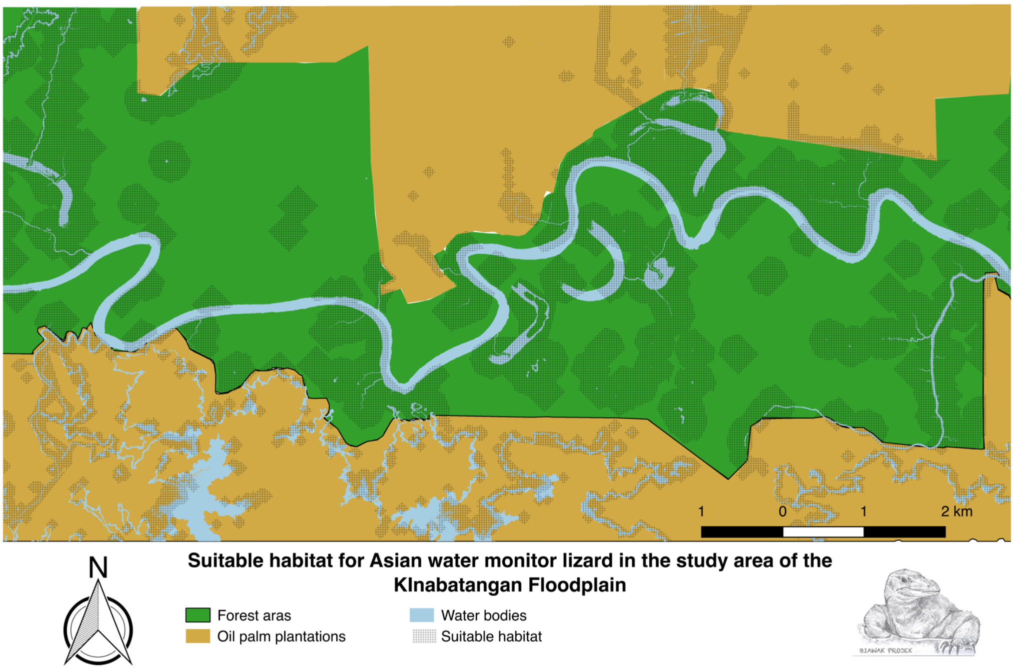

Fig. 2.2. Distribution of suitable areas (grey grilled shades) for Asian water monitor lizard populations in the Kinabatangan Floodplain.

2.2.4. Growth rate and survival

Growth rates were calculated in Mark with the Pradel Survival and λ analysis using the same data set and considering 18 different combinations between the analysed variables. The model gives the growth rate estimation for each inter-season period which means, for this case, the periods between the first and second season, and between the second and third season. This model differentiates survival from recruitment and considers them separately, avoiding over or underestimations (Pradel, 1996). No time variations (·) or variations over time (*t*) and between groups (*g*) were considered for Φ and *p*. Meanwhile, variations between groups (*g*) were considered for λ. Pradel's survival estimation gives a factor that explains how the population size varies in the timeline, and can be understood either as increasing ($\lambda > 1.0$), decreasing ($\lambda < 1.0$) or stable ($\lambda = 1.0$) across time (Pradel, 1996; Sibly and Hone, 2002). The best fit model was selected as the model with the lowest AIC value.

2.2.5. Body weight and size distribution

In order to understand how the body size is distributed within the population in the landscape, analysis of variance (ANOVA) were performed to assess differences between weight and snout to vent length (SVL). The selected independent variables for comparation were (i) habitat, (ii) study area (n= 4; Forest North and South and plantation North and South) and (iii) study sites (n= 6). Therefore, although the distribution of both SVL and weight was considered normal, the values were transformed to a natural logarithm (ln) so a Pearson's correlation test for the whole data set could be performed and therefore, grouped by study site and class size, i.e. small (≤ 5 kg), medium (5.1 -10 Kg) and large (>10 Kg).

2.2.6. Potential of study sites as population sources

Determining the sex of Asian water monitor lizards in the field is a difficult task. The muscles surrounding the cloaca are very strong and make the insertion of a probe difficult and harmful to the animals. Sometimes during handling, males may relax the sphincter and expose the hemipenis. Nevertheless, females can also expose a hemiclitoris that could be confused with an incompletely exposed hemipenis (Böhme, 1995). Sexual dimorphism in varanids has been discussed and related to adults' body size, where males are reported to be three to five times larger than females, depending on the species. Sex determination in varanids by molecular tools is still not well developed. The most complete work at the moment has been done on Komodo dragons, the only species for which sexing primers have been developed and tested successfully (Halverson and Spelman, 2002; Sulandari et al., 2014). These primers were eventually applied to a population of *V. varius* in Australia (Jessop et al., 2012).

For this study, two categories were created according to body weight as proxy for sex determination. Individuals smaller than five kilos were considered to be infants or young females, while individuals above five kilos were assumed to be either young or adult males. Therefore, study sites with higher recruitment rates and higher proportions of infant individuals could be considered as source of the super-population.

2.3. Results

A total of 3,055 day/traps were carried out with a 25% of recorded trapping success (774 events) and 402 individuals marked and sampled. During the whole period, no animals were recaptured in different sites, and only a few GPS tagged individuals crossed the main river for very short periods of time, supporting the decision of treating the forested areas north and south from the river separately. The information generated by the telemetry data suggested that the Asian water monitor lizards have selective habitat utilization; therefore, each study site's surface needed to be adjusted correspondingly. The buffer estimated for suitable areas in plantations has a radius of 74 m, while the forested areas generated an estimated radius of 252 m.

The best fit model for the population size estimation considered survival (Φ) with no variation over time, while recapture probability (p) and population size (N) present differences among groups and the probability of entering (*Pent*) differs over time (Table 1, Appendix II). The overall population size for the study area was estimated at 4,448 individuals (3,660 – 5,475) with an overall density of ~145.77 animals per km^2. Forested areas showed larger overall populations compared to plantations, as well as higher densities (Table 2.1).

Table 2.1. Population size of the Asian water monitor lizard in the Kinabatangan Floodplain. Adjusted area and adjusted *N* are estimated according to suitable habitats for the species distribution. *% of the study site's area. **Density was estimated as individual/km^2.

Study site	*N* ± SE (95%CI)	Sampling area (km^2)	Study site area (km^2)	Adjusted area (%*)	Adjusted N ± SE (95% CI)	Density** ± SE (95% CI)
Forest (north)	725.54 ± 55.79 (624-843)	3.42	22.534	11.527 (51.16)	2445.4 ± 188.04 (2103 – 2841)	212.14 ± 16.3 (182 – 246)
Forest (south)	199.45 ± 24.03 (158-252)	1.47	18.404	10.621 (57.71)	1439.57 ± 173.62 (1142 –1820)	135.53 ±16.34 (108 – 171)
OPP (north)	78.27 ± 2.29 (74-82)	2.87	17.943	2.487 (13.86)	263.81 ± 7.72 (249 – 276)	106 ± 3.1 (100 – 111)
OPP (south)	187.05 ± 57.47 (104-337)	3.68	23.687	5.878 (24.61)	298.77 ± 91.80 (166 – 538)	50.82 ± 15.61 (28 – 92)
Overall abundance of Asian water monitor lizard s in the study area					4448 ± 461 (3660 – 5475)	145.77 ± 15.11 (120– 179.43)

The model that best fit population growth rates considered a constant Φ and p, while λ was different between groups (Table 2, Appendix II). The population growth rate demonstrates that the overall population is near stable (λ = 0.995 – 1) with a survival rate of Φ = 98.32 ± 0.002. (Table 2.2).

Table 2.2. Population growth and survival rates of the Asian water monitor lizard populations in the Kinabatangan Floodplain.

Habitat	Site	Survival			Growth rate (λ)		
		Φ	SE	95% CI	λ	SE	95% CI
Forest	**North**	98.32	0.002	97.94 – 98.64	0.996	0.01	0.994 – 0.998
	South				0.999	0.002	0.997 – 1.003
Oil palm plantation	**North**				1	0.002	0.996 – 1.005
	South				.995	0.003	0.989 – 1

Recruitment estimates were, on average, higher in forested areas than in plantations in both inter-season periods. The highest recruitment was recorded in the northern forested area between the first and second trapping season (16.49 ± 16.61), while the lowest was recorded in the southern plantations between the second and the third seasons (12.65 ± 1.21; Table 2.3).

Table 2.3. Recruitment estimation (birth/immigration) per inter-seasonal period for each one of the four study sites within the Kinabatangan Floodplain.

Inter-Season	Birth/immigration estimates ±SE (95% CI)			
	Forest North	Forest South	OPP North	OPP South
1	161.49 ± 16.61 (132 – 197)	44.39 ± 6.27 (34 – 58)	17.42 ± 1.45 (15 – 20)	41.63 ± 13.03 (23 – 76)
2	117.25 ± 13.78 (93 – 147)	32.23 ± 4.72 (24 – 43)	12.65 ± 1.21 (10 – 15)	30.23 ± 9.71 (16 – 56)

The body weight of the lizards ranged from 1.1 up to 25 kg, while the SVL ranged from 34.4 up to 107 cm. In total, 15 monitor lizards weighed more than 22 Kg and just one reached 25Kg. Five individuals had a body length over 1 m. Both SVL and Body weight (BW) were normally distributed ($W_{SVL} = 0.961$, $p < 0.0001$; $W_{BW} = 0.8148$, $p < 0.0001$). Both forested areas and plantations show similar mean values of body weight ($BW_{Forest} = 5.85$ Kg ± 0.387 SE vs. $BW_{Plantation} = 5.86$ ± 0.272 SE; F = 0; p = 0.985) and SVL ($SVL_{Forest} = 63.58$ cm ± 1.196 SE vs. $SVL_{Plantation} = 64.16$ ± 0.907; F= 0.158; p = 0.691). Nonetheless, when comparing the same values among study sites, Lot 5 showed the highest values of both body weight (6.98 Kg ± 0.719; F = 5.529; p = 0.0043) and SVL (67.57 ± 2.187; F = 6.533; p = 0.0016). Both distributions show that Lot 5 has the larger individuals of the forested areas while the oil palm plantation subpopulation was similarly distributed around the mean (Fig. 2.3). A higher proportion of lizards under five kilos (infants and young females) was found in forested areas (65.07%), while plantations showed a more balanced proportion of the two classes of lizards.

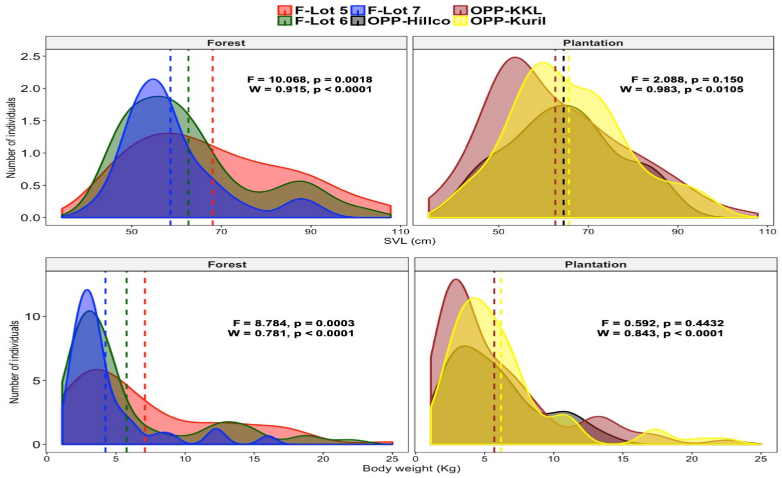

Fig.2.3. Distribution of (a) SVL and (b) body weight of the monitor lizard subpopulations per study site within the Kinabatangan Floodplain. Scatter lines show the mean value for each subpopulation.

2.4. Discussion

This study provides robust information regarding the population status of *V. salvator* within the Kinabatangan Floodplain using mark-recapture models applied to a large-scale collection of data. Data on the distribution of suitable habitats within the landscape allowed for a more accurate estimation of the number of lizards inhabiting the area as well as the population density.

Different studies, mostly performed by distance survey methods, have suggested higher occupancy of Asian water monitor lizards in human dominated areas compared to non-disturbed areas (Uyeda, 2009; Jessop, 2012; Twining et al., 2017). In Tinji Island (Indonesia), a total of 1,400 individuals/km^2 Asian water monitor lizards have been estimated in disturbed areas, while 4 individuals/km^2 in non-disturbed areas, which suggests that food leftovers and waste management in the villages of the area are important drivers of these differences, as well as the absence of predators (Uyeda, 2009). In Australia, the use of distance surveys for *V. varius* detected 35 times higher counts of individuals in disturbed areas than in non-disturbed areas (Jessop et al., 2012), suggesting that human trophic subsides are attractive to lizards, and also warning that a high abundance of lizards in interface areas could represent a risk to other wild populations, such as ring-tailed possums (*Pseudocheirus peregrinus*).

In Bengal, *V. bengalensis* tends to prefer protected areas than those subjected to forestry management and exotic species planting (Ghimire and Phuyal 2013). The authors suggest that the features of trees (eucalyptus and teak) do not satisfy the requirements of this species as shelter (too vertical and small branches). In West Bengal, *V. salvator* were reported in anthropogenic coastal estuarine areas and floodplains, but none in the highlands. *V. bengalensis* and *V. falvensis,* on the other hand, were less abundant but more widely distributed within four different type of agro-ecological zones than *V. salvator*. Livestock disposal, as well as the presence of ponds and small wetlands in the villages (naturally stocked with fish and crabs), and a high population of rats and other prey within farmlands and around the villages, seem to provide those three species with sufficient food resources in such human-modified territories (Chatterjee and Bhattacharyya, 2014). At the same time, the authors highlight the preference of *V. salvator* for floodplains and wetlands.

The estimated densities in this study are much lower than those estimated by Uyeda (2009) for the same species in an anthropogenic habitat in Indonesia. This difference could be influenced by methods used in this study. Regarding MR methods, it has been suggested that distance surveys may have a high risk of false absences due to the cryptic features of *V. komodensis* and large variability (Ariefiandy et al., 2014). Using mark and recapture methods, Bennett (2000) calculated a density of 357 individuals/km^2 for *V. exanthemicus*, a half-sized varanid, in mixed farmland and grassland habitats in Ghana, while Purduwana et al. (2007) estimated a total abundance of 2,448 *V. komodensis*, the largest varanid in the world (twice the size of *V. salvator*) in the whole Komodo Dragon National Park. Regarding the body mass of these three species and the abundances estimated in each study, the population estimated for the Kinabatangan Floodplain could be considered within the range for varanids.

Micro-climate variables may have an impact on nesting behaviour and/or egg survival (Shine and Harlow, 1993; Horn and Visser, 1997; Elphick and Shine, 1998). Characteristics of some tree species used in commercial crops, such as eucalyptus and teak, have been found unsuitable for *V. bengalensis* requirements (Ghimire and Phuyal, 2013). It is very likely that oil palm plantations might not offer enough suitable habitat for nesting, and that the high temperatures of those sites may have a negative impact on egg survival. These environmental factors could explain why the inter-season recruitment estimations are higher in forested areas than in plantations. The higher proportion of individuals under five kilos, also suggests higher number of young individuals in forested areas than in plantations.

Growth rates reported in this study are similar to those of Komodo dragons, while survival rate estimations are much higher (Purwandana et al., 2014). Growth rates in Komodo dragon populations are stable on islands with relatively short distance between them and with enough prey availability, while the smallest and more isolated islands presented both the lowest survival and growth rates (Purwandana et al., 2014). This study shows that the Asian water monitor lizard population in the Kinabatangan Floodplain has remained stable, which suggests that the landscape provides enough resources to maintain the current population. Personal observations during the study period and telemetry data suggest that the Asian water monitor lizards are more likely to utilize areas with dense understory and presence of water, as well as the boundaries between the plantations and the forested areas. Although forested areas of the LKWS are considered as non-disturbed sites, the influence of surrounding oil palm plantations may have a positive influence on the dynamics of the population.

The landscape matrix of the Kinabatangan Floodplain offers a highly suitable habitat for the Asian water monitor lizard, one of the most abundant predators in the area. The population size seems to be stable in time and the survival rates are very high. The absence of larger predators and competition could play an important role in the dynamics of the population, as well as the abundance of resources within the area. Future studies on sex identification and population genetics may give more complete information regarding the demography of the species in the Kinabatangan Floodplain. On the other hand, it is recommendable to assess the impacts of their abundance on communities of small vertebrates and invertebrates that inhabit the floodplain, particularly those with vulnerable populations.

Chapter 3

Home range and habitat selection of *Varanus salvator* in a highly fragmented landscape

3.1. Introduction

Knowing how certain species interact with the habitat within their distribution range is an important element to understanding what their requirements are for performing essential ecological functions (i.e. mating, feeding, nesting, resting). The home range can be considered as the area where an individual finds the necessary elements for these functions (Jewel, 1966; Baker, 1978). Understanding how individuals utilize resources within their home range provides information regarding the basic needs for the survival of the species within the landscape and helps to predict where the species is more likely to occur, as well as assess a potential over-utilisation of resources when the species is highly abundant compared with the availability of these resources (Ciofi et al., 2007; Huck et al., 2008; Kie et al., 2010).

The concept of 'resource preferences' within a home range is known as habitat selection and describes the environmental variables that influence the species' population dynamics, resource utilisation, and therefore, potential impacts on the ecosystem (Fretwell and Lucas, 1970; Morris, 2003; Aarts et al., 2008). Forest dynamics and succession processes can be negatively affected by the over-utilisation of herbivorous populations and the absence of predators (Brown et al., 2001). Different studies have analysed the proportion of resource availability and utilization within human dominated landscape and the effects of fragmentation (i.e. Leuthold and Sale, 1973; Brøseth et al., 1997; Topping et al., 2005; Ripple and Beshta, 2014, Gara et al., 2017). A study on *Varanus varius* in anthropogenic landscapes suggested that the species' abundance in edge areas may have an impact on the ringtail opossum (*Pseudocheirus peregrinus*) populations in Australia (Jessop et al., 2012). Habitat preferences also help to identify the habitat features that species prefer within the landscape and their availability. Thus, it is possible to predict whether a species is more (or less) likely to be found in a given landscape (Guisaan and Zimmermann, 2000; Scott et al., 2002).

Global positioning system (GPS) technologies have been used in fragmented landscapes to understand how some species adapt to the loss of their habitat, as well as the mechanisms of either avoidance or preference of anthropogenic habitats such as crops, farms and human settlements (Hints et al., 2006; Houle et al., 2010; Cristescu et al., 2016; Stark et al., 2017; Hearn et al., 2018). Furthermore, GPS approaches have also provided useful information for species distribution models and have allowed researchers to estimate the amount of habitat that target species need to satisfy their requirements, such as protection, nutrition and reproduction (Dyer et al., 2001; Sastrawan and Ciofi, 2002; Hebblewhite and Merril, 2008; Graham et al., 2009; Hearn et al., 2018). For generalist species that may occur in both forested areas and plantations, GPS telemetry can aid researchers to understand activity patterns and describe how resources are distributed and utilised within the landscape (McCue et al., 2013, Bastille-Rousseau et al., 2016).

There are only a few studies using telemetry data to understand home ranges and habitat use in varanids (Auffemberg, 1981; Christian and Wavers, 1994; Gaulke et al., 1999; Ibrahim, 2000; Guarino, 2002; Ciofi et al., 2007; Imansyah et al., 2008; Bennett, 2014), with the majority using very high frequency (VHF) radio-telemetry, and only a couple of studies using GPS telemetry (*V. varius*; Flesh et al., 2009; Lei and Booth, 2018). GPS telemetry has a substantial advantage over the VHF system. It provides more accurate, constant and abundant data on the locations of the target individual, while VHF depends on (1) being relatively close to the target animal, (2) expertise in triangulation, and (3) the time spent in the field for tracking (Rodgers, 2001; Kochanny et al., 2002; Hebblewhite and Haydon, 2010; Tomkiewicz et al., 2010). The GPS system has evolved quickly and currently it provides more information regarding environmental variables (e.g. temperature) and animal activity (e.g. inactivity, speed and mortality). However, GPS telemetry presents limitations of its own. For example, current GPS tags need to be of a safe and comfortable size for the target species, which limit their use and / or longevity on certain small species (Kochanny et al., 2002; Land et al., 2002). On the other hand, environmental factors, such as canopy cover, topography and weather, may also influence the efficiency of GPS tags (Rempel et al., 1995; Gau et al., 2004; Blackie et al., 2010; Chadwick et al., 2010; Evans et al., 2015; Lehrke et al., 2017; Bailey, 2018; Henderson et al., 2018). Therefore, researchers need to weigh the trade-offs carefully when using this technology to answer specific questions.

This study represents the first example of GPS/VHF tagging of Asian water monitor lizards in Sabah, in order to estimate their home range and habitat use. The purpose of this study is to understand the spatial dynamics of *V. salvator* in the Kinabatangan Floodplain, a highly fragmented landscape in Sabah, Malaysian Borneo. Specifically, it aims to (1) estimate home range sizes in both forested areas and oil palm plantations, and (2) determine the habitat selection ratio of different environmental elements within the landscape, such as habitat type, vegetation height, slope, and potential of flooding. It was hypothesised that lizards living in or nearby plantations have smaller home ranges than those inhabiting forested areas; however, their habitat preference is determined by the same environmental elements in both areas (forest and plantation) albeit with different levels of utilization of each.

3.2. Methods

3.2.1. *GPS/VHF tagging*

Twenty lizards heavier than 15 kilos were tagged with GPS/VHF devices (Advanced Telemetry Systems Inc., North Isanty, MN USA) between January 2015 and December 2016. Although the weight of the tags was small enough to be used on lizards above five kilos, it was preferable to choose individuals above 15 kilos due to the tag's size and attachment system (which otherwise would have been too large and may have slipped off from the smaller animals). Regarding sex selection, all the animals tagged were likely to be males, considering their weight and size. As female lizards seem to be much smaller it was not possible to GPS tag any during this study. All the lizards tagged were selected during the trapping period or hand-caught if they happened to be seen opportunistically.

Ten lizards were chosen in the boundaries or within oil palm plantations, while the other 10 were found inhabiting the forested areas. In order to avoid pseudo-replication, each lizard tagged within the same period of time was trapped with a minimum distance of 2 km from each other. This way, the influence of one individual over each other (territoriality) was also avoided. Tags were slightly modified from the VHF tags designed by Ciofi et al. (2007) and Harlow et al. (2010) for the Komodo dragon. The backpack-like device consisted of a block of waterproof resin that wrapped three different elements: (1) a GPS sensor connecting to the satellite to record the current location, (2) a VHF transmitter sending a high frequency pulse to the receptor in order to identify the current location of the individual on the ground, and (3) an ultra-high frequency UHF transmitter connecting to the base-station/computer in order for the user to be able to download the data collected from the tag (Fig 3.1). Besides the GPS locations, the device provides environmental temperature, location accuracy, number of satellites used, and the date and time of each record. Since the Asian water monitor lizard is a diurnal species, the GPS schedule was fixed to record one point every 90 minutes from 5:00 a.m. until 8:00 p.m. every day, while the VHF/UHF system was set to operate from 7:00 a.m until 12:00 p.m. These settings would allow the tags to work from three up to nine months, depending on the effort that it takes to reach the satellite, being easier when the lizard is in an area with little canopy cover.

Fig 3.1. a) Deployment of the GPS/VHF back-pack on an Asian water monitor lizard in the study site, and b) the same lizard after being released with the device.

Data were downloaded once a week, but lizards were monitored every other day for the first two weeks to confirm that tags had been properly attached and the animals do not show any damage associated with the tag. Additionally, this process provided valuable information regarding the potential locations for future tracking. Since the tags are equipped with a battery detector, it was possible to identify the status of the battery and decide when the device should be taken off the lizard so that it would not stay on the lizard for a lengthy period of time while non-functional.

In order to get sufficient data to estimate home ranges, it was necessary to discard data from individuals whose tags lasted for a short period of time. The number of effective days needed for an accurate estimation was determined by the rate of increasing area of the individual’s movements during the time they were tracked until the moment the area did not increase any more for a period of 1 or two weeks (Sastrawan and Ciofi, 2002; Ciofi et al., 2007; Imansyah et al., 2008).

3.2.2. *Home Range Estimation*

Location data generated per each individual was organized as a shape file in Q-GIS 2.18.20 (Free Software Foundation Inc., MA. USA) and analysed in the R package ADEHABITAT-HR v 0.4.15 (R-Core Team) (Calenge, 2015,). A Minimum Convex Polygon (MCP) with 100% of density points was calculated as home range to be considered in the habitat selection analysis. A more accurate estimation was carried out using Local Convex Hulls (LoCoH), with i) the core habitat of an animal represented by the area where 50% of the animal observations were made, ii) a buffer area defined as the area where the 75% of the GPS locations occur, and iii) a transient habitat including up to 95% of the observations (Ciofi et al., 2007; Huck 2008; Kie et al., 2018). Although Kernel Density Utilization (KDU) methods are very accurate to estimate home ranges compared with MCP methods, there is a risk of over or under-estimation of the home range, due to the buffer estimation, whereas LoCoH offers a more accurate calculation by triangulation of the nearest neighbour points (Getz *et al.*, 2007; Huck, 2008). Although the area estimated with this method is much smaller when compared with Kernel methods, this method is much more accurate (Getz et al., 2007; Huck, 2008; Stark et al., 2017; Kie et al., 2018). The adaptive algorithm (a-LoCoH) was used for the home range estimation, which creates the home range from the smallest to the largest area limited by the maximum distance between two points (Getz et al., 2007).

3.2.3. *Habitat Selection Analysis*

The 100% Minimum Convex Polygon was considered as the available area per each tagged individual (whole home range) (Aebischer *et al.*, 1993). Rasterized images of (1) canopy height, (2) slope, (3) elevation, and (4) type of habitat were used to assess the type of habitat preferred by the lizards. Raster files were created utilizing Light Detection And Ranging (LiDAR) images provided by the Sabah Forestry Department and generated by the Carnegie Airborne Observatory of Stanford University. LiDAR images are one of the newest generations of 3D land imagery with very high resolution in horizontal and vertical axes (Vierling et al., 2008; Asner et al., 2012; Davies and Asner, 2014). Laser technology is used to detect variations in the landscape in terms of topography (elevation and slope), vegetation structure (canopy height, canopy cover, tree diameter) and even composition, with a precision of one up to two meters (Asner et al., 2012; Davies and Asner, 2014).

Two analyses were carried out to describe the habitats of the tagged Asian water monitor lizards under the Third Order Analysis (TOA) assumption which considers that all the individuals within the study have been identified with GPS tags and their home ranges are independent of each other (Thomas and Taylor, 1990). As mentioned above, to avoid territory issues, each site had only one lizard tagged per period and the distance between individuals tagged in the same period was of a minimum of 2 Km.

Firstly, in order to describe the importance of the different environmental variables in the habitat selection, K-select analysis was used. K-select analysis is a multivariate approach to understand the importance of variables according with their distribution within the landscape and their utilization by different individuals using radio or GPS telemetry (Calenge et al., 2005). Afterwards, each raster file was re-classified as follows: *Vegetation height* was classified into: (1) Low understory, below 2m height, (2) low canopy, 2- 4 m height, and (3) high canopy, above 4 m. *Slope* was classified into (1) flat, (2) smooth, and (3) steep. *Habitat* was classified into (1) forested areas, and (2) oil palm plantations. Since the study area is a floodplain with few hills, it was convenient to classify the *Elevation* raster image according to the likelihood of flooding into: (1) permanently flooded, (2) seasonally flooded and (3) highland. Each lizard's home range was analysed separately to estimate the proportions of each category per each variable available and used within the whole home range (Aebischer et al., 1993; Manly et al., 2002).

Due to the amount of data to be processed, the analysis was first performed per individual using the First Order Analysis instead (FOA; Aebischer et al., 1993; Manly et al., 2002). FOA considers the occurrence of any individual within a determined area without the need of any identification. Each individual's location was recorded as independent occurrence within the polygon as study sub-area (Thomas and Taylor, 1990). Afterwards, the results of these analyses were then sorted in an overall data set and analysed with the TOA method to have an overall estimation of the ratio between utilized and available resources within the whole study site (Aebischer et al., 1993). The ratios between the availability and use of each resource within each home range was used to describe habitat selection per individual, assuming independence between individuals in how they select the resources available within their home range (Manly et al., 2002).

In order to investigate if there is any difference between the selection of habitat for the daily activities and as sleeping sites utilization, the ratios between availability and use of habitat was estimated using exclusively the GPS locations recorded at 20:00 hours of every day. This was assumed after several field observations were made of individuals feeding on dead animals between 6:00 a.m. and 19:30 pm (*pers. observ.*). The results generated were compared with the daily utilization ratios. Ratio values closer to the unit indicate that such proportion is even and, therefore, the pattern of selection of sleeping sites does not differ from the overall pattern. Distance from the unit indicates either higher (>1) or lower (<1) preference of habitat during the night than on the day.

3.3. Results

3.3.1. *Tag Performance*

Fourteen out of 20 tagged individuals were considered for the study. The remaining six individuals were discarded due to the little amount of information provided by the tags. These failures happened essentially during the first part of the study period. At the beginning it was easy for the lizards to get the backpack off when they walked under the vines or into burrows. The first-generation belts were made of leather and, being afraid of causing skin damage on the animals, the attachment was a bit loose and therefore easy to slip past from the lizard’s hip. For the second generation, the belts were covered with a soft rubber tube and the device had a little slope in the front to avoid it from being stuck in vines (Fig 3.1). Before the batteries’ life ends, the lizards were caught to retrieve the devices.

Six out of the 20 individuals held the tag for less than 55 days and the data of one individual for which the collar lasted for 60 days was discarded due to inefficient GPS performance. The maximum period of work was recorded in one lizard that held the tag for about 300 days while the average performance was of 154 days (Fig 3.2).

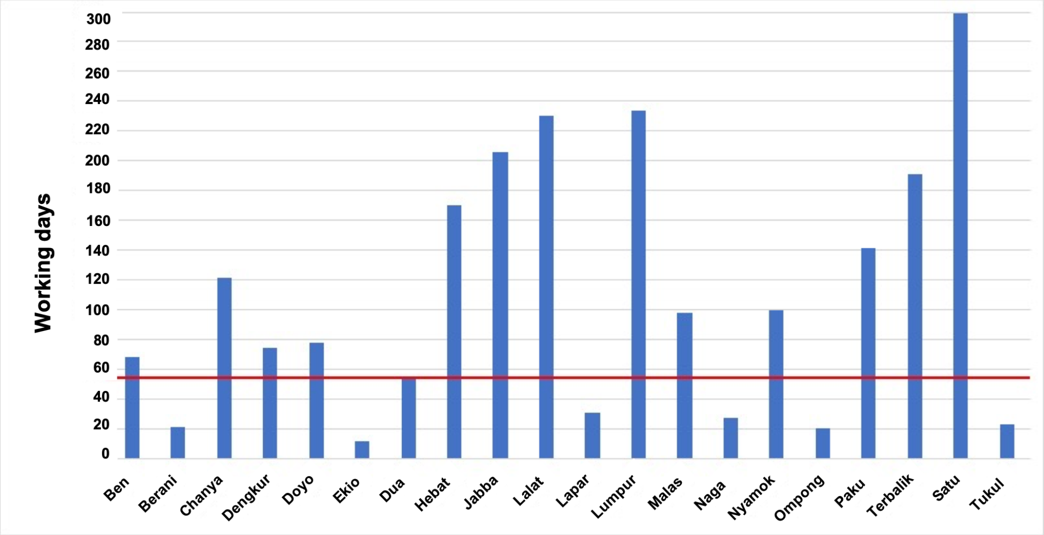

Fig 3.2. GPS/VHF tag performance. Each bar represents the number of days recorded by each tag. The red line represents a threshold for data selection in this study. All individuals below this threshold were discarded, as well as the first individual (Ben) due to a GPS failure.

Out of the 14 individuals used in this study, seven (n = 7) were captured in forested areas while the other seven were found in oil palm plantations. GPS data showed that three animals made exclusive use of oil palm plantations and one of forested areas. Thus, the habitat selection analyses included both area types for almost all individuals.

3.3.2. *Home Range*

The adaptive approach of the Local Convex Hull method was used to estimate three different levels of home range per individual according with the density of GPS locations. The core area was identified as the area where 50% of the locations occurred, while the buffer area was estimated with 75% of density and the transient area was estimated as the 95% of density (Fig 3.3).

The maximum home range (MCP-100) calculated was 6.611 km^2 in forest while the minimum home range in the same habitat was 1.416 km^2. Home range in oil palm plantations varied from 0.277 km^2 to 3.321 km^2. The maximum core area using the

LoCoH-50% estimation for forest was 0.144 km^2 (4.4% of the MCP-100) and the minimum core area was 0.063 km^2, which was observed for two individuals.

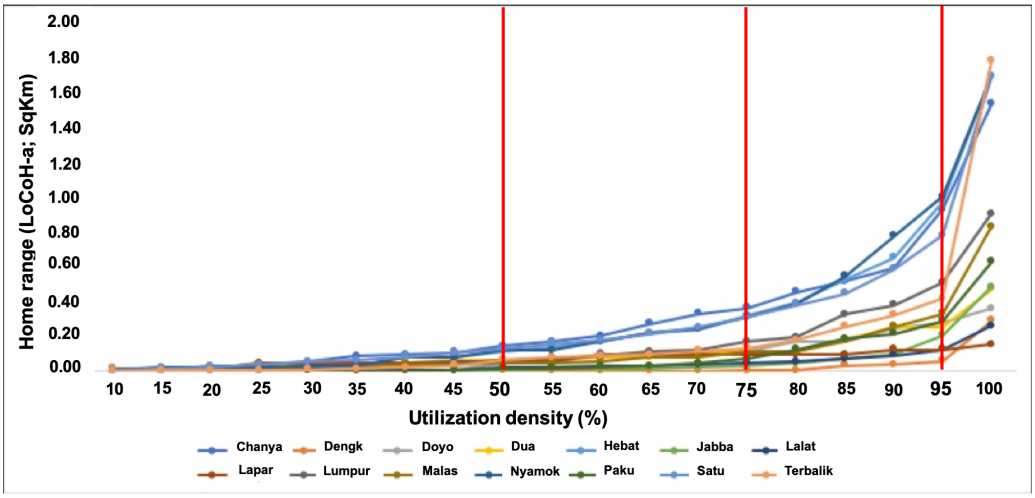

Fig 3.3. Calculated home range for different levels of utilisation density (in %) using the adaptive approach of the Local Convex Hull method. Red vertical lines identify the 50, 75 and 95% of density that were taken as core, buffer and transient areas respectively.

In plantations, the maximum core area was estimated at 0.128 km^2, which represents around 4 to 5% of the whole home range and the minimum core area was estimated at 0.001 km^2 (0.17%). The maximum percentage of utilisation (core area vs. MCP-100) occur in plantations, where one lizard used the 19.13% (0.053 km^2) of its own home range as core area. These results suggest that the individuals inhabiting plantations seem to optimize their whole home range even if this is much smaller than in forested areas, where lizards have more land to explore and use different sites as core areas (Table 3.1).

MCP calculation showed that individuals in the forest have significantly larger home ranges than those mostly living in plantations ($\text{MCP}_{\text{Forest}}$ = 3.913 km^2 vs $\text{MCP}_{\text{Plantation}}$ = 1.586 km^2; t = 2.78; df = 10.55; p = 0.018). Similarly, the LoCoH-method found larger home ranges in forested areas than in plantations ($\text{LoCoH-95}_{\text{Forest}}$ = 0.631 km^2 vs $\text{LoCoH-95}_{\text{Plantation}}$ = 0.262 km^2; t = 2.4428; df = 11.14; p = 0.03241), but there was no significant difference between both habitats when comparing buffer ($\text{LoCoH-75}_{\text{Forest}}$ = 0.244 km^2 vs $\text{LoCoH-75}_{\text{Plantation}}$ = 0.125 km^2; t = 1.8389; df = 11.571, p = 0.09172) and core areas ($\text{LoCoH-50}_{\text{Forest}}$ = 0.089km^2 vs $\text{LoCoH-50}_{\text{Plantation}}$ = 0.065 km^2; t = 0.91; df = 10.356; p = 0.382) (Fig. 3.4).

Table 3.1. Home range calculated per tagged lizard during the study period in the Lower Kinabatangan Wildlife Sanctuary. Areas MCP-100 represent the whole available territory per individual calculated as Minimum Convex Polygon in sq. Km. *The percentage of utilisation of Local Convex Hull estimated for transient (95%), buffer (75%) and core (50%) areas compared with the MCP-100 is indicated in brackets.

