The Price of Persistence: Small Carnivore Ecology within the Anthropogenically-Degraded Kinabatangan Landscape

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DECLARATION

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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This thesis is being submitted in partial fulfilment of the requirements for the degree of PhD.

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Summary

Habitat fragmentation and degradation by human activities, particularly agricultural development, threatens global biodiversity. This thesis presents a multifaceted evaluation of the ecology of Malay and common palm civets in the Lower Kinabatangan Floodplain (Sabah, Borneo), a patchwork forest landscape heavily fragmented by oil palm plantations. Morphometric measurements, reproductive observations, parasitic infections, blood samples for haematology and serum biochemistry analyses, and hair samples for heavy metal analysis were collected from wild civets captured between 2012 and 2018. The pioneering deployment of GPS-collars on four common palm and 17 Malay civets enabled the determination of home ranges, diurnal sleeping sites, home range overlaps, and movement behaviours.

Haematological and biochemical blood profiles indicated potential anaemia, immunosuppression, and consumption of a low-protein diet in civets captured closer to oil palm plantations. Civets expressed significantly elevated liver enzyme levels relative to domestic animals. Individuals of both species used oil palm plantations for nocturnal foraging and diurnal rest sites; however, all collared individuals accessed forests. Home ranges of civets that accessed plantations were significantly larger than civets that did not, suggesting oil palm poses low habitat suitability. Civet hair concentrations of 13 heavy metals indicated detectable exposure to varying quantities of metals, with levels impacted by biological and landscape factors. Exposure to Ba, Cd, Cr, and Fe was associated with Malay civet proximity to tributaries, whilst elevated Al, Cd, and Pb concentrations were documented from GPS-collared civets using plantations. The extent of exposure scaled with the intensity of an individual's usage of plantations. Finally, correlations between hair metal concentrations and blood parameters suggested exposure to Al, Cd, Cr, Ba, and Pb may impact civet physiology. This study represents a step change in the understanding of civet ecology, and provides novel insights into the price of carnivore persistence in degraded landscapes.

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Co-Author Statement

Appendix I is a co-authored and peer-reviewed published manuscript, while Chapter 3 is adapted from a co-authored and peer-reviewed published manuscript.

Appendix I:
Evans, M.N., Vickers, S.H., Bakar, M.S.A., & Goossens, B. (2016). Small carnivores of the Lower Kinabatangan Wildlife Sanctuary, Sabah, Borneo, including a new locality for the Otter Civet *Cynogale bennettii. Small Carnivore Conservation, 54,* 26–38.

MNE designed and executed the study with supervision from BG; SHV managed the camera trap inventory and conducted the data analysis under MNE's supervision; MSAB acted as local collaborator within the government; MNE wrote the manuscript. All authors contributed to manuscript drafts.

Chapter 3:
Evans, M.N., Guerrero-Sanchez, 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,* 475–481.

MNE designed and executed the study with supervision from PK and BG; SG-S provided the veterinarian support in animal captures; MSAB acted as local collaborator within the government; MNE collected the data, performed the statistical analyses, and wrote the manuscript. All authors contributed to manuscript drafts.

Table of Contents

Chapter 1. Habitat fragmentation and biodiversity: Review and general introduction

Chapter 2: Health of small carnivores in the fragmented landscape of the Lower Kinabatangan

Chapter 3. First known satellite collaring of a viverrid: results and implications of GPS-collaring Malay civets (*Viverra tangalunga*)

Chapter 4. Spatial ecology of small carnivores in the fragmented Lower Kinabatangan landscape

Chapter 5. Landscape sentinels: metal biomonitoring with model small carnivores in a fragmented ecosystem

Chapter 6. Synthesis: Life on the edge

Chapter 7. Conclusions

List of Tables

List of Figures

Glossary of Abbreviated Terms

ABM – Agent-Based Model
AIC – Akaike’s Information Criterion
AICc – Akaike’s Information Criterion with small sample adjustment
ATSDR – Agency for Toxic Substance and Disease Registry, of the US Department of Health and Human Services
BEC – Background Equivalent Concentration
BRB – Biased Random Bridges
DF – Degrees of Freedom
DGFC – Danau Girang Field Centre
DL – Batch Detection Limit
DOE – Department of Environment (Malaysia)
DVCA– Danum Valley Conservation Area
EDTA – Ethylenediaminetetraacetic Acid
EIA – Environmental Impact Assessment
ENSO – El Niño Southern Oscillation
EPA – Environmental Protection Agency (USA)
FAO – Food and Agricultural Organization of the United Nations
GAM – General Additive Model
GAMM – Generalised Additive Mixed Model
GLM – General (or Generalised) Linear Model
GLMM – General (or Generalised) Linear Mixed Model
GPS – Global Positioning System
IBT – Island Biogeography Theory
IPBES – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPM – Integrated Pest Management
IQR – Interquartile Range
IUCN – International Union for Conservation of Nature
LD – Detection Limit
LD-50 – Lethal Dose-50 Value
LKWS – Lower Kinabatangan Wildlife Sanctuary
MCP – Minimum Convex Polygon
MPOC – Malaysian Palm Oil Council
MPOB – Malaysian Palm Oil Board
MSPO – Malaysian Sustainable Palm Oil
MWU – Mann-Whitney U Statistical Test
NOAEL – No Observable Adverse Effect Level
NPL – Nightly Path Length
NS – Non-significant
PC – Principal Component
PCA – Principal Component Analysis
PCR – Polymerase Chain Reaction
POME – Palm Oil Mill Effluent
RFID – Radio-Frequency Identification
RSPO– Roundtable on Sustainable Palm Oil
SD – Standard Deviation
SE – Standard Error
SS – Sleeping Site
TA – Mean Nightly Turning Angle
UD – Utilisation Distribution
UHF – Ultra-High Frequency
VHF – Very-High Frequency
WHO – World Health Organization

Blood parameter abbreviations– refer to Tables A2.1 & A2.2

Chemical symbology follows those of the International Union of Pure and Applied Chemistry (IUPAC)

Chapter 1. Habitat fragmentation and biodiversity: Review and general introduction