Name	Habitat	Territory (km^2)			
		MCP-100	LoCoH-95 (%*)	LoCoH-75 (%*)	LoCoH-50 (%*)
Chanya	**Forest**	3.271	0.922 (28.18)	0.364 (11.12)	0.144 (4.40)
Doyo		1.416	0.274 (19.35)	0.112 (7.90)	0.063 (4.44)
Hebat		4.835	0.967 (20)	0.319 (6.59)	0.116 (2.39)
Malas		1.945	0.329 (16.91)	0.111 (5.70)	0.046 (2.36)
Lumpur		4.187	0.507 (12.10)	0.17 (4.06)	0.063 (1.50)
Nyamok		6.611	0.999 (15.11)	0.312 (4.72)	0.122 (1.84)
Terbalik		5.127	0.417 (8.13)	0.32 (6.24)	0.069 (1.34)
Satu	**Oil palm plantation**	3.321	0.776 (23.36)	0.309 (9.30)	0.128 (3.85)
Paku		2.486	0.288 (11.58)	0.071 (2.85)	0.128 (5.14)
Lalat		0.705	0.126 (17.87)	0.045 (6.38)	0.021 (2.97)
Lapar		0.277	0.126 (45.48)	0.094 (33.93)	0.053 (19.13)
Jabba		0.917	0.207 (22.57)	0.033 (3.59)	0.011 (1.19)
Dua		2.818	0.249 (8.83)	0.319 (11.32)	0.116 (4.11)
Dengkur		0.58	0.059 (10.17)	0.004 (0.68)	0.001 (0.17)

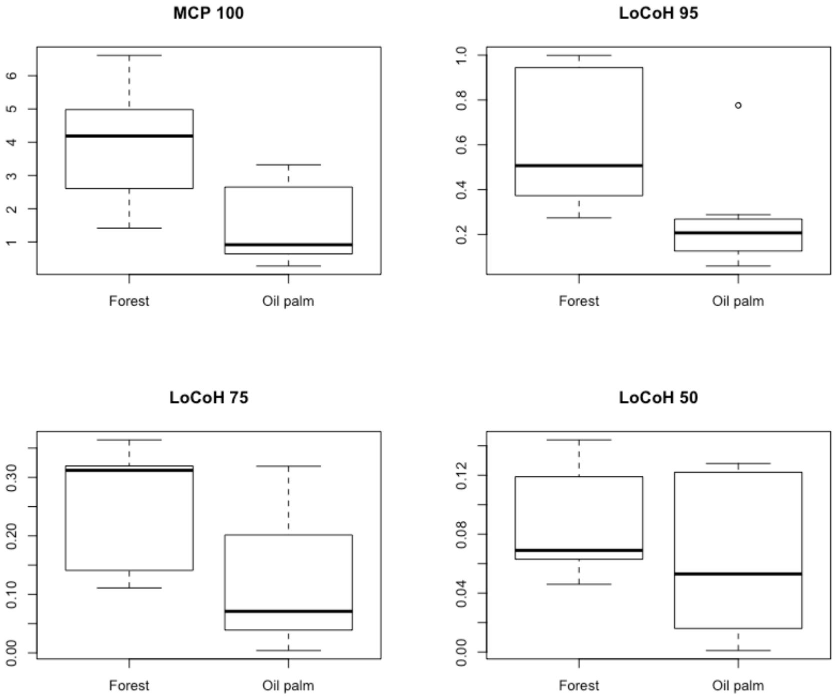

Fig 3.4. Differences in home ranges between forested areas and plantations for the whole territory (MCP-100), transient (LoCoH-95), buffer (LoCoH-75) and core (LoCoH-50) areas of the Asian water monitor lizard GPS/tagged within the Lower Kinabatangan Wildlife Sanctuary and the surrounding plantations.

3.3.3. *Habitat Selection*

To understand the habitat preference, the full area of the Minimum Convex Polygon (MCP) was used to define the entire potential area available for each individual. Since not all the individuals were tracked during the same period of time, it is not advisable to assume territoriality.

Inspection of the data showed that tagged individuals were using mostly sites with low understory and low canopy, with low or null preference for those sites with high canopy in oil palm plantations. Just two monitor lizards showed greater occurrence in oil palm plantations than in forested areas where both habitats were present within their home range. Although less abundant, areas with null potential of being flooded were less used compared with those sites with high or low flooding probability (edges of water bodies and seasonally flooded areas) (Fig. 3.5).

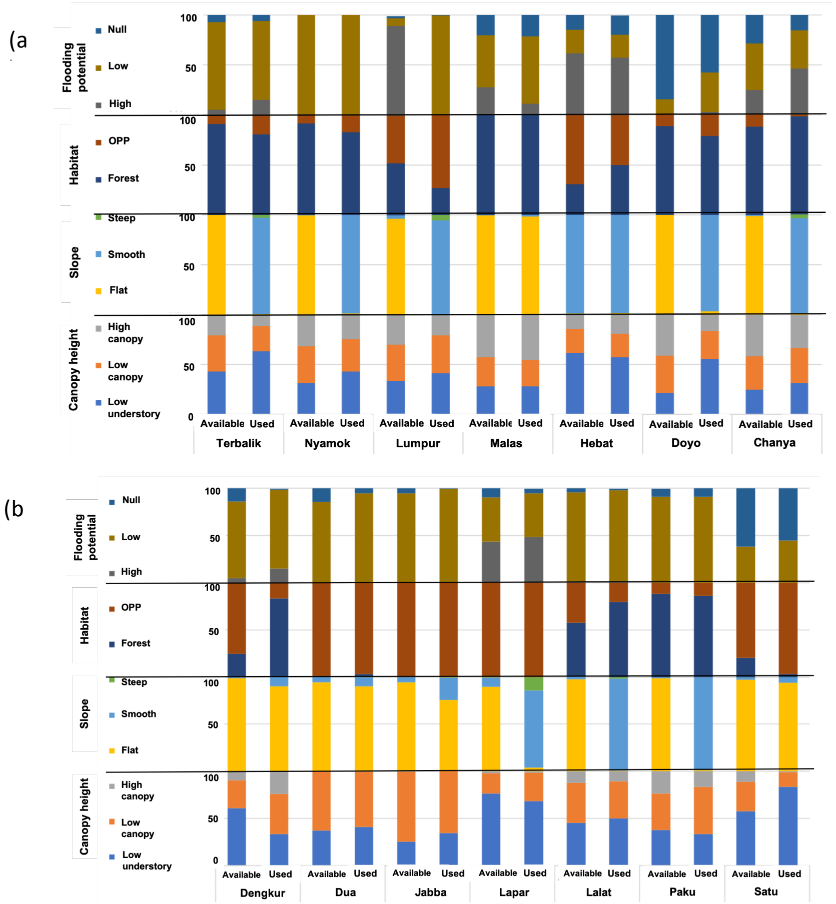

Fig 3.5. Proportion of available and used environmental features within each lizard's home range. As the categories' distribution of each variable is given in percentage, each variable is separated at the hundreds mark. Upper graph (a) corresponds to the individual caught in forested areas while those trapped in oil palm plantations are represented in the lower graph (b).

The k-select analysis showed that vegetation height and flooding potential are important variables influencing landscape use in *V. salvator* in both plantations and forested areas. The weight of slope as variable is influenced by the flooding variable. This suggests that the lizards' habitat use might rely on water presence with specific vegetation structure features (Fig. 3.6).

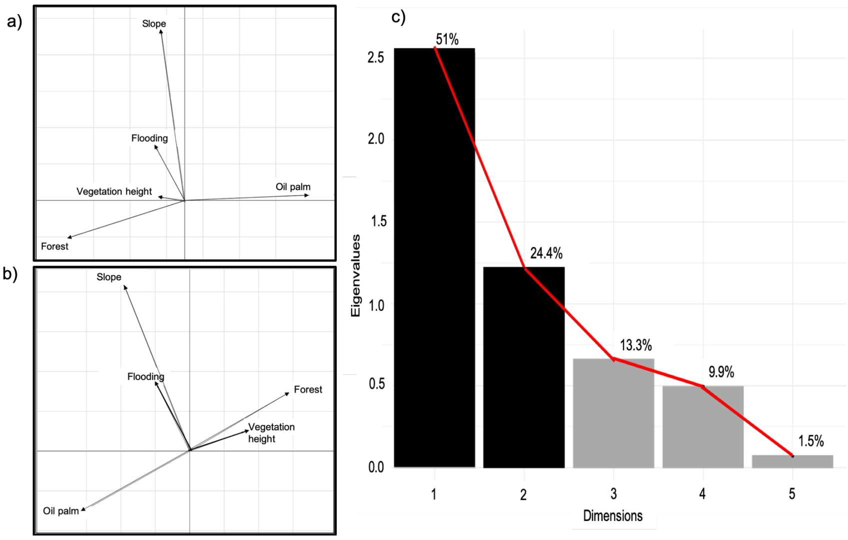

Fig 3.6. Principal Component Analysis representation of the weights of each variable and its influence in the *V. salvator*'s habitat selection in (a) forest and (b) plantation. Plot c represents the eigenvalues and the percentage of the contribution on the model.

The overall compositional analysis of habitat selection demonstrated either a nonrandomised selection of habitat or independence between the way how each individual uses its own home range (Table 3.2). Therefore, it was necessary to analyse each individual selection ratio separately.

Table 3.2. Values of Λ (MANOVA) and p of the compositional analysis of habitat use by *V. salvator* in the Lower Kinabatangan Wildlife Sanctuary and surrounding plantations. $p < 0.001$ indicate that the selection is nonrandomized or the process for each individual is independent of each other (Aebischer *et al.*, 1993).

Variable	**Λ**	**p**
Habitat	0.999	0.998
Vegetation height	0.7917	0.260
Slope	0.288	0.002
Flooding	0.591	0.154

Looking at the individual selection ratio, most cases show a significant over-utilisation of plantations, even for those individuals captured in forested areas. Grasslands were slightly preferred over bush and canopy areas, but this was significant for two individuals only. Only one lizard seemed to be more comfortable within the high canopy areas. Smooth and steep slopes as well as permanent and seasonally flooded areas were the most preferred sites by most of the individuals with very high over-utilisation of those areas (Table 3, Figs 4.15- 4.17 of Appendix 4).

Lizards with home ranges entirely within plantations showed very low utilisation ratio of high canopy areas (tall oil palm trees) where the understory is absent or at very low densities and, therefore, with no protection for the lizards. In the same way, the preference for areas with seasonal or permanent presence of water (i.e. related to drains and streams) is highly significant (Table 3.3).

Ratios between selection of sleeping sites over overall selection ratios show a high preference for bush and grasslands. However, it is unexpected that the preference between forested areas and plantations was not different from the general pattern. This could be explained by specific features in plantations that could provide good shelter for lizards. Three individuals that spent the whole study period within plantations showed a higher preference for sites with dense understory (Table 3.4).

Table 3.3. Individual selection ratios of *V. salvator* in the Lower Kinabtangan Wildlife Sanctuary. Habitat was divided into forest (Fst) and oil palm plantation (OPP). Vegetation height was divided into understory (Uds), low canopy (LC) and high canopy (HC). Slope was categorized as flat (Ft), smooth (Sth) and steep (Stp). Flooding probability was divided into permanently flooded (Pm), seasonally flooded (Ssl) and highland (Hld). Site (*) corresponded to the site where each individual was captured, and differs from habitat in that it represents the ratio of availability/use for each category per individual. Values < 1 represent a sub-utilization of the resource, meanwhile values >1 represent an over-utilisation. (p^+) is the p value of Xi^2 that was used as statistical method to assess the significance of the selection with 95% of confidence.

		Selection ratios														
Site*	**Name**	**Habitat**			**Vegetation height**				**Slope**				**Flooding**			
		Fst	**OPP**	**p^+**	**Uds**	**LC**	**HC**	**p^+**	**Ft**	**Sth**	**Stp**	**p^+**	**Pm**	**Ssl**	**Hld**	**p^+**
Forest	**Chanya**	1.12	0.12	**0.005**	1.28	1.04	0.80	0.411	0.01	95.10	3.50	**0.000**	1.83	0.83	0.54	**0.003**
	Doyo	0.89	1.82	0.058	1.93	0.75	0.75	**0.001**	0.03	971.00	NA	**0.000**	29.00	2.58	0.68	**0.000**
	Hebat	1.63	0.72	**0.005**	0.93	0.98	1.32	0.667	0.90	1.00	NA	0.950	0.93	0.98	1.32	0.670
	Malas	1.00	NA	NA	1.00	0.91	1.07	0.896	0.99	1.78	4.00	0.790	0.39	1.32	1.03	**0.010**
	Lumpur	0.29	8.69	**0.000**	1.22	1.05	0.69	0.304	0.00	30.36	56.94	**0.000**	0.00	12.45	0.09	**0.000**
	Nyamok	0.90	2.06	**0.046**	1.38	0.88	0.77	0.202	0.01	99.30	NA	**0.000**	0.70	1.00	NA	0.800
	Terbalik	0.89	2.12	**0.027**	1.47	0.70	0.56	**0.015**	0.00	322.00	31.00	**0.000**	2.76	0.90	0.86	**0.060**
Plantation	**Satu**	0.16	1.21	**0.000**	1.46	0.49	0.11	**0.000**	0.97	2.07	3.00	0.490	NA	1.17	0.89	**0.300**
	Paku	0.97	1.22	0.577	0.88	1.30	0.70	0.216	0.01	99.10	NA	**0.000**	NA	0.92	9.29	**0.000**
	Lalat	1.39	0.48	**0.001**	1.10	0.93	0.86	0.806	0.01	40.67	17.02	**0.000**	1.00	1.02	0.50	0.720
	Lapar	Na	1.00	NA	0.90	1.39	0.70	0.368	0.04	8.65	14.21	**0.000**	1.12	0.99	0.53	0.460
	Jabba	Na	1.00	NA	1.37	0.88	0.14	0.288	0.80	4.31	8.00	**0.000**	NA	1.05	0.06	**0.046**
	Dua	3.22	0.98	0.234	1.09	0.94	1.33	0.875	0.96	1.73	1.50	0.520	NA	1.11	0.36	**0.030**
	Dengkur	3.37	0.22	**0.000**	0.55	1.43	2.48	**0.000**	0.91	9.00	NA	**0.000**	2.92	1.03	0.08	**0.000**

Table 3.4. Ratios between the overnight and the overall habitat selection ratios of *Varanus salvator* in the Kinabatangan floodplain. Each value represents the coefficient of the overnight over the overall habitat selection ratios obtained by Selection ratio estimation. Values closer to the unit indicate that such proportion is even and therefore, the selection patterns of sleeping sites do not differ from the overall patterns. Distance from the unit indicate higher (>1) or lower (<1) preference during the night than the general pattern.

Site	**Name**	**Habitat**		**Vegetation height**			**Slope**			**Flooding**		
		Forest	**OPP**	**Uds**	**Low canopy**	**High canopy**	**Flat**	**Smooth**	**Steep**	**Permanent**	**Seasonal**	**Highland**
Forest	**Chanya**	1.000	0.847	1.175	1.108	0.729	1.000	1.005	0.943	0.950	1.041	0.947
	Doyo	1.016	0.956	1.125	1.441	0.427	2.169	0.963	NA	2.241	0.980	1.050
	Hebat	0.953	1.054	1.133	0.935	0.690	1.333	0.998	NA	0.021	4.218	NA
	Malas	1.000	NA	1.038	1.004	0.966	0.992	0.875	3.504	0.996	1.041	1.138
	Lumpur	1.002	1.003	1.029	1.002	0.946	NA	0.980	1.228	NA	0.996	NA
	Nyamok	0.958	1.222	1.016	1.068	0.882	1.010	0.997	NA	1.429	1.000	NA
	Terbalik	0.704	2.231	0.989	1.142	0.747	NA	0.987	1.387	0.893	1.007	0.824
Plantation	**Satu**	0.531	1.015	1.012	0.939	0.805	1.052	0.155	0.000	NA	0.962	0.965
	Paku	1.033	0.806	0.895	1.085	0.945	0.606	1.003	NA	NA	0.966	0.758
	Lalat	0.254	3.893	1.024	0.953	1.081	0.410	1.020	0.000	0.400	0.999	0.714
	Lapar	NA	1.000	0.693	1.238	10.714	1.397	0.943	1.232	0.103	1.068	0.110
	Jabba	NA	1.000	1.498	0.235	341.837	1.221	0.329	0.000	NA	0.996	0.500
	Dua	NA	1.030	0.385	0.532	66.792	1.002	0.736	7.667	NA	0.926	0.433
	Dengkur	1.051	0.978	1.160	0.982	0.811	1.010	0.919	NA	2.961	0.668	NA

3.4. Discussion

3.4.1. *Tag performance*

Although the use of GPS tags is becoming more common in landscape ecology, it is still a challenging methodology for species which spend most of their time close to the ground and in dense covered areas, such as is the case for many tropical forest species. The ultimate design of the backpacks that were used during the study demonstrated to be efficient in terms of durability and functionality, recording data for more than seven months with high efficiency even in forested areas. Such modifications make the GPS tags an important tool for the study of movement ecology of varanids, however, the reliance on two “AA” batteries to ensure long-term data recording forced the tags to be more voluminous than those used in other studies (Flesh et al., 2009). It was observed in this study that Asian water monitor lizards shed skin very often resulting in glued attachments being less likely to remain attached for long time. However, the tangling issues previously reported by others (Ciofi et al., 2007) can be overcome by smoothing the front side of the device as done here.

Although tags used in this study did not have a drop-off mechanism, lizards could be re-captured in order to retrieve the device and no signs of injuries on the individuals were observed. This suggests that tags can last for enough time to get accurate data to answer some crucial questions in movement ecology, without causing any damage to the animals. The crossed-belt tag proved to be a good option for this species since it is waterproof, as well as hard to lose if the animal gets under vegetation or in burrows. The GPS data recovered by the tags did not show any alterations in the animal’s behaviour or movement limitations of the tagged individuals. Studies on Komodo dragons have reported a period of working days between 14 and 56 days (Ciofi et al., 2007; Imansyah et al., 2008) using VHF and between 18 and 66 points recorded (Imansyah et al., 2008). Unfortunately, Flesh et al. (2009) did not mention the success rate of fixing GPS points or the time that each lizard was monitored. Therefore, the average number of 154 working days with more than 50% of fixing success represent a robust amount of data to evaluate home range and habitat selection.

3.4.2. *Home Range*

Home ranges of *V. salvator* were very similar to those recorded by Ciofi et al. (2007) and Imansyah et al. (2008) for *V. komodensis*. Nevertheless, the amount of data generated by these studies made it difficult to compare with the data obtained in this study.

Larger home ranges in forested areas rather than in plantations are expected due to the large availability of food in plantations. Gehring and Swihart (2004) found that the home range of long-tailed weasels (*Mustela frenata*) is reduced in agricultural fragmented landscapes. The authors suggest that the abundance of prey in the area may influence this observation. Saïd and Servanty (2005) found a similar effect in roe deer (*Capreolus capreolus*) in fragmented landscapes. They suggested that roe deer may reduce their home range when inhabiting edges with dense vegetation, where they can find abundant food and protection at the same time. A different observation was reported from female meadow voles (*Microtus pennsylvanicus*), which have larger home ranges in edges than interior sites, but in this case, the home range size could be influenced by intraspecific dominance more by than availability of resources (Bowers et al., 1996). Oil palm plantations are highly dominated by rodents that feed on palm fruits, and build their nests in palm trees and wasted leaves. Therefore, oil palm plantations offer lizards, as well as other carnivores, an abundant food source sparing the need for long quests for food, contrary to what happens to lizards with larger home ranges in forested areas, where they might feel more comfortable exploring larger areas under the protection of the forest.

Core areas represent hotspots within the whole home range where the individual spent most of the time or made repetitive visits. Ciofi et al. (2007) used 25% and 50% of utilisation density in their study. In this study, 50% was considered enough to determine the core areas since the curve does not differ very much from 25% or 30% (Fig. 3.3). During ground-truthing expeditions, it was observed that core areas consist mainly of riparian habitats with abundant water supply and dense understory. Majevski (2017) found great abundance of potential preys in those areas for both plantations and forested sites.

Although the intensity of use is more distributed within forested areas than in plantations, there is a pattern in the selection of those sites that provide the lizards not only with good shelter but also may represent a good food source (Saïd and Servanty, 2005). The distribution of the core areas within forested sites demonstrate that lizards inhabiting the forest are more able or willing to explore and establish different core areas within their home range, which may optimize the use of the resource under the protection of the forest. Meanwhile, lizards in plantations seem more comfortable staying in the same spot instead of venturing to other potential sites. The lack of understory outside of the core areas in the plantations and the unsuitability of the palm trees as refuge for these large reptiles, seem to be the cause of this behaviour. These patterns may have different impacts on the ecosystem, by over-utilising some areas and under-utilising others.

3.4.3. *Habitat selection*

Beyond the food source, habitat features seem to be important for the selection of the core areas. They determine the prey community structure and provide shelter and protection (Saïd and Servanty, 2005). Auffenberg (1981) suggested that around 50% of the activities of Komodo dragons happen within a core area that rarely overlaps with other dragons' home range and have specific features that make it differ from less utilised areas. *V. salvator* was found to have a strong preference for those sites with either permanent or seasonal presence of water and with dense understory, as it has been suggested by Wikramanayake and Dryden (1993). These places provide a suitable microhabitat with more stable temperature, when the individuals warm up during the nights and cool down during the days (Wikramanayake and Green, 1989; Wikramanayake and Dryden, 1993).

This thermoregulatory behaviour benefits reptiles to optimize energy but may represent a risk for predation if they have to spend a long time basking in open areas to warm their bodies (Dawson, 1975; Huey, 1982). Harlow et al. (2010) concluded that forested habitats offer the most suitable thermal habitat for Komodo dragons with long periods of stable temperature. In the Kinabatangan Floodplain, Asian water monitor lizards find in the riparian zones and swamps with dense bush and grassland a suitable environment to keep their body temperature stable. This study found that the limited presence of dense understory (grass) and water in the plantations seem to be determinant in the preference of sites and the establishment of smaller home ranges within these human-modified areas, whereas the forest offers a good protection that allow them to search for the adequate habitats within a larger area.

Some generalist species inhabiting anthropogenic landscapes can establish their home ranges in the boundaries between crops and forested areas in order to reduce the cost-effect between food and protection (Gehring and Swihart, 2004; Saïd and Servanty, 2005). Places with water source and its associate vegetation may offer a good shelter for other animal species that could be potentially harvested by the Asian water monitor lizards. On the other hand, rodents are certainly highly abundant in plantations and widely distributed within the crops. Therefore, Asian water monitor lizards would not need to walk too far away from the core area to find food, which allows them to have small home ranges with relatively small transient zone.

Uyeda et al. (2013) reported nocturnal activity of *V. salvator* in Indonesia as a possible strategy to increase food consumption and avoid competition as well as human encounters. Although the authors just reported two individuals having this nocturnal behaviour, other authors have reported the same activity in *V. durmeri* (Yong et al., 2008) and *V. gouldii* (Cota et al., 2008). Nonetheless, nocturnal activity was not recorded during the time of this study.

As the very last GPS point was recorded at 20:00 hours, these locations were considered as sleeping sites. The results from this study demonstrate that both forest and oil palm plantations offer shelter to the Asian water monitor lizards in the floodplain. Nonetheless, these sites are close to water bodies such as streams and drains with permanent running water and dense riparian vegetation.

3.4.4. Generalist vs Specialist

Specialisation is a characteristic that explains the ecological requirements of certain species (Levins, 1968). This feature is often determined in terms of nutritional requirements, food behaviour and niche occupied within the landscape (i.e. disturbed vs undisturbed habitats) (Futuyama and Moreno, 1988; Kassen, 2002; Devictor et al., 2008). The Asian water monitor lizard is considered a generalist due to the great range of elements identified as part of its diet, from invertebrates and small vertebrates up to monkeys and chickens, as well as dead animals that can be found within the forest (Traeholt, 1993; Traeholt, 1994). In this sense, anthropogenic habitats such as oil palm crops, farms and, rural and sub-urban house-holds have become a good opportunity for the survival of the species due to the increased presence of rodents, unattended poultry and human waste (Uyeda, 2009).

The core area size in both forest and plantation did not show a significant difference. This might be due to the reduced suitable habitat in plantations, although in both cases, habitats seem to provide the necessary resources for survival. High environmental temperature in plantations and the high risk of encounters with humans and domestic dogs may explain why these lizards are strongly attached to their core areas where they have enough food and protection. Contrary to their counterparts living in forested areas, where they may be more confident to establish more core areas within a larger home range.

Jessop et al. (2012) found that the high occurrence of lace monitor *V. varius* in the boundaries between forested areas and human-mediated habitats, may have a negative impact on the small mammals' community in the forest, affecting even endangered species such as the ring-tailed opossum (*Pseudocheirus peregrinus*). The distribution of two or more core areas within the home ranges in the forest may suggest a sustainable optimisation of the resources and a balanced dynamic of the ecosystem, which may not happen in the plantations.

Although it is difficult to determine, in this stage, the impact of the over-utilization of some resources in the interior and edges of the plantations, it is possible to consider that, in the long term, there could be a negative impact on the ecosystem of those small and isolated spots within the plantations as well as in the boundaries between forest and plantations. On the other hand, accessibility to a less diverse food source such as the high number of rodents surrounding the core areas in the plantations as well as human waste, may have impact on the lizard's nutrition and physiology.

As it was expected, Asian water monitor lizard's home ranges are much smaller in oil palm plantations than in forested areas. Nonetheless, for a generalist species, habitat structure seems to be an important element for the population's distribution within the landscape. The availability and distribution of specific habitat features, such as water, dense riparian understory and food within the landscape favour the presence of the species in the landscape. Therefore, the limited distribution of this resource in oil palm-associated fragmented landscapes, limiting lizard movements and abundance might have an important impact on the prey community in the short or long-term. Thus, it is of importance to assess this impact, essentially for species with low reproduction rate.

Chapter 4

Fast food effect I: Diet, body condition and health of *Varanus salvator* in a human-modified landscape

4.1. Introduction

Oil palm plantations, as well as many industrial crops, are not only low in biodiversity (Edwards et al., 2010; Azhar et al., 2011; Edwards et al, 2014a, 2014b;), but they have also become an abundant and inviting food source for species which seem to be well adapted to anthropogenic landscapes (McClure et al., 1995; Beasley et al., 2007; Morey et al., 2007; Abbas et al., 2011; Bastille-Rousseau et al., 2016). In this sense, the Asian water monitor lizard is one of the most familiar examples in the Asian wetlands, where its populations seem to be favoured by increasing habitat fragmentation and expansion of human-modified habitats (Traeholt, 1997; Uyeda, 2009; Uyeda, 2015). In the previous chapter, it was showed that the home range of lizards in plantations is much smaller than the home range in the forest. These observations suggest that Asian water monitor lizards can satisfy most, if not all, of their vital requirements (i.e. food and shelter) in specific small areas without the need of traveling long distances.

The abundance of generalist species within human-modified landscapes has been recorded several times (Saïd and Servanty, 2005; Beasley et al., 2007; Morey et al., 2007; Devictor et al., 2008; Abbas et al., 2011; Jessop, 2012; Bevan, 2016). Different species, such as raccoons (*Procyon lotor*), coyotes (*Canis latrans*), macaques (*Macaca nemestrina and M. ochreata*) and wild boars (*Sus scrofa*) have been described as pests in both rural (Hill, 1997; Bealsey et al., 2007; Linkie et al., 2007; Priston et al., 2012) and urban ecosystems (Morey et al., 2007), having strong negative economic and public health implications. Regarding the impact on the wildlife communities, the increase in abundance of generalist carnivore species in the boundaries between crops and forested areas have a negative effect on native prey species inhabiting those areas (Glen and Dickman, 2005; Johnson et al., 2007).

Furthermore, the adaptability of those generalist species in the human-wildlife interphase, plays an important role in the dynamics of diseases between anthropogenic and natural habitats, i.e. through the facilitation of the movement of diseases between the human-modified environment and the wild (Dobson, 2004; Randolf, 2004; Vanwambeke et al., 2010).

Changes in available resources translate into changes in the dietary diversity. The composition of the gut microbiome can be modified according to the modification of the components of the diet (i.e. amount of fiber, quantity and quality of protein) (Amato et al., 2013; Barelli et al., 2015; Cheng et al., 2015). In the same way, the nutritional composition of the diet is reflected on the biochemical profile of animals' blood (Artacho et al., 2012; Way Rose and Allender, 2012; Bolten et al., 2013; Fernandez- García et al., 2013; Harms et al., 2013; Mitchell et al., 2013; Kelley et al, 2016; Scheelings et al., 2016). Fatty-acid levels in blood, have been used to assess the health status of stingrays (*Dasyatis americana*) fed by tourists in Cayman Islands (Semeniuk et al., 2007). High levels of phosphorus and sodium have been reported in lace lizards (*V. varius*) feeding on human food waste in human-modified habitats in Australia (Jessop et al., 2012).

The level of biochemical markers varies according to the composition of the diet, among other factors. Cholesterol and triglycerides are elevated when the food contains high amount of lipids or carbohydrates, uric acid levels increase if the diet is extremely rich in proteins (Benjamin, 1984; Meyer and Harvey, 2004; Harms et al., 2013). Electrolytes and other minerals can be augmented with the ingestion of processed or industrialized food (Jessop et al., 2012). Hepatic enzymes (i.e. aminotransferase) and kidney-associated markers such as urea and creatinine can be either elevated or reduced due to chronic or acute failure in the hepatic or renal functions, as consequence of the effort to metabolise, store and eliminate the excess of lipids, carbohydrates and proteins, as well as the amount of minerals consumed with industrialised food. (Benjamin, 1984; Meyer and Harvey, 2004; Bolten and Bjorndal, 2013; Harms et al., 2013)

The main goal of this study is to assess the health of the Asian water monitor lizard population in relation to its dietary diversity in the Kinabatangan Floodplain. It is hypothesised that the feeding habits of Asian water monitor lizards inhabiting the oil palm plantations is less diverse than those living in forested areas which can be reflected in an increased level of markers such as cholesterol, lipids, uric acid and sodium, among others. The association between these and other biological markers with the dietary diversity, as well as the body condition (measures as the ratio of the body weight to the snout vent length) and size of the lizards will be analysed in this chapter.

4.2. Methods

4.2.1. *Sampling*

Trapping protocols used for this study were the same that have been explained in Chapter 1 and during the same period of time (October 2013-September 2017). During the handling process, some lizards emptied their stomach as a response to stress or as a defence mechanism (Greene, 1988), and therefore the content of the vomit was identified and counted. Since the content does not necessarily inform about individual preferences, but food availability, the inventory was grouped by study site (Fig 4.1).

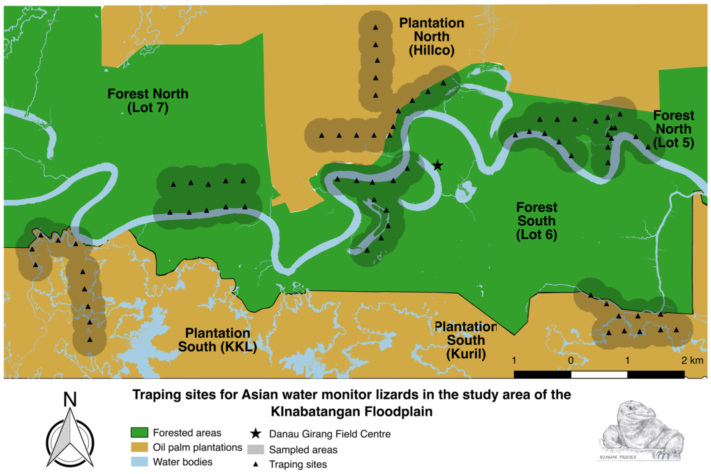

Fig 4.1. Distribution of trapping sites within the study area.

Morphometric measures such as body weight (BW), total length, tail length and snout to vent length (SVL) were recorded for each individual. Body condition (BC) was estimated, as it has been shown to be a more accurate size estimator than BW and SVL (Green, 2001; Jessop et al., 2012; Smith et al., 2014):

$$\mathrm{BC} = \frac{Log10(BW)}{Log10\ (SVL)}$$

where BC corresponded to the coefficient extracted from the log10 of both BW (expressed in kilograms), and SVL (expressed in centimetres) (Green, 2001; Jessop et al., 2012; Smith et al., 2014).

Up to 2 ml of blood were taken from the coccygeal vein of each trapped lizard larger than 3 kilograms. Blood was collected with a 3cc syringe and a 23G needle and immediately placed into a collection tube with no additive. Samples were centrifuged for 10 minutes at 1000 xG. Afterwards the serum was separated from the blood cell package and stored in a freezer until processing (Benjamin, 1984; Calama, 1994; Fudge, 2000). Samples were sent to a private laboratory (Gribbles Sdn. Bhd; Sandakan, Malaysia) for analysis of 20 biochemical markers (Table 4.1).

4.2.2. *Analysis*

Descriptive and comparative analyses were performed to describe the health condition of the Asian water monitor lizards in the study area. For these analyses, individuals were grouped in three different ways according to three spatial criteria: (1) habitat: forest vs. plantation, (2) study site: Forest North and South and Plantation North and South, and (3) transect site: each forest lot and plantation estate analysed separately (Fig 4.1). Forest North study site was comprised by Lots 5 and 7 while Lot 6 was the only forest lot for the forest South study site. At the same time, Plantation North study site was comprised of Hilco estate while Kuril and KKL estates were part of the Plantation South study site.

The stomach content was identified according to morphological features observed, and the observations were listed in an inventory grouped by study site. Dietary diversity was calculated using the Simpson's Dominance Index (D) in each study site (Heip, 1974; Heip et al., 1998). For each biochemical marker the mean, standard deviation and 95% confidence intervals for each group were estimated. Variances were compared between the different groups by using ANOVA.

Generalized Estimation Equations (GEE) were used to calculate the association between (1) body measures (weight and body condition) and biochemical markers with the calculated prey's dominance index, and (2) between body measures and the biochemical markers. Contrary to generalised linear models that need to estimate a within group variance component, GEE models estimate the average group (i.e. habitat, study site, and transect) response independently of the correlative structure between the groups (Liang and Zeger, 1986; Yan and Fine, 2004; Zuur et al., 2009). Two correlative structures were tested and compared in order to find the best model: the *exchangeable* structure of the model assumes that there is no linearity between the observations and that all the individuals within the group respond to the same correlation parameter, while the *independence* structure considers no correlation between the sampled individuals (Liang and Zeger, 1986; Yan and Fine, 2004; Zuur et al., 2009). The best-fit model between those two correlative structures was chosen by the lowest value of *quasi likelihood* under the independence model information criterion (QIC) (Pan, 2001; Zuur et al., 2009). GEE models were run for the three different group categories (habitat, study site and transect) using the package geepack v. 1.2-1 in R v. 1.1.4 (Højsgard, 2016; R Core Team).

4.3. Results

A total of 256 individuals were sampled and analysed for dietary diversity, body measures and biochemical analysis. Serum samples were tested for 20 biochemical markers (Table 4.1).

Table 4.1. List of variables evaluated for the Asian water monitor lizard population in the Kinabatangan Floodplain.

Profile group	Marker
Lipids profile	Cholesterol
	High Density Cholesterol (HDL-Ch)
	Low Density Cholesterol (LDL-Ch)
	Triglyceride
Electrolytes	Sodium
	Potassium
	Chloride
Kidney function	Urea
	Creatinine
	Uric Acid
Calcium metabolism	Phosphate
	Calcium
Protein profile	Total protein
	Albumin
	Globulin
Liver function	Alkaline Phosphatase (AkPhs)
	Bilirubin
	Gamma Glutamyl Transferase (GGT)
	Aspartate Amino Transferase (AST)
	Alanine Amino Transferase (ALT)

Across all vomit contents analyses, 14 different types of prey were identified. Vomit content varied in prey size from woodlice and snails up to wild boars. Dominance was far higher in plantations (D_{OPPN} = 0.685; D_{OPPS} = 0.551), where rodents were the most common prey, while forested areas showed more diverse diets ($D_{Forest.N}$ = 0.139; $D_{Forest.S}$ = 0.079). Rodents were the most abundant prey in plantations with a maximum of 24 out of 29 identified prey, while in forest sites, the number of rodents was no more than 5 out of 64 prey identified. Crabs and woodlice were the most dominant group of prey in forested sites (Table 4.2).

Table 4.2. Inventory of prey identified in the vomit of Asian water monitor lizards sampled in the Kinabatangan Floodplain and Simpson's dominance index per study site.

Prey	Bat	Centipede	Crab	Egg	Fish	Frog	Macaque	Rodent	Scorpion	Snail	Snake	Tortoise	Wild boar	Wood-louse	Simpsons Diversity (D)
Forest N	0	7	16	1	1	6	1	5	2	7	2	1	1	14	**0.139**
Forest S	1	1	6	1	4	1	3	2	1	3	1	2	0	2	**0.079**
OPP N	0	2	0	0	0	0	0	24	0	0	0	1	0	2	**0.685**
OPP S	0	1	0	0	2	2	0	23	0	2	0	1	0	0	**0.551**

Biochemical results were grouped by (i) habitat type (forest vs. plantation), (ii) study site (Forest North and South and plantation North and South) and (iii) transect sites (each forest lot and plantation estate separated, Table 4.3). Regarding the habitat type comparison (Forest vs Plantation), Asian water monitor lizards inhabiting forested areas presented higher levels of cholesterol (F = 0.3; df = 100; $p < 0.001$), calcium (F = 3; df = 90; $p < 0.001$) and urea (F = 2; df = 90; $p < 0.001$), while those living in plantations showed larger body condition (F = 0.2; df = 100; p = 0.02), and higher level of HDL-Ch (F = 0.9; df = 100; $p < 0.05$), LDL-Ch (F = 0.002; df = 100; $p < 0.001$) and uric acid (F = 0.6; df = 100; p = 0.002), total protein (F = 20; df = 90; $p < 0.001$), bilirubin (F = 0.6; df = 90; p = 0.02) and ALT (F = 3; df = 90; $p < 0.001$) (Fig. 4.2 and Table 1 of Appendix IV).