1.1 Global biodiversity crisis

Worldwide, large and sudden declines in biodiversity numbers have led the scientific community to predict the onset of an anthropogenic sixth mass extinction (Ceballos et al., 2015; Ceballos et al., 2017; Ceballos & Ehrlich, 2018; Pimm & Raven, 2000). In Earth's history, five mass extinctions have previously occurred, each marked by spiking extinction rates and losses of over 75% of global species (Barnosky et al., 2011). These events occurred at the end of the Ordovician, late Devonian, Permian, Triassic, and Cretaceous (K-T) periods, and proposed causes were varied but natural, such as catastrophes, climate change, and hyper-disease prevalence (Barnosky et al., 2011; Koch & Barnosky, 2006; Raup, 1994). The current biodiversity loss is, however, the direct result of extreme anthropogenic pressures, and the past century alone has seen an estimated thousand-fold increase of the global species' extinction rate (Ceballos et al., 2015; Pimm et al., 1995; Pimm et al., 2014). According to the 2018 Living Planet Index, the global species population size has declined by 60% between 1970 and 2014 (WWF, 2018). Between 1975 and 2008, the global percentage of threatened species thus increased from 7.8% to 36.3% (Di Marco et al., 2014). Based on best recent estimates, over 25% of all known mammalian species, 40% of amphibians, 14% of birds, and 34% of reptiles are imminently vulnerable to extinction (Ceballos et al., 2010; IUCN, 2018; Visconti et al., 2011). The 2019 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global Assessment report estimates over a million species are threatened with imminent extinction. A multitude of factors facilitate these large-scale losses, but the anthropogenic destruction and conversion of natural ecosystems into alternate usages, such as large-scale agriculture or urban spaces, pose the greatest threats to global biodiversity (Crooks et al., 2011; Newbold et al., 2015; Ripple et al., 2015; Schipper et al., 2008). Acting in parallel, and occasionally additively, to agricultural expansion, are other drivers of modern biodiversity losses such as urbanisation, industrial expansion, burgeoning localised human populations, natural resource exploitation, and climate change

(Ehrlich & Harte, 2015; Laurance et al., 2014; Mcdonald et al., 2008; Struebig et al., 2015; Thomas et al., 2004; Woodroffe, 2000).

1.2 Land use change

Over 40% of global land has been converted to human-dominated usage, expansions which have coincided with large-scale losses of native species (Foley et al., 2005; Prugh et al., 2008). The scale of loss varies from region to region; at the upper threshold, small countries, such as Singapore, have lost over 95% of all natural habitat and at least 28% of all native species in less than 185 years (Brook et al., 2003; Turner et al., 1994). In the past 300 years alone, anthropogenic land use changes have resulted in a loss of between 7 and 11 million km^2 of forests across the globe (FAOSTAT, 2004; Foley et al., 2005), with drivers of this loss regionally varied but nonetheless anthropogenic (Curtis et al., 2018; Watson et al., 2016). In a recent assessment, IPBES (2018) reported that a mere 25% of Earth's total land area was void of impacts from human activities.

One of the main reasons habitat destruction and fragmentation is the major threat to biodiversity is that the global distribution of species is non-random, with large numbers of species occurring in relatively small geographic regions, coined biodiversity hotspots (Myers et al., 2000; Pimm et al., 2014). This unequal distribution of biodiversity equates to over half of Earth's threatened species occupying 1.4% of the world's land surface (Brooks et al., 2002). As an example, tropical forests hold an estimated 67% of all terrestrial biodiversity, yet cover a mere 10% of the planet (Pimm & Raven, 2000). These relatively small, endemic-rich regions represent the frontlines of extinction events, as they contain large quantities of unique biodiversity that can be lost with a slight amount of ecosystem degradation or loss (Pimm et al., 1995; Ribeiro et al., 2009). Jantz et al. (2015) expressed that projected land use changes within biodiversity hotspots would result in an additional 220–21,000 species extinctions by 2100. Tropical hotspots contain significantly greater counts of threatened endemic amphibians, birds, and mammal species than non-tropical hotspots (Brook et al., 2008). The loss of tropical forests is occurring daily, however; between 2000 and 2012, Hansen et al. (2013) reported a complete loss of 2.3 million km^2 of global forest, the majority of which was tropical forest. Curtis et al. (2018) further refined those estimates to elucidate that approximately 27% of 2001–2015 global forest loss occurred due to human demand for commodities, a deforestation driver they defined as encompassing agriculture, mining, and human infrastructure establishment.

With increasing global demand for commodities, agricultural expansion is the world's largest driver of land use change, and is thought to affect at least 40% of all terrestrial mammals and most biodiversity hotspots negatively (Carvalho et al., 2009; Godfray & Garnet, 2014; Kuyper & Struik, 2014; Tilman et al., 2001; Tscharntke et al., 2012; Visconti et al., 2011). According to Meijaard et al. (2018), over 9,200 species categorised as threatened on the International Union for the Conservation of Nature (IUCN) Red List (Critically Endangered, Endangered, and Vulnerable categories) are stated as sensitive to agriculture and aquaculture, making it the most common threat on the Red List. Projections by Kok et al. (2018) estimate agricultural practices will account for 54% of expected mean species abundance losses by 2050. The establishment of new agricultural lands has resulted in the loss of large tracts of tropical forests (Gibbs et al., 2010); agricultural land in tropically biodiverse regions increased by over 400 million hectares between 1995 and 2007 (Visconti et al., 2011).

1.3 Habitat fragmentation and biodiversity

Habitat loss and fragmentation are considered the primary threats to the world's mammals (Crooks et al., 2017; Fletcher Jr. et al., 2017; Haddad et al., 2015; Schipper et al., 2008). Habitat fragmentation is defined as the landscape-scale process whereby the loss of continuous habitat results in smaller, isolated habitat fragments persisting in a 'matrix' of new land use types (Ewers & Didham, 2006; Fahrig, 2003). This intrinsically implies four alterations to landscape-scale habitat patterns, which are the most frequent indices used to measure habitat fragmentation quantitatively: 1) total reduction in original habitat amount, 2) increase in the number of habitat patches, 3) decrease in the area of habitat patches, and 4) increased isolation of patches (Fahrig, 2003). Through these pattern changes, fragmentation intrinsically creates a series of edges between the original and new land use types. Fragmentation itself is not a purely anthropogenic event, as it occurs naturally in many ecosystems such as island archipelagos, alpine glaciers, and riverine systems; habitat modification by human intervention, however, is the most significant factor in increased global fragmentation rates (Ewers & Didham, 2006). Haddad et al. (2015) reported that forest edges could be found less than 1 km from a given location in 70% of remaining global forests.