For the comparison between study sites (Forest North and South and Plantation North and South), significant differences were found on body condition (F = 3.29; df = 3; p = 0.021), cholesterol (F = 9.4; df = 3; $p < 0.001$), HDL-Ch (F = 4.46; df = 3; p = 0.005), sodium (F = 3.47; df = 3; p = 0.018), creatinine (F = 3.25; df = 3; p = 0.024), albumin (F = 4.33; df = 3; p = 0.006) and alkaline phosphatase (F = 3.46; df = 3; p = 0.018) (Fig. 4 and Table 1 of Appendix IV).

Table 4.3. Mean value of the body measures and biochemical markers analysed on the Asian water monitor lizards within the Kinabatangan Floodplain. Significant differences were estimated using ANOVA with a 95% of confidence interval between (*) habitat, (†) study site and (œ) transect

Habitat	**Study Site**	**Transect**	**MEAN VALUE ± SE (95 % CI)**								
			Weight (kg)	**Body Condition*,†**	**Cholesterol (mmol/L)*,†,œ**	**HDL-Ch (mmol/L)*,†**	**LDL-Ch (mmol/L)***	**Triglyceride (mmol/L)**	**Sodium (mmol/L)†**	**Potassium (mmol/L)**	**Chloride (mmol/L)**
Forest (n= 132)	**Forest North (n= 69)**	**Lot5 (n= 31)**	5.806 ± 0.63 (4.56 - 7.05)	0.386 ± 0.02 (0.34 - 0.43)	2.18 ± 0.12 (1.96 -2.41)	0.177 ± 0.02 (0.131 - 0.22)	1.65 ± 0.16 (1.3 - 1.97)	1.602 ± 0.436 (0.79 - 2.46)	156.857 ± 1.35 (154 - 160)	33.179 ± 2.52 (28.2 - 38.1)	98.143 ± 2.05 (94.1 - 102)
		Lot7 (n= 38)	5.368 ± 0.71 (3.97 - 6.77)	0.352 ± 0.20 (0.31 - 0.39)	1.91 ± 0.11 (1.68 - 2.13)	0.182 ± 0.03 (0.12 - 0.24)	1.68 ± 0.32 (1.0 - 2.31)	2.076 ± 0.65 (0.81 - 3.34)	157.5 ± 1.07 (155 - 160)	31.775 ± 1.89 (28.1 - 35.5)	103.25 ± 1.09 (101 - 105)
		Total Forest N	5.565 ± 0.48 (4.62 - 6.51)	0.368 ± 0.01 (0.34 - 0.40)	2.03 ± 0.08 (1.87 - 2.19)	0.18 ± 0.02 (0.14 - 0.21)	1.66 ± 0.19 (1.3 - 2.04)	1.867 ± 0.41 (1.07 - 2.67)	157.2 ± 0.84 (156 - 159)	32.531 ± 1.59 (29.4 - 35.6)	100.867 ± 1.2 (98.5 - 103)
	Forest South (n= 63)	**Lot6 (n= 63)**	5.79 ± 0.58 (4.65 - 6.93)	0.347 ± 0.02 (0.31 - 0.39)	2.07 ± 0.08 (1.92 - 2.22)	0.11 ± 0.004 (0.09 - 0.12)	1.62 ± 0.09 (1.46 - 1.8)	1.842 ± 0.44 (0.97 - 2.71)	160.536 ± 0.69 (159 - 162)	37.154 ± 6.07 (15.2 - 49.1)	102.72 ± 0.83 (101 - 104)
		Total Forest	5.673 ± 0.37 (4.94 - 6.41)	0.358 ± 0.01 (0.33 - 0.38)	2.05 ± 0.06 (1.94 - 2.16)	0.15 ± 0.01 (0.13 - 0.17)	1.65 ± 0.12 (1.4 - 1.87)	1.856 ± 0.29 (1.27 - 2.44)	159.436 ± 0.56 (158 - 161)	35.572 ± 4.03 (27.7 - 43.5)	102.11 ± 0.68 (101 - 103)
Plantation (n= 124)	**OPP North (n= 37)**	**Hillco (n= 37)**	6.408 ± 0.55 (5.33 - 7.49)	0.402 ± 0.02 (0.36 - 0.44)	2.17 ± 0.12 (1.93 - 2.41)	0.14 ± 0.01 (0.12 - 0.16)	1.71 ± 0.15 (1.3 - 2)	1.571 ± 0.40 (0.78 - 2.36)	159.08 ± 1.23 (157 - 161)	30.408 ± 1.45 (27.6 - 33.3)	104.4 ±1.29 (102 - 107)
	OPP South (n= 87)	**KKL (n= 61)**	6.328 ± 0.5 (5.34 - 7.32)	0.394 ± 0.02 (0.36 - 0.42)	1.55 ± 0.16 (1.23 - 1.86)	0.15 ± 0.02 (0.12 - 0.19)	2.64 ± 1.66 (0.0 - 5.9)	0.874 ± 0.21 (0.45 - 1.3)	160.5 ± 0.95 (159 - 162)	30.523 ± 0.79 (29 - 32.1)	103.09 ± 1.19 (101 - 105)
		Kuril (n= 26)	6.173 ± 0.71 (4.77 - 7.58)	0.398 ± 0.02 (0.35 - 0.44)	2.17 ± 0.11 (1.96 - 2.38)	0.21 ± 0.11 (0.0 - 0.43)	1.74 ± 0.15 (1.43 - 2.0)	1.894 ± 0.51 (0.88 - 2.9)	161.615 ± 1.37 (159 - 164)	28.362 ± 1.63 (25.2 - 31.6)	102.85 ± 1.11 (101 - 105)
		Total OPP S.	6.282 ± 0.41 (5.48 - 7.09)	0.395 ± 0.01 (0.37 - 0.42)	1.73 ± 0.12 (1.49 - 1.97)†	0.17 ± 0.04 (0.10 - 0.25)	2.38 ± 1.19 (0.06 - 4.7)	1.185 ± 0.22 (0.75 - 1.62)	161.104 ± 0.85 (159 - 163)	29.352 ± 0.96 (27.5 - 31.2)	102.96 ± 0.80 (101 - 105)
		Total OPP	6.319 ± 0.33 (5.67 - 6.97)	0.397 ± 0.01 (0.37 - 0.41)	1.86 ± 0.09 (1.68 - 2.05)	0.16 ± 0.027 (0.11 - 0.22)	2.19 ± 0.84 (0.54 - 3.8)	1.291 ± 0.19 (0.91 - 1.67)	160.411 ± 0.70 (159 - 162)	29.704 ± 0.80 (28.1 - 31.3)	103.45 ± 0.68 (102 - 105

Table 4.3 (cont.). Mean value of body measures and biochemical markers analysed on the Asian water monitor lizards within the Kinabatangan Floodplain. Significant differences were estimated with ANOVA with 95% of confidence interval between (*) habitat, (†) study site and (^{œ}) transect

Habitat	Study Site	Transect	MEAN VALUE ± SE (95 % CI)								
			Urea (mmol/L)*	Creatinine (µmol/L)†	Uric Acid (mmol/L)^{*,œ}	Calcium (mmol/L)*	Phosphate (mmol/L)	Total protein (g/L)*	Albumin (g/L)†	Globulin (g/L)	AkPhs (U/L)^{†,œ}
Forest (n= 132)	Forest North (n= 69)	Lot5 (n= 31)	0.907 ± 0.05 (0.81 - 1.01)	20.786 ± 1.9 (17.1 - 24.5)	0.66 ± 0.05 (0.56 - 0.76)	0.485 ± 0.05 (0.38 - 0.59)	2.374 ± 0.13 (2.11 - 2.63)	72.134 ± 5.84 (60.7 - 83.6)	26.214 ± 0.76 (24.7 - 27.7)	52.143 ± 1.49 (49.2 - 55.1)	24.714 ± 4.15 (16.6 - 32.8)
		Lot7 (n= 38)	0.793 ± 0.05 (0.691 - 0.89)	36.063 ± 15.4 (5.84 - 66.3)	0.604 ± 0.07 (0.47 - 0.73)	0.495 ± 0.03 (0.43 - 0.56)	2.245 ± 0.16 (1.92 - 2.57)	75.125 ±1.75 (71.7 - 78.5)	25.25 ± 0.54 (24.2 - 26.3)	49.875 ± 1.39 (47.2 - 52.6)	25.25 ± 3.61 (18.2 - 32.3)
		Total Forest N	0.846 ± 0.04 (0.77 - 0.92)	28.933 ± 8.27 (12.7 - 45.1)	0.629 ± 0.04 (0.54 - 0.71)	0.49 ± 0.03 (0.43 - 0.55)	2.305 ± 0.11 (2.1 - 2.51)	73.729 ± 2.84 (68.2 - 79.3)	25.7 ± 0.46 (24.8 - 26.6)	50.933 ± 1.02 (48.9 - 52.9)	25 ± 2.68 (19.7 - 30.3)
	Forest South (n= 63)	Lot6 (n= 63)	0.961 ± 0.12 (0.73 - 1.19)	24.59 ±1.6 (21.5 - 27.7)	1.78 ± 1.12 (0.0 - 3.97)	1.654 ± 1.17 (0.0 - 3.94)	2.193 ± 0.07 (2.05 - 2.33)	77.066 ± 1.29 (74.5 - 79.6)	25.066 ± 0.66 (23.8 - 26.4)	52.328 ± 1.18 (50 - 54.6)	33.401 ± 1.84 (29.8 - 37)
		Total Forest	0.923 ± 0.08 (0.76 - 1.08)	26.022 ± 2.91 (20.3 - 31.7)	1.178 ± 0.53 (0.13 - 2.22)	1.253 ± 0.76 (0.0 - 2.75)	2.23 ± 0.06 (2.11 - 2.35)	75.966 ± 1.28 (73.5 - 78.5)	25.275 ± 0.46 (24.4 - 26.2)	51.868 ± 0.86 (50.2 - 53.5)	30.632 ± 1.57 (27.6 - 33.7)
Plantation (n= 124)	OPP North (n= 37)	Hillco (n= 37)	0.876 ± 0.04 (0.79 - 0.96)	33.12 ± 4 (25.3 - 41)	1.192 ± 0.57 (0.07 - 2.31)	0.656 ± 0.11 (0.42 - 0.88)	2.286 ± 0.15 (1.98 - 2.59)	78.92 ± 2.31 (74.4 - 83.4)	23.52 ± 1.29 (21 - 26)	56.16 ± 3.04 (50.2 - 62.1)	26.84 ± 2.83 (21.3 - 32.4)
	OPP South (n= 87)	KKL (n= 61)	0.812 ± 0.01 (0.79 - 0.83)	19.909 ±1.26 (17.4 - 22.4)	0.948 ± 0.5 (0.0 - 1.92)	0.525 ± 0.04 (0.44 - 0.61)	2.409 ± 0.11 (2.18 - 2.64)	83.364 ± 1.28 (80.9 - 85.9)	27.54 ± 0.39 (26.8 - 28.3)	55.818 ± 0.92 (54 - 57.6)	16.091 ± 1.9 (12.4 - 19.8)
		Kuril (n= 26)	1.0 ± 0.13 (0.74 - 1.26)	21.56 ± 1.66 (18.3 - 24.8)	2.469 ±1.81 (0.0 - 6.03)	0.604 ± 0.07 (0.46 - 0.74)	2.304 ± 0.12 (2.07 - 2.53)	79.56 ± 1.27 (77.1 - 82)	26.76 ± 0.5 (25.8 - 27.7)	52.8 ± 0.97 (50.9 - 54.7)	36.04 ± 4.17 (27.9 - 44.2)
		Total OPP S.	0.913 ± 0.07 (0.77 - 1.05)	20.787 ± 1.06 (18.7 - 22.9)	1.395 ± 0.63 (0.15 - 2.64)	0.567 ± 0.04 (0.48 - 0.65)	2.353 ± 0.08 (2.19 - 2.51)	81.34 ± 0.93 (79.5 - 83.2)	27.128 ± 0.32 (26.5 - 27.8)	54.213 ± 0.7 (52.8 - 55.6)	26.70 ± 2.78 (21.2 - 32.2)
		Total OPP	0.9 ± 0.05 (0.80 - 0.99)	25.069 ± 1.68 (21.8 - 28.4)	1.334 ± 0.47 (0.40 - 2.26)	0.594 ± 0.05 (0.50 - 0.69)	2.33 ± 0.07 (2.18 - 2.48)	80.5 ± 1.01 (78.5 - 82.5)	25.875 ± 0.53 (24.8 - 26.9)	54.889 ± 1.14 (52.7 - 57.1)	26.75 ± 2.05 (22.7 - 30.8)

Table 4.3 (cont.). Mean value of body measures and biochemical markers analysed on the Asian water monitor lizards within the Kinabatangan Floodplain. Significant differences were estimated with ANOVA with 95% of confidence interval between (*) habitat, (†) study site and (œ) transect

Habitat	Study Site	Transect	MEAN VALUE ± SE (95 % CI)			
			Bilirubine (µmol/L)*	**GGT (U/L)**	**AST (U/L)**	**ALT (U/L)***
Forest (n= 132)	**Forest North (n= 69)**	**Lot5 (n= 31)**	2	36.071 ± 5.8 (24.7 - 47.4)	41.071 ± 6.1 (29.1 - 53)	38.429 ± 4.75 (29.1 - 47.7)
		Lot7 (n= 38)	2.063 ± 0.06 (1.94 - 2.19)	31.563 ± 4.84 (22.1 - 41)	46.75 ± 8.59 (29.9 - 63.6)	58.188 ± 10.6 (37.5 - 78.9)
		Total Forest N	2.033 ± 0.03 (1.97 - 2.1)	33.667 ± 3.7 (26.4 - 40.9)	44.1 ± 5.33 (33.6 - 54.6)	48.967± 6.24 (36.7 - 61.2)
	Forest South (n= 63)	**Lot6 (n= 63)**	2.18 ± 0.1 (1.99 - 2.37)	26.754 ±1.85 (23.1 - 30.4)	49.18 ± 4.76 (39.8 - 58.5)	67.639 ± 7.98 (52 - 83.3)
		Total Forest	2.132 ± 0.07 (2 - 2.26)	29.033 ± 1.76 (25.6 - 32.5)	47.51 ± 3.64 (40.4 - 54.6)	61.484 ± 5.79 (50.1 - 72.8)
Plantation (n= 124)	**OPP North (n= 37)**	**Hillco (n= 37)**	2.24 ± 0.2 (1.84 - 2.64)	34.32 ± 3.06 (28.3 - 40.3)	47.32 ± 6.58 (34.4 - 60.2)	65.44 ± 6.15 (53.4 - 77.5)
	OPP South (n= 87)	**KKL (n= 61)**	2.182 ± 0.11 (1.97 - 2.39)	27 ± 2.12 (22.8 - 31.2)	43.95 ± 5.46 (33.3 - 54.7)	62.95 ± 7.08 (49.1 - 76.8)
		Kuril (n= 26)	2.2 ± 0.2 (1.81 - 2.59)	25.32 ± 2.94 (19.6 - 31.1)	51.52 ± 6.87 (38.1 - 65)	57.2 ± 5.3 (46.8 - 67.6)
		Total OPP S.	2.191 ± 0.12 (1.96 - 2.42)	26.106 ± 1.84 (22.5 - 29.7)	47.98 ± 4.45 (39.3 - 56.7)	59.89 ± 4.32 (51.4 - 68.4)
		Total OPP	2.208 ± 0.10 (2.01 - 2.41)	28.958 ± 1.66 (25.7 - 32.2)	47.75 ± 3.67 (40.6 - 54.9)	61.819 ± 3.53 (54.9 - 68.7)

Forest South site (Lot 6) presented the lowest body condition, HDL-Ch and creatinine, and the highest values for alkaline phosphatase. Plantation North site was one of the lowest for cholesterol and HDL cholesterol, while it was the highest for albumin. Forest and OPP in the northern sites showed very similar values for alkaline phosphatase, creatinine and albumin (Table 4.3; Fig 4.3).

Lastly, the comparison between transect (Forest lots and plantation estates separately), revealed significant differences in cholesterol ($F = 14$; $df = 2$; $p < 0.001$), uric acid ($F = 5.37$; $df = 2$; $p = 0.005$) and alkaline phosphatase ($F = 8.68$; $df = 2$; $p = < 0.00$) (Fig. 4.5 and Table 1 of Appendix IV) between transects. Lot 5, in the forest North study site, and Hilco plantation had the highest values of cholesterol, while Lot 7 presented the lowest. Uric acid was also higher in Lot 5 and lower in Lot 7. Alkaline phosphatase was lower in KKL plantation than in the other transects. Values' dispersion and mean values show similar patterns between Lot 5 and Hilco, its adjacent plantation estate (Fig 4.4).

Regarding the association with prey diversity, the highest dominance index was detected in the Plantation North. This site also presented the highest levels of biochemical markers, even those that were not statistically significant, such as alanine ALT and GGT. Lizards inhabiting the forest south showed higher levels of uric acid, AST and alkaline phosphatase than those in the northern forest. Nonetheless, the northern forest had higher levels of HDL cholesterol, GGT, creatinine and albumin. Biochemical markers levels were more similar between Hilco plantation and Lot 5 than between the same plantation and Lot 7.

Strong association was detected between diet dominance and HDL cholesterol (1.96 ± 0.62; Wald $Xi^2 = 9.87$; $p = 0.001$), sodium (0.06 ± 0.02; Wald $Xi^2 = 7.23$; $p = 0.0071$), uric acid (0.03 ± 0.004; Wald $Xi^2 = 71.82$; $p < 0.0001$), total protein (0.009 ± 0.002; Wald $Xi^2 = 13.15$; $p = 0.0003$) and a weak association with body condition (2.57 ± 1.01; Wald $Xi^2 = 6.43$; $p = 0.011$), triglyceride (-0.09 ± 0.04; Wald $Xi^2 = 3.79$; $p =0.05$) and calcium (-0.009 ± 0.004; Wald $Xi^2 = 4.53$; $p = 0.033$) (Table 2 of Appendix IV).

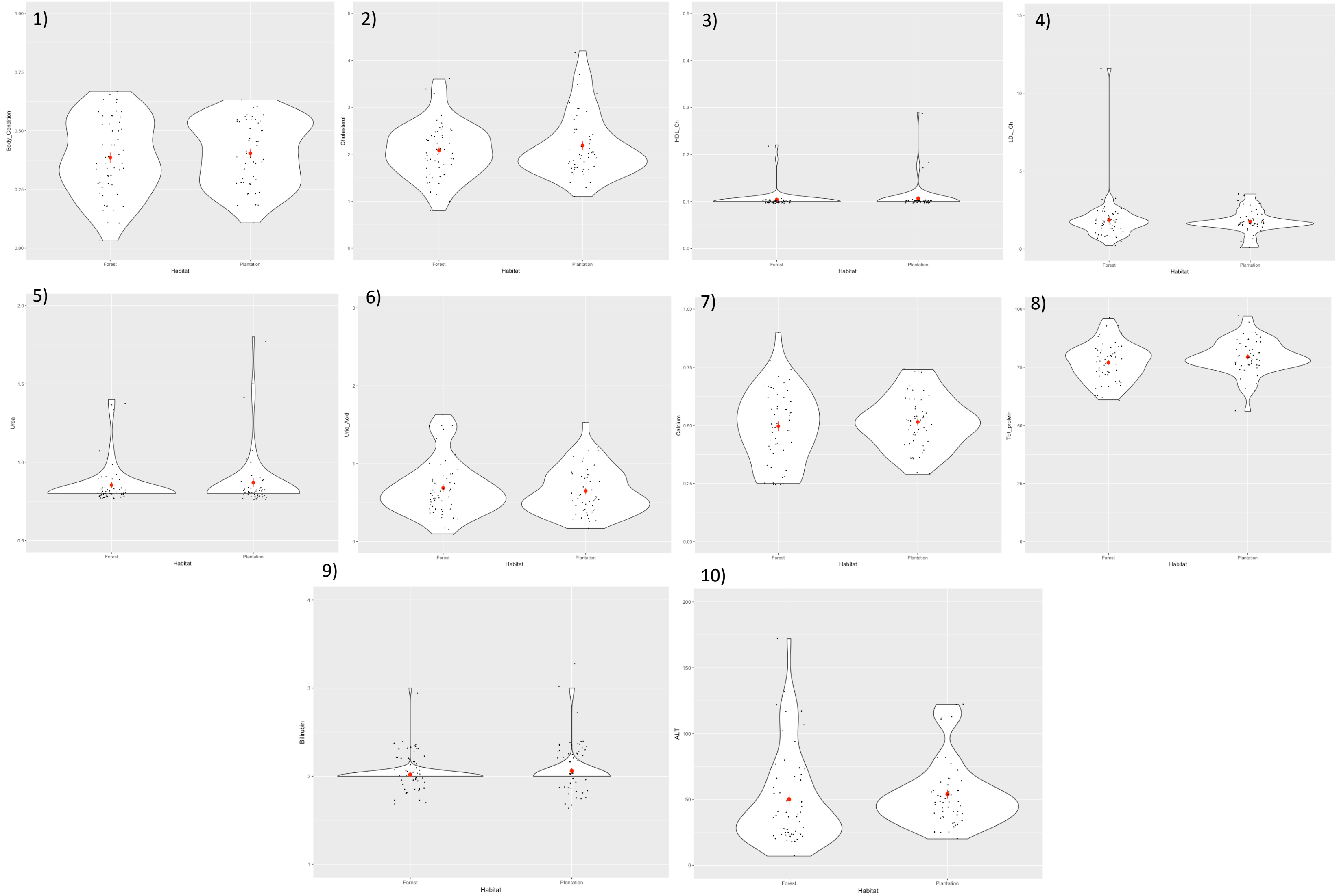

Fig 4.2. Comparative plots of (1) body condition, (2) cholesterol, (3) high and (4) low density cholesterol, (5) urea, (6) uric acid, (7) calcium, (8) total protein, (9) bilirubin and, (10) alanine amino transferase for Asian water monitor lizards between forested areas and plantations. Violin plots show the dispersion of values while the mean and SE are shown in red.

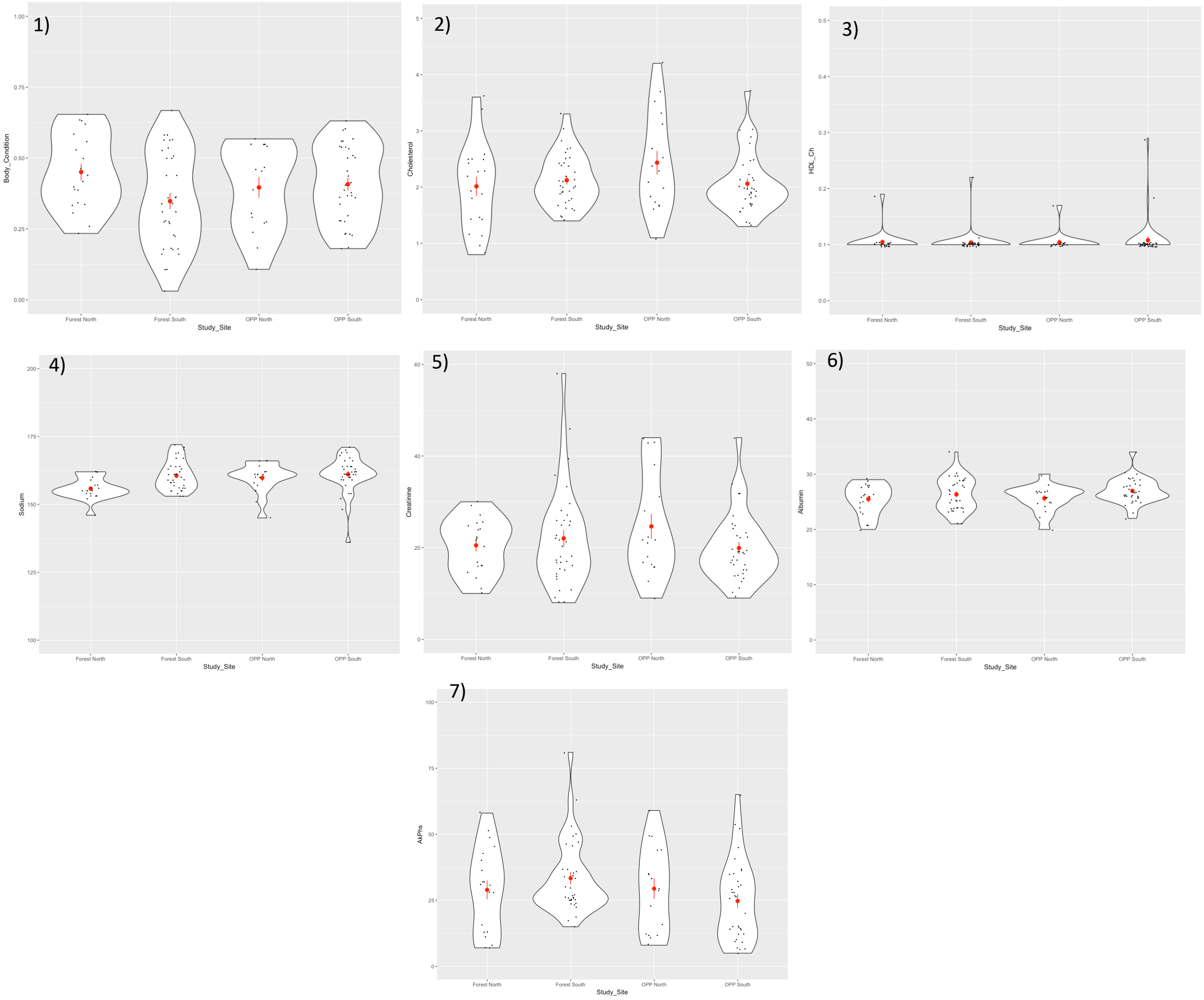

Fig 4.3. Comparative plots of (1) body condition, (2) cholesterol, (3) high density cholesterol (HDL-Ch), (4) Sodium, (5) creatinine, (6) Albumin and, (7) alkaline phosphatase (AkPhs) for Asian water monitor lizards between four study sites (Forest North and South and OPP North and South). Violin plots show the dispersion of the values while the mean and SE are shown in red.

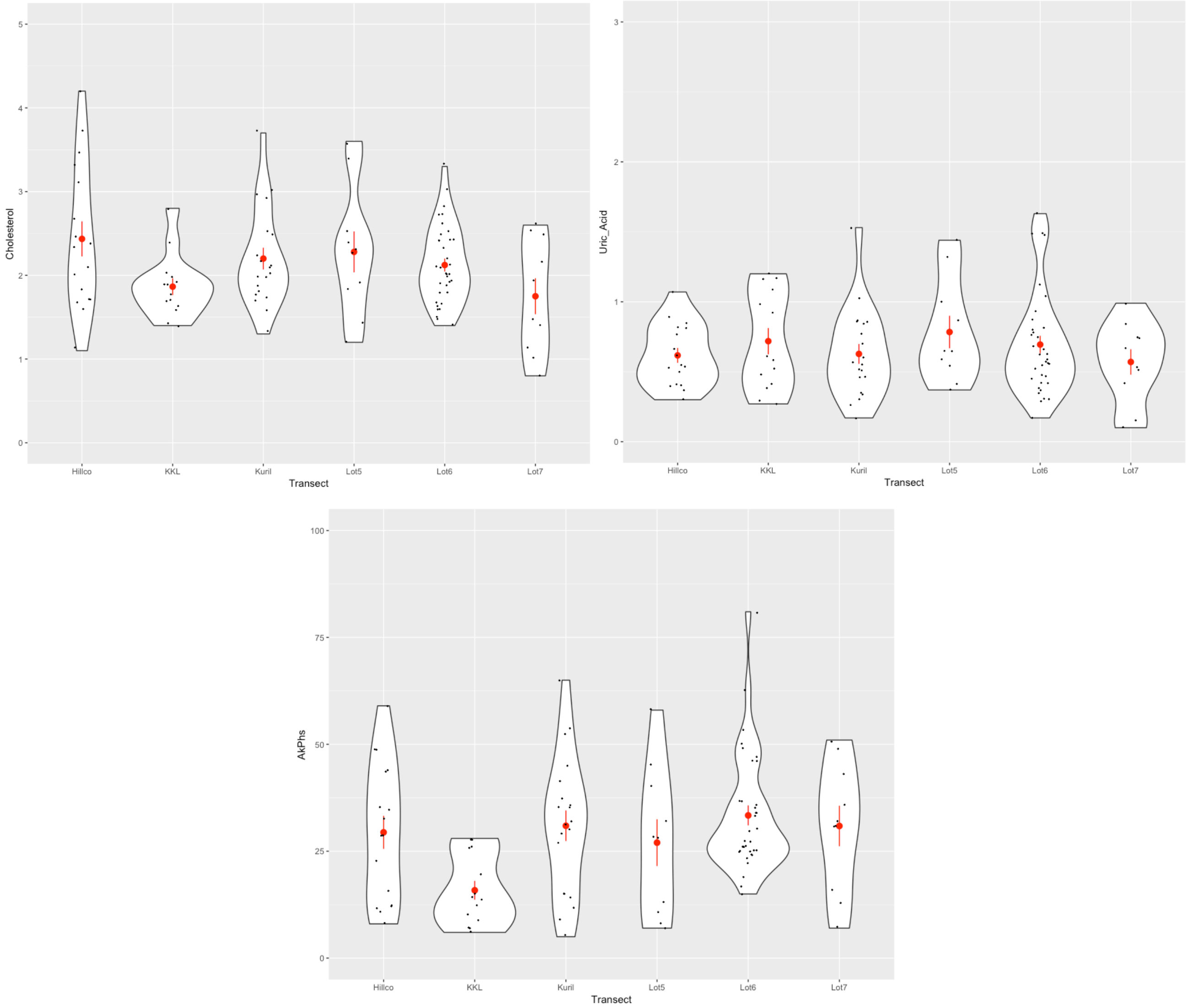

Fig 4.4. Comparative plots of (1) cholesterol, (2) uric acid, and (3) alkaline phosphatase for Asian water monitor lizards between transect sites (Hilco, KKL, Kuril, Lot 5, Lot 6 and Lot 7). Violin plots show the dispersion of the values and the red line represents the mean value.

4.4. Discussion

The abundance of Asian water monitor lizards in the study area offers a great advantage for the assessment of the implications of a fragmented landscape on this species' ecology, feeding behaviour, physiology and health. Although reptiles are much more resilient than mammals or birds to physiological alterations due to changes in food intake, the effects of the ingestion of pollutants or the presence of pathogens in their environment can be monitored with biochemical markers present in blood (Burger, 1992; Jones and Holladay, 2006). This study provides information regarding the health status of a wild population of Asian water monitor lizards associated with dietary diversity in a human-modified landscape.

Oil palm plantations, as well as other industrial crops, are a threat to biodiversity by turning natural forests into large extensions of land dominated by a very reduced number of species (Edwards et al., 2010; Azhar et al., 2011; Edwards et al., 2013: Edwards et al., 2014). For Southeast Asia, where large areas of forest have been converted to agriculture, in particular OPP, the resulting changes in ecosystem dynamics have been documented through the alteration of the trophic behaviour of Asian water monitor lizards (Traeholt, 1997; Uyeda, 2009; Uyeda, 2015), as well as other meso-predators, such as leopard cats (*Prionailurus bengalensis*) and civets (*Viverra tangalunga* and *Paradoxurus hermaphroditus*), all of which feel comfortable venturing into plantations where they can feed on rodents (Jennings et al., 2014; Yue et al., 2015). Such trend was also observed in these data where the number of rodents found in the vomit of lizards from plantations was up to 12 times higher than in lizards from the forest. This suggests that these small mammals are the main element in the Asian water monitor lizards' diet in oil palm plantations. While it is uncertain if nourishing through rats is a strategy dictated by choice or by opportunity, it is evident that these rodents make a substantial part of the OPP Asian water monitor lizard's prey despite of only corresponding to one out of the six taxa identified in the lizard's vomit, while the number of taxa in the forest ascended up to 14.

The higher number of crabs and woodlice in the Forest North site in comparison to the Forest South site may be a consequence of the topographic differences between sites (e.g. Forest North site is flooded more often than the Forest South site). These differences in dietary diversity are reflected in some, but not all biochemical markers analysed in this study, such as cholesterol, urea, uric acid, sodium, and proteins, as well as in body condition. Although it remains to be seen whether these levels lie or not within a healthy range for both populations, the amounts are associated to high levels of protein, carbohydrates and lipids ingested constantly (Meyer and Harvey, 2004). ALT levels can be associated to high cortisol levels caused by stress (Meyer and Harvey, 2004). Unfortunately, cortisol could not be evaluated during this study.

Cholesterol is an essential lipid that is part of the cellular membrane's structure and is in charge of the transport of other vital substances such as vitamin D and hormones. It is created in the body through the metabolism of lipids and carbohydrates, and it can be differentiated in two main types according with the density of the molecule: The Cholesterol with high density lipoproteins (HDL- Ch) is easier to be transported and metabolized in the liver, while the Cholesterol with low density lipoproteins (LDL-Ch) flow slower along the blood stream and gets attached to vessels' walls with the subsequent impact on the blood flow (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004), although other factors have to be involved to create systemic problems (Sinatra et al., 2014), high levels of these marker is a risk factor for heart disease.

Urea is a Nitrogen's metabolite associated directly with the amount of protein ingested. Urea levels in blood may depend on two main factors: the most common is an insufficient kidney filtration but also a very high amount of proteins in the diet, larger than the amount that a normal kidney can filter (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004). Creatinine, on the other side, is produced as part of muscular activity and is also eliminated by the kidney. High level of creatinine means either muscular activity (i.e. exercise, stress) or kidney failure (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004). Uric acid is another marker originated from the proteins' metabolism and is the main component in the urine of birds and reptiles (Fudge, 2000). Increased values of this marker are consequence of the ingest of high amount of proteins and, since is an element that crystalize, it can produce either kidney stones (urolithiasis) or, in the worst-case scenario, the crystals can get attached to the different organs (i.e. liver, kidney) and originate a visceral gout (Fudge, 2000; Meyer and Harvey, 2004).

Calcium is an essential mineral as principal component of the bones structure. A deficient amount of vitamin D, as well as kidney failure or pancreatic disease could generate a consequent low level of calcium in blood (Meyer and Harvey, 2004). On the other side, high ingest of food rich in calcium and vitamin D may drive to an increased amount of calcium in blood, although there are other factors, such as hyperthyroidism and cancer (Meyer and Harvey, 2004).

Albumin is one of the two plasmatic proteins usually analysed in blood and is the one directly associated with the amount of protein ingested. While the globulin's function is to support the immune system, albumin is in charge of the transportation of different substances (i.e. hormones, fatty acids) along the body system, as well as control the pH and the osmotic pressure of the cells (Devlin, 2004; Meyer and Harvey, 2004). Although the deficiency is of medical concern more than the high levels, an increase of the amount of albumin in blood is directly associated to high amount of protein in the diet (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004). The bilirubin is a product created from the destruction of the red blood cells and is eliminated by the liver. During the process in gets attached to the albumin for transport. Thus, besides the erythrocytes' destruction, the levels of bilirubin are linked to the levels of albumin (Fudge, 2000; Meyer and Harvey, 2004).

Sodium is, along with the potassium, an important electrolyte strongly associated with the homeostasis of the system. Sodium levels in blood are directly associated to the amount ingested during the meals. Food rich in salt and preservatives such as mono-sodic glutamate, as well as a low ingest of water are the main factors to increase the levels of sodium in the blood (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004).

Alkaline phosphatase (AkPh) is an enzyme present in almost all the body tissues, specially, in the liver, kidney and bones. Normally, this enzyme is produced from the cellular destruction of these tissues. Thus, high levels of AkPh can be associated with anaemia, due to the erythrocytes' destruction, but also to liver and kidney damage. On the other side, low levels of the enzyme can be associated to nutritional issues due to the lack of proteins in the diet (Fudge, 2000; Devlin, 2004; Meyer and Harvey, 2004). Another enzyme associated with cellular damage, especially with liver and muscles damage, is the alanine aminotransferase (ALT). The enzyme is not directly linked to the quality of the diet, although it can be elevated as consequence of diet-related stress (Fudge, 2000; Meyer and Harvey, 2004).

Regarding the comparison between transect sites, the higher levels of cholesterol detected in Forest South may be a consequence of the intake of fish and aquatic food. Although the prey inventory did not record high amounts of fish, the trapping sites in the Forest South were very close to two oxbow lakes, which may act as a food source for this semi-aquatic species (Bulliya, 2002). High levels of sodium in plantation sites may indicate the intake of leftovers of processed or industrialized food, such as packed noodles, snacks, artificial flavoured food, etc. (Jessop et al, 2012). The same explanation may apply for the observation of higher levels of sodium in the Forest South, due to the presence of human activities in Lot 6 (e.g. fishing in the oxbow lakes and the presence of the research centre). Similarities between both the northern forest and the adjacent plantation may suggest an influence of the plantation on the forest's population, especially in Lot 5 and the narrow corridor between it and Lot 7 (Fig 1).

Interestingly, the dispersion of cholesterol, uric acid and phosphatase alkaline values behaves very similarly in adjacent forests and plantations transects. Lloyd *et al.* (2016) suggested that disturbed areas in Tennessee may have an influence in the high levels of white blood cells and low packed cell volume in box turtles (*Terrapene carolina carolina*) inhabiting adjacent forested areas. Comparable to what was presented in Chapter 2, the similarities found in this study may suggest a sort of influence of these plantations and their adjacent forests. This influence could go more than 500 meters deep into the forest regarding the Asian water monitor lizard populations and this could explain the similarities between Hillco plantation and Lot 5 which is the smallest patch of forest within the study area with ~700 m of distance between the main river and the plantation in its widest part.

Food abundance is an important driver of the ecology of predators, as their behaviour and activity patterns will respond to the presence of food and the absence of threat (Uyeda, 2009; Jennings et al., 2014; Jessop et al., 2014; Yue et al., 2015). Oil palm plantations provide Asian water monitor lizards, and other small carnivores, with an environment where the effort of finding food is much lower than in the forested areas, and the rewards are much higher, as seen by the abundant sources of animal protein, and the human subside of wasted food. This direct effect can be observed in the reduced home ranges within the plantations compared with forested sites, as described in Chapter 3.

Metabolic effects due to shifts in dietary diversity are only one of the consequences on the health of this population. This *fast food effect* could be imperceptible for the lizards' population in the short term, but not for mammals or birds (i.e. leopard cats, macaques, raptors, and even wild boars and sun bears, among others) that have walked into this trade-off. Therefore, including the health component of populations becomes an imperative measure in order to adequately assess the impact of anthropogenic fragmentation on the ecosystem. An assessment of the metabolic markers in rodents and a nutritional quality evaluation of the preys will be of great value for a deeper understanding of the nutrients supplied through the food web in fragmented landscapes.

Chapter 5

Fast food effect II: Host abundance, feeding behaviour and parasites diversity in *Varanus salvator* in a fragmented landscape

5.1. Introduction

Anthropogenic habitat fragmentation alters the risk and occurrence of infection in wildlife populations due to subsequent changes in their ecology (Gillespie and Chapman, 2005; Cardoso et al., 2015; Bonnell et al., 2018). Although the majority of studies have been conducted in primates (Gillespie and Chapman, 2005; Trejo-Macias et al., 2007; Arroyo-Rodriguez and Dias, 2010), alterations to host-parasites associations have been observed in other taxa as well (Lafferty and Kuris, 1999; Patz et al., 2000; Horwitz and Wilcox, 2005). Wells et al. (2018) suggest that the crescent interaction between domestic and wild animals, as well as the introduction of invasive species into the habitats, increases the risk of parasite transmission to non-usual hosts and even humans.

Host-parasite associations are important drivers of ecological structure and function (Gomez and Nichols, 2013), and important components of ecosystems in terms of species diversity (Poulin and Morand, 2004), and their role in food webs (Dunne et al., 2013). However, parasites can also shape community composition (Fenton and Brockhurst, 2008), and alter their patterns of distribution and density at larger spatial scales (Thomas et al., 2005). At smaller scales, parasites can be responsible for the survival, growth and reproductive rates of the host (Thomas et al., 2009; Jessop et al., 2012; Gomez and Nichols, 2013).

Feeding behaviour is commonly associated to host-parasites interactions (Dunne et al., 2013; Leung and Koprivnikar, 2018; Wells et al., 2018). Leung and Koprivnikar (2018) found that carnivore reptiles held a larger richness of helminths than those which diet is essentially herbivorous. This phenomenon applies mostly to those parasites with simple life cycle and able to infect a new host through predation. However, Lafferty et al. (2006) mentioned that predation by the host could be translated as parasite predation when the parasite is unable to adapt to the new host or, it has a complex life cycle which requires free-ranging stages, such as *Fasciola hepatica* that have a free-ranging stage between the intermediary and the ultimate host (Lafferty et al., 2006).

Several studies have reported gastrointestinal parasites associated to reptiles, although most of them correspond to records of parasite occurrence, and they are not necessarily related to the ecology of either the host or the parasite (Jones, 1983; Shine and Harlow, 1998; Jones, 2003; Jones, 2004; Jones 2010; Jones 2014; Ribeiro et al., 2018). Most gastrointestinal helminths reported from Varanidae are nematodes of the family Physalopteridae, belonging to the genus *Abbreviata* (Jones, 2010). Nevertheless, some species of this genus that infect snakes, are not able to survive in *V. goudii* (Jones, 1983). Several nematodes, trematodes, and a single cestode (*Oochoristica vacuolate*) have been recorded to occur most frequently within larger varanids (Pinnell and Schmidt, 1977; Jones, 2004; Scheeling et al., 2009; Jones, 2010, Zhang et al., 2011). Leishangthem et al. (2018) reported an incidental case of *Strongyloides stercoralis* infecting *V. bengalensis* in India.

This study aims to elucidate how alterations in feeding behaviour driven by anthropogenic changes to natural habitats influence parasite diversity. The working hypothesis is that a less diverse diet will be (1) associated to a low parasite diversity in the Asian water monitor lizards, and (2) generalist species will dominate the parasites community due to this homogeneous diet.

5.2. Methods

5.2.1. Trapping and sampling

Sampling took place between October 2013 and September 2016, parallel to the population assessment fieldwork. A clean plastic tarp was placed under the cage trap every day to collect lizard droppings and prevent these from getting contaminated by touching the ground. Samples were collected during the afternoon right after the individual was taken out of the trap. Those contaminated with mud (because of rain splatter or individual’s dirtiness) were discarded. Each sample was placed in a 15 mL tube and stored until it was processed for parasitological diagnostics.

5.2.2. *Diet assessment*

During the handling of the lizards, some individuals vomited as a consequence of stress or as a defence mechanism (Greene, 1988). The vomit was then used as sample material, and every prey item in it was identified and recorded in an inventory. Classification was carried up to order when possible, while species and genus levels were often not possible for most prey items undergone the lizards' digestion process (Tiranti, 1994; Reed et al., 2002; Bonvicino et al., 2003).

5.2.3. *Sample processing*

Samples were processed using a modified formalin-ethyl acetate sedimentation protocol (Young et al., 1979; Manser et al., 2016) to concentrate parasite eggs, and then samples were examined with a sequential sedimentation-flotation procedure. Fecal samples were mixed thoroughly before being strained through fine gauze into a 15 mL centrifugation tube. The filtrate was centrifuged at 3,000 rpm for 3 min, after the supernatant was discarded the fecal pellet was weighed before being re-suspended in 8 mL saline and 4 mL of ethyl acetate. Each sample was mixed thoroughly, centrifuged, and the supernatant was discarded again. The final pellet was re-suspended in sodium acetate – acetic acid – formaldehyde, and a 1 mL aliquot was placed into a vial containing saline and put on a magnetic stirrer to keep well homogenized throughout the analysis. Parasite abundance was estimated as the number of eggs per gram of feces (EPG) in each sample. An aliquot was removed from the homogeneous suspension, placed in a McMaster counting chamber and the sedimented material was examined at 100x magnification. The average of five replicate counts of all nematode eggs observed under the chamber's grid was used to calculate the EPG, given the known weight of fecal sediment in the 0.15 ml volume of suspension in the McMaster chamber. After quantification, each sample was centrifuged, the supernatant was discarded and the concentrated pellet was re-suspended in salt solution with a specific gravity of 1.27. Two slides were examined to minimize the risk of missing less-abundant helminth eggs. EPG was not quantified from flotation data; as we used the mass of the filtered sediment following the first centrifugation, the estimate of EPG is in fact eggs per gram of fecal sediment. Measurements and picture digitalization were performed in Image J 1.38 (Wayne Rasband, National Institute of Health, USA, 2011).

5.2.4. *Statistical analysis*

The Asian water monitor lizard population size for each site was reported in Chapter 2 (Table 5.1). Simpson Dominance Index (D) for prey and parasite diversity was calculated in Biodiversity PRO 2.0 (The Natural History Museum & The Scottish Association for Marine Sciences, 1997). In both cases, the number of taxon encounters was considered instead of the amount found in each sample in order to avoid over estimations. D values close to zero indicate an even distribution across taxa in the sample, while values close to one indicate the dominance of one or a few taxa in the sample.

Table 5.1. Abundance of *Varanus salvator* per study site in the Lower Kinabatangan Wildlife Sanctuary

Site	Abundance		
	N	**S.E.**	**95% IC**
Forest North	2445.50	188.04	2103 – 2841
Forest South	1439.57	173.62	1142 – 1820
OPP North	263.81	7.72	249 – 276
OPP South	298.77	91.80	166 – 538

Parasite prevalence (number of individuals positive among the total sampled population) was estimated using the package Prevalence (v. 0.4.0 for R 3.4.4. R Core Team). The statistical difference between prevalence by habitat was estimated using Wilcoxon test with a significant threshold (alpha) of 0.05%. Parasites abundance was log10 transformed in order to normalize the values. For those normalized values, differences between sites were assessed by t-Student meanwhile those which could not be normalized were assessed using Wilcoxon test.

In order to understand how different ecological variables affect the prevalence and abundance of each parasite in the Asian water monitor lizard populations, General Linear Mixed Effect Model (glmmADMB; glmmADMB v. 0.6.7.1, ADMB Project.) and Linear Mixed Effect Model (lmer; lme4 v. 1.1-17, R Core Team) fitted with Maximum Likelihood were applied.

Prevalence was assessed using the binomial presence/absence data. Models were run assuming two different distributions (Poisson and negative binomial) and a Zero-inflation effect to account for the large number of samples without parasite observations. The model with the lowest AIC value was chosen to explain how eight different co-variables affect the prevalence of each parasite group. The variables considered as drivers for parasite prevalence were: diet diversity (D), host abundance, EPG. Richness was estimated as the number of parasite taxa found in each sample. Co-infection was not considered appropriate to be included in the statistical models since it is uncertain whether multiple parasite taxa actually infect the lizards or whether such infections, when found, are just incidental due to the lizard's feeding behaviour (Zuur et al., 2009; Bolker et al., 2012; Bates et al., 2015).

The variables were arranged in 5 co-variable groups to assess a combined influence of parasites abundance: (1) diet diversity and host abundance, (2) prevalence and host abundance, (3) diet diversity and prevalence, (4) host abundance and parasite richness, and (5) diet diversity and parasite richness. The statistical model testing these variables was run considering either restricted or not restricted Maximum Likelihood (REML and ML, respectively). The model with the lowest AIC value was chosen to explain eggs shedding intensity. Since parasite eggs are not shed continuously, absence of parasites does not necessarily mean that there is no infection, and therefore samples with zero EPG were considered in this model (Bates et al., 2015).

5.3. Results

5.3.1. *Diet*

A total of 152 prey items were recorded from the vomit samples collected. Records for some animals are missing due to two main factors: 1) not all the individuals vomited during the process and 2) sometimes, the individuals only vomited the bait. Fourteen different types of prey were identified as part of the diet of *V. salvator* in this study, and rodents showed the highest occurrence. Consistent with this pattern, it was observed that lizards in the forest were feeding on 14 different taxonomic groups, whereas seven different prey were identified in plantation sites (Table 2). Invertebrates such as crabs, centipedes and woodlice seem to be an important part of the diet of the forest inhabitants, while rodents dominated the diet in plantations. Rodents were mainly represented by rats followed by mice and squirrels. Fish, on the other hand, included the tiger fish *Hypostomus plecostomus*, an invasive species that inhabit the main river and tributaries. Simpson Dominance Index (D) showed that diet diversity was significant higher in plantation areas than in forest (Kruskal-Wallis $Xi^2 = 14.37$, df = 3, p = 0.002).

The number of rodents recorded in plantation sites were up to 12 times higher than in forested areas, where woodlice and crabs were the dominant preys. Forest South dietary diversity seemed to be more even than the Forest North site, where woodlice and crabs were highly abundant. Although the number of rodents recorded in both plantations' sites were similar, OPP South site presented slightly higher richness (6 types) of preys than the OPP North site (4 types). This plantation site showed the highest dominance index (D = 0.658) while Forest South held the lower index (D = 0.079; Table 5.2).

Table 5.2. Inventory of prey identified in the vomit of Asian water monitor lizards sampled in the Kinabatangan floodplain and Simpson's dominance index per study site.

Prey	Bat	Centipide	Crab	Egg	Fish	Frog	Macaque	Rodent	Scorpion	Snail	Snake	Tortoise	Wild boar	Wood-louse	Simpsons Diversity (D)
Forest N	0	7	16	1	1	6	1	5	2	7	2	1	1	14	**0.139**
Forest S	1	1	6	1	4	1	3	2	1	3	1	2	0	2	**0.079**
OPP N	0	2	0	0	0	0	0	24	0	0	0	1	0	2	**0.685**
OPP S	0	1	0	0	2	2	0	23	0	2	0	1	0	0	**0.551**

5.3.2. Parasite prevalence and intensity

A total of 92 samples were considered adequate for the analysis in the laboratory. Nevertheless, due to the small sample size for one of the study sites (n=1), the comparative and association analyses were performed with 91 samples ($n_{forest} = 44$ samples; $n_{plantation} = 47$ samples). There were 11 parasite taxonomic groups identified from lizards' faeces corresponding to the phyla Platyhelminthes (2), Apicomplexa (1) and Nematoda (8) (Appendix V, section 1).

Thirteen samples were reported with no parasites, and just one individual presented six different kind of parasites. Samples collected in plantation sites showed lower parasite richness than those inhabiting the forested areas. However, the individual with the highest richness recorded was sampled in a plantation (Fig 5.1.).

Forested areas recorded 11 different type of parasites (D = 0.146) while nine types were recorded in plantations (D = 0.196; W = 71.5, p = 0.49). Soil-transmitted parasites were found in both forest and plantations, while trematodes and ascarids, that usually need one or two intermediary host, were found only in forested areas.

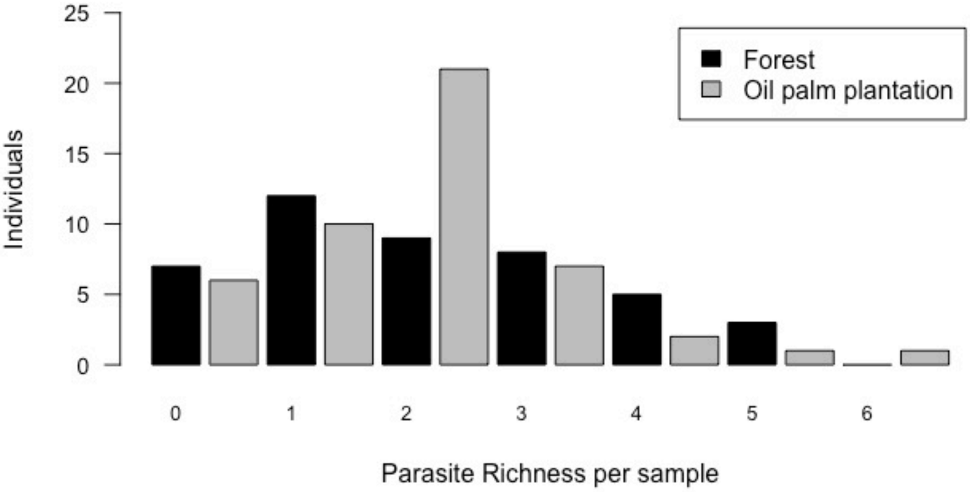

Figure 5.1. Parasite richness found in individual fecal samples in both forested and plantation areas.

Prevalence was higher in plantations for capillarids, strongyles, *Strongyloides spp*. and protists; nevertheless, protists were the only ones that presented statistically significant difference (21.27 vs 6.82; W = 884.50; p < 0.001). Trichurids were the only group with significantly higher prevalence in forest than in plantations (13.64 vs 2.13; W = 1153; p = 0.04). Ascarids and trematodes were only recorded in forest dwelling animals (Fig 5.2. and Table 5.3).

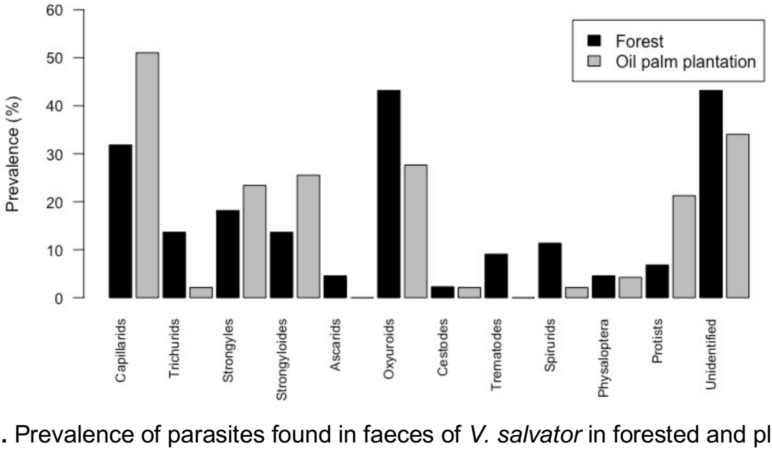

Figure 5.2. Prevalence of parasites found in faeces of *V. salvator* in forested and plantation areas.

Table 5.3. Prevalence of parasites found in faeces of *V. salvator* in forest and plantation. Prevalence is shown in percentage (%); minimum and maximum ranges were estimated with CI= 95%. Wilcoxon test was performed to assess the differences with alpha = 0.05.

PARASITE GROUP	**PREVALENCE**		**W**	**p**
	FOREST	**OIL PALM PLANTATION**		
Capillarids	31.82 (19.55-46.39)	51.06 (37.06-64.93)	835.00	0.65
Trichurids	**13.64 (5.90-25.96)**	**2.13 (0.23-9.51)**	**1153.00**	**0.04**
Strongyles	18.18 (8.99-31.40)	23.40 (13.11-36.84)	980.00	0.55
Strongyloides spp.	13.63 (5.89-25.96)	25.53 (14.78-39.19)	911.00	0.16
Ascarids	4.55 (0.95-13.79)	0.00	NA	NA
Oxyuroids	43.18 (29.36-57.86)	27.65 (16.47-41.49)	1194.00	0.12
Cestodes	2.27 (0.24-10.13)	2.12 (0.23-9.51)	1035.00	0.98
Trematodes	9.09 (3.14-20.18)	0.00	NA	NA
Spirurids	11.36 (4.47-23.12)	2.12 (0.23-9.51)	1129.00	0.08
Physaloptera spp.	4.55 (0.95-13.79)	4.25 (0.89-12.95)	1037.00	0.96
Protists	**6.82 (1.95-17.09)**	**21.27 (11.49-34.47)**	**884.50**	**<0.001**

Results from the GLMM are presented in section 2 of the Appendix V. The prevalence of capillarids was associated with parasite abundance combined with either host abundance (z = 1.91; p = 0.05) or food diversity (z = -1.95; p = 0.05). Oxyuroids were also positively associated with parasite diversity (z = -2.90; p = 0.003) alone and combined with diet diversity (z = 3.39; p = 0.0007).

Strongyles were the only taxa that showed significantly higher parasite abundance in forested areas than in plantations (1134.5 vs 509.27; F = 7.907 p = 0.01). Although not significant, capillarids, *Strongyloides spp*. and protists presented higher abundance in plantations than in forested sites. Ascarids and trematodes were only present in forested areas in high abundance, while cestodes were collected from one individual in plantation and one in forest, so the abundances could not be compared statistically (Table 5.4 and Fig 5.3).

Table 5.4. Eggs shedding intensity of parasites found in faeces of *V. salvator* in forest and plantation, presented as the number of eggs per gram of faeces (EPG; mean +/-SD). Values were log10 transformed before being evaluated with Wilcoxon test and ANOVA (*) with alpha= 0.05.

	EPG			
PARASITE	**Forest (+/-SD)**	**OPP (+/-SD)**	**value**	**p**
Capillarids	683.43 (108.91-1257.94)	5410.42 (658.50-10162)	124	0.18
Trichurids	12476.67 (5487.29-19466)	2162	NA	NA
Strongyles	**1134.5 (855.37-1413.63)**	**509.27 (240.81-777.73)**	**7.907***	**0.012**
Strongyloides spp.	141.66 (98.04-185.29)	314.16 (130.42-497.91)	38	0.88
Ascarids	134 (118-150)	0	NA	NA
Oxyuroids	458.36 (239.61-677.12)	357.69 (283.47-431.91)	97	0.31
Cestodes	8900	1100	NA	NA
Trematodes	96.75 (77.93-115.57)	0	NA	NA
Spirurids	1894.4 (234.65-3554.15)	152	4	0.66
Physaloptera spp.	201 (102-300)	200 (100-300)	2.5	1
Protists	2077.67 (641.73-3513.60)	7496 (3986.2-11005.8)	0.064*	0.80

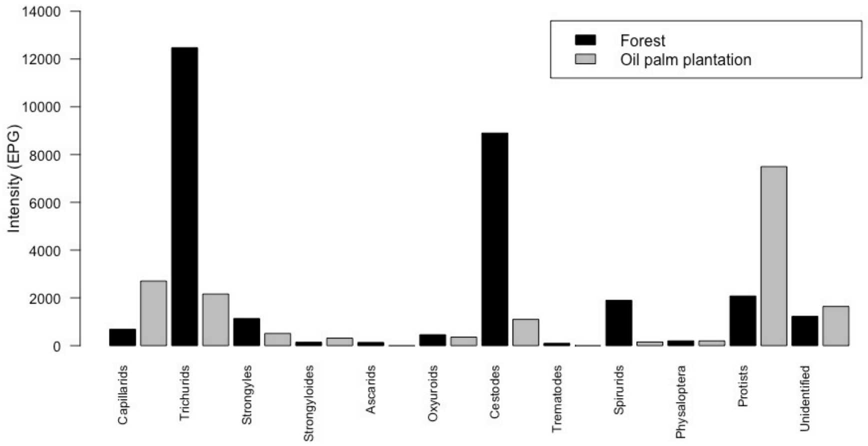

Fig 5.3. Egg shedding intensity of parasites found in faeces of *V. salvator* in forested and plantation areas.

Linear Mixed-Effect Models (LMEM) were used to assess how different ecological variables were associated with parasite abundance. Dietary diversity (Dominance), prevalence and host abundance were strongly associated with six out of nine parasite groups evaluated. Ascarids, trematodes and cestodes were not tested due to the distribution and number of the samples. Prevalence, alone and mixed with food diversity, showed a positive influence on the abundance of trichurids, strongylids, *Strongyloides spp.*, oxyuroids, spirurids, *Physaloptera spp.*, and protists (see section 3 of the Appendix). *Physaloptera spp.* and protists were the only parasite groups that seem to be also affected by the mixed effect of the host abundance/prevalence (see section 3 of the Appendix V).

5.4. Discussion

There is a reasonable amount of studies of parasites in Asian water monitor lizards in Asia but most of them focus on taxonomic questions (Singh, 1964; Self and Kunts, 1966; Pinnell and Schmidt, 1977; Jones, 1983; Adamson, 1986; Shine et al., 1998; Zhang et al., 2011; Jones and de Chambrier, 2016; Agustin et al., 2017; Leishangthem et al., 2018). Jones (1983) found that some species of *Abbreviata spp*., nematodes that infect elapid snakes, are not able to survive when infecting *V. gouldii* in Australia. Leishangthem et al. (2018) reported an incidental case of *Strongyloides stercoralis* infecting *V. bengalensis* in India. Twining et al. (2017) reported the presence of unidentified pentastomids in one individual of *V. salvator*. It is challenging to determine whether parasites shed in lizards' faeces are truly infecting the lizards, or are just paratenic hosts in the life history dynamics of these parasites in the area.

Although the differences between study sites were not significant, the study shows an influence of host abundance and diet diversity in the prevalence and abundance of some groups of parasites. The loss of diversity in the ecosystem may influence the diversity and abundance of parasites (Daszak et al., 2000). Specialist parasites, could be drastically affected by fragmentation while generalist parasites relay in their plasticity to adapt to a wider range of host and survive (Frias and MacIntosh, 2019). Host diversity plays also an important role in the transmission of parasites (Dobson, 2004). An example of this is *Ribeiroia ondatrae*, a multi-host trematode, that shows a limited transmission rate when the host community is more diverse, due to the interspecific differences in resistance (Johnson et al., 2008), suggesting that higher host diversity may act as a buffer against parasite transmission. Abundance of rodents in the diet of Asian water monitor lizards in the plantation suggest that either the lizards prefer them over other type of prey or they are much easier to catch in these areas. High catchability could be influenced either by the abundance or a possible vulnerability caused by parasitism. Lafferty et al. (2006) suggest that parasites divert host energy onto the immune activity affecting other survival functions such as reduction of mating success and increase of stress and susceptibility to predators.

Soil-transmitted parasites, such as capillarids, trichurids, strongyles, *Strongyloides spp.* and oxyuroids have a simple and direct life cycles and can be transmitted either by ingest from the environment or through predation (Foryet, 2001). Other parasites such as spirurids, physaloptera, cestodes and trematodes have more complex life cycles and need one or more intermediary hosts in order to develop into infecting stages (Foryet, 2001). The low occurrence of snails and invertebrates in the diet of lizards inhabiting plantations could explain the null prevalence of trematodes and cestodes in those lizards. However, this does not indicate that parasites are absent from plantations, as they may be affecting other animals in the area, such as long tail macaques and birds that feed more on invertebrates.

The lower diversity of parasites in plantations and the dominance of parasites such as capillarids, strongylids and *Strongyloides spp.* can be explained by the rodent-dominated diet of the lizards that inhabit the crops. Leung and Koprivnikar (2018) found that host diet is the best predictor to explain parasite diversity and community composition and that carnivore lizards play an important role maintaining parasites biodiversity. On the other hand, Frias and MacIntosh (2019) suggest that parasite diversity helps to keep low the abundances of generalist parasites maintaining a healthy parasite infracommunity. Diversity of parasites in forest also works as dilution factor increasing the interspecific competition and reducing the rates of transmission (Daszak et al., 2000; Fenton et al., 2002; Dobson, 2004).

It has been suggested that habitat fragmentation by human activities is a contributing factor to i) the increasing number of individuals in lizard populations, ii) the observed shift in their habits, as well as iii) the change in lizard behaviour, physiology and size

(Jessop et al., 2012). Although it is difficult to determine if the parasites found in this study are certainly affecting the ecology and survival of the lizards' populations, as a generalist widely distributed within the landscape, Asian water monitor lizard could be contributing in the dynamics of some species of parasites, either as dispersers or as end point host. This study suggests that the abundance of rodents in the plantation is playing an important role in the parasite diversity in oil palm plantations. Nevertheless, the impact on the population's health remain uncertain. Although the survival and growth rates found in Chapter 2 indicate that the population is healthy, changes in the dietary diversity and the abundance and dispersion of lizards within the landscape may have a strong significance in the survival of generalist parasites, which also may represent a risk of infection for some other generalist carnivores that inhabit the plantations and feed on rodents, such as raptors, leopard cats, civets, among others. Therefore, A multi-host landscape study would bring more light on the role of Asian water monitor lizards as part of parasite dynamics and potential for zoonotic risk.

Chapter 6

Ecology of *Amblyomma helvolum* (acarina; ixodidae) associated to *Varanus salvator* in a fragmented landscape

6.1. Introduction

Habitat fragmentation is generally linked to altered host-parasite interactions driving parasites either to increase their populations or walk into the extinction path (Dobson, 2004; Gillespie and Chapman, 2008; Froeshke et al., 2013). Frias and MacIntosh (2019) suggest that habitat fragmentation may drive specialist helminth parasites to extinction while generalist will adapt to the new environment and availability of resources. Habitat fragmentation, as well as land management have a relevant role in the ecology of ticks and the risk of transmission of rickettsial diseases (*e.g.* Lyme borreliosis or tick-borne encephalitis virus), including host community diversity and relative abundance (Krasnov et al., 2007; Vanwambeke et al., 2010). Krasnov et al. (2007) suggested that the dilution effect in *Ixodes ricinus* associated with two rodent species, is strongly associated with how the hosts use their habitat; while Vanwambake et al. (2010) described the role of forest type and land use as important factors for the dispersion of *I. ricinus* and *I. scapularis*.

Amblyomma helvolum is a hard-shell tick from the family Ixodoidea, widely distributed in Southeast Asia. It has been described as a reptile specialist, commonly found in the Asian water monitor lizard, and other members of the family Varanidae, Scinidae and Agamidae (Auffenberg, 1988; Durden, 2008), although it has also been recorded in Sulawesi black racer (*Pytas dipsa*) and in other large species such as water buffalo (*Bubalus bubalis*), wild pigs (*Sus barbatus*) and deer (*Rusa unicolor*) (Durden et al., 2008; Volzit and Kerians, 2002). Ixodid species have been well studied in countries of the northern hemisphere due to their importance in public and animal health (Ostfeld et al., 2000; Randolph, 2004; Estrada- Peña et al., 2006; Stein et al., 2008). Spotted Fever Group Rickettsiae (SFGR), such as Lyme's borreliosis and Ehrlichiosis, as well as and anaplasmosis are just some of the pathogens that can be transmitted through ticks, along with some protists such as *Babesia spp*. and *Hepatozoon spp.* which are of medical relevance to livestock and human health (Randolph, 2004; Parola et al., 2005; Reeves, 2006; Doornbos et al., 2013). In Sabah, East Malaysia, Salgado Lynn et al. (2018) suggested that, although tick-borne rickettsiosis is present in Borneo, the disease is not diagnosed due to the lack of information about the ecology of the pathogen and its vector, as well as the lack of diagnostic tools.

Varanus salvator is one of the main hosts for *A. helvolum*, with ticks having been found infecting monitor lizards across its distribution range (Auffemberg, 1988; Durden et al., 2008). Among the 104 species of ticks reported in Southeast Asia (Petney et al., 2007), *A. helvolum* seems to be the most prevalent in the Asian water monitor lizard (Durden et al., 2008), although the presence of *Aponnoma* spp. on in Malaysia has been reported as well (MacDonald, 1960, Hussain et al., 2010). *A. helvolum* has been identified in Asian water monitor lizards in Sulawesi, Indonesia (Durden et al., 2008) and the Philippines (Auffemberg, 1998). Twining et al. (2017), opportunistically reported the presence of 14 ticks identified as *A. helvolum* in five Asian water monitor lizards, although the identification method is not clear.

The population dynamics of *V. salvator* in the Kinabatangan Floodplain may have some influence in the dynamics of *A. helvolum* within the landscape. Tick population dynamics greatly depend on their host's abundance, with this being particularly important for those species exhibiting host-specialisation (Arneberg, 1998; Gray, 1998; Daszak et al., 2000; Ostfeld and Keesing, 2000). Nevertheless, the survival opportunity for ticks in non-parasitic stages may depend on environmental factors such as humidity and temperature (Eisen et al., 2003; Jouda et al., 2004; Diuk-Waser et al., 2006). Thus, vegetation structure, propensity to flooding and seasonality contribute to parasite abundance (Gray, 1998; Randolph, 2004; Stein et al., 2008; Vanwambeke et al., 2010; Pfäffle et al., 2013).

Fragmented landscapes dominated by oil palm plantations seem to offer a suitable habitat for the distribution and abundance of Asian water monitor lizards no just within the crops but also within the adjacent forested areas (see chapter 1). This anthropogenic landscape offers a highly abundant food source that not only favours the lizards' population size but also their body size. This advantage for the lizards may be also an advantage for the presence of *A. helvolum,* which may find in lizards' preferred habitats a suitable place to survive. Larger hosts offer better surface for ixodids to feed on and reduce the inter- and intra-specific competition (Auffenberg, 1988). Varanids, when small, spend long periods of time on trees hiding from predators and basking. On the other hand, larger individuals spend most of the time basking on the ground, or hiding under vines or inside burrows, becoming more susceptible to be infected by ticks (Auffenberg, 1981; Auffenberg, 1988; King et al., 2002). Thus, *A. helvolum* may find in larger lizards a better opportunity to feed on than in smaller ones.

This study aims to understand how the ecology of *A. helvolum* and *V. salvator* are linked within a fragmented landscape, and how different environmental variables, such as seasonality, vegetation cover and propensity to flood, influence the presence and abundance of this ixodid. It is hypothesised that the prevalence and intensity of ticks will be directly associated with host abundance as well as with the presence of dense understory. In order to assess this hypothesis, high resolution maps (Light Detection And Ranging, LiDAR) will be used, as they offer a very small scale image of habitat structure which allows to identify slight differences in forest structure and topography to assess the heterogeneity of both plantations and forested areas (Asner et al., 2007; Levick et al., 2010).

6.2. Methods

6.2.1. <u>Sampling</u>

Following the same trapping protocol mentioned in earlier chapters, once the lizards were secured and measured, the whole body was scanned for ectoparasite detection. The most common areas for ectoparasites were around the shoulders and hip joints, however, legs and the head were also searched for ticks as these areas are considered to be good spots for ticks due to the softness of the tissue. Nevertheless, for heavily-infected individuals, ticks could be found in any part of the body, even over the dorsal region (Auffenberg, 1988; *pers. obs.*) (Fig. 6.1).

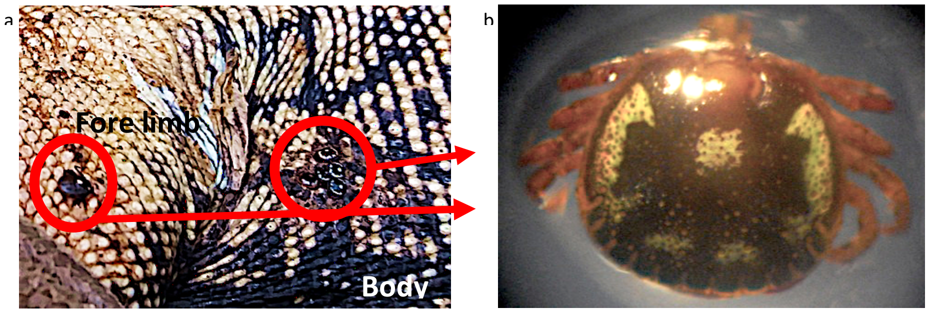

Figure 6.1. Ticks are usually found around the Asian water monitor lizard's shoulders or around the hip (a), as well as on limbs and neck. When the intensity is high, they can be found in any part of the body. The colour pattern of the ticks' shell is very similar to the lizard's skin, making them difficult to see (b).

All ticks were counted and collected for each sampled individual, placed in 2 mL tubes with absolute ethanol, and marked with the animal's identification code. Ticks were identified with an optic microscope using standardized keys (Kohls, 1957). *Amblyomma helvolum* is characterized by an ornate scutum, long palpi, hypostome with 3/3 dentition, triangular spurs on coxae I-IV, indistinct eyes and no lateral groove (Kohls, 1957) (Fig. 6.1b).

6.2.2. *Statistical analysis*

Ticks prevalence, intensity and density (measures of parasite infection; MPI) were assessed and compared between groups according with different variables such as type of habitat, location of the study site (north or south from the main river), transect (forest lot or plantation estate), distance from the river, canopy height, potential of flooding and season. Prevalence was measured as the proportion (%) of individuals carrying at least one tick among the whole sampled population (Bush et al., 1997). Intensity was calculated as the residual of the number of ticks per individual among the tick-positive group (Auffenberg, 1998). In the same way, density was estimated as the residual of the number of ticks in relation to the body length (in centimetres) of the tick-positive individuals (SVL) (Auffenberg, 1988). Prevalence was calculated with the package Prevalence 0.4.0 (R Core Team) and using Jeffrey's method to estimate the 95% confidence intervals of the prevalence estimate. Mean intensity and density and their own confidence interval (95%) were estimated using the base package 3.4.4 for R (R Core Team).

Host variables such as abundance and SVL were considered while sampling site (six sites), habitat (oil palm crop vs. forest), canopy height (four categories), flooding potential (three categories) and seasonality (dry season vs. monsoon) were accounted as environmental variables. Location from the river was considered, although it may be influenced by habitat features. The monsoon season comprises the months from October to January, while dry season extends from March to August (Data from nearest weather station in Sandakan, Malaysia). These variables were evaluated individually and in combination with each other resulting in 24 different single and mixed effects for the model. Generalized linear mixed models were used to evaluate the effect of these variables on ticks' epidemiological indexes (MCMCglmm V 2.26, R Core Team) (Hadfield, 2018). MCMCglmm models allow to fit the prior distribution of the random variables and to adjust the number of Markov Chain Monte Carlo (MCMC) iterations manually.

The amount of mixed effects acted as dilution factor when assessing single effects, thus, single effects were evaluated individually first and then mixed. In both cases, the individual identification was used as random effect to reduce the influence of recaptures in the model. MCMC models were set to run 100,000 iterations with a default burn-in of 1,000 and a thinning interval of 100. The prior of each random variable was increased from the default (V=1; nu=0.002) by adding an α value of 1,000 for the G structure, while the R structure was set with V=1, n=1 and the fix factor value of 1 (fix=1). These values reduced the influence of the random variables on the statistical analysis (Hadfield, 2010). Ordinal distribution was considered for prevalence, while a Poisson distribution was fit for intensity and exponential distribution for density (Hadfield, 2010).