Quantifying the impacts of habitat fragmentation on biodiversity is a difficult undertaking and requires a well-designed set of research questions. Most studies wrestle to tease apart the biological effects and responses to habitat fragmentation from those of discrete habitat loss, and theoretical debates regarding the relative importance of scale versus configuration are ongoing (Ewers & Didham, 2006; Fahrig, 2003; Fahrig, 2017; Fletcher Jr. et al., 2018; Hadley & Betts, 2016). Despite the abundance of evidence underlining a deleterious relationship between forest loss and biodiversity richness and abundances, the mechanisms facilitating these losses are complex and often difficult to derive empirically (Ewers & Didham, 2006; Fahrig, 2003; Hanski, 2015). In terms of research effort and focus on the biological responses to habitat fragmentation, two investigative lenses exist (Didham et al., 2012; Fischer & Lindenmayer, 2007): 1) species-driven models, and 2) landscape pattern-oriented examinations. Species-focused efforts seek to determine the relationship between habitat fragmentation and a focal species' responses in terms of their own biological constraints, such as dietary requirements or interspecific relations. Landscape pattern research traditionally examined the biological consequences of fragmentation through applied island biogeography theory (IBT; MacArthur & Wilson, 1967), where patch size and degree of isolation or connectivity were the main determinants of landscape-level biodiversity. Advancements in the field of landscape ecology have since led to the development of more holistic analyses to explore the effects of fragmentation on species' persistence, including an additional focus on the spatial arrangement of remnant fragments, additive edge effects, connectivity indices, matrix structure, and overall landscape permeability (Begotti et al. 2018; Ewers & Didham, 2006; Fardila et al., 2017; Haddad et al., 2015; Kupfer et al., 2006; Laurance, 2008; Porensky & Young, 2013). The losses of biodiversity following habitat fragmentation can be thus attributed to a variety of factors; for example, altered microclimate features, time since fragmentation, predator-prey relations, and invasive species all impact biodiversity (Debinski & Holt, 2000; Evans et al., 2017a; Haddad et al., 2015; Laurance, 2008; Laurance et al., 2018). Here, several of the deleterious aspects associated with habitat fragmentation are explored, beginning with landscape-oriented considerations, moving towards a discussion of species-focused concerns, and concluding with a description of patterns of mammalian carnivore responses to stressors associated with anthropogenic land use modification.

1.3.1 Patches: habitat reduction and isolation

The most apparent consequence of habitat fragmentation is the implicit loss of crucial habitat, and thus resources, for native species. Species require access to specific habitat features and resources to survive, such as water, food, and areas of reproductive significance, such as mating, lekking, or nesting sites; as such, the loss of native habitat will inevitably lead to a decreased survival ability for a given individual and thus population (Crooks et al., 2011; Rybicki & Hanski, 2013). Generally, and with all other factors held equal, smaller patches of native vegetation support smaller populations and fewer species than larger patches (Azhar et al. 2014; Fischer & Lindenmayer, 2007; Vieira et al. 2009). This concept forms the basis of species-area relationships, and a wide array of models exists predicting the extinction rates of species given decreasing habitat fragment sizes (Keinath et al., 2017). Although each model carries implicit shortcomings, assumptions, and caveats, there is general agreement regarding the decreasing, nonlinear trend between species extinction rates and habitat area (Prugh et al., 2008; Rybicki & Hanski, 2013). With the loss of native flora, habitat heterogeneity plummets, and the number of niches available to the native biotic community is similarly diminished (Fahrig, 2001; Rybicki & Hanski, 2013; Vaughn et al., 2015). Trophic chains are often shortened following patch area reduction, as more individuals and species become extirpated by the loss of required habitat parameters and resources, destabilizing the ecological community (Dobson et al., 2006; Hill et al., 2011; Komonen et al., 2000).

Fragmentation events create remnant habitat patches that are not only smaller, but also compositionally disconnected or isolated from other similar habitat patches (Prugh et al., 2008). Functional connectivity is crucial for landscape-level ecosystem processes (Taylor et al., 1993); indeed, the relative importance of a patch's total area to biodiversity conservation can be modulated by the degree of connectivity to other remnant patches, at least in some systems (Martensen et al., 2008). The degree to which patch isolation impacts biodiversity, however, is a function of individual species' traits, such as locomotive capabilities and behavioural dispersal systems, taken with respect to the new matrix's permeability. Some species may be completely unable to disperse, and thus persist, in fragmented landscapes because the new land use poses a functional barrier to movement (as per traditional IBT theory; Haddad et al., 2015; Tucker et al., 2018; jaguar *Panthera onca,* Zemanova et al., 2017), while other species may be able to navigate the mosaic of matrix and remnant habitat patches to obtain necessary resources and, more importantly for population stability, disperse (bird *spp.,* Brambilla et al., 2015; reviewed by Kupfer et al., 2006; LaPoint et al., 2015). Analyses conducted by Crooks et al. (2011) determined that both the decrease of total available habitat and functional habitat connectivity threaten the survival of global mammalian carnivores.

1.3.2 Patch features, edges, and degradation

In addition to the concerns following the reduction in total area and functional configuration of original habitat, a suite of microclimate changes occur in the recently converted land, the remnant native fragments, and along the edge interface. These microclimatic changes often result in additional deterioration of the remaining fragments, and thus compound the damages sustained to the biotic community (Harper et al., 2005; Matlack, 1993; Pfeifer et al., 2017; Porensky & Young, 2013). Skole and Tucker (1993) reported that following a deforestation event in the Amazon, the cleared area was not the only area negatively affected; in total, the study documented negative biodiversity impacts and edge effects caused by the deforestation actually spanned an area 1.5 times greater than the directly removed patch. Barlow et al. (2016) reported similar trends, whereby patch size reduction facilitated greater than expected losses of biodiversity due to synergetic disturbances and pressures beyond the direct impacts of deforestation. According to Pfeifer et al. (2017), the presence of forest edges impacted, in some form, the abundance measures of 85% of studied forest vertebrates.

Radiation fluxes between the surface of the Earth and the surrounding atmosphere (surface albedo) are altered with the loss of native flora, resulting in greater temperature extremes and gradients in both the new matrix and at fragment edges than in contiguous habitat (Joshi et al., 2009; Laurance, 2008; Saunders et al., 1991). Increased temperature fluxes in habitat fragments can restrict foraging opportunities for temperature-dependent species (forest vertebrates, Pfeifer et al., 2017; Carnaby's cockatoo *Calyptorhynchus funereus latirostris,* Saunders, 1990). Post-fragmentation events in tropical forests can result in rapid, sun and heat-tolerant pioneer vegetative growth, such as vines, around fragment edges, while shade-preferring plants are severely restricted to the patch interior (Lovejoy et al., 1986; Saunders et al., 1991). This altered phenology can result in changed resource availability for native consumers (e.g. diademed sifaka *Propithecus diadema,* Irwin, 2008; Saunders et al., 1991), which can impact further up the trophic chain.

With the creation of edges in landscape features, increased wind exposure can result in elevated tree mortality both along edge boundaries (Harper et al., 2005) and within patches (Vaughn et al., 2015). Intensification of wind exposure within the interior of the fragment can also lead to habitat desiccation, lowering the survival rates of seedlings and preventing the establishment of species requiring native, humid, and moist soil conditions, thus expediting additional forest loss (Chen et al., 1992). Desiccation alters nutrient cycling processes by negatively impacting litter decomposition rates (Harper et al., 2005).

Following the removal of the natural surface cover, nutrient and hydrological cycles become greatly altered, and habitat fragmentation is often associated with extreme erosion, nutrient leaching, river sedimentation, and run-off events (Douglas, 1999; Saunders et al., 1991), particularly in lowland areas (Gregersen et al., 2003). In Brazil, the conversion of riparian forests to agriculture resulted in a 25% flow increase within the Tocantins River basin, with no change in annual precipitation rates (Foley et al., 2005). Elevated sedimentation rates further exacerbate global aquatic biodiversity losses (Dudgeon et al., 2006).

1.3.3 Species interactions

With structural habitat changes and altered microclimatic variables, remnant fragments often become the site of increased invasion from alien or otherwise suppressed species. The disturbance regime associated with fragmentation events creates otherwise unnatural opportunities for invasive species to establish within or around a fragment (Sakai et al., 2001; Doherty et al., 2015). In North America, extensive habitat fragmentation has been linked to the proliferation of kudzu (*Pueraria lobata*), an invasive, edge-preferring strangling vine now outcompeting native flora (Waldner, 2008). In Thailand, Gibson et al. (2013) reported a positive relationship between habitat fragmentation and invasion by non-native Malayan field rats (*Rattus tiomanicus*), and the resultant destabilisation accelerated the complete extinction of native small mammals. Fragmentation events in Madagascar disturbed the carnivorous species composition such that exotic carnivores (*Felis* spp.) severely threatened the survival of native fauna (Gerber et al., 2012). In fragmented ecosystems, the altered proximity and thus accessibility to remnant habitat patches by domesticated species, such as the domestic dog (*Canis familiaris*), has been documented globally, and the repercussions of interspecific interactions can be serious (Doherty et al., 2017; Hughes & Macdonald, 2013).

Habitat fragmentation can alter a variety of endogenous species interactions on multiple scales, such as shifting food or prey availability, influencing intra- and interspecific competition, altering predation rates, and undermining mutualisms (Banks et al., 2007; Fischer & Lindenmayer, 2007; Hagen et al., 2012). Herbivory rates and pressures are influenced by fragmentation; in the US, sensitive interior-dwelling plants became more accessible to non-selective browsing species such as white-tailed deer (*Odocoileus virginianus*) following fragmentation, which, in turn, further degraded the remaining mature forests (Alverson et al., 1988). Similar degradation loops have been initiated by wild boar (*Sus scrofus*) surviving near oil palm agriculture in Indonesia (Luskin et al., 2017). Relations between herbivorous insects and plant communities can be negatively impacted by fragmentation, and complex trophic relationships between plants, insect herbivores, and insect parasites become significantly destabilised (Valladares et al., 2006). Seed predation rates, which carry landscape-level implications for forest regrowth and establishment, are also altered by fragmentation (García & Chacoff, 2007). In Venezuela, the loss of top-down regulatory predators in forest fragments resulted in dramatic trophic cascades, described by Terborgh et al. (2001) as 'ecological meltdown', where unbounded populations of herbivores devastated flora assemblages, further exacerbating the rate of habitat loss. Through ecological network manipulations, Solé & Montoya (2006) demonstrated habitat fragmentation triggered similar ecological meltdowns via the disruption of and resultant feedback cascades within the biotic trophic web; further, this interplay was mediated by the diversity and structure of the original network. Increased predation of birds at patch edges compared with rates in contiguous habitat has been documented globally, and can represent a significant threat to native avian species (Chalfoun et al., 2002). Similarly, predation rates by a diverse carnivore guild in landscapes of the eastern United States were elevated after fragmentation disturbances (Oehler & Litvaitis, 1996).

With shifts in prey abundance and predation pressures, both inter- and intraspecific competition rates are similarly affected. The trophic organisation of native communities is altered following disturbances (*Lepidoptera* spp., Hill et al., 2011; insect communities, Komonen et al., 2000; Valladares et al., 2006). As time progresses past a fragmentation event, the assemblage of surviving fauna shifts to favour those species with significant ecological flexibility, be it in the form of spatial adaptations, niche breadth, or other coping mechanisms (Cooke et al., 2019; Ramiadantsoa et al., 2018). Following most fragmentation events, patches suffer a reduction in the number of specialist species, due to either direct conflict where the patch fails to meets its specific requirements, or indirect conflict of unsustainable competition with 'hardier' generalist species (Fitzherbert et al., 2008; Komonen et al., 2000; Oehler & Litvaitis, 1996). Generalist species with broad ecological niches persist as specialist species struggle, as with the raccoon (*Procyon lotor*) and opossum (*Didelphis virginianus*) in North America, and the small Indian civet (*Viverricula indica*) in Asia (Crooks & Soulé, 1999; Mudappa et al., 2007). The loss of specialist species significantly truncates food webs and community richness indices of fragments (Komonen et al., 2000), which can have dramatic repercussions for the long-term functioning of an ecosystem (Galetti & Dirzo, 2013).

1.3.4 Genetic implications

Habitat fragmentation events can result in serious genetic implications (Brunke et al., 2019; Lino et al., 2018). The concepts of IBT can apply to isolated habitat patches, as gene flow can be significantly reduced or even completely blocked due to the fragmentation of a population's range by a dispersal-resistant matrix (Crooks et al., 2011). The complexity in understanding and documenting genetic responses to fragmentation is pervasive in the literature, and is not to be disregarded (Kramer et al., 2008; Lino et al., 2018). On one hand, if the isolated fragment is large enough to sustain a significantly genetically diverse population, speciation through genetic divergence may occur over time, assuming all other biological requirements are fulfilled (Gibbs, 2001; Schluter, 2009; Thomas, 2000). The rate and scale of anthropogenic habitat fragmentation are, however, surpassing many metapopulations' flexibility to such selective pressures, so fragmentation events can instead directly result in localised and, theoretically, complete extinctions (toad *Rhinella ornata,* Dixo et al., 2009; Bornean orang-utan *Pongo pygmaeus,* Goossens et al., 2005; Asiatic lion *Panthera leo persica,* Singh & Gibson, 2011; *Lepidoptera* spp., Thomas, 2000). Over time, metapopulations persisting in small, isolated fragments can suffer from an elevated inbreeding risk (Keller & Waller, 2002; Iberian lynx *Lynx pardinus,* Johnson et al., 2004; puma *Puma concolor,* Loxterman, 2011); although this pattern only occurs if time since fragmentation aligns with that of detectable genetic change, which can be particularly prolonged for carnivore species (Aguilar et al., 2008; reviewed by Lino et al., 2018; maned wolves *Chrysocyon brachyurus*, Mannise et al., 2017). The importance of patch demographics in determining a population's genetic response to fragmentation events over time can be critical (Gibbs, 2001; arthropod spp., Habel & Schmitt, 2018; Lino et al., 2018). Following fragmentation events, the loss of individuals from a metapopulation simultaneously results in the loss of potentially adaptive genetic mutations, the impact of which could further undermine a population's resistance to stressors (Keyghobadi, 2007). Similarly, isolation of a given metapopulation could lead to the accumulation of deleterious mutations within the patch's overall genetic diversity, which could further accelerate localised extinctions.