Ticks have specific requirements for their development, including temperature, humidity and the presence of low vegetation to hide while waiting for the new host to pass over (Eisen et al., 2003; Jouda et al., 2004; Diuk-Waser et al., 2006). Tropical places with high humidity during most part of the year can be suitable for the presence of ticks during the whole year. Although grasslands are the most common areas for ticks, open areas receiving too much sunlight would increase the temperature of the ground, affecting their development (Diuk-Waser et al., 2006).

To assess the influence of flooding levels and vegetation structure, LiDAR images were utilized within the study area (Asner et al., 2007). The 1 m resolution of the elevation raster images allowed the classification of the area according to its probability of being flooded: (1) permanent flooded, including drains, rivers and lakes that hold water most part of the year, (2) seasonally flooded, including areas covered by water during the monsoon season, also the most common category in the study area, representing those sites adjacent to rivers or drains in plantations, and (3) high ground, which corresponds to areas that never got affected by floods during the time of the study. The canopy height layer was classified in four categories: (1) low understory (up to 2 meters high, this includes grasslands), (2) high understory (2-5 meters high, including vines and bush), (3) low canopy (small trees from 5 to 10 meters high), and (4) high canopy (trees higher than 10 meters). Four years of fieldwork allowed validating the classification of the sites at specific points. LiDAR images were generated by the Stanford University Carnegie Airborne Observatory (CAO), and access was provided by the Sabah Forestry Department. Ground elevations represent height above WGS84 ellipsoid and tree canopy height (TCH) values are height above ground.

Although oil palm plantations seem to be a uniform matrix and are usually compared at a large scale with forested areas, the sites where sampling took place are somehow heterogenous. Each one of the forested and plantation transects presented differences in canopy height and flooding not just between transects but also between trap spots, therefore the sampling site selection was chosen randomly. Since LiDAR images offer a high-resolution landscape description (within 1 m accuracy), they provide a finer description of the area where each trap was deployed (Asner et al., 2007; Levick et al., 2010). A buffer zone of 400 meters radius around each trap was described taking in account the flooding potential and the dominant type of vegetation structure. This buffer area is the same value estimated as the influence radius for each trap, as described in chapter 2.

Some varanids have an arboreal behaviour when small, using the tree branches to hide from predators and reach the sunlight in forested areas (Auffenberg, 1988; King et al., 2002). Asian water monitor lizards also present this behaviour as it was observed during the study. Although larger lizards (up to 15 kilos) have been seen resting on high trees, it is more common to spot them hidden under burrows and vines, as well as basking among the grasslands where sunlight is more available. This behaviour, tree and body size dependent, may play an important role in the association of *A. helvolum* and *V. salvator* (Auffenberg, 1998; Gray, 1998; Stein et al., 2008), thus, they were also tested as single and mixed effects.

Host abundance is an important variable to consider in parasites' ecology, essentially when it can explain how diversity influences in the presence and intensity of parasites (dilution factor; Arneberg et al., 1998; Gray, 1998; Daszak et al., 2000; Dobson, 2004). However, in cases when the study is focused in a population instead of a community, its relevance could be influenced or masked by other variables such as distribution within the landscape and habitat suitability for the survival of the parasite. In this study, host abundance was assessed as host-related variable; nevertheless, its interpretation might have to consider the influence by the sampling site features.

6.3. Results

The description of each trapping site and the differences in abundance and mean body length of the Asian water monitor lizards inhabiting them is shown in table 6.1. Sites from both sides of the main river differ mainly in the intensity of flooding. While the north side of the river (Hilco and Lots 5 and 7) are flooded most part of the year, the south side is just flooded during the monsoon season (Table 6.1). Only two sites, Hilco and Lot 5 presented high dominance of low canopy (bushland). Hilco and KKL presented some patches of grasslands, while this is scarce or absent in other trapping sites (Table 6.1 and Fig. 6.2).

Within the six different sampling sites, there were 348 individuals sampled. All recaptures were considered as different individuals due to inconsistencies of the inter-capture periods, and thus the overall number of animals samples was 683, with 312 samples collected in oil palm sites (Hilco = 52; KKL = 168; Kuril = 92) and 371 corresponding to animals in forested areas (Lot 5 = 108; Lot 6 = 170; Lot 7 = 93).

Table 6.1. Features of the sampling sites. Descriptions were made at the time of the study. *SVL is given in centimetres (cm).

Site	Habitat	Canopy structure	Flooding potential	Lizards' abundance	SVL*; mean (SD; min-max)
Hilco	OPP	Dominated by different size of palms. Dense understory is present in both riverside and interior because of the presence of a large swamp dominated by grass and bush.	Flooded most part of the year	263.81	67.70 (12.33;43.4-87)
KKL	OPP	Dominated by old palms with some areas of understory, mainly along the rivers and within the drains.	Seasonally flooded in the riverbank, the interior transect has some areas of high ground.	298.77	64.99 (14.11; 42.2-97)
Kuril	OPP	High palms above 10 m with areas covered by herbs and ferns.	Seasonally flooded in interior although hills are present. Riverbank is flooded most part of the time.	298.77	64.99 (14.11; 42.2-97)
Lot 5	Forest	Dominated by trees above 10 m with high density of ground vines and bush.	Flooded most part of the year. The area is surrounded by tributaries.	2445.4	64.66 (15.88; 43.4-103.8)
Lot 6	Forest	Dominated by high trees with dense understory surrounding the lakes and along the riverside	Seasonally flooded in the interior, there are two oxbow lakes within the area.	1439.6	60.61 (13.19;43-102.4)
Lot 7	Forest	Dominated by high trees with dense understory surrounding the lakes and along the riverside	Flooded most part of the year in the interior, influence of two small tributaries	2445.4	64.66 (15.88; 43.4-103.8)

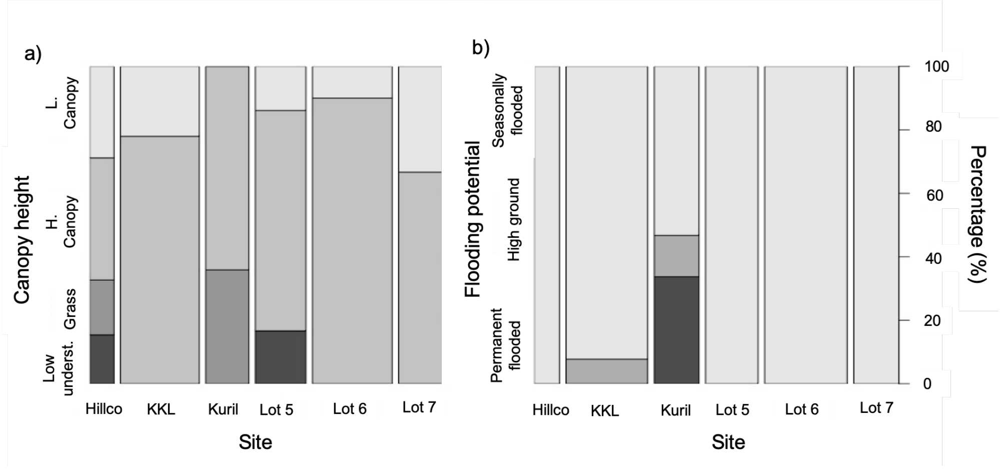

Fig 6.2. Heterogeneity of the study sites during the study period regarding canopy height and flooding. Lots 5, 6 and 7 belong to the LKWS, while Hilco, Kuril and KKL are the oil palm estates where the sampling was carried out. Categories are referenced by the patterns showed by Hilco (a; canopy height) and Kuril (b; flooding).

6.3.1. *Measures of Parasite Infection*

Prevalence, intensity and density were significantly higher in oil palm plantations (OPP) than in forested sites (pMCMC <0.001; table 6.2). Tick prevalence was significantly higher in Kuril, KKL and Lot 7 ($\text{pMCMC}_{\text{Kuril}} < 0.0001$; $\text{pMCMC}_{\text{KKL}} < 0.0001$; $\text{pMCMC}_{\text{Lot7}} = 0.016$; Table 6.2). Lot 6 presented higher tick intensity among forested sites ($\text{pMCMC}_{\text{Lot6}} = 0.002$; $\text{pMCMC}_{\text{Lot7}} = 0.038$; Table 6.2), while for plantation sites, Kuril presented the highest intensity ($\text{pMCMC}_{\text{Kuril}} < 0.0001$; $\text{pMCMC}_{\text{KKL}} < 0.0001$; Table 6.2). Tick density was significantly higher in Lot 6 (pMCMC = 0.013), KKL (pMCMC = 0.0006) and Kuril (pMCMC = 0.0002; Table 6.2).

Table 6.2. Prevalence, intensity and density of *A. helvolum* on *V. salvator* within the Kinabatangan Floodplain. Intensity is shown in ticks/individual, while density is presented in ticks/cm.

Habitat	Site	Prevalence (%; min-max)	Intensity (mean; min-max)	Density (mean; min-max)
Forest	**Lot5**	29.62 (21.64-38.69)	4.5 (1.23-6.34)	0.054 (0.036-0.071)
	Lot6	43.52 (36.23-51.03)	5.8 (3.94-6.44)	0.086 (0.076-0.095)
	Lot7	51.61 (41.53-61.58)	4.22 (2.54-4.81)	0.069 (0.059-0.079)
	Total	**63.77 (57.73-69.50)**	**5.03 (4.50-5.55)**	**0.074 (0.067-0.080)**
Oil Palm Plantation	**Hillco**	30.76 (19.52-44.09)	1.87 (1.52-2.22)	0.026 (0.022-0.030)
	KKL	67.85 (60.53-74.56)	7.94 (7.26-8.62)	0.109 (0.108-0.128)
	Kuril	70.65 (60.81-79.21)	15.58 (11.9-19.26)	0.236 (0.181-0.290)
	Total	**72.4 (66.94-77.39)**	**10 (8.68-11.33)**	**0.150 (0.130-0.169)**

6.3.2. *Single effects*

Sites in the interior of the forest presented higher tick intensity (pMCMC = 0.0001) and density (pMCMC = 0.006) compared to those placed nearby the rivers. Both intensity and density were also significantly higher during the rainy season ($\text{pMCMC}_{\text{Intensity}} = 0.0006$; $\text{pMCMC}_{\text{Density}} = 0.0092$). Regarding canopy height, grasslands showed the highest tick prevalence (pMCMC = 0.002) and intensity (pMCMC = 0.02), while, regarding flooding levels, high ground presented significantly higher tick intensity (pMCMC = 0.0004) and density (pMCMC = 0.01; (Figs 6.3, 6.4 and 6.5) than those areas that are highly flooded.

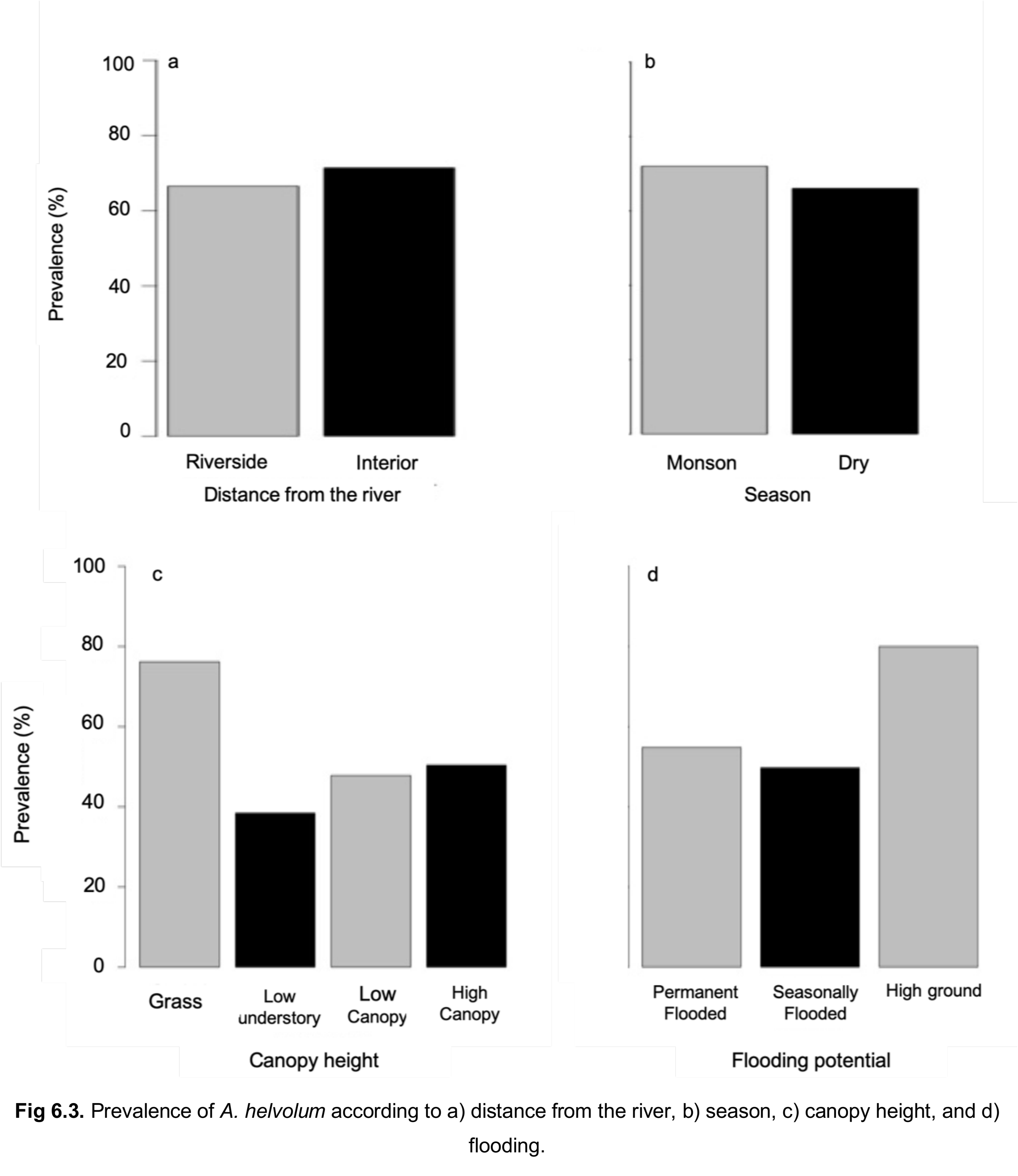

Fig 6.3. Prevalence of *A. helvolum* according to a) distance from the river, b) season, c) canopy height, and d) flooding.

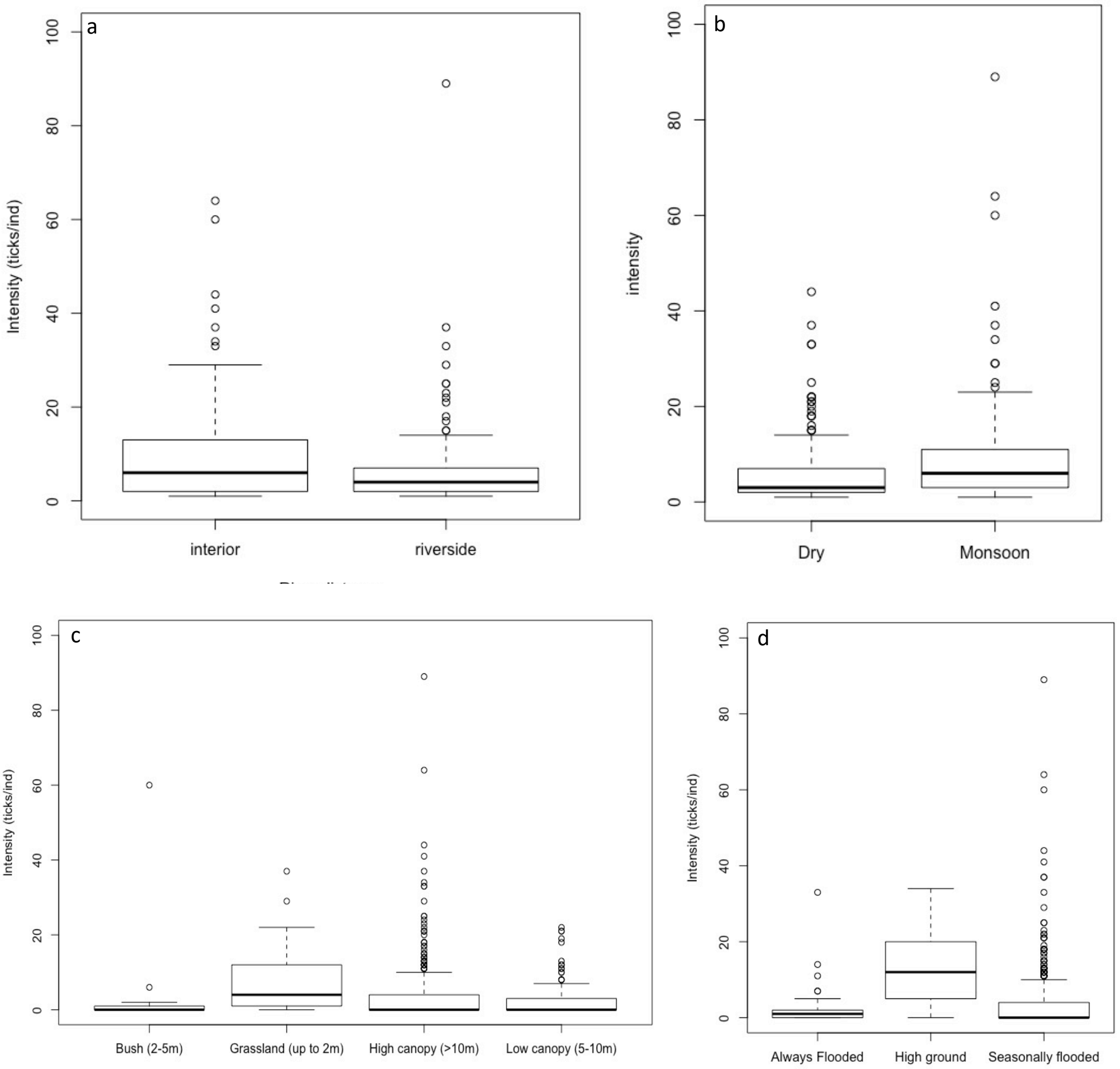

Fig 6.4. Intensity of *A. helvolum* according to a) distance from the river, b) season, c) canopy height and d) flooding.

The abundance of lizards seems to have a positive influence on tick intensity (pMCMC = 0.043), but not on prevalence (pMCMC = 0.26) or density (pMCMC = 0.12). Although it seems like the higher the abundance of lizards the higher the prevalence and density, it is likely that there are other factors involved since the site with the highest lizards abundance (Hilco = 187.32) is the one with the lowest epidemiological values (Fig. 6.6).

Body size also showed a strong significant association with prevalence (pMCMC < 0.0001) and tick intensity (pMCMC = 0.0008), but the number of ticks per cm (density) does not seem to be influenced by this single effect (Fig. 6.7).

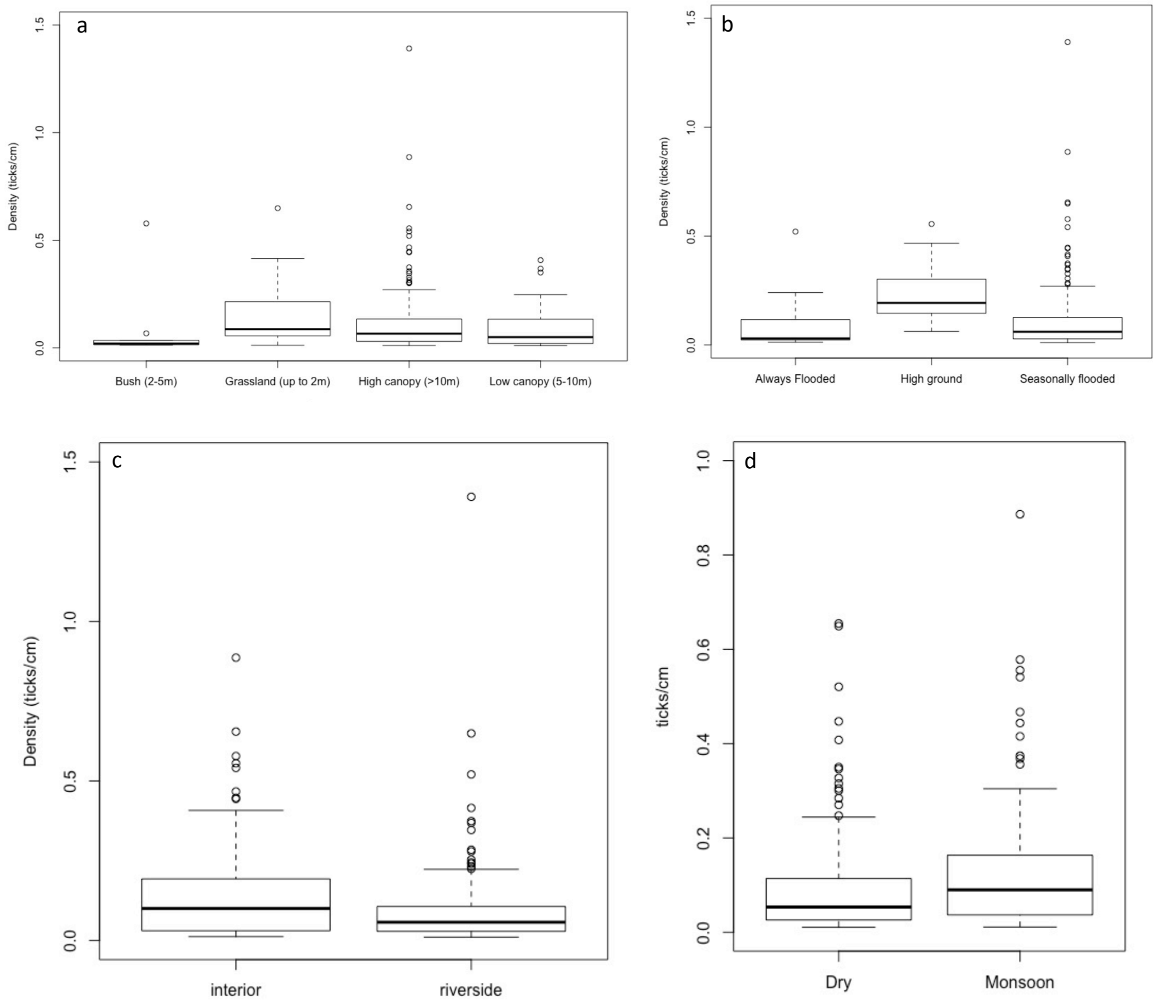

Fig 6.5. Density of *A. helvolum* according to a) distance from the river, b) season, c) canopy height and d) flooding.

6.3.3. *Mixed effects*

The combination of spatial distribution of the epidemiological index and the significant differences between the six sites resulted in no single variable influencing the distribution of ticks, rather the mixed effects between them seems to explain tick distribution better (Fig. 6.8).

Although host abundance may be influenced by the site, it is evident that the interior forest sites have higher tick prevalence, which increases with lizards' abundance (pMCMC = 0.05; Fig 6.9a). In the same way, prevalence increases directly with the size of the lizards, and it is higher in sites where lizard abundance is higher. Environmental factors may be affecting the low prevalence observed in the site with highest lizard abundance, however the association with body size is still positive (pMCMC = 0.04; Fig. 6.9d).

Interior sites do not seem to be affected by seasonality, but prevalence increases in riverside sites during the dry season (pMCMC = 0.03; fig 6.9c). Prevalence increases during the rainy season in high spots, although this association is not observed in lower lands (pMCMC = 0.02; fig 6.9b).

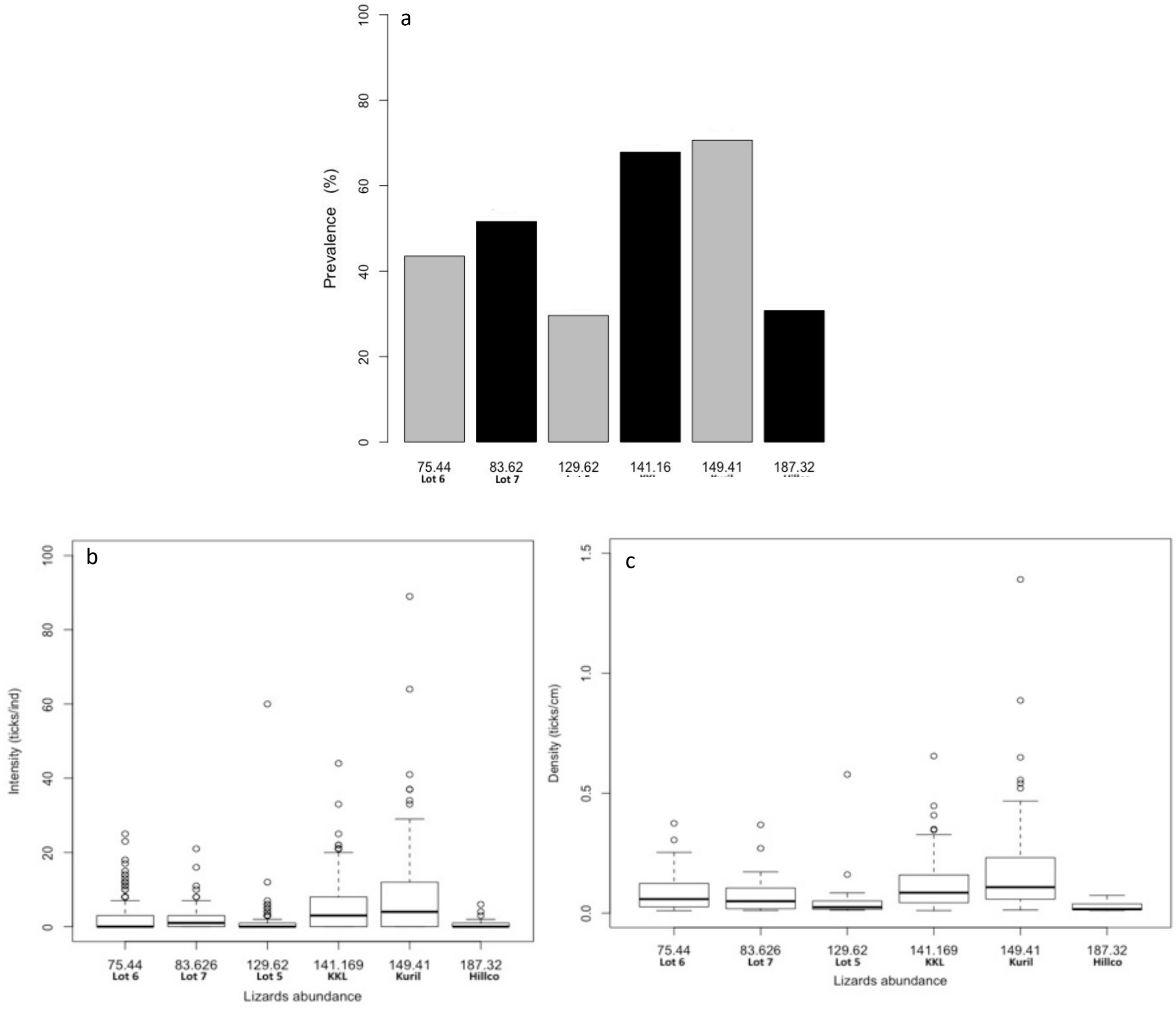

Fig 6.6. Measures of parasite infection of *A. helvolum* according to sampling site and abundance of lizards. For this study, abundances were calculated for the influence area of each of the trapping site (400m). Measure of parasite infection are a) prevalence, b) intensity of infection, and c) density.

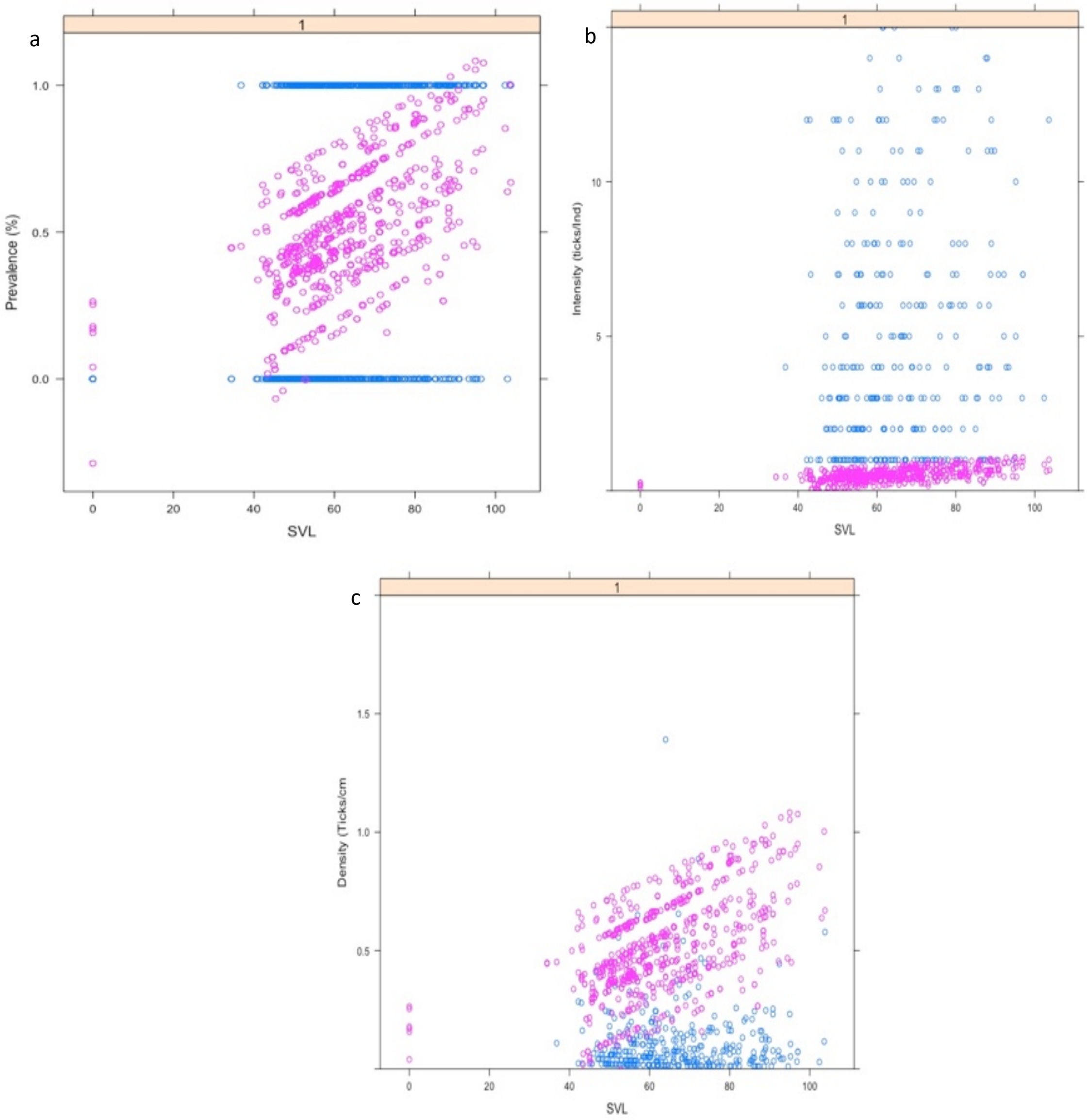

Fig 6.7. Association between the different epidemiological values of *A. helvolum* and the lizards body size (SVL). Epidemiological values are a) prevalence, b) intensity of infection, and c) density. Blue dots represent the data values while the red dots represent the trend.

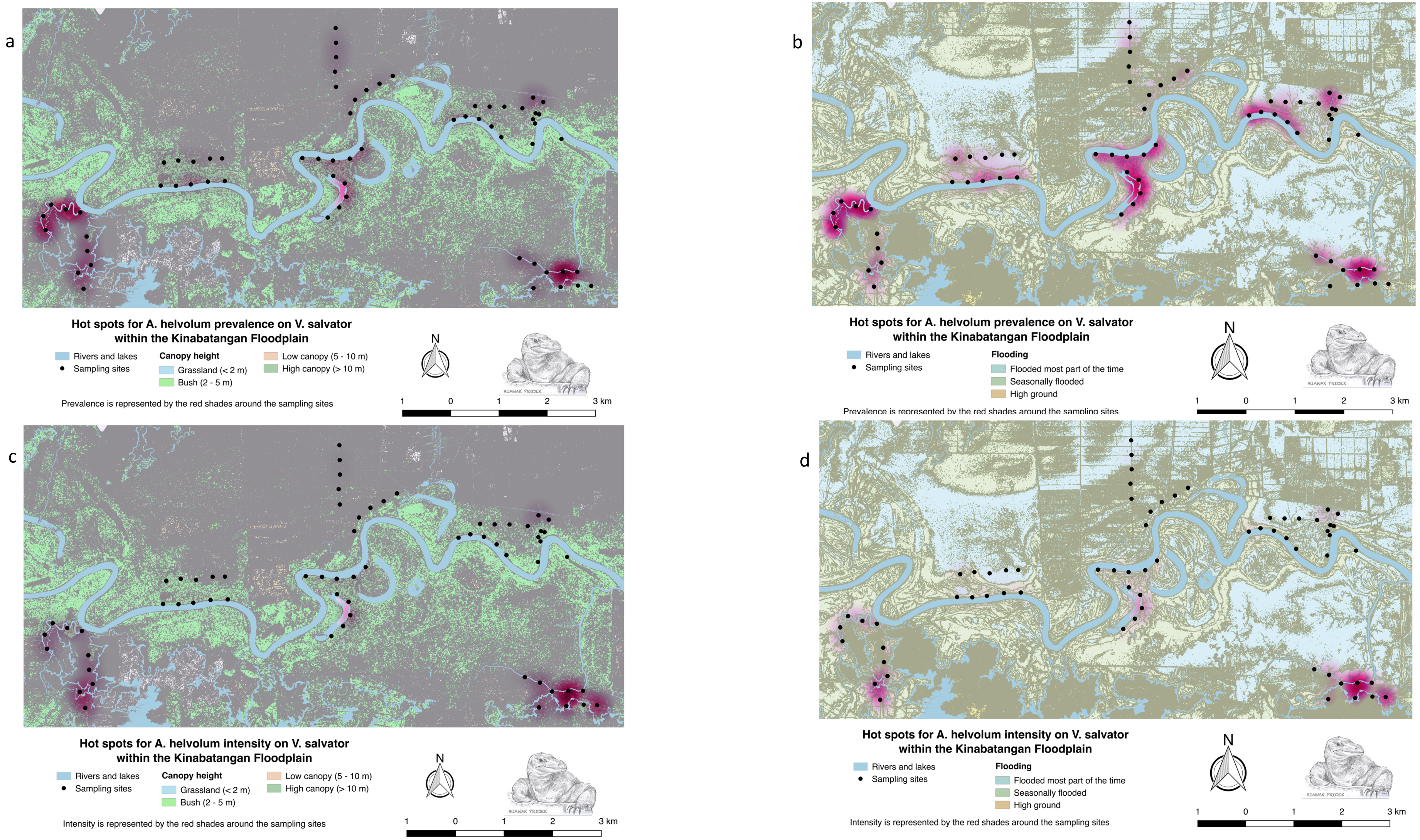

Fig 6.8. Spatial distribution of the epidemiological indexes of *A. helvolum* in relation to canopy height (a, c) and flooding (b, d). Black dots represent the trap's distribution within the landscape and the red halloes represent both the prevalence (a and c) and the intensity (b and d). Density is not represented in the figure, as its values are very similar to intensity

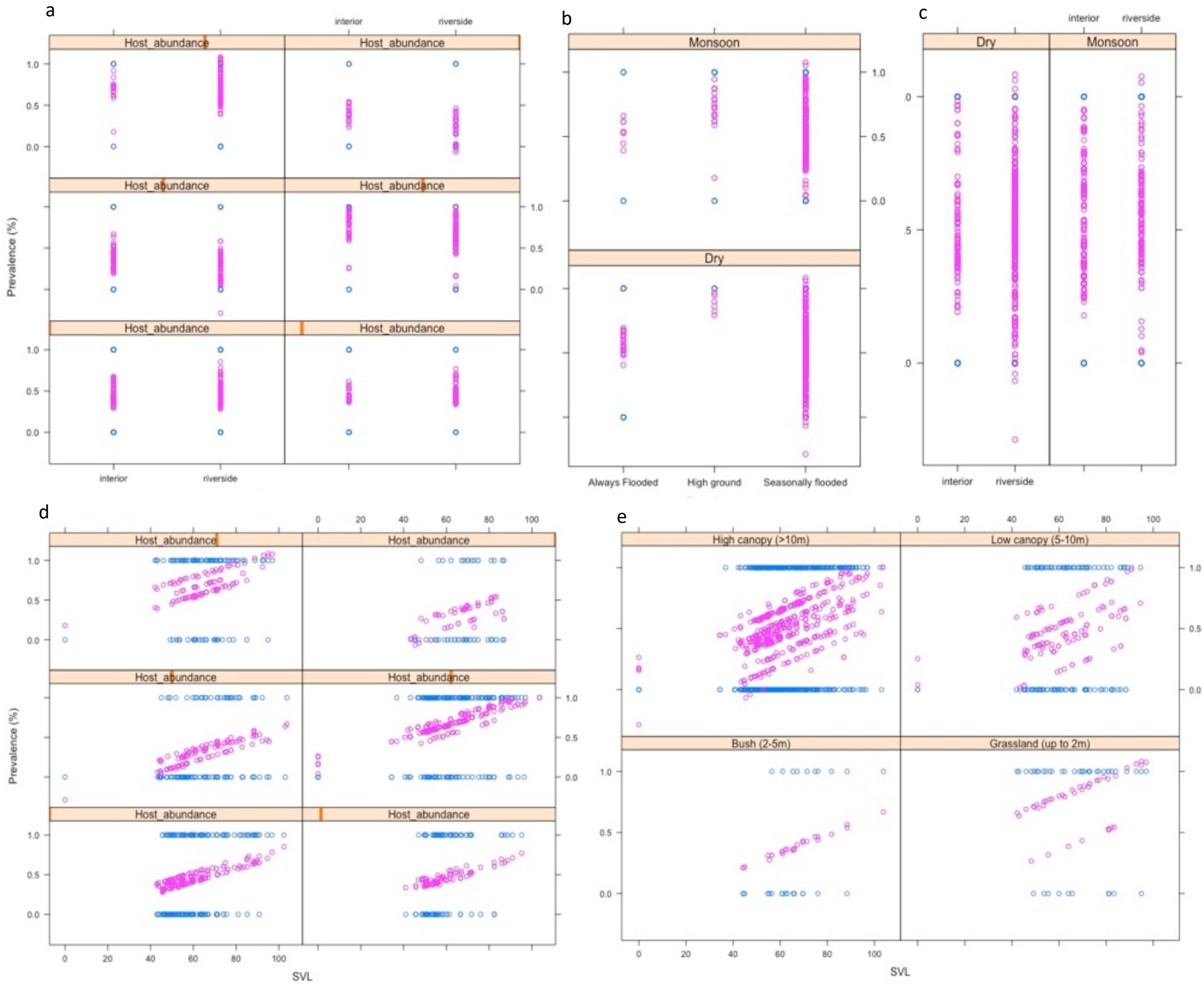

Fig 6.9. Prevalence of *A. helvolum* and its response to mixed effects: a) host abundance/river distance; b) season/flooding; c) season/river distance; d) host abundance/body size; e) canopy height/body size. Blue dots represent data values, while red dots represent the trend.