Anthropogenic land use change also raises the probability of hybridisation between wild and domestic species; this has been documented in an array of carnivore species persisting in human-modified landscapes (African wildcat *Felis silvestris lybica,* Le Roux et al., 2014; dingo *Canis lupus dingo,* Stephens et al., 2015; Iberian wolf *Canis lupus signatus,* Torres et al., 2017). Negative impacts of fragmentation on the genetic structuring, allelic diversity, and genetic richness of isolated populations have been documented in plants (Aguilar et al., 2008), birds (Khimoun et al., 2016), reptiles (Delaney et al., 2010; Velo-Antón et al., 2014), amphibians (Cushman, 2006), mammals (small mammals, Gaines et al., 1990; Sumatran rhinoceros *Dicerorhinus sumatrensis,* Goossens et al., 2013; bobcat *Lynx rufus* and ocelot *Leopardus pardalis,* Janecka et al., 2016; ringtail possum *Pseudocheirus peregrinus,* Lancaster et al., 2016; leopard *Panthera pardus,* McManus et al., 2014; black bears *Ursus americanus,* Murphy et al., 2017), fish (white-spotted charr *Salvelinus leucomaenis*, Yamamoto et al., 2004), and invertebrates (ground beetle *Carabus violaceus,* Keller & Largiadèr, 2003), and the field of landscape genetics continues to expand.

1.3.5 Species health

The interplay between land use changes and wildlife disease prevalence is an intensely studied field (Brearley et al., 2013). According to density-dependent transmission epidemiological theory, elevated host densities in remnant patches increase the probability of infectious agents, such as viruses or parasitic larva, contacting their required targets or hosts (Anderson & May, 1979). Further, if the habitat patch is significantly isolated and surrounded by a functionally impermeable matrix, the remnant wildlife population may not be able to ‘escape’ a disease, further hastening species declines (McCallum & Dobson, 2002). Increased parasite prevalence, richness, and infection rates have been documented in species persisting within habitat fragments, such as primates (red colobus *Procolobus rufomitratus,* Gillespie & Chapman, 2008; mangabey *Cerocebus galeritus galeritus,* Mbora & McPeek, 2009), birds (Lesser Antillean bullfinch *Loxigilla noctis,* Pérez-Rodríguez et al., 2018), Bornean elephants (*Elephas maximus borneensis,* Hing, 2012), and small mammal communities (Vaz et al., 2007). A meta-analysis conducted by Pedersen et al. (2007) revealed carnivores to be more threatened by parasite and pathogen exposure events than any other mammalian orders, excluding ungulates. Alternatively, frequency-dependent transmission theories suggest that post-fragmented disease transmission rates could increase due to a relative inflation of the proportion of total infected individuals within the remnant population, regardless of population density changes (Ryder et al., 2007). This theory hinges upon how disease prevalence is modulated by transmission modes (e.g. direct contact, vector-borne, or sexual transmission modes), and how the variety of behavioural responses of wildlife to fragmentation can additively exacerbate localised transmission dynamics (Brearley et al., 2013; Sanchez & Hudgens, 2015). For example, following urban development of native habitats in south California, the movement patterns of resident bobcats displayed active avoidance of urbanised regions, in turn intensifying the usage of remnant forest patches by the population (Tracey et al., 2013). This resultant concentration of spatial behaviours led to increases in the transmission probability of feline immunodeficiency virus, a contact-transmitted disease (Fountain-Jones et al., 2017).

Additionally, the introduction of habitat edges and matrices facilitate exposure to novel diseases otherwise functionally absent from continuous habitats. The presence of livestock and other domestic animals in fragmented regions increases the risk of disease transmission to wild species, and can lead to devastating effects (Aguirre, 2009). Carnivores across the globe have experienced population declines from diseases associated with domestic animals, such as canine distemper virus or rabies (African wild dogs *Lycaon pictus,* Kat et al., 1995; Ethiopian wolves *Canis simensis,* Laurenson et al., 1998; Iberian lynx, Millán et al., 2009a; African lions *P. leo,* Viana et al., 2015). In Mexico City, the wild mammal assemblage demonstrated elevated seroprevalence of infectious pathogens including rabies, *Toxoplasmosis*, and canine parvovirus, findings attributed to the large populations of feral cats and dogs surrounding and permeating forest patches (Suzán & Ceballos, 2005). With the increased accessibility to forest interiors, the potential for zoonotic disease transmission grows both for wildlife and humans. Human diseases such as AIDS, plague, smallpox, nipah, Ebola, rabies, and severe acute respiratory syndrome (SARS) coronavirus originated from wild animals, and fragmentation events can create future human epidemiological risks worldwide (Bell et al., 2004; Daszak et al., 2001; Molyneux, 2002). With the loss of natural habitat, local population densities and assemblage diversity of both wildlife and zoonotic disease vectors and reservoirs can dramatically shift, the effects of which have resulted in widespread zoonotic disease outbreaks across the globe (e.g. Lyme disease, Allan et al., 2003; mosquito vectors and malaria, Brant, 2011; Fornace et al, 2016; Patz & Wolf, 2002; *Bartonella* spp., Young et al., 2014).

Beyond the risks of infectious disease or parasitic transmission, species persisting in fragmented habitats can display decreased overall measures of health, be this assessed as body condition (Irwin et al., 2019; Johnstone et al., 2011), haematological parameters (Irwin et al. 2010; Junge et al. 2011), immune system functioning (Murray et al., 2016), gastrointestinal microbiomes (Amato et al. 2013), or reproductive capabilities (Acevedo-Whitehouse & Duffus, 2009). The field of organism health is relatively underrepresented in the literature and difficult to study in the wild, given the invasive nature of most associated veterinarian procedures, but is nonetheless an important aspect of consideration regarding biodiversity responses to fragmentation. Individuals unable to obtain sufficient amounts of appropriate quality natural food sources suffer from nutrient deficiencies (Birnie-Gauvin et al., 2017), anemia (García-Feria et al., 2017), or dehydration (Singleton et al., 2015), all which can ultimately lead to death (Irwin et al., 2019; Irwin, 2008). Alternatively, species with adequate dietary flexibility can supplement their natural diets with anthropogenic food sources, as documented by coyotes (*Canis latrans,* Newsome et al., 2015) or red foxes (*Vulpes vulpes*, Cancio et al., 2017). Such behavioural plasticity staves off immediate death, but can present its own suite of perils to these individuals' overall health, be this inadequate nutrient intake, elevated cholesterol, or exposure to toxins (Murray et al., 2016; Murray et al., 2015; Oro et al., 2013; Sorensen et al., 2014).

Recent developments in the field of organismal research have begun to explore the role of chronic stress in species health and persistence within fragmented habitats (Ellis et al., 2012; Messina et al., 2018; Meyer & Novak, 2012; Wikelski & Cooke, 2006). The production of stress hormones, namely glucocorticoids, is, in the short term, adaptive for a species, as they work to regulate responses to destabilizing or unexpected situations (Busch & Hayward, 2009; Nelson, 2005). Long-term exposure to elevated stress hormones is, however, maladaptive to the physiological health of an individual, and often linked to the development of disorders and tissue damage (Charmandari et al., 2005). Further, stress can negatively affect an individual's reproductive success, a finding that carries population-level conservation implications (Vitousek et al., 2014). Some studies have positively correlated detectable mammalian stress hormone levels with the degree of habitat fragmentation and degradation (tiger *Panthera tigris,* Bhattacharjee et al., 2015; agile antechinus *Antechinus agilis,* Johnstone et al. 2012; brown bear *Ursus arctos,* Macbeth et al., 2010; Støen et al., 2015; bat spp. Seltmann et al., 2017). Contrasting trends have also been reported, however (e.g. spider monkey *Ateles geoffroyi,* Ordóñez-Gómez et al., 2016), highlighting the importance of future development and conservation application of this field (Busch & Hayward, 2009; Millspaugh & Washburn, 2004; Russell et al., 2012).

Lastly, habitat fragmentation can increase the probability of biodiversity being exposed to anthropogenic pollutants, such as persistent organic pollutants (Acevedo-Whitehouse & Duffus, 2009), pest control chemicals (Sánchez-Barbudo et al., 2012), heavy metals (Schuler & Relyea, 2018), microplastics (Barletta et al., 2019), or estrogenic agents (Vos et al., 2000). Forest edges themselves can act as concentrators of pollutants, and as such, fragmentation poses risks to wildlife persisting both within the directly treated matrices and within remnant patches (Weathers et al., 2001). Given their high trophic positions and long lifespans, carnivore species are particularly vulnerable to anthropogenic pollution through both bioaccumulation and biomagnification processes (killer whales *Orcinus orca,* Desforges et al., 2018; Arctic megafauna, Dietz et al., 2013; Smith et al., 2007). Of specific concern are the implications of habitat fragmentation for agricultural development and the subsequent application of a wide array of chemicals and minerals otherwise absent in the natural habitat (Geiger et al., 2010; Gibbs et al., 2009; McLaughlin & Mineau, 1995). According to Pretty and Bharucha (2015), global synthetic pesticide usage has grown to an annual application rate exceeding 3.5 billion kg of active ingredients per year, the application of which carries negative consequences for global biodiversity (Devine & Furlong, 2007). Carnivores are frequent victims of both direct and indirect pesticide poisonings, with significant population-level repercussions documented globally (Köhler & Triebskorn, 2013; San Joaquin kit fox *Vulpes macrotis mutica* Nogeire et al. 2015; Oriental white-backed vulture *Gyps bengalensis* Oaks et al., 2004; Eurasian otter *Lutra lutra* Prigioni et al., 2007; bobcat Serieys et al., 2018).

1.3.6 Human-wildlife conflict

Habitat fragmentation increases the potential for human-wildlife conflict (Pooley et al., 2017; Treves & Karanth, 2003). Direct conflicts between humans and wildlife, such as physical attacks, livestock predation, road mortalities, and crop damage, intensify with increased habitat fragmentation (black bear, Beckmann & Berger, 2003; Ceia-Hasse et al., 2018; Asian elephant *E. maximus,* Choudhury, 2004; sun bear *Helarctos malayanus,* Guharajan et al., 2017; Brazilian wildlife, Marchini & Crawshaw, 2015). Woodroffe and Ginsberg (1998) report habitat fragmentation increased the extinction rates of African carnivores, due specifically to the increased risk of human-carnivore contact outside of native land cover, and the resultant persecution of ‘problem’ animals. Beyond these examples of direct conflict, fragmentation is linked to increases in hunting, poaching, and further human-facilitated degradation of remaining patches, such as illegal logging; these actions inflict even more pressure on wildlife managing to persist within altered landscapes (Cullen et al., 2000; Gray et al, 2018; Laurance, 2008; Naughton-Treves et al., 2003; Nielsen et al. 2017; Sandom et al., 2017; Woodroffe & Ginsberg, 1998). Analysis by Sandom et al. (2017) highlighted human-induced defaunation of target prey species poses a major threat to the survival of felid species. Indeed, even in areas specifically protected from human presence and modifications, Jones et al. (2018) found that one-third of supposed preserves were subjected to immense human pressure. With international and local wildlife and botanic trade markets flourishing (Phelps & Webb, 2015; Symes et al., 2018), fragmented areas are often the first regions decimated by poaching due to the relative ease of access to target species (e.g. hornbill spp., Holbech et al., 2018; Thai wildlife, Pattanavibool & Dearden, 2002).

1.3.7 Interplay

The relations between patch size, edge effects, species interactions, genetic considerations, disease ecology, deleterious agents, and human-wildlife conflict are dynamic, often complementary, and even more often synergistic, and together inflict multifarious pressure on global biodiversity (Brook et al., 2008; Côté et al., 2016; Fletcher Jr. et al., 2018). Not to be overlooked, stochastic threats often serve to complicate these already intricate issues. Global processes, most notably climate change, will further exacerbate species' loss in fragmented ecosystems, particularly if remnant patches no longer represent suitable habitat for the species in question (Jantz et al., 2015; Littlefield et al., 2017; Struebig et al., 2015). Species' responses to fragmentation depend not only on the severity of landscape-level changes, but also on their own intrinsic population and species traits, such as trophic level, body size, home range size, reproductive rates, dispersal capabilities, and population genetic variance (Crooks et al., 2017; Fahrig, 2001; Ferreira et al., 2018; Shamoon et al., 2017; Vetter et al., 2011). Rybicki and Hanski (2013) demonstrated that the theoretical relationship between habitat fragmentation events and extinction rates is a direct function of area lost, spatial organization of the remaining fragments, and species' traits. The topic of a species', indeed an individual's, sensitivity to habitat change and fragmentation is common in the literature (Crooks, 2002; Gehring & Swihart, 2002; Orme et al., 2019; Purvis et al., 2000; Swihart et al., 2003), and efforts to evaluate species' requirements for surviving fragmentation events are increasingly important for conservation. The combination and interplay of these factors determine the resultant survival or demise of species across anthropogenically modified landscapes; it is therefore critical to tease apart the complexities of such systems to determine how best to offset large-scale biodiversity losses.