Prevalence in grasslands and areas with a canopy height ranging between 5-10 m was higher than other sites. Sampling size may be influencing low prevalence in bush lands, however in all four types of sites, the association between body size and prevalence was positive ($pMCMC_{Grassland} = 0.03$; $pMCMC_{Low\ canopy} = 0.04$; Fig. 6.9e). Although plantations showed elevated tick intensity compared with forested areas, in both habitats, interior sites seem to be more likely to host higher number of ticks per individual (pMCMC = 0.5; Fig. 6.10a). Rainy season contributed to an increased tick intensity in forest interior sites (pMCMC = 0.03; Fig. 6.10b), and although the differences in intensity between canopy heights were significant ($pMCMC_{Grassland} = 0.02$; $pMCMC_{Low\ canopy} = 0.04$; $pMCMC_{High\ canopy} = 0.03$; all in relation to bushland), all of them showed a positive association with lizards' body size (pMCMC= 0.007; Fig. 6.10c). MCMCglmm did not show any influence of mixed effects on tick density.

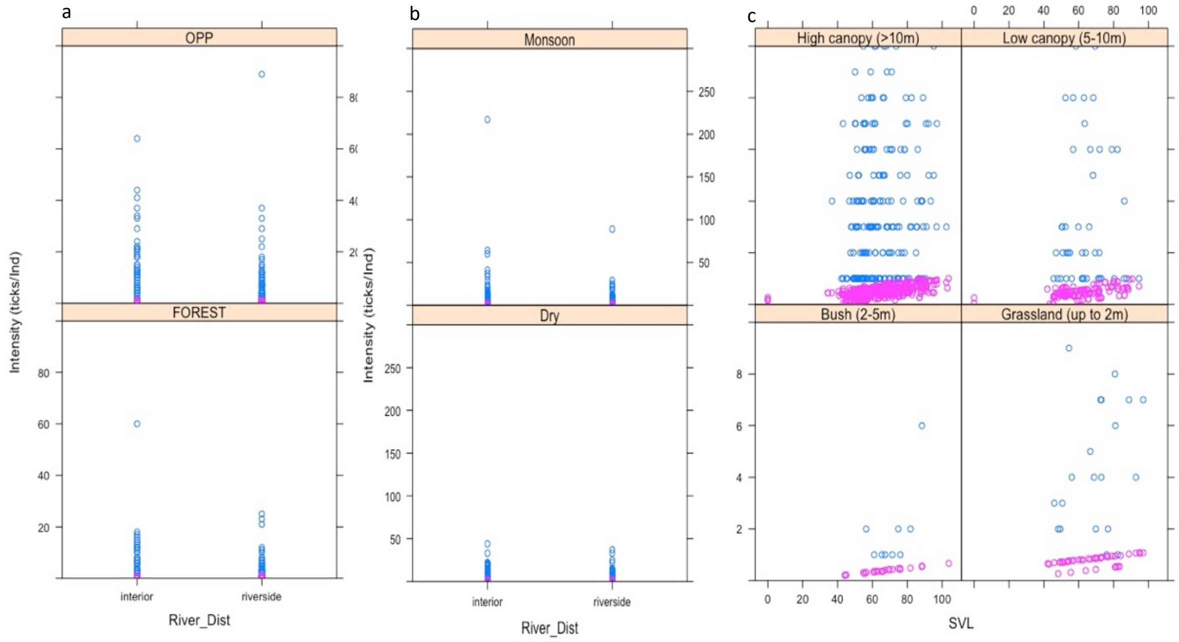

Fig 6.10. Effect of mixed factors on ticks' intensity: a) habitat/river distance; b) season/river distance; c) canopy height/body size. Blue dots represent data values, while red dots represent the trend.

6.4. Discussion

A. helvolum has been described as a reptile specialist (Volzit and Keirans, 2002; Petney et al., 2007;), although there are some records of large mammals being infected by this species (Durden, 2008). *A. helvolum* is associated to the presence of Spotted Fever Group Rickettsiae vector (Doornbos et al., 2013), thus its ecology is relevant to understanding the potential risk of disease transmission to different wildlife species other than reptiles, and humans.

Anthropogenic landscapes, like those composed by oil palm plantations surrounding forested areas, favour the existence of large populations of Asian water monitor lizards. As these are one of the main hosts for those ticks, it becomes relevant to understand how host and parasite associate in a landscape like the Kinabatangan Floodplain. In this study, lizards' body size was strongly associated to the prevalence, intensity and density of ticks (post mean = 0.52, p < 0.001), in accordance to previous reports in other varanid species (*V. salvator* and *V. grayi*, Auffenberg 1988). This association may be explained by the fact that larger hosts offer larger surface areas for attachment and reduce tick intra-specific competition. It also increases the opportunity to infect individuals that spend more time on the ground than on the trees (Auffenberg, 1981; Auffenberg, 1988; King, 2002). Host distribution has a strong influence on tick distribution (Estrada-Peña, 2002; Stein et al., 2008), determining where adult ticks will lay their eggs and where larvae and nymphs will appear next season (Stein et al., 2008).

For *A. helvolum*, a reptile specialist and the only tick species identified in the sampled lizards, the abundance of lizards in the floodplain may play a particularly important role in the ecology of the tick, although it does not seem to be determinant, as other factors such as host size and vegetation structure. Unfortunately, at the moment there are no inventories of ectoparasites infecting wildlife species in the area, and no studies regarding the association of *A. helvolum* with other hosts. *A. helvolum* could be potentially found on other reptiles, such as reticulated pythons (*Malayopython reticulatus*), as well as rodents and domestic animals inhabiting plantations.

In this study, sites with more homogeneous canopy structure in plantations and forested areas showed the highest abundances of ticks. Ixodid ticks are sensitive to desiccation during the free-ranging stages (Gray, 1998; Diuk-Waser et al., 2006), and thus, vegetation density is essential for their survival (Semtner, 1971; Koch, 1984; Gray, 1998). Sites with a microenvironment of ~80% humidity are considered optimal for the development of ticks, while areas that exceed that percentage, such as flooded sites, have a negative impact on their development. Habitats with good vegetation cover, as well as abundance of decaying vegetation, may also provide an excellent micro-environment for their development (Gray, 1998). Old plots of oil palm plantation that usually have a dense understory, like those in the southern side of the river, offer a suitable habitat for the survival of the free-ranging stages of this parasite. These environmental circumstances can explain the higher prevalence and intensity of ticks per individual.

The intensity and aggregation of ectoparasites is influenced by a mixture of variables that include seasonality, and host abundance, habitat use and distribution (Brunner and Ostfeld, 2008). Asian water monitor lizards' abundance has a significant effect on the intensity of ticks in the study sites, as well as their body size and the presence of dense understory. These dense areas, such as grassland and riparian sites, bring the perfect combination of factors for the survival of *A. helvolum*. During the sampling period, we detected both nymphs and adults (female and male) attached to the body of the lizards. The axillar, chest, and inguinal region do not only provide an easy access to feeding, but also protection from sunlight and desiccation (Auffemberg, 1998). This suggests that lizards cover all the requirements for the full development of *A. helvolum* and that their distribution across the landscape may be determinant for the spatial distribution of ticks (Stein et al., 2008).

In most of the sites, the dry season provides the adequate humidity for the development of ticks, while the flood caused by monsonic weather seems to have an impact on ticks in these seasonally flooded areas, benefitting those living in high ground. Ixodid ticks are able to get into a diapause period (i.e. delay in development in response to adverse environmental conditions) whenever weather conditions or host availability are not favourable for their survival and wait for suitable conditions for their development (Gray, 1998; Brunner and Ostfeld, 2008, Randolph, 2004). In this case, the rainy season brings flooding to the study site, negatively affecting the survival of ticks in lowlands while favouring it in high ground, by providing adequate level of humidity.

Although some studies suggest that reptiles may be affected by ticks through pathogen transmission (Shall and Houle, 1992), others suggest that certain species may act as barriers against infection, as they are less efficient replicating *B. burgdorferi* than other animal host, despite of presenting seasonally higher intensities of ixodid ticks (Talleklint-Eisen and Eisen, 1999). *A. helvolum* has been identified as vector for Spotted Fever Group Rickettsia (Doornbos et al., 2013), however, the efficiency of *V. salvator* as a carrier is still uncertain. Therefore, the abundance of lizards in anthropogenic habitats such as plantations may represent a risk of infection to accidental hosts, such as domestic animals and humans (Durden et al., 2008). But if Asian water monitor lizards are inefficient carriers for the pathogen, their populations may act as biological barrier for *Rickettsia* transmission. Therefore, it is of great importance to understand, from a wider perspective, the ecology of *A. helvolum*, its specialization on Asian water monitor lizards and its interaction with other species of ticks, as well as the susceptibility of the Asian water monitor lizard as a carrier of rickettsial pathogens.

Habitat fragmentation has provided the Asian water monitor lizards, and other generalist species in Sabah, a suitable environment to inhabit. At the same time, the abundance of this large lizard in the landscape and the features of the preferred habitat, offer to *A. helvolum* a highly suitable collection of circumstances for survival. These findings bring out more questions regarding the specialization of this ixodid and its significance in mater of animal and human health within a fragmented landscape such as the Kinabatangan Floodplain.

Chapter 7
General Discussion

7.1. Summary of Aims

The main goal of this thesis was to understand how the *Varanus salvator* population has adapted to the forest lost and expansion of oil palm plantations within the fragmented landscape of the Kinabatangan Floodplain. By describing their demography and habitat preferences, this study aimed to understand the drivers behind the abundance and apparent preferences of *V. salvator* for anthropogenic habitats within the landscape and therefore, within its distribution range.

This study also intended to describe the possible consequences of *V. salvator*'s adaptation in terms of population health and parasite transmission. For this purpose, the goal was to address the question of how does the feeding behaviour differ between individuals living in the forested areas and those inhabiting the plantations, and how do these differences impact on the body condition and metabolic health of the Asian water monitor lizards. The study also aimed to understand how this dietary difference has an influence on the diversity of endoparasites, such as helminths and protozoans. In the same context of population health, the study attempted to understand how the population's dynamic within this fragmented landscape has impacted in the prevalence and intensity of an apparently Asian water monitor lizard's specialist ectoparasite, the tick *Amblyomma helvolum*.

7.2. Summary of findings

In **Chapter 2**, I showed that the Asian water monitor lizard's sub-populations are not only much lower in plantations than in forested areas, contrary to what has been suggested by others (Uyeda, 2009; Twining et al., 2017), but also that those sub-populations have lower rates of recruitment (birth or immigration) than in the forest. This finding suggests that the forest emits new individuals for the plantations. Since both sub-populations are stable with high survival probability and a balanced growth rate with higher proportion of young individuals, it is possible to suggest forested areas function as population sources supplying the plantations with new individuals.

Two different studies using mark and recapture have estimated abundances of 357 individuals/km^2 for *V. exanthematicus* (Bennett, 2000), a lizard that is half the size of *V. salvator*, and of 2,448 individuals of *V. komodensis* (Purwandana et al., 2007). The number of Asian water monitor lizards in this study and their estimated densities can be compared with these other two species relative to their body size. Consistently with *V. salvator*'s size being intermediate between that of *V. exanthematicus* and *V. komodensis,* its density estimation numbers are also between those of these two species. Thus, this study suggests that the Kinabatangan Floodplain is neither under- nor overpopulated by Asian water monitor lizards. On the contrary, the population is stable and in healthy numbers.

Long-term mark and recapture methods have proved to offer accurate estimations for the populations of Asian water monitor lizards, a cryptic species for which the population can be overestimated by either repeated counts or differences in catchability. On the one hand, morphological features of Asian water monitor lizards are very uniform among individuals and differentiation by distance surveys is almost impossible. On the other hand, food availability and habitat characteristics may have an influence in the success of trapping different individuals and, therefore, if catchability is not considered in the model, it is highly possible to under- or overestimate population sizes.

Chapter 3 demonstrated that Asian water monitor lizards have smaller home ranges in oil palm plantations than in forested areas, and that these differences could be explained by the abundance of food in plantations and the limited habitat needed for protection. Food and shelter availability are the main elements within an established home range that ensure the individual’s survival (Jewel, 1966; Baker, 1978). The core areas in both forest and plantations have a great abundance of prey (Majevsky, 2017) and also offer shelter and protection to the Asian water monitor lizards. Nonetheless, the characteristics of the terrain within the plantations, with low dense or absent understory and reduced connectivity between preferred habitats (with presence of water and riparian vegetation), limit the movements of the lizards. The abundance of food and protected sites in plantation results in the establishment of small home ranges with proportionally larger core areas relative to those observed in forest, where the home range can be as large as 4.5 km^2 with 1.5% of core areas dispersed within the whole home range.

The habitat selection analysis showed that the Asian water monitor lizard is not necessarily a generalist, in terms of habitat preferences. The GPS-tagged individuals presented high preference for those sites close to water bodies, such as rivers, small streams, dense understory and riparian vegetation (Wikramanayake and Green, 1989; Wikramanayake and Dryden, 1993; Harlow et al., 2010). The difference found between the two groups (forest and plantations) is that the utilization rate of the core areas is much higher in plantations than in forested areas, where the lizards are able to move between different core areas and maintain a balanced utilization of them. Although the previous chapter mentioned that there is no overpopulation of lizards in the study area, how the species uses the available resources may have consequences in the prey community, and this is a topic that needs to be further assessed.

The *fast food effect* is described in **Chapters 4** and **5**. Both chapters describe how the differences in dietary diversity between plantation and forest individuals impact their body condition, and the presence and abundance of endoparasites. In Chapter 3, I discussed how smaller home ranges in plantations could be influenced by the abundance of prey. In these chapters, the diet proved to be more diverse in forested areas than in plantations, where rodents were dominant. This quasi-homogeneous diet has an impact on some biochemical markers, such as cholesterol, uric acid and total proteins. All of them strongly associated with lizards feeding behaviour.

Even more interesting was the fact that, although the diet is different, the biochemical values are more similar between forested areas and the adjacent plantations. This effect is more evident between the smallest and narrowest patch of forest (Lot 5; north bank) and Hillco plantation, where values of cholesterol, uric acid and alkaline phosphatase show more similar patterns, than those between Lot 7 (also in the north bank) and the same plantation. It is possible that lizards inhabiting Lot 5 are no strangers to the adjacent plantation and, in contrast, lizards from Lot 7, which are far more distant from the plantation, are not influenced by it. The findings suggest that this influence is strong and goes as deep in the forest as to 700 meters (maximum distance between the main river and the plantation in the trapping area of Lot 5).

Regarding parasite diversity, the dominance of helminths such as capillarids, strongylids and *Strongyloides spp*. in plantations can be explained by the dominance of rodents in the diet of these lizards. Host diet is the best predictor to explain parasites diversity in carnivores (Leung and Koprivnikar, 2018) and this diversity helps to maintain a balanced community of parasites in the ecosystem, increasing competition and reducing rates of transmission, especially for those generalist parasites (Daszak et al., 2000; Fenton et al., 2002; Dobson, 2004; Frias and MacIntosh, 2019).

The high number of rodents in the diet, as well as the abundance of Asian water monitor lizards with limited dispersion, may have some influence on the survival of generalist parasites and therefore, in the rates of infection to other generalist carnivores, such as small felids and raptors. Similarly, this quasi-homogeneous diet may have a major impact on the body condition and health of other generalist carnivores, such as leopard cats (*Prionailurus bengalensis*) or civets (*e.g. Viverra tangalunga*, *Paradoxurus hermaphroditus*). These mammals also comfortably inhabit plantations and feed on rodents, probably at similar rates as Asian water monitor lizards, however as mammals, they are more susceptible to be affected by these biochemical and parasitic alterations.

Chapter 6 described the prevalence and abundance of a quasi-specialist ixodid tick, *Amblyomma helvolum* as the only ectoparasite identified on Asian water monitor lizards within the study area. The relevance of this ectoparasite is that, although it is considered a lizard's specialist, it has been collected also from mammals such as water buffaloes, pigs and deer (Volzit and Kerians, 2002; Durden et al., 2008). The tick is also catalogued as vector for spotted fever group rickettsiosis (Doornbos et al., 2013) and therefore, relevant in terms of veterinary and public health. The presence and abundance of ticks, is influenced by (1) the abundance and distribution of the host or hosts and (2) the characteristics of the habitat that will provide the resources to survive (Brunner and Ostfeld 2008). The abundance and distribution of Asian water monitor lizards, as well as their body size, play an important role in the distribution and abundance of *A. helvolum* which finds in riparian vegetation and grasslands a suitable habitat for survival, as well as development of larvae and nymphs.

Suitable habitats for lizards in plantations are equally suitable for the survival of *A. helvolum* and, therefore, the Asian water monitor lizard plays an important role in the dispersion of ticks in plantations. Nonetheless, the role of the lizards as carriers of pathogens such as *Rickettsia* is still uncertain. Asian water monitor lizards could be acting either as carriers or barriers for the transmission of these pathogens, and this is something worth exploring, as well as the risk of infection to other wild and domestic animals, humans included.

7.3. Limitations and future prospects of this study

This thesis provides a wide range of information regarding one of the most understudied varanids and represents the first long-term population assessment and distribution of *V. salvator* within its distribution range, as well as the description of the diet and its impact on the population’s health. Nonetheless, there are still questions that remain unanswered and which are of importance to increase our knowledge of Asian water monitor lizards in the fragmented landscape of the Kinabatangan Floodplain.

The demographic assessment will not be completed without information of the population’s sex ratio in the study area. A proper understanding of the distribution and proportion of males and females within the ecosystem may provide a more complete understanding of the dynamics of the population, and the identification of potential reproduction sites. As mentioned in Chapter 2, the determination of individual’s sex by conventional methods is complicated, can be potentially harmful to the animal during manual handling, and can be ambiguous (Böme, 1995). Therefore, there is a need for suitable molecular methods to be developed. In collaboration with Danau Girang Field Centre in Sabah, molecular primers have been designed to determine the sex of Asian water monitor lizards, however, PCR protocols are not fully functional and require further optimization (work in progress). Future work on molecular analysis will provide information regarding the sex of the individuals sampled, and to provide a more comprehensive description of the population dynamics in the area.

Asian water monitor lizards can be good bioindicators of the ecosystem’s health. As a top predator, the species is highly susceptible to accumulate several pollutants such as heavy metals and agrochemicals through the food web (Burger, 1996; Jones and Holladay, 2004). Studies suggest that the skin that lizards periodically shed can be a bio-accumulator of heavy metals and other pollutants, making it a suitable target for less invasive assays to assess the level of toxic elements ingested through the food web (Jones and Holladay, 2004). This also means that the prey needs to be tested in order to better understand the route of accumulation of the pollutants, all the way from invertebrates to rodents and other small mammals, and ending on the Asian water monitor lizard. Unfortunately, specialist laboratories are required to perform these analyses and no suitable facilities are yet available in Sabah. Future research will focus on the optimization of the toxicological analysis by using monitor lizard shedding.

A prey inventory conducted within the home ranges of the GPS tagged lizards during this project (Majevsky, 2017) suggests that the abundance of prey in core areas are higher than in transient ones. A parasitological survey, as well as a biochemical assessment of the preys in the core areas would provide relevant information to better understand parasite transmission through the trophic network. At the same time, it would be important to complement the information on *A. helvolum* by looking into the lizards’ distribution areas, and evaluate their suitability for the survival of ticks. Moreover, it would be of great relevance to assess the presence of *Rickettsia* in the Asian water monitor lizard population, and that of other pathogens transmitted by ixodids, in order to describe the role of the lizard in the dynamics of vector-borne diseases within the landscape (Krasnov et al., 2007; Vanwambeke et al., 2010). A multi-host survey is also highly recommended in order to understand how the interaction of other species, (i.e. rodents, leopard cats, deers, wild boars) and *V. salvator* influence in the distribution and abundance of *A. helvolum.*

Lastly, this study provided information regarding the home range of lizards inhabiting forested areas and oil palm plantations, but we still lack information regarding their behaviour in other anthropogenic habitats, such as touristic places, farms, villages and smallholder plantations. The Kinabatangan Floodplain has some sites with caves and limestone hills, as well as permanent swamps. How the Asian water monitor lizards use these habitats is also a question that needs to be addressed.

7.4. Implications for the management and conservation of the Kinabatangan Floodplain ecosystem.

Identifying biological, chemical and physical changes in the ecosystem is the main goal of the subject known as Ecosystem Health (Huges et al., 1992). To achieve this goal, indicator species are often used (Fausch et al., 1990). When choosing an indicator species, there should be enough information available about the species and its distribution range, as well as its role in the ecosystem (Rice, 2003). Specialist species are frequently the focus of attention for researchers and, although substantial bodies of information may become available for them, they are frequently not representative of the ecosystem's complexity, and due to their typically low densities and reduced distribution, they cannot be used as indicators of environmental status (Landres et al., 1988; Menge, 1995; Rice, 2003). Moreover, if those species are threatened or at risk of extinction, their densities can be further reduced, making them more complicated and expensive to study (Rice, 2003). Generalist species, on the other hand, are more abundant, often well distributed within the ecosystem, and can provide more representative information of the ecosystem's status. Nonetheless, generalist species are frequently adaptable to changes in the ecosystem and may fail to reflect the impact of those changes in the whole community in terms of diversity changes and species distribution (Hilty and Merelender, 2000). As they are also highly abundant and common in human modified landscapes, they result in lower costs and lower efforts when compared to the use of specialist and less abundant species (Morelli, 2015). Therefore, by combining information from generalist and specialist species we will be able to build a more comprehensive model that explains the effects of fragmentation, and that offers a more efficient and cost-effective strategy to explain landscape homogenization (Morelli, 2015).

Throughout this study it was assumed that the Asian water monitor lizard was doing perfectly well in fragmented landscapes and, therefore, in the Kinabatangan Floodplain as well. However, this study demonstrated that individuals are more abundant in forested areas than in plantations, and that they present larger home ranges and more opportunities for dispersion in the forest relative to plantations. The abundance and restricted dispersion in plantations, coupled with a homogenous diet, impact the lizard's body condition and the distribution of associated parasites without apparent consequences on the whole population's health, although representing what could occur on other generalist species, even more susceptible to be affected by these dietary switches.

The distribution of generalist predators can be used to understand the distribution of species that are lower in the food chain (Sergio et al., 2005). As a reptile, the Asian water monitor lizard has the quality of being more resilient to metabolic alterations, as well as to infection or diseases and, as a top predator, it can be indicative of the health condition of the prey community and other predators in the ecosystem (Burger, 1992; Jones and Holladay, 2006). Ideally, results like the ones observed here could be obtained from other top predators or species exposed to similar diet conditions, *e.g.* carnivores such as clouded leopards, leopard cats, or primates such as macaques. However, assessing the population health of those species is hardly affordable and requires larger sampling efforts without the guarantee of getting a sufficient sample size (Holt & Miller 2010, Rainio & Niemela 2003). The utilization of Asian water monitor lizards to understand effects of habitat fragmentation, *e.g*. the *fast food effect*, may represent an efficient tool for generating information from a large number of individuals well distributed within the landscape in a short period of time.

Due to the broad diet, and selective habitat requirements, monitoring the dispersion of the Asian water monitor lizards' populations can be an indicator of the abundance and distribution of the prey community, from amphibians and invertebrates up to rodents and other small mammals (Majevsky, 2017). This dynamic can be also an indicator of the presence in the same area of other meso-predators that feed on the same preys. In the same way, it is very likely that predators sharing the niche with Asian water monitor lizards are affected by the same *fast food effect*. Furthermore, although Asian water monitor lizards can be resilient to the effect of some parasites and metabolic alterations, mammals and birds are more susceptible and vulnerable. Therefore, the impact of a quasi-homogeneous diet might be more disastrous for the latter.

7.5. Highlights and conclusions

Habitat fragmentation and the expansion of oil palm and other anthropogenic activities are still an ongoing process and go at very quick rates. Therefore, there is an urgent need to understand how this habitat transformation impacts on the animal communities. Long-term projects are necessary to understand how the animals adapt to the newly transformed landscape through time, but it is also important to consider species that are already abundant and widely distributed to build stronger models that explain the consequences of fragmentation, especially regarding carnivores. This study highlights the importance of using a generalist species as a model to understand how human-modified habitats, such as oil palm plantations, influence the dynamic of the forest ecosystem beyond its boundaries. It also highlights the importance of evaluating not only the ecological aspects of this influence but also the impact on the health of animal communities.

The information generated during this study must be complemented with subsequent work focused on (1) parasite transmission through trophic networks, (2) ecotoxicology and bioaccumulation as a third element of the *fast food effect*, (3) the dispersion of *Amblyomma helvolum* and the role of *V. salvator* in the ecology of tick-borne diseases, (4) the impact of other human-modified habitats, and (5) genetic health of the lizard population. The more we know about Varanus salvator, the more useful the species will become as an indicator of the ecosystem health.

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APPENDIX I

Table I. 1. List of varanid species, their distribution ranges, size, and IUCN Red List status (CE = Critically Endangered; E = Endangered; V = Vulnerable; NT = Near Threatened; LC =Least Concern; DD = Data Deficient; NL = Not Listed). Size is estimated as Snout to Vent Length (SVL), unless stated otherwise.

Species	Distribution	SVL (mm)	IUCN status
AFRICA			
V. albigularis	South and East Africa	500	NL
V. exanthemicus	Central Africa	320	LC
V. griseus	Northern Africa /Arabia / West Asia	830[†]	NL
V. niloticus	Central and Southern Africa	600	NL
V. ornatus	West Africa	1900[†]	NL
ASIA			
V. yemensis	Southern Arabia	470	DD
V. bengalensis	Southeast Asia, except Borneo, Philippines and Sulawesi	580	LC
V. dumerili	Malaysia and Indonesia	292	NL
V. flavensis	North India	315	LC
V. komodensis	Southern islands of Indonesia	1540	V
V. juxtindicus	Solomon Islands	504	LC
V. macraei	Indonesian New Guinea	350	E
V. olivaceous	Philippines	509	V
V. rudicollis	Malaysia / Sumatra	590	NL
V. mabitang	Philippines	527	E
V. salvator[§]	Sri Lanka / North India /South east Asia (Mainland, Philippines and Sunda Islands)	1650[†]	LC[œ]
V. caerulivirens	Moluccas islands	400	NL
V. cerambonensis	Moluccas islands	409	NL
V. yuwonoi	Moluccas islands	532	NL
OCEANIA			
V. acanthurus	Northern Australia	241	LC
V. baritji	Northern Australia	171	LC
V. brevicauda	Central and North west Australia	110	LC
V. caudolineatus	Central and West Australia	118	LC
V. doreanus	New Guinea	460	LC
V. eremius	Central and West Australia	160	LC
V. finschi	New Guinea /Australia	305	LC
V. giganteus	Central and West Australia	880	LC
V. gilleni	Central, South and West Australia	186	LC

[†] = size estimated as Total Length; [§] = includes the eight known subspecies; [œ] = subspecies *V. s. nuchalis* is the only one listed as NT.

Table 1 (Cont.). List of varanid species, their distribution ranges, size, and IUCN Red List status (CE = Critically Endangered; E = Endangered; V = Vulnerable; NT = Near Threatened; LC =Least Concern; DD = Data Deficient; NL = Not Listed). Size is estimated as Snout to Vent Length (SVL), unless stated otherwise.

Species	Distribution	SVL (mm)	IUCN status
OCEANIA			
V. glauteri	North west coast of Australia	215	LC
V. glebopalma	Northern Australia	290	LC
V. gouldii	Australia (Widely distributed)	590	LC
V. indicus	North Australia / New Guinea	340	LC
V. jobensis	New Guinea	445	LC
V. keithhornei	Cape York Peninsula, Australia	260	LC
V. kingorum	Northern Australia	114	LC
V. kordensis	Papua New Guinea	900†	DD
V. melinus	Moluccas Islands	420	NL
V. mertensi	Northern Australia	48	CE
V. mitchelli	Northern Australia	320	CE
V. panoptes	North and West Australia / New Guinea	740	LC
V. pilbarensis	East Australia	169	LC
V. primordius	Northern Australia	120	LC
V. prasinus	New Guinea	295	LC
V. rosenbergi	Southern Australia	395	LC
V. salvadorii	New Guinea	1160	LC
V. scalaris	Northern Australia / New Guinea	250	LC
V. semiremex	North east Australia	250	LC
V. spenceri	North- Central Australia	550	LC
V. spinulosus	Solomon Islands	312	LC
V. storri	Northern Australia	132	LC
V. timorensis	Timor Islands	600†	NL
V. tristis	Australia (Widely distributed)	305	LC
V. varius	East and Southern Australia	765	LC

† = size estimated as Total Length; § = includes the eight known subspecies; œ = subspecies *V. s. nuchalis* is the only one listed as NT.

APPENDIX II

Table 1. Ranking of POPAN models for Population size and survival estimations performed in program Mark. Ranking is according with the AICc value.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
{Φ (·) *p*(*g*) *pent*(*t*) *N*(*g*) PIM}	823.9098	0	0.39075	1	9	0	805.6881
{Φ (*t*) *p*(*g*) *pent*(t) *N*(*g*) PIM}	825.8285	1.9187	0.14971	0.3831	10	0	805.5572
{Φ (·) *p*(*g*) *pent*(*g*) *N*(*g*) PIM}	825.9173	2.0075	0.14321	0.3665	11	0	803.5913
{Φ (*g*) *p*(*g*) *pent*(*t*) *N*(g) PIM}	826.3258	2.416	0.11675	0.2988	12	0	801.9401
{Φ (*t*) *p*(*g*) *pent*(*g*) *N*(*g*) PIM}	827.945	4.0352	0.05196	0.133	12	0	803.5594
{Φ (·) *p*(*g*) *pent*(*g*t*) *N*(*g*) PIM}**	828.0084	4.0986	0.05034	0.1288	15	0	797.4129
{Φ (*t*) *p*(*g*t*) *pent*(*t*) *N*(*g*) PIM}**	828.4279	4.5181	0.04081	0.1044	16	0	795.7521
{Φ (*t*) *p*(*g*) *pent*(*g*t*) *N*(*g*) PIM}**	829.9438	6.034	0.01913	0.049	16	0	797.268
{Φ (*g*) *p*(*g*t*) *pent*(*t*) *N*(*g*) PIM}**	830.6168	6.707	0.01366	0.035	12	0	806.2312
{Φ (·) *p*(*g*t*) *pent*(*g*) *N*(*g*) PIM}**	832.7639	8.8541	0.00467	0.012	17	0	798.0027
{Φ (*g*) *p*(*t*) *pent*(*t*) *N*(*g*) PIM}	833.0379	9.1281	0.00407	0.0104	10	0	812.7666
{Φ (*t*) *p*(*g*t*) *pent*(*g***t*) *N*(*g*) PIM}**	833.2671	9.3573	0.00363	0.0093	18	0	796.4153
{Φ (*g*) *p*(*g*) *pent*(*g*t*) *N*(*g*) PIM}**	833.3663	9.4565	0.00345	0.0088	18	0	796.5145
{Φ (*g*t*) *p*(*t*) *pent*(*t*) *N*(*g*) PIM}**	833.954	10.0442	0.00258	0.0066	15	0	803.3585
{Φ (*g*) *p*(*g*) *pent*(*g*) *N*(*g*) PIM}	835.3466	11.4368	0.00128	0.0033	13	0	808.8962
{Φ (·) *p*(*g*t*) *pent*(*t*) *N*(*g*) PIM}**	835.9567	12.0469	0.00095	0.0024	9	0	817.7351
{Φ (*g*t*) *p*(*g***t*) *pent*(*g***t*) *N*(*g*) PIM}**	837.0645	13.1547	0.00054	0.0014	21	0	793.9095
{Φ (*g*) *p*(*g*t*) *pent*(*g***t*) *N*(*g*) PIM}**	837.1141	13.2043	0.00053	0.0014	21	0	793.9591
{Φ (·) *p*(*t*) *pent*(*t*) *N*(*g*) PIM}	838.318	14.4082	0.00029	0.0007	9	0	820.0964
{Φ (*g*t*) *p*(*g***t*) *pent*(*t*) *N*(*g*) PIM}**	838.403	14.4932	0.00028	0.0007	19	0	799.4554
{Φ (·) *p*(*g*t*) *pent*(*g***t*) *N*(·) PIM}**	839.6435	15.7337	0.00015	0.0004	17	0	804.8823
{Φ (*t*) p(*g*t*) *pent*(*g***t*) *N*(·) PIM}**	839.9932	16.0834	0.00013	0.0003	17	0	805.232
{Φ (*g*) *p*(*g*t*) *pent*(*g***t*) *N*(·) PIM}**	840.0581	16.1483	0.00012	0.0003	19	0	801.1105
{Φ (*t*) *p*(*t*) *pent*(*t*) *N*(*g*) PIM}	840.5078	16.598	0.0001	0.0003	8	0	824.3307
{Φ (*g*) *p*(·) *pent*(*g*) *N*(*g*) PIM}	840.6465	16.7367	0.00009	0.0002	13	0	814.196
{Φ (*g*t*) *p*(*g*) *pent*(*g***t*) *N*(*g*) PIM}**	840.7822	16.8724	0.00008	0.0002	21	0	797.6272
{Φ (*g*) *p*(*t*) *pent*(*g*t*) *N*(*g*) PIM}**	840.8953	16.9855	0.00008	0.0002	18	0	804.0435
{Φ (*g*t*) *p*(*g*) *pent*(*g*) *N*(*g*) PIM}**	840.9479	17.0381	0.00008	0.0002	17	0	806.1867
{Φ (*g*) *p*(·) *pent*(*g*t*) *N*(*g*) PIM}**	840.9687	17.0589	0.00008	0.0002	17	0	806.2075
{Φ (*g*) *p*(*t*) *pent*(*g*) *N*(*g*) PIM}	840.9938	17.084	0.00008	0.0002	15	0	810.3983
{Φ (*g*) *p*(*g*t*) *pent*(*g*) *N*(*g*) PIM}**	841.2733	17.3635	0.00007	0.0002	15	0	810.6778
{Φ (*g*t*) *p*(*t*) *pent*(*g***t*) *N*(*g*) PIM}**	842.1494	18.2396	0.00004	0.0001	21	0	798.9944
{Φ (*g*) *p*(*t*) *pent*(*t*) *N*(·) PIM}	842.2749	18.3651	0.00004	0.0001	8	0	826.0978
{Φ (*t*) *p*(*g*t*) *pent*(*t*) *N*(·) PIM}**	842.2879	18.3781	0.00004	0.0001	13	0	815.8374
{Φ (·) *p*(*g*t*) *pent*(*g***t*) *N*(*g*) PIM}**	842.8266	18.9168	0.00003	0.0001	16	0	810.1509
{Φ (·) *p*(*g*t*) *pent*(*t*) *N*(·) PIM}**	843.7158	19.806	0.00002	0.0001	13	0	817.2654
{Φ (*g*) *p*(*g*) *pent*(*t*) *N*(·) PIM}	843.8202	19.9104	0.00002	0.0001	11	0	821.4943