1.4 Habitat fragmentation and carnivores

As with global biodiversity, mammalian carnivores are in decline across the world (Ripple et al., 2014), and this is largely attributed to anthropogenically-mediated habitat loss, fragmentation, and degradation (Crooks et al., 2011), with agricultural development highlighted as a major threat (Dobrovolski et al., 2013). As a group, carnivores are considered sensitive to habitat fragmentation due to biological and ecological traits such as long lifespans, slow reproduction rates, large body mass, high trophic level, large home ranges, and/or naturally low metapopulation densities (Carbone et al., 2005; Crooks, 2002; Gehring & Swihart, 2002; Hawkins & Racey, 2005; Keinath et al., 2017; Pfeifer et al., 2017; Purvis et al., 2000; Solé & Montoya, 2006). The full extent of carnivore responses to fragmentation and degradation is however strongly mediated by the ecology of the focal species (Brodie et al., 2015; Ryall & Fahrig, 2006; Swihart et al., 2003), and carnivores demonstrate a range of tolerance thresholds and adaptations. The importance of evaluating carnivore responses to human-mediated land use changes is amplified given the value of these species to ecosystem functionality. Carnivores are traditionally considered both a value to and a symptom of a healthy ecosystem (Miller et al., 2001; O'Bryan et al., 2018; Ripple & Beschta, 2012; Roemer et al., 2009; Suraci et al. 2016). To reiterate the analyses by Terborgh et al. (2001), the repercussions of predator loss from forest fragments have been described as ecological meltdown. Noss et al. (1996) went so far as to state that the mere presence of carnivores within forest fragments is indicative of the 'integrity of an entire ecosystem'; although this is a largely simplified paradigm given the complex factors involved in carnivore survival following fragmentation, it remains a valuable conservation discourse. In this section, the diversity of mammalian carnivore responses to habitat fragmentation patterns and processes are briefly discussed.

Carnivore extant ranges have been severely reduced by anthropogenic habitat loss and fragmentation, which has contracted carnivore distribution and site occupancy patterns across the world (Crooks et al., 2017; Di Minin et al., 2016). Only 54.3% of all mammalian extant carnivore ranges occur in areas considered high quality habitat, and these regions are rapidly shrinking as a result of human activities (Crooks et al., 2011). Both large and small carnivore species are experiencing significant extant range contractions thanks, at least in part, to habitat fragmentation (e.g. leopards*,* Jacobson et al., 2016; North American carnivore species, Laliberte & Ripple, 2004), realities that could serve to facilitate localised and, if unimpeded, total extirpation of carnivore species (Crooks et al., 2017; Gibson et al., 2013). Lower carnivore occupancy rates have been documented in patchy and disturbed landscapes than in contiguous habitats worldwide (Madagascan carnivores, Farris et al., 2015; Gerber et al., 2012; Bornean carnivores, Mathai et al., 2017; Amazonian species Michalski & Peres, 2007; Andean carnivores, Zapata-Ríos et al., 2018). This impact is particularly apparent in regions where carnivores are unable to recolonise any remaining 'unoccupied' habitat due to extreme patch isolation via low matrix permeability (beech marten *Martes foina* and badger *Meles meles,* Mortelliti & Boitani, 2008; Evans et al., 2017a; Bornean carnivores, Yue et al., 2015).

Complementarily, the patterns of carnivore abundance and density are altered by habitat fragmentation, as carnivore density is directly and positively related to available prey density (Carbone & Gittleman, 2002). Habitat fragmentation is largely reported to decrease landscape carnivore population densities; mechanistically, the creation of small and isolated habitat patches can result in resource scarcity for top trophic species, be the resource dietary, spatial, or reproductive (Banks et al., 2007). Decreased carnivore abundances and densities in fragmented landscapes have been documented in both large- and small-bodied carnivores (African golden cat *Caracal aurata*, Bahaa-el-din et al., 2016; coyote and bobcat, Flores-Morales et al., 2018; Sunda clouded leopard *Neofelis diardi,* Hearn et al., 2017; Malay civet *Viverra tangalunga,* Heydon & Bulloh, 1996; black bears*,* Murphy et al., 2017). Contrastingly, carnivores have been documented at greater densities in disturbed landscapes than in contiguous habitats (e.g. leopard cat *Prionailurus bengalensis,* Mohamed et al., 2013); this increase is most often attributed to two (not necessarily exclusive) mechanisms: a 'crowding effect' (Debinski & Holt, 2000; Collinge & Forman, 1998; Irwin, 2008), or a 'magnet effect' (Greene et al., 2002). The crowding effect is a process whereby the loss of native habitat inflates carnivore density in remnant patches through immediate patch immigration, and has been documented mainly in small mammals (Lynam & Bilick, 1999) and insects (Grez et al., 2004). The magnet effect relates to fragmentation-facilitated increases in the patch-level availability or productivity of critical resources; as examples, the literature review by Sálek et al. (2015) reported significantly increased densities of coyote, raccoon, and red fox along an increasing gradient of anthropogenic disturbance, and attributed this to the availability of alternative food sources. Similarly, Mudappa et al. (2007) suggested increased the abundance of the omnivorous small Indian civet in fragmented habitats was due to increased availability of litter arthropods following disturbance. Such patterns have been considered an indication of species' tolerance to human disturbance, and have been described in a diverse array of species (review, Bateman & Fleming, 2012; feral cats *Felis catus,* Bengsen et al., 2015; caracals *Caracal caracal,* Ramesh & Downs, 2013). As always, the time since fragmentation can alter the directionality and strength of the carnivore density fragmentation relationship (Banks et al., 2007; Gibson et al., 2013), as can the scale of habitat loss relative to the spatial ecology of target carnivore species (Bowers & Matter, 1997; Oehler & Litvaitis, 1996).

Finally, fragmentation events can alter landscape-level carnivore assemblages and diversity indices (Dalerum et al., 2009). As time progresses past a fragmentation event, the assemblage of surviving fauna tends to shift towards favouring those species with significant ecological flexibility, be it in the form of spatial adaptations, dietary niche breadth, or other coping mechanisms (Madagascan carnivores, Gerber et al., 2012; leopard cat, Mohamed et al., 2013; Mediterranean carnivores, Pita et al., 2009; theory Ramiadantsoa et al., 2018; Ryall & Fahrig, 2006). This pattern of shifting assemblage composition can occur due to either direct resource scarcities discussed above, whereby a remnant patch fails to provide the specialist with required resources and they perish; or through process-driven conflict, whereby unsustainable competition with 'hardier' generalist species drives the demise of specialist species (Fitzherbert et al., 2008). Following the loss of large-bodied, top-down apex regulators, populations of mesopredators (defined as small or medium-sized carnivores) increase, a process coined 'mesopredator release' (Crooks & Soulé, 1999; Mudappa et al., 2007; Newsome & Ripple, 2015; Roemer et al., 2009). This increases the predation pressure on smaller prey animals, in turn diminishing herbivory rates, which can result in a full trophic cascade, defined as a community-wide response triggered by altered species dynamics, originating at the apex trophic positions (Crooks & Soulé, 1999). In California, the loss of the top carnivore, the coyote, in forest fragments resulted in large, unbounded patch populations of raccoon, grey fox (*Urocyon cinereoargenteus*), and both feral and domestic cats. The fragments with higher mesopredator densities were, in term, found to contain significantly smaller populations of native bird species due to

the increased predation pressure (Crooks & Soulé, 1999).
Given the diversity of species' responses to anthropogenic land use changes, it remains critically important to evaluate carnivore ecology within human-impacted systems. Through the study of carnivore physiology, behaviour, and population demography within such dynamic landscapes, it may be possible to determine how to best mitigate further anthropogenic extinction events in this crucially important guild.