Table 1 (cont.). Ranking of POPAN models for Population size and survival estimations performed in program Mark. Ranking is according with the AICc value.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
{Φ (t) p(t) pent(g*t) N(g) PIM}	843.9997	20.0899	0.00002	0.0001	15	0	813.4042
{Φ (g*t) p(g*t) pent(g) N(g) PIM}	844.2262	20.3164	0.00002	0.0001	18	0	807.3744
{Φ (g*t) p(g) pent(t) N(g) PIM}	844.2875	20.3777	0.00001	0	15	0	813.6919
{Φ (t) p(t) pent(g) N(g) PIM}	844.4546	20.5448	0.00001	0	12	0	820.0689
{Φ (g*t) p(g*t) pent(g*t) N(·) PIM}	844.7163	20.8065	0.00001	0	23	0	797.3329
{Φ (·) p(t) pent(g) N(g) PIM}	844.7359	20.8261	0.00001	0	12	0	820.3503
{Φ (·) p(·) pent(g) N(g) PIM}	844.8757	20.9659	0.00001	0	10	0	824.6044
{Φ (g*t) p(·) pent(g) N(g) PIM}	845.1726	21.2628	0.00001	0	17	0	810.4114
{Φ (g) p(g*t) pent(t) N(·) PIM}	845.4359	21.5261	0.00001	0	17	0	810.6747
{Φ (·) p(·) pent(g*t) N(g) PIM}	845.6579	21.7481	0.00001	0	14	0	817.1375
{Φ (·) p(t) pent(g*t) N(g) PIM}	845.663	21.7532	0.00001	0	15	0	815.0675
{Φ (g*t) p(g*t) pent(t) N(·) PIM}	846.6081	22.6983	0	0	21	0	803.4531
{Φ (t) p(·) pent(g) N(g) PIM}	846.8975	22.9877	0	0	11	0	824.5716
{Φ (g*t) p(t) pent(t) N(·) PIM}	847.2983	23.3885	0	0	12	0	822.9126
{Φ (·) p(t) pent(t) N(·) PIM}	847.5136	23.6038	0	0	5	0	837.4401
{Φ (t) p(·) pent(g*t) N(g) PIM}	847.6209	23.7111	0	0	15	0	817.0253
{Φ (g*t) p(g) pent(t) N(·) PIM}	847.8142	23.9044	0	0	15	0	817.2187
{Φ (g) p(t) pent(g*t) N(·) PIM}	848.0706	24.1608	0	0	14	0	819.5501
{Φ (t) p(g*t) pent(g) N(g) PIM}	848.3417	24.4319	0	0	15	0	817.7462
{Φ (·) p(g*t) pent(g) N(·) PIM}	848.4958	24.586	0	0	14	0	819.9754
{Φ (t) p(t) pent(t) N(·) PIM}	849.1897	25.2799	0	0	6	0	837.0866
{Φ (g) p(g*t) pent(g) N(·) PIM}	849.4912	25.5814	0	0	18	0	812.6394
{Φ (g*t) p(g*t) pent(g) N(·) PIM}	851.8501	27.9403	0	0	21	0	808.6951
{Φ (·) p(t) pent(g*t) N(·) PIM}	852.8064	28.8966	0	0	11	0	830.4805
{Φ (g) p(·) pent(t) N(g) PIM}	852.9074	28.9976	0	0	9	0	834.6857
{Φ (g*t) p(t) pent(g*t) N(·) PIM}	853.0155	29.1057	0	0	18	0	816.1637
{Φ (g) p(g) pent(g*t) N(·) PIM}	853.5505	29.6407	0	0	17	0	818.7893
{Φ (g) p(g) pent(g) N(·) PIM}	854.295	30.3852	0	0	13	0	827.8446
{Φ (t) p(t) pent(g*t) N(·) PIM}	854.3141	30.4043	0	0	12	0	829.9284
{Φ (g*t) p(g) pent(g*t) N(·) PIM}	857.3459	33.4361	0	0	15	0	826.7503
{Φ (g) p(t) pent(g) N(·) PIM}	859.7631	35.8533	0	0	10	0	839.4918
{Φ (·) p(g) pent(g*t) N(·) PIM}	860.2042	36.2944	0	0	14	0	831.6837
{Φ (g*t) p(·) pent(t) N(g) PIM}	861.0104	37.1006	0	0	14	0	832.49
{Φ (·) p(g) pent(g) N(·) PIM}	861.5992	37.6894	0	0	10	0	841.3279
{Φ (t) p(g) pent(g*t) N(·) PIM}	862.1718	38.262	0	0	15	0	831.5762
{Φ (g) p(·) pent(t) N(·) PIM}	863.6276	39.7178	0	0	8	0	847.4505
{Φ (t) p(g) pent(g) N(·) PIM}	863.6533	39.7435	0	0	11	0	841.3273
{Φ (t) p(·) pent(t) N(g) PIM}	864.4453	40.5355	0	0	8	0	848.2682
{Φ (g*t) p(t) pent(g) N(·) PIM}	864.9747	41.0649	0	0	14	0	836.4542

Table 1 (cont.). Ranking of POPAN models for Population size and survival estimations performed in program Mark. Ranking is according with the AICc value.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
{Φ (·) *p*(*t*) *pent*(*g*) *N*(·) PIM}	865.1147	41.2049	0	0	7	0	850.9772
{Φ (*t*) *p*(*t*) *pent*(*g*) *N*(·) PIM}	866.9715	43.0617	0	0	8	0	850.7944
{Φ (*t*) *p*(*g*t*) *pent*(*g*) *N*(·) PIM}	868.7532	44.8434	0	0	16	0	836.0774
{Φ (·) *p*(·) *pent*(*t*) *N*(·) PIM}	868.8003	44.8905	0	0	5	0	858.7268
{Φ (*g*t*) *p*(·) *pent*(*t*) *N*(·) PIM}	868.8313	44.9215	0	0	12	0	844.4456
{Φ (*g*) *p*(·) *pent*(*g*t*) *N*(·) PIM}	870.7836	46.8738	0	0	14	0	842.2631
{Φ (*g*t*) *p*(*t*) *pent*(*g*) *N*(*g*) PIM}	871.8674	47.9576	0	0	16	0	839.1916
{Φ (*g*) *p*(·) *pent*(*g*) *N*(·) PIM}	874.4532	50.5434	0	0	10	0	854.1819
{Φ (·) *p*(·) *pent*(*gt) *N*(·) PIM}**	875.8345	51.9247	0	0	11	0	853.5086
{Φ (*g*t*) *p*(·) *pent*(*g*t*) *N*(·) PIM}	876.1389	52.2291	0	0	18	0	839.2871
{Φ (*t*) *p*(·) *pent*(*g*t*) *N*(·) PIM}	877.882	53.9722	0	0	12	0	853.4963
{Φ (*g*t*) *p*(·) *pent*(*g*) *N*(·) PIM}	879.7201	55.8103	0	0	14	0	851.1996
{Φ (·) *p*(*g*) *pent*(*t*) *N*(·) PIM}	879.9857	56.0759	0	0	6	0	867.8826
{Φ (*t*) *p*(·) *pent*(*t*) *N*(·) PIM}	880.7939	56.8841	0	0	5	0	870.7204
{Φ (*t*) *p*(·) *pent*(*g*) *N*(·) PIM}	881.5418	57.632	0	0	8	0	865.3647
{Φ (*t*) *p*(*g*) *pent*(*t*) *N*(·) PIM}	882.0074	58.0976	0	0	7	0	867.8698
{Φ (*g*t*) *p*(*g*) *pent*(*g*) *N*(·) PIM}	891.519	67.6092	0	0	15	0	860.9235

Table 2. Ranking of Pradel models for Population growth rates and survival estimations performed in program Mark. Ranking is according with the AICc value.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
{Φ (·) *p*(*g*) λ (*g*) PIM}	2152.6293	0	0.28119	1	9	10.5331	2134.4076
{Φ (·) *p*(*g*) λ (*g*) PIM}	2152.6293	0	0.28119	1	9	10.5331	2134.4076
{Φ (*t*) *p*(*g*) λ (*g*) PIM}	2153.7416	1.1123	0.16124	0.5734	10	9.5959	2133.4703
{Φ (*t*) *p*(*g*) λ (*g*) PIM}	2153.7416	1.1123	0.16124	0.5734	10	9.5959	2133.4703
{Φ (*g*) *p*(·) λ (g) PIM}	2157.543	4.9137	0.0241	0.0857	9	15.4469	2139.3213
{Φ (*g*) *p*(·) λ (*g*) PIM}	2157.543	4.9137	0.0241	0.0857	9	15.4469	2139.3213
{Φ (*g*) *p*(*g*) λ (*g*) PIM}	2157.8021	5.1728	0.02117	0.0753	12	9.5419	2133.4164
{Φ (*g*) *p*(*g*) λ (*g*) PIM}	2157.8021	5.1728	0.02117	0.0753	12	9.5419	2133.4164
{Φ (*g*) *p*(*t*) λ (*g*) PIM}	2159.8357	7.2064	0.00766	0.0272	11	13.6353	2137.5098
{Φ (*g*) *p*(*t*) λ (*g*) PIM}	2159.8357	7.2064	0.00766	0.0272	11	13.6353	2137.5098
{Φ (·) *p*(·) λ (g) PIM}	2162.432	9.8027	0.00209	0.0074	6	26.4544	2150.3289
{Φ (·) *p*(·) λ (*g*) PIM}	2162.432	9.8027	0.00209	0.0074	6	26.4544	2150.3289
{Φ (*t*) *p*(·) λ (*g*) PIM}	2163.6021	10.9728	0.00116	0.0041	7	25.59	2149.4645
{Φ (*t*) *p*(·) λ (*g*) PIM}	2163.6021	10.9728	0.00116	0.0041	7	25.59	2149.4645
{Φ (·) *p*(*t*) λ (*g*) PIM}	2164.6501	12.0208	0.00069	0.0025	8	24.5985	2148.473
{Φ (*t*) *p*(*t*) λ (*g*) PIM}	2164.6501	12.0208	0.00069	0.0025	8	24.5985	2148.473
{Φ (·) *p*(*t*) λ (*g*) PIM}	2164.6501	12.0208	0.00069	0.0025	8	24.5985	2148.473
{Φ (*t*) *p*(*t*) λ (*g*) PIM}	2164.6501	12.0208	0.00069	0.0025	8	24.5985	2148.473

APPENDIX III

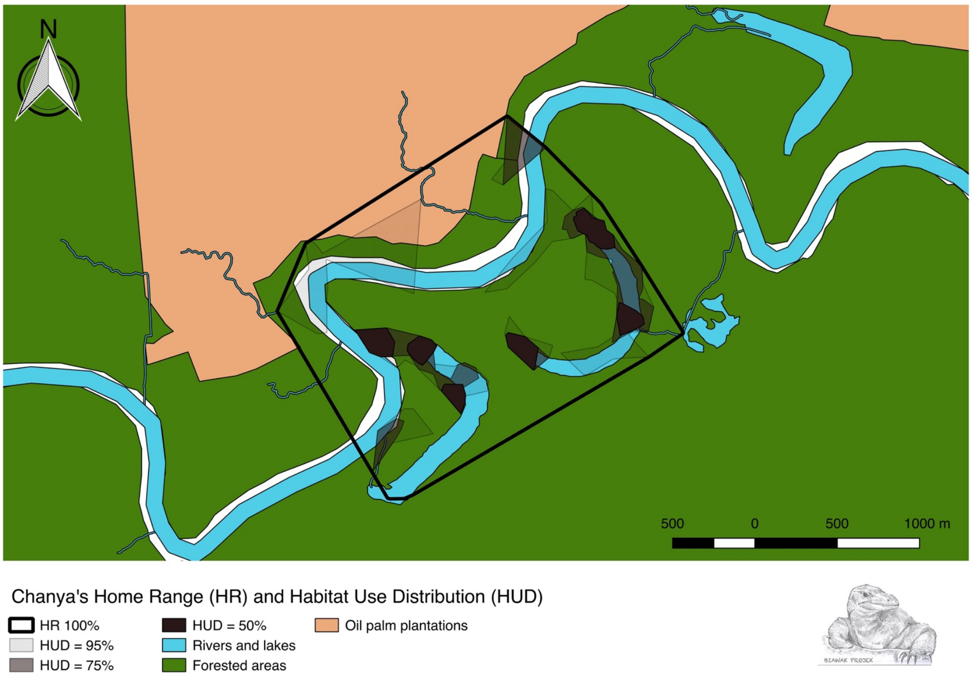


Fig 1. Home range and Habitat use distribution of Chanya. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

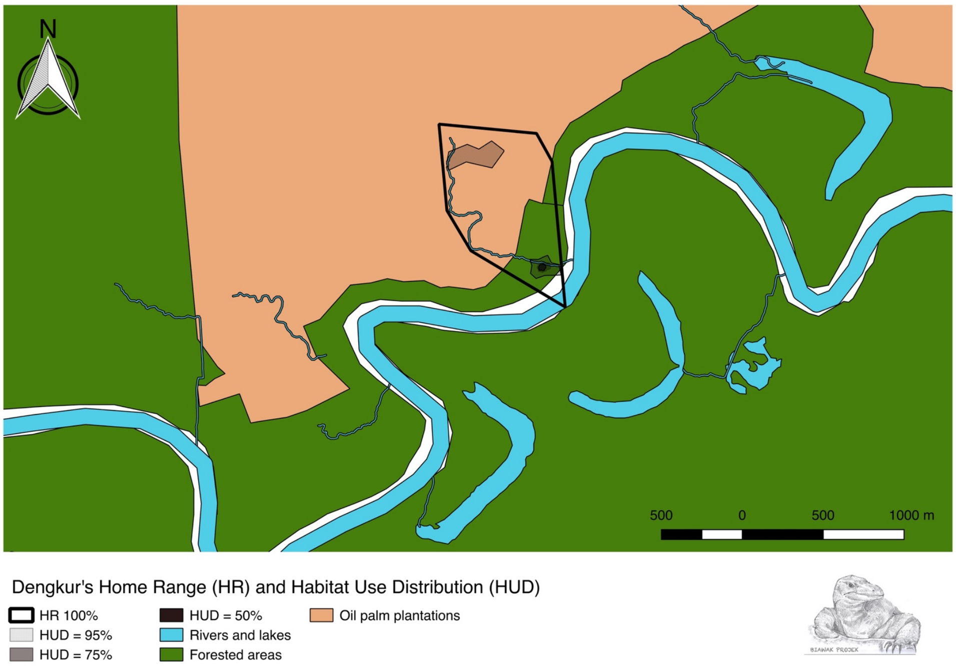


Fig 2. Home range and Habitat use distribution of Dengkur. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

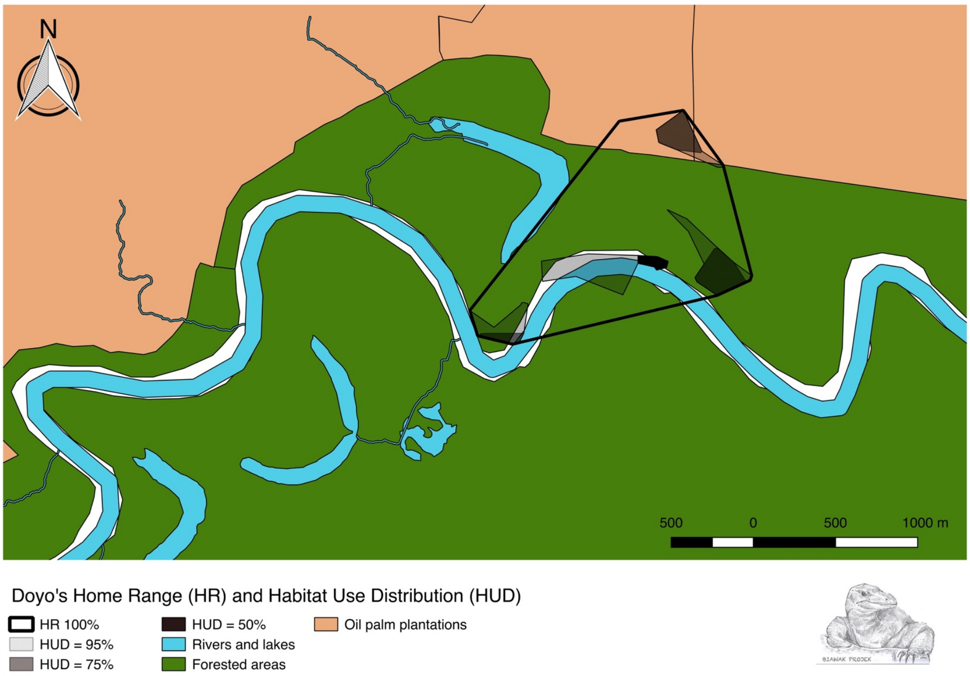


Fig 3. Home range and Habitat use distribution of Doyo. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method

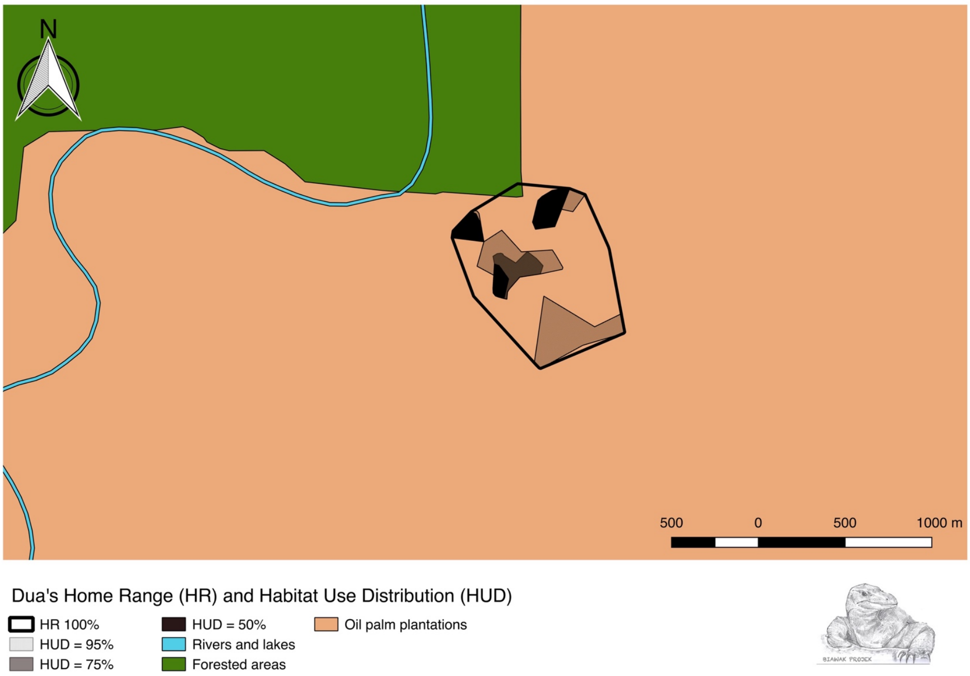


Fig 4. Home range and Habitat use distribution of Dua. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

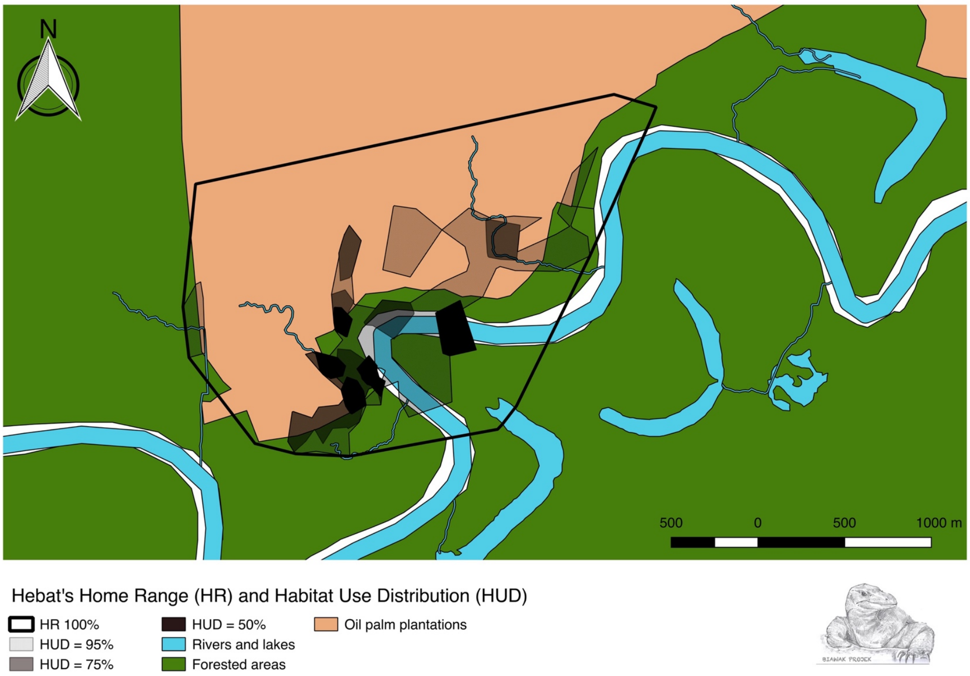


Fig 5. Home range and Habitat use distribution of Hebat. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

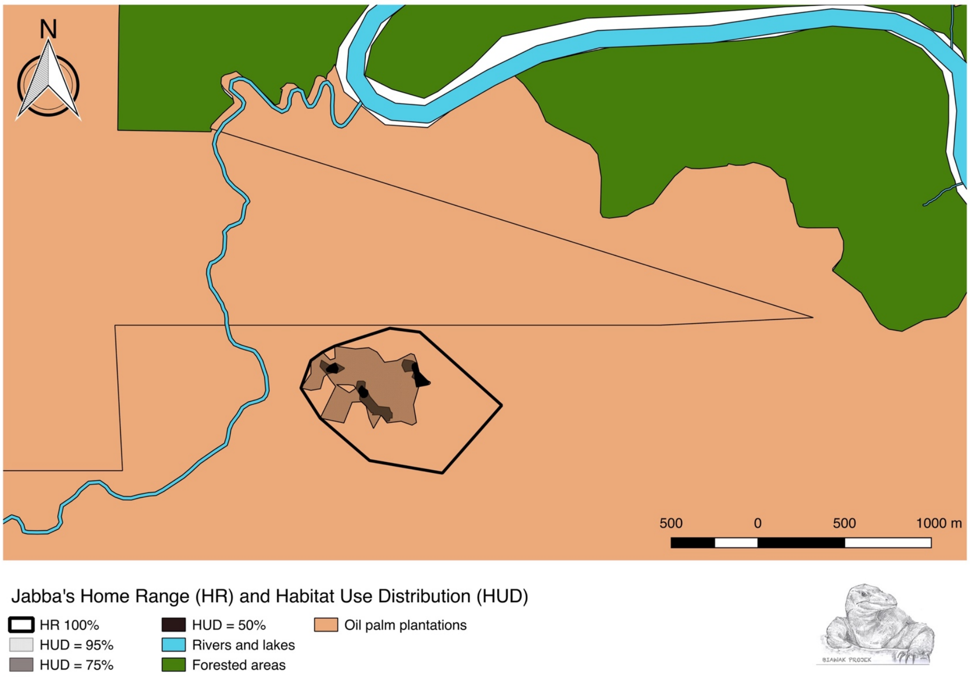


Fig 6. Home range and Habitat use distribution of Jabba. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

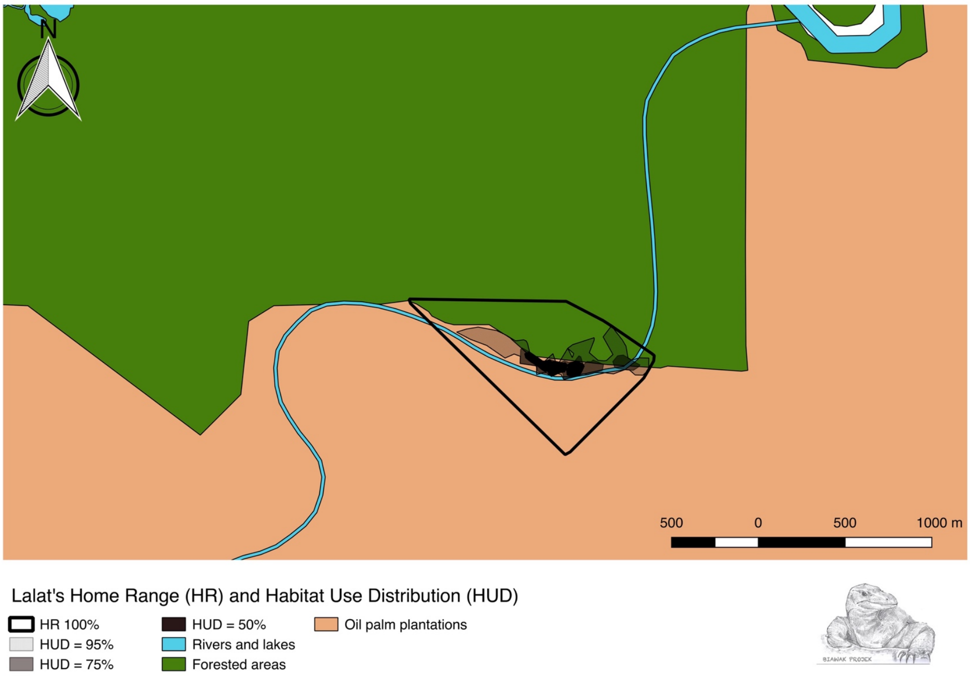


Fig 7. Home range and Habitat use distribution of Lalat. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

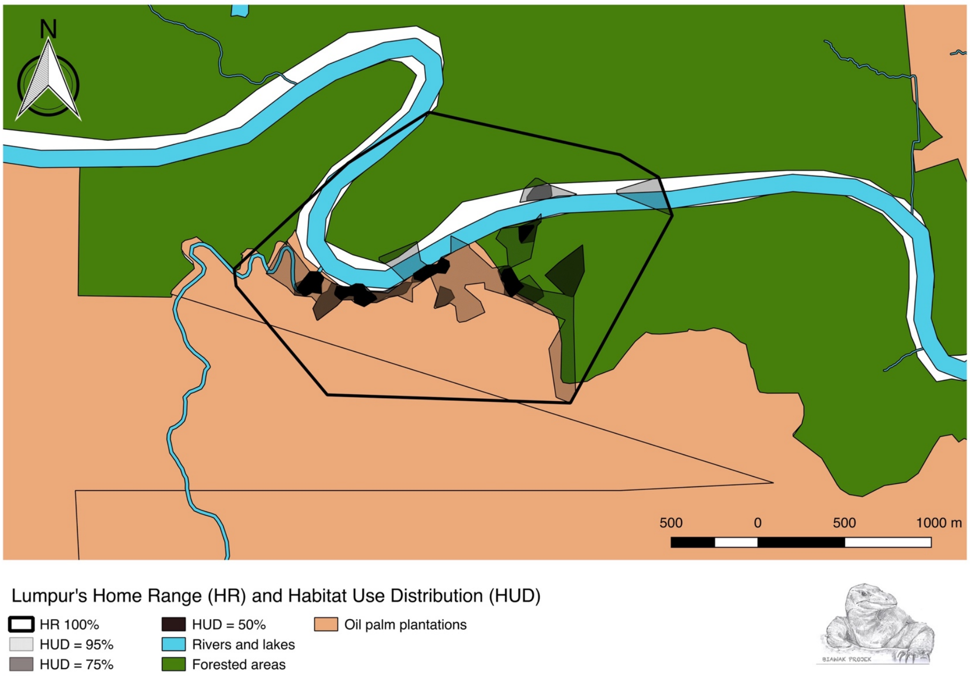


Fig 8. Home range and Habitat use distribution of Lumpur. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

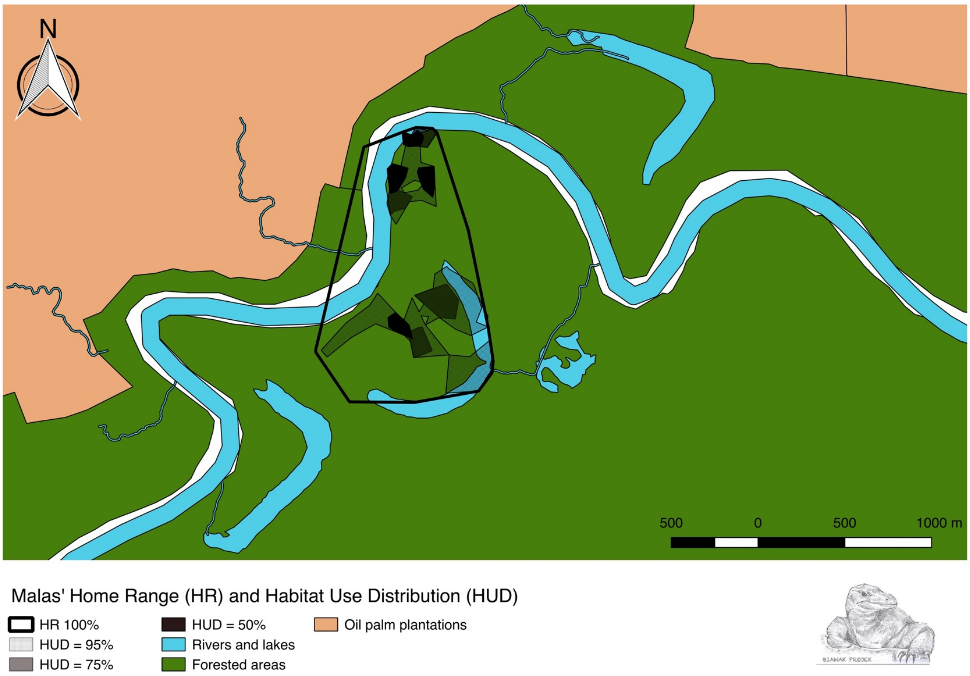


Fig 9. Home range and Habitat use distribution of Malas. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

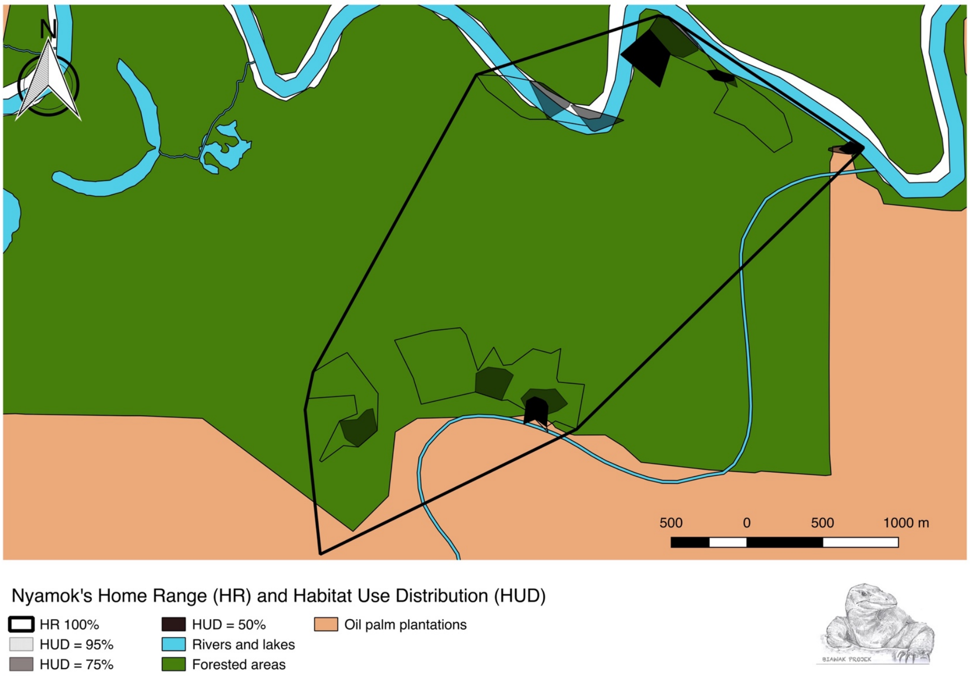


Fig 10. Home range and Habitat use distribution of Nyamok. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

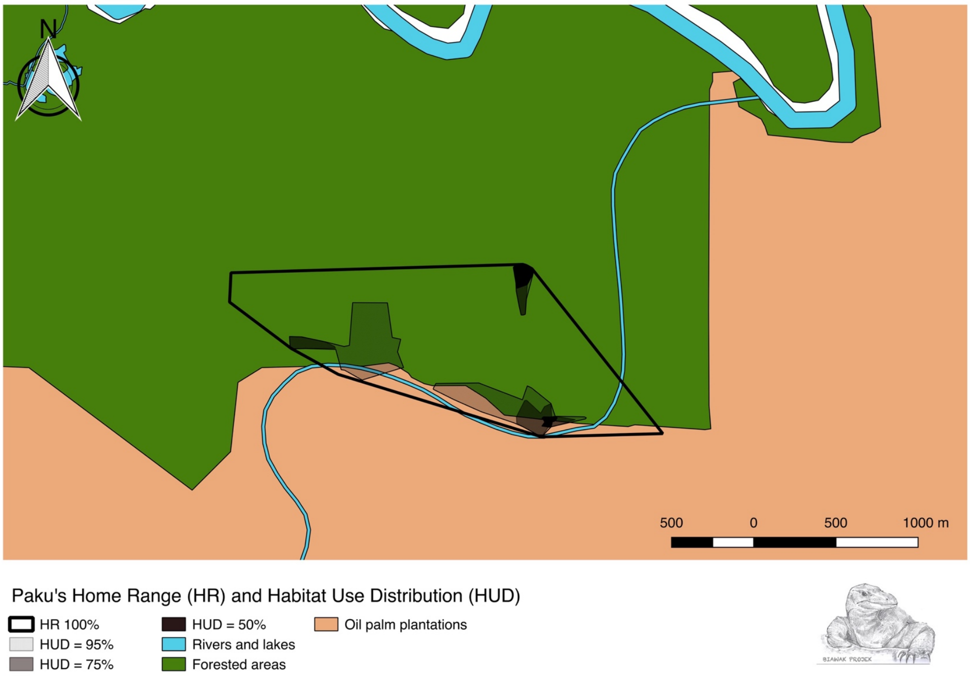


Fig 11. Home range and Habitat use distribution of Paku. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

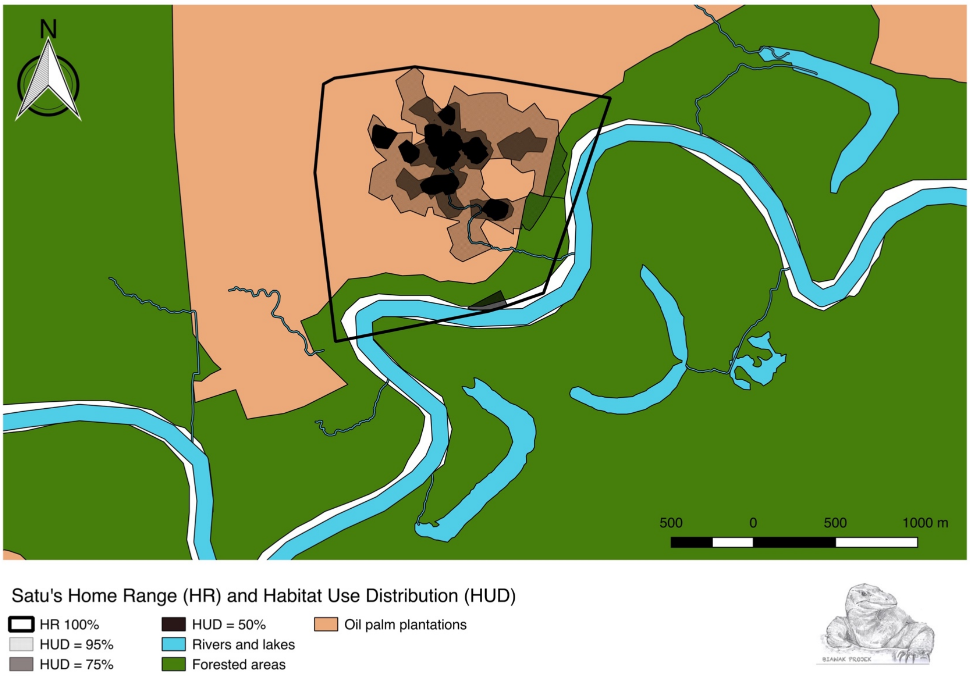


Fig 12. Home range and Habitat use distribution of Satu. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

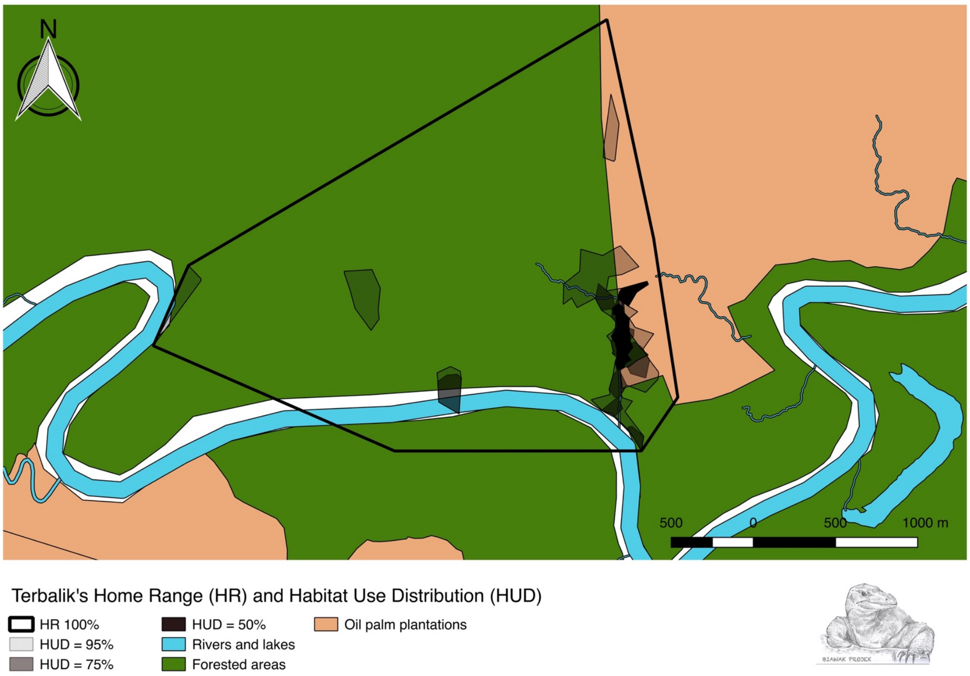


Fig 13. Home range and Habitat use distribution of Terbalik. Home ranges are expressed according to the MCP 100% method and three levels of the a-LoCoH method.

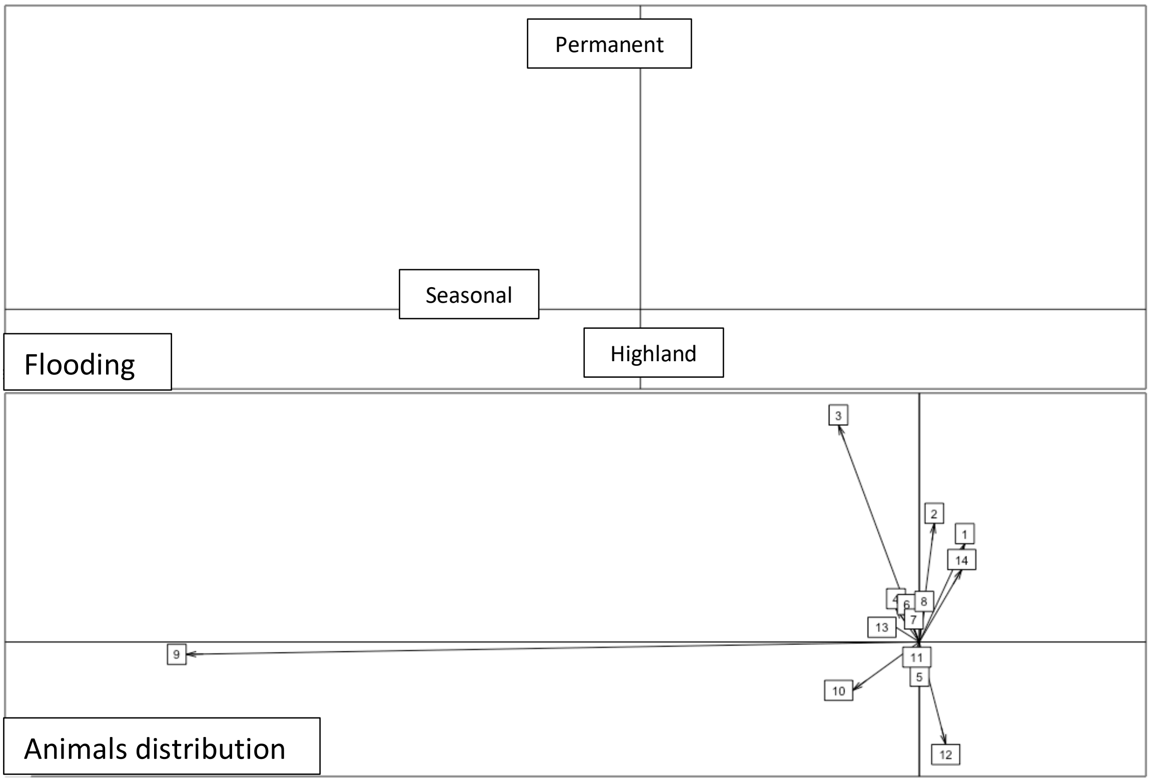


Fig 15. Graphic representation of the animal distribution according with the selection ratios for the different categories of flooding. The above plot represents the position of each one of the three levels of flooding. The bellow plot represents the distribution of the tagged individuals towards those categories. Each number correspond to the individuals according with the disposition of the maps in this appendix.

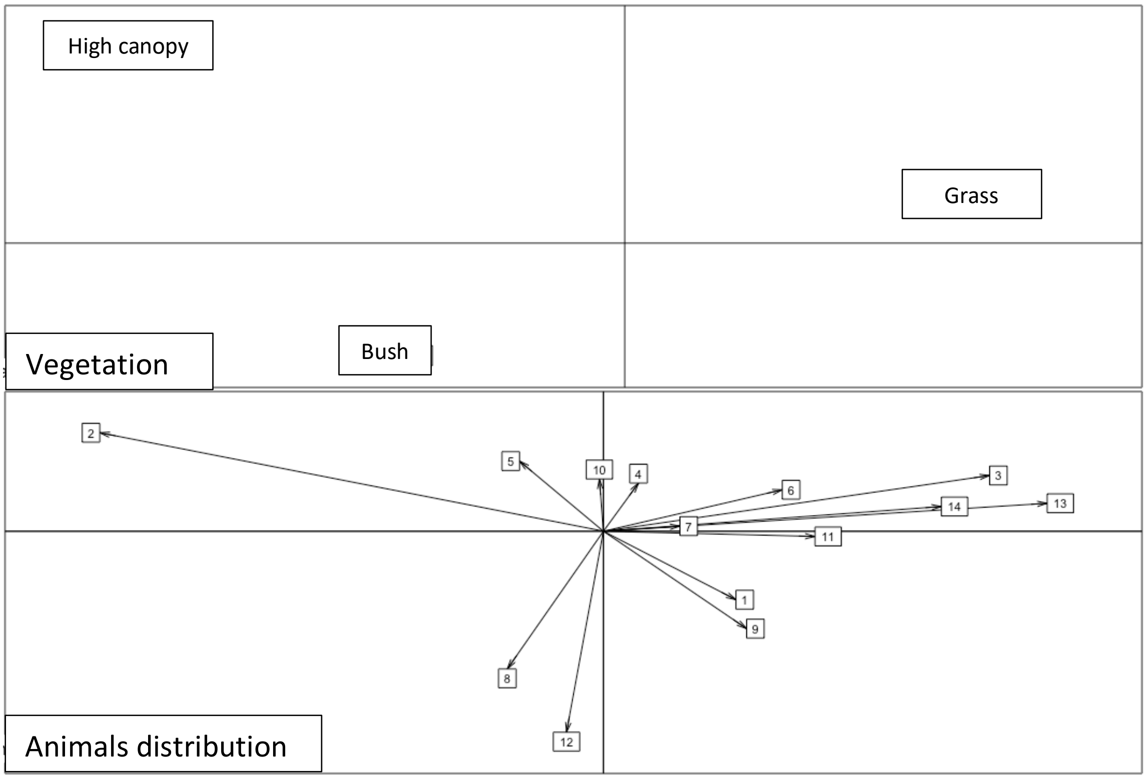


Fig 16. Graphic representation of the animal distribution according with the selection ratios for the different categories of vegetation. The above plot represents the position of each one of the three levels of vegetation height. The bellow plot represents the distribution of the tagged individuals towards those categories. Each number correspond to the individuals according with the disposition of the maps in this appendix.

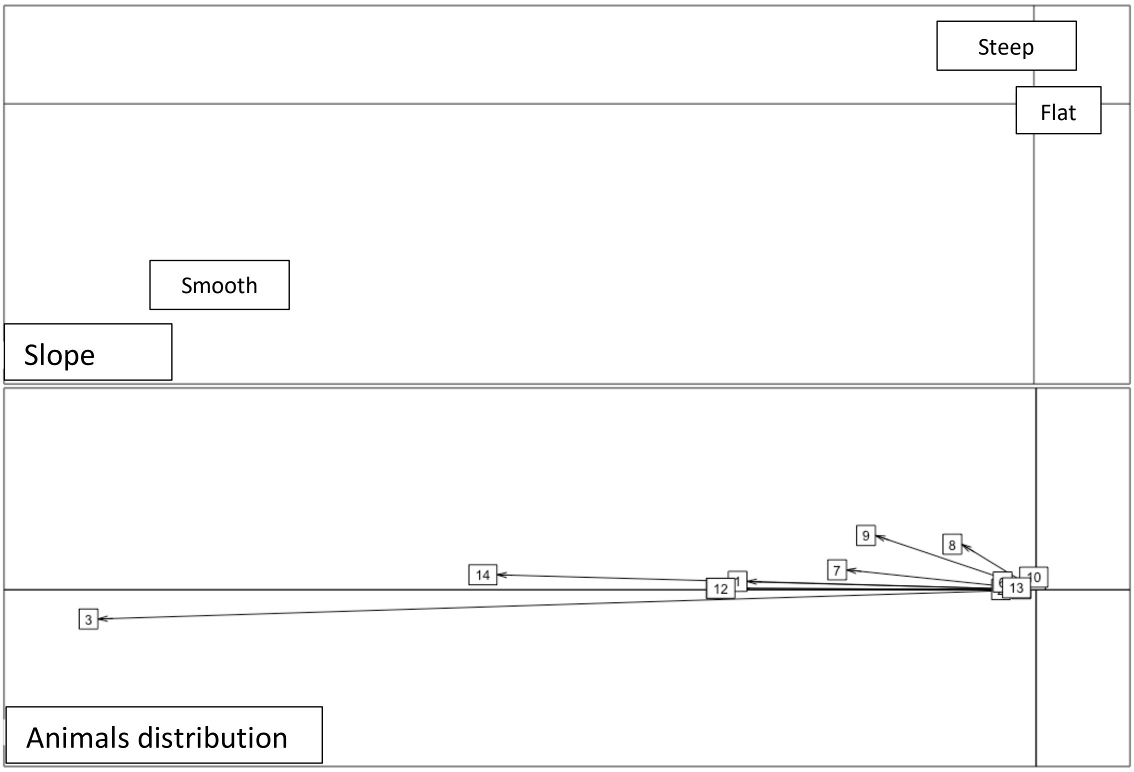


Fig 17. Graphic representation of the animal distribution according with the selection ratios for the different categories of Slope. The above plot represents the position of each one of the three levels of Slope. The bellow plot represents the distribution of the tagged individuals towards those categories. Each number correspond to the individuals according with the disposition of the maps in this appendix.

APPENDIX IV

Table 1. Normality test for the biochemical values obtained from *V. salvator*

Variable	W	p
Weight (Log)	1	0.00004
Body condition (Log)	0.9	< 0.0001
Cholesterol (Log)	0.9	< 0.0001
HDL_Ch (Log)	0.6	< 0.0001
LDL_Ch	**0.1**	< 0.0001
Triglyceride (Log)	0.9	< 0.0001
Sodium (Log)	1	0.001
Potasium (Log)	0.6	< 0.0001
chloride (Log)	0.9	< 0.0001
Urea (Log)	0.4	< 0.0001
Creatinine (Log)	0.9	< 0.0001
Uric_Acid (Log)	0.8	< 0.0001
phosphate	**1**	0.0002
Calcium (Log)	0.6	< 0.0001
Tot_protein (Log)	0.3	< 0.0001
Albumin (Log)	0.6	< 0.0001
Globulin (Log)	0.9	< 0.0001
AkPhs (Log)	0.9	< 0.0001
Bilirubine (Log)	0.3	< 0.0001
GGT (Log)	1	0.0009
AST	**0.8**	< 0.0001
ALT	**0.8**	< 0.0001

Table 2. ANOVA test for the biochemical values obtained from *V. salvator*

Variable	**F (df; p)**		
	HABITAT	**Study site**	**Transect**
Weight	1 (100;0.2)	1.67 (3; 0.17)	0.46 (2;0.63)
Body condition	**2 (100; 0.002)**	**3.29 (3; 0.021)**	0.33 (2; 0.716)
Cholesterol	**0.3 (100; <0.0001)**	**9.4 (3; < 0.0001)**	**14.4 (2; < 0.0001)**
HDL_Ch (Log)	**0.9 (100; 0.5)**	**4.46 (3; 0.005)**	0.71 (2; 0.4923)
LDL_Ch	**0.002 (100; <0.0001)**	0.23 (3;0.87)	0.17 (2; 0.85)
Triglyceride (Log)	1 (100;0.4)	0.86 (3; 0.462)	2.79 (2; 0.063)
Sodium (Log)	0.7 (90; 0.2)	**3.47 (3; 0.018)**	0.25 (2; 0.781)
Potasium (Log)	1 (80; 1)	1.40 (3; 0.24)	0.85 (2; 0.43)
chloride (Log)	1 (90; 0.2)	1.49 (3; 0.219)	2.73 (2; 0.068)
Urea (Log)	**2 (90; <0.0001)**	0.56 (3; 0.643)	2.50 (2; 0.086)
Creatinine (Log)	1 (90; 0.5)	**3.25 (3; 0.024)**	0.48 (2; 0.622)
Uric_Acid (Log)	**0.6 (100; 0.002)**	2.49 (3; 0.0606)	**5.37 (2; 0.0052)**
phosphate	0.8 (90; 0.3)	0.67 (3; 0.57)	0.35 (2; 0.70)
Calcium (Log)	**3 (90; < 0.0001)**	0.74 (3; 0.53)	0.22 (2; 0.80)
Tot_protein (Log)	**20 (90; <0.0001)**	2.26 (3; 0.083)	2.45 (2; 0.090)
Albumin (Log)	0.9 (90; 0.5)	**4.33 (3; 0.006)**	0.2 (2; 0.821)
Globulin (Log)	1 (90; 0.9)	1.85 (3; 0.14)	1.09 (2; 0.34)
AkPhs (Log)	1 (90; 0.8)	**3.46 (3; 0.018)**	**8.68 (2; 0.0003)**
Bilirubine (Log)	**0.6 (90; 0.02)**	0.41 (3; 0.75)	0.1 (2; 0.9)
GGT (Log)	1 (90; 0.08)	2.15 (3; 0.096)	0.54 (2; 0.581)
AST	1 (90; 0.3)	0.16 (3; 0.92)	0.41 (2; 0.67)
ALT	**3 (90; < 0.0001)**	1.20 (3; 0.31)	0.79 (2; 0.45)

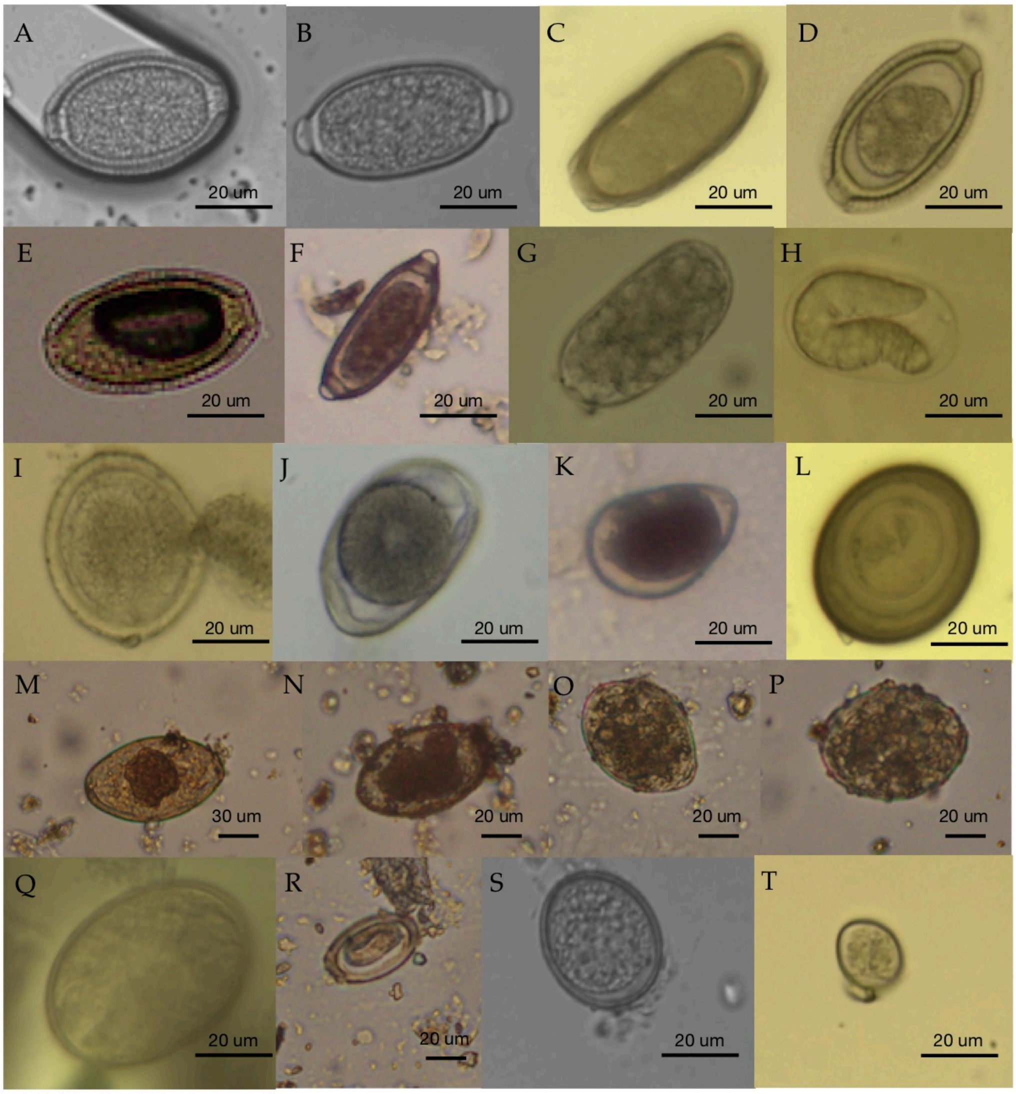
Table 3. GEE results for the biochemical values obtained from *V. salvator.*
alpha = 1.229 ± 0.832; Scale parameter 0.65 ± 0.404

	Estimate	Std.err	Wald	Pr(>|W|)	
(Intercept)	-8.92051	3.83702	5.4	0.02008	*
Weight	-0.04546	0.04321	1.11	0.29274	
Body_Condition	2.57262	1.01426	6.43	0.0112	*
Cholesterol	-0.09456	0.14662	0.42	0.51897	
HDL_Ch	1.96898	0.62658	9.87	0.00168	**
LDL_Ch	-0.06111	0.11757	0.27	0.6032	
Triglyceride	-0.09004	0.04627	3.79	0.05166	.
Sodium	0.06164	0.02292	7.23	0.00716	**
Potasium	0.00428	0.00259	2.72	0.09901	.
Chloride	0.00326	0.01146	0.08	0.77584	
Urea	-0.29607	0.36764	0.65	0.42063	
Creatinine	-0.00732	0.00906	0.65	0.41915	
Uric_Acid	0.03881	0.00458	71.82	< 2e-16	***
Phosphate	0.19775	0.11402	3.01	0.08285	.
Calcium	-0.0094	0.00442	4.53	0.0334	*
Tot_protein	0.00951	0.00262	13.15	0.00029	***
Albumin	-0.1099	0.05829	3.56	0.05935	.
Globulin	0.03817	0.02098	3.31	0.0688	.
AkPhs	0.00328	0.00838	0.15	0.69597	
Bilirubine	-0.05204	0.19576	0.07	0.79036	
GGT	-0.00464	0.0046	1.02	0.31268	
AST	0.00218	0.00252	0.75	0.38704	
ALT	-0.00347	0.00263	1.74	0.18705	

APPENDIX V

SECTION V-1.

PARASITES (MORPHO-TYPES) FOUND IN *Varanus salvator* IN THE LOWER KINABATANGAN WILDLIFE SANCTUARY



Gastrointestinal helminths recovered from fecal samples of monitor lizards. A-E: *Capillaria* spp.; F: *Trichuris* sp.; G: Strongylida; H: *Strongyloides* spp.; I: Ascarididae; J-K: Oxyuridae; L: Taeniidae; M-P: Trematoda spp.; Q: *Physaloptera* spp.; R: Spirurida; S-T: protists.

SECTION V-2.
OUTCOMES FROM THE GENERALIZED LIENAR MIXED MODELS FOR THE PREVALENCE OFPARASITES ASSOCIATED WITH *Varanus salvator*

Capillarids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.99e+02	3.69e+04	-0.01	0.99
Diet diversity (D)	2.67e+02	3.26e+04	0.01	0.99
Host abundundance	2.55e+00	3.12e+02	0.01	0.99
Eggs loadind (EPG)	8.24e-04	5.52e-04	1.49	0.13
Diet div. / Host Abundance	-1.97e+00	2.41e+02	-0.01	0.99
Host abundance / EPG	**1.44e-05**	**7.53e-06**	**1.91**	**0.05**
Diet Diversity / EPG	**-1.56e-03**	**8.03e-04**	**-1.95**	**0.05**
Host abundance / PCI*	9.26e-04	3.95e-03	0.23	0.81
DomDiet/ PCI	-2.76e-02	4.67e-01	-0.06	0.95

Trichurids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.17e+01	1.99e+01	1.10	0.27
Diet diversity (D)	-2.07e+01	1.90e+01	-1.09	0.27
Host abundundance	-1.70e-01	2.35e-01	-0.72	0.47
Eggs loadind (EPG)	-1.15e-02	8.27e-03	-1.39	0.17
Diet div. / Host Abundance	1.08e-01	1.61e-01	0.67	0.50
Host abundance / EPG	3.71e-05	2.55e-05	1.45	0.15
Diet Diversity / EPG	6.59e-03	4.91e-03	0.18	1.34
Host abundance / PCI	-9.00e-03	3.76e-02	-0.24	0.81
DomDiet/ PCI	1.50e+00	2.62e+00	0.57	0.57

Strongylids	Estimate	Std. Error	z value	Pr(>|z|)
Diet diversity (D)	2.39e+01	4.23e+01	0.56	0.57
Host abundundance	-2.68e+01	5.00e+01	-0.54	0.59
Eggs loadind (EPG)	-2.86e-01	5.11e-01	-0.56	0.57
Diet div. / Host Abundance	3.88e-03	1.87e-03	2.07	0.03
Host abundance / EPG	2.16e-01	3.91e-01	0.55	0.58
Diet Diversity / EPG	-1.67e-05	1.66e-05	-1.00	0.31
Host abundance / PCI	-5.26e-04	1.00e-03	-0.52	0.60
DomDiet/ PCI	2.96e-03	5.88e-03	0.50	0.61

Strongyloids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.33e+02	1.87e+04	-0.02	0.98
Diet diversity (D)	3.69e+02	1.77e+04	0.02	0.98
Host abundundance	3.96e+00	1.79e+02	0.02	0.98
Eggs loadind (EPG)	-5.75e-03	2.23e-02	-0.26	0.79
Diet div. / Host Abundance	-2.88e+00	1.33e+02	-0.02	0.98
Host abundance / EPG	1.68e-04	1.44e-04	1.16	0.24
Diet Diversity / EPG	-9.41e-03	5.21e-03	-1.81	0.07
Host abundance / PCI	5.30e-05	7.31e-03	0.01	0.99
DomDiet/ PCI	1.29e+00	6.87e-01	1.88	0.06

***PCI = Parasite Coinfecton**

Ascarids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.70e+01	5.33e+07	0.00	1.00
Diet diversity (D)	4.12e+01	6.55e+07	0.00	1.00
Host abundundance	5.90e-01	6.57e+05	0.00	1.00
Eggs loadind (EPG)	2.96e+14	2.24e+21	0.00	1.00
Diet div. / Host Abundance	-3.70e-01	5.19e+05	0.00	1.00
Host abundance / EPG	-5.23e+12	3.88e+19	0.00	1.00
Diet Diversity / EPG	1.11e+14	7.90e+20	0.00	1.00
Host abundance / PCI	-1.53e-03	1.35e+00	0.00	1.00
DomDiet/ PCI	-1.38e+00	2.96e+02	0.00	1.00

Oxyuroids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.88e+02	3.04e+04	-0.01	0.99
Diet diversity (D)	2.55e+02	2.69e+04	0.01	0.99
Host abundundance	2.47e+00	2.58e+02	0.01	0.99
Eggs loadind (EPG)	**-1.01e-02**	**3.48e-03**	**-2.90**	**0.003**
Diet div. / Host Abundance	-1.91e+00	1.99e+02	-0.01	0.99
Host abundance / EPG	1.96e-06	1.62e-05	0.12	0.90
Diet Diversity / EPG	**9.39e-03**	**2.77e-03**	**3.39**	**0.00069**
Host abundance / PCI	-1.04e-04	2.98e-03	-0.03	0.97
DomDiet/ PCI	-5.11e-02	6.55e-01	-0.08	0.93

Cestodes	Estimate	Std. Error	z value	Pr(>|z|)
Diet diversity (D)	-1.75e+01	4.27e+04	0	1
Host abundundance	-6.01e-01	3.83e+04	0	1
Eggs loadind (EPG)	2.33e-02	3.24e+02	0	1
Diet div. / Host Abundance	1.71e+11	3.84e+16	0	1
Host abundance / EPG	-1.81e-02	2.75e+02	0	1
Diet Diversity / EPG	1.06e+07	2.39e+12	0	1
Host abundance / PCI	-1.35e+11	3.03e+16	0	1
DomDiet/ PCI	1.98e-04	1.10e+01	0	1

Trematodes	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-8.63e+01	1.98e+05	0	1
Diet diversity (D)	6.85e+01	2.24e+05	0	1
Host abundundance	6.72e-01	2.30e+03	0	1
Eggs loadind (EPG)	6.65e+14	1.58e+17	0	1
Diet div. / Host Abundance	-5.19e-01	1.73e+03	0	1
Host abundance / EPG	-2.36e+13	5.62e+15	0	1
Diet Diversity / EPG	1.03e+15	2.44e+17	0	1
Host abundance / PCI	-1.61e-02	2.76e+01	0	1
DomDiet/ PCI	-1.15e+00	5.39e+03	0	1

Spirurids	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.74e+02	1.88e+05	0.00	1
Diet diversity (D)	-1.83e+02	2.21e+05	0.00	1
Host abundundance	-2.02e+00	2.25e+03	0.00	1
Eggs loadind (EPG)	-1.23e-01	2.10e+01	-0.01	1
Diet div. / Host Abundance	1.31e+00	1.68e+03	0.00	1
Host abundance / EPG	1.81e-03	7.45e-01	0.00	1
Diet Diversity / EPG	-1.02e-02	3.24e+01	0.00	1
Host abundance / PCI	7.32e-03	5.31e+01	0.00	1
DomDiet/ PCI	5.66e+00	2.31e+03	0.00	1

Physaloptera	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.55e+02	6.44e+04	0.00	1
Diet diversity (D)	-3.27e+02	6.85e+04	0.00	1
Host abundundance	-3.17e+00	7.04e+02	0.00	1
Eggs loadind (EPG)	-3.32e-02	8.22e+01	0.00	1
Diet div. / Host Abundance	2.48e+00	5.34e+02	0.00	1
Host abundance / EPG	-2.10e-03	5.42e-01	0.00	1
Diet Diversity / EPG	3.39e-01	1.39e+02	0.00	1
Host abundance / PCI	5.55e-03	7.06e+00	0.00	1
DomDiet/ PCI	-3.99e-01	2.12e+03	0.00	1

Protist	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.02e+03	1.79e+07	0.00	1.00
Diet diversity (D)	3.39e+03	1.59e+07	0.00	1.00
Host abundundance	3.72e+01	1.52e+05	0.00	1.00
Eggs loadind (EPG)	1.21e-01	4.53e-01	0.27	0.79
Diet div. / Host Abundance	-2.62e+01	1.17e+05	0.00	1.00
Host abundance / EPG	-4.04e-04	1.52e-03	-0.27	0.79
Diet Diversity / EPG	-3.53e-02	1.31e-01	-0.27	0.79
Host abundance / PCI	-7.78e-02	2.54e-01	-0.31	0.76
DomDiet/ PCI	-4.66e+00	2.19e+01	-0.21	0.83

SECTION V-3.
OUTCOMES FROM THE GENERALIZED LIENAR MIXED-EFFECT MODELS FOR THE PARASITES' ABUNDANCE ASSOCIATED WITH *Varanus salvator*

Capillarids	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	4.85e+03	3.11e+04	91	0.156	0.999
Diet diversity (D)	6.34e+03	5.35e+04	5.59e-07	0.118	1.000
Host abundance	6.21e+00	1.38e+02	8.05e-06	0.045	1.000
prevalence	3.95e+03	1.68e+04	8.00e+01	0.235	0.815
PCI	-3.44e+02	5.18e+03	8.00e+01	-0.066	0.947
Parasite diversity	-7.30e+03	3.00e+04	6.96e-06	-0.243	1.000
Diet div. / Host abundance	1.72e+00	2.99e+02	2.13e-06	0.006	1.000
Host abund. / prevalence	-3.13e+01	2.01e+02	8.00e+01	-0.156	0.877
Diet diversity / prevalence	1.48e+04	3.35e+04	8.00e+01	0.443	0.659
Host abundance / PCI	2.83e+00	6.17e+01	8.00e+01	0.046	0.964
Diet diversity / PCI	-4.16e+03	1.04e+04	8.00e+01	-0.400	0.690

Trichurids	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-2.77e+04	9.64e+03	3.40e-05	-2.874	0.9998
Diet diversity (D)	3.00e+04	1.79e+04	7.44e-08	1.674	1.0000
Host abundance	4.91e+01	4.62e+01	1.06e-06	1.063	1.0000
prevalence	**1.60e+04**	**7.43e+03**	**8.00e+01**	**2.156**	**0.0341**
PCI	1.48e+03	1.77e+03	8.00e+01	0.836	0.4057
Parasite diversity	2.51e+04	9.58e+03	7.68e-07	2.624	1.0000
Diet div. / Host abundance	-1.91e+02	9.59e+01	2.38e-07	-1.994	1.0000
Host abund. / prevalence	-3.52e+01	1.00e+02	8.00e+01	-0.352	0.7256
Diet diversity / prevalence	-6.73e+03	1.80e+04	8.00e+01	-0.373	0.7099
Host abundance / PCI	-1.28e+01	1.90e+01	8.00e+01	-0.674	0.5020
Diet diversity / PCI	1.24e+03	2.90e+03	8.00e+01	0.428	0.6701

Strongylids	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-7.67e+01	1.08e+03	5.70e-04	-0.071	0.99897
Diet diversity (D)	-3.58e+02	1.67e+03	5.95e-07	-0.214	1.00000
Host abundance	-4.39e-01	4.38e+00	9.13e-06	-0.100	0.99996
prevalence	4.37e+02	5.69e+02	8.00e+01	0.769	0.44433
PCI	-6.63e+01	1.34e+02	8.00e+01	-0.493	0.62358
Parasite diversity	3.00e+02	1.02e+03	1.04e-05	0.294	0.99995
Diet div. / Host abundance	4.46e-01	9.51e+00	2.42e-06	0.047	0.99999
Host abund. / prevalence	1.39e+01	7.37e+00	8.00e+01	1.896	0.06152
Diet diversity / prevalence	**-3.85e+03**	**1.27e+03**	**8.00e+01**	**-3.014**	**0.00345**
Host abundance / PCI	1.024e-01	1.60e+00	8.00e+01	0.064	0.94934
Diet diversity / PCI	1.36e+02	2.73e+02	8.00e+01	0.497	0.62041

***PCI = Parasite Coinfecton**

Strongyloids	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	1.80e+01	5.38e+02	6.93e-05	0.034	0.9999
Diet diversity (D)	3.84e+01	9.68e+02	1.33e-07	0.040	1.0000
Host abundance	-5.88e-01	2.58e+00	2.20e-06	-0.228	1.0000
prevalence	**1.49e+03**	**7.71e+02**	**8.00e+01**	**1.940**	**0.0560**
PCI	-7.18e+00	8.19e+01	8.00e+01	-0.088	0.9303
Parasite diversity	3.03e+01	5.26e+02	1.47e-06	0.058	1.0000
Diet div. / Host abundance	8.23e-01	5.35e+00	4.87e-07	0.154	1.0000
Host abund. / prevalence	-1.19e+01	6.92e+00	8.00e+01	-1.727	0.0880
Diet diversity / prevalence	1.31e+03	7.04e+02	8.00e+01	1.868	0.0655
Host abundance / PCI	2.20e-01	9.52e-01	8.00e+01	0.232	0.8173
Diet diversity / PCI	-9.87e+01	1.63e+02	8.00e+01	-0.604	0.5479

Oxyuroids	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	-236.637	1141.711	80.000	0.8363	-0.207
Diet diversity (D)	-688.840	1881.619	80.000	-0.366	0.7153
Host abundance	1.833	4.921	80.000	0.372	0.7106
prevalence	-498.297	573.860	80.000	-0.868	0.3878
PCI	121.949	182.251	80.000	0.669	0.5053
Parasite diversity	227.683	1130.929	80.000	0.201	0.8410
Diet div. / Host abundance	1.873	10.494	80.000	0.179	0.8588
Host abund. / prevalence	**12.952**	**6.694**	**80.000**	**1.935**	**0.0565**
Diet diversity / prevalence	-2092.306	1096.760	80.000	-1.908	0.0600
Host abundance / PCI	-2.120	2.110	80.000	-1.005	0.3180
Diet diversity / PCI	359.179	346.074	80.000	1.038	0.3025

Spirurids	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	3.96e+03	1.84e+03	2.36e-04	2.152	0.998671
Diet diversity (D)	-6.00e+03	3.05e+03	3.28e-07	-1.966	0.999997
Host abundance	-1.60e+00	8.38e+00	6.05e-06	-0.192	0.9999
prevalence	**4.15e+03**	**1.21e+03**	**8.00e+01**	**3.429**	**0.000961**
PCI	2.67e+02	2.60e+02	8.00e+01	1.027	0.307476
Parasite diversity	-4.31e+03	1.75e+03	4.47e-06	-2.467	0.999965
Diet div. / Host abundance	3.47e+01	1.71e+01	1.25e-06	2.033	0.999990
Host abund. / prevalence	-3.09e+01	1.68e+01	8.00e+01	-1.837	0.069890
Diet diversity / prevalence	1.85e+03	3.11e+03	8.00e+01	0.594	0.553860
Host abundance / PCI	-2.21e+00	2.97e+00	8.00e+01	-0.745	0.458612
Diet diversity / PCI	1.41e+02	4.90e+02	8.00e+01	0.288	0.774188

Physaloptera	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	2.52e+00	3.81e+01	9.61e+00	0.066	0.9485
Diet diversity (D)	8.63e-01	6.38e+01	1.59e-02	0.014	0.9983
Host abundance	-3.61e-03	1.72e-01	2.75e-01	-0.021	0.9907
prevalence	**-9.97e+01**	**4.24e+01**	**8.00e+01**	**-2.350**	**0.0212**
PCI	-2.11e+00	5.73e+00	8.00e+01	-0.368	0.7136
Parasite diversity	-7.96e-01	3.72e+01	2.31e-01	-0.021	0.9911
Diet div. / Host abundance	-6.56e-02	3.55e-01	5.94e-02	-0.185	0.9603
Host abund. / prevalence	**3.66e+00**	**4.73e-01**	**8.00e+01**	**7.724**	**2.80e-11**
Diet diversity / prevalence	**-5.29e+02**	**7.34e+01**	**8.00e+01**	**-7.215**	**2.74e-10**
Host abundance / PCI	9.93e-03	6.55e-02	8.00e+01	0.152	0.8799
Diet diversity / PCI	4.73e+00	1.09e+01	8.00e+01	0.434	0.6653

Protist	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	1230.40	8531.102	80.000	0.144	0.88569
Diet diversity (D)	7695.67	15397.507	79.998	0.500	0.61859
Host abundance	11.667	40.791	79.999	0.286	0.77561
prevalence	**21553.5**	**7868.617**	**80.000**	**2.739**	**0.00759**
PCI	-230.443	1255.118	80.000	-0.184	0.85479
Parasite diversity	-3571.28	8343.668	79.999	-0.428	0.66978
Diet div. / Host abundance	-45.335	83.727	79.999	-0.541	0.58969
Host abund. / prevalence	**-178.606**	**81.492**	**80.000**	**-2.192**	**0.03131**
Diet diversity / prevalence	**23182.3**	**11288.92**	**80.000**	**2.054**	**0.04329**
Host abundance / PCI	1.372	14.165	80.000	0.097	0.92307
Diet diversity / PCI	-194.367	2317.212	80.000	-0.084	0.93336