1.5 Case study: Southeast Asia and the oil palm

1.5.1 Southeast Asia and the oil palm: a history

Southeast Asia is one of the most biodiverse areas of Earth, and contains four biodiversity hotspots (Brooks et al., 2002; Myers et al., 2000; Sodhi et al., 2004). Southeast Asia has one of the most rich and diverse carnivore guilds in the world, with 22 species from five families present (Dalerum et al., 2009), along with the highest global mean proportion of country-endemic bird and mammal species (Sodhi et al., 2009). Over 700 endemic vertebrates have been documented throughout the Sundaland region, with new species identifications still occurring (Brooks et al., 2002; Pimm et al., 2014). The Southeast Asian region of Sundaland is however also one of the top five hotspots poised to lose the most vertebrates and plants due to habitat destruction and degradation (Butchart et al., 2004; Brooks et al., 2002; Ceballos & Ehrlich, 2002; Cushman et al., 2017); indeed, Wilcove et al. (2013) report that as of 2010, 70% of the natural lowland forests of Sundaland had been cleared by human activities. As such, across all taxonomic groups except amphibians, the region claims the highest global proportion of threatened species (Sodhi et al., 2010).

Southeast Asian forest destruction and fragmentation is unparalleled by any other global region (Curtis et al., 2018; Rautner et al., 2005). Currently, the endemic biodiversity of the area is directly threatened by the conversion and thus loss of over 70% of natural species' habitats (Myers et al., 2000), and significant degradation of those remaining natural ecosystems recorded (Zhao et al., 2006). Broad species-area-relationship estimates propose a total loss of anywhere from 13 to a staggering 85% of all Southeast Asian species by 2100 (Sodhi et al., 2009; Wilcove et al., 2013). With dramatically growing regional human populations paired with booming technological advancements and quality of life expectations, natural landscapes are the first to suffer; with a fraction of Southeast Asian forests legally protected, the future rate of habitat loss and further degradation appears to be unbounded (Cushman et al., 2017; Sodhi et al., 2010).

Most notably, the expansion of the palm oil (*Elaeis guineensis*) sector is considered the largest single threat to the remaining biodiversity of the region (Phalan et al., 2013; Wilcove & Koh, 2010; Wilcove et al., 2013). A lucrative business, the palm oil sector is a multi-billion dollar industry, and has swiftly surpassed all other oil crop production, such as soybean and rapeseed, to account for over 30% of global oil and fat production (Carter et al., 2007; Kushairi et al., 2018). As of 2017, nearly 68 million tons of palm oil and over 7 million tons of palm kernel oil were produced globally per annum (Oil World, 2018). Native to western Africa, *E. guineensis* has been successfully established in tropical regions within 15–20° of the Equator (Henderson & Osborne, 2000); according to Kushairi et al. (2018), the world contains over 19 million total hectares of planted palm oil. Production is currently centered around Southeast Asia; Indonesia and Malaysia are the top global producers of crude palm oil, accounting for over 85% of total cultivation (Teoh, 2010; Varkkey et al. 2018). An additional 41 countries are reported to produce the crop (Meijaard et al., 2018; Sheil et al., 2009).

The oil palm was introduced to Southeast Asia in 1848 in Java by the Dutch, primarily as an ornamental species (Henderson & Osborne, 2000). The first commercial plantation was established in Peninsular Malaysia in 1917, and the sector grew exponentially, replacing rubber plantations as the area's dominant agriculture (Sheil et al*.,* 2009). To date, palm oil is the largest industry sector of oilseed producing crops in the world (Fitzherbert et al., 2008; USDA, 2014).

The tree produces large bundles of fruit from the trunk of the palm, with each bunch weighing between 20-30 kg and female bunches bearing a maximum of 2500 fruits (Basiron & Weng, 2004). These fruits are comprised of two parts, each with economic value: a hard kernel and a surrounding fleshy mesocarp. The major product of the crop is oil contained in the mesocarp as palm oil, or crude palm oil. The oil contains a large amount of antioxidants and linoleic acid, both which contribute to a long product shelf life (Basiron & Weng, 2004). Palm oil is also trans-fat free, although it is relatively high in saturated fats (Henderson & Osborne, 2000). Crude palm oil is used in a wide variety of manners, mostly edible, such as cooking oil, margarine, coffee creamers and confectionaries (Sheil et al., 2009). The kernel produces a different type of oil, called palm kernel oil, which is utilised in soaps, cosmetics, some edible products, and in oleo-chemical creation, compounds used widely in industrial sectors as lubricants, plastics, and as pharmaceutical additives (Wahid et al., 2004). Both crude palm oil and palm kernel oil also hold the potential to be utilised as biodiesel fuel (Fargione et al., 2010).

Economically, one of the attractive qualities of *E. guineensis* is its prolific yield. Compared to other major oil crops, oil palm far surpasses the per hectare yield, producing an average of four tons of product per hectare on commercial plantations, although this figure varies by region and treatment (Meijaard et al., 2018; Murphy, 2014). Trees begin producing fruit at the age of 2–3 years old, and continue to do so at a high rate until they are 25–30 years old. This results in a lifespan yield that easily eclipses other oil-producing crops such as rapeseed, coconut, sunflower, and soybean (approximately 0.5–1 tonnes of oil produced per hectare of crop; Basiron, 2002; Sheil et al., 2009).

The environmental concerns associated with palm oil plantation establishment and upkeep are vast and represented by a growing body of literature (*selection*: Aratrakorn et al., 2006; Barnes et al., 2014; Dislich et al., 2017; Donald, 2004; Drescher et al., 2016; Fitzherbert et al., 2008; Koh & Wilcove, 2008; Savilaakso et al., 2014; Turner & Foster, 2008; Turner et al., 2011; Yaap et al., 2010). The conversion of natural forest habitat to oil palm agriculture has been demonstrated to affect most levels of biodiversity, soil microbiomes (Tripathi et al. 2016), fungal communities (Kerfahi et al., 2014), vegetation (Rembold et al. 2017), invertebrates (Brühl & Eltz, 2010; Sabrina et al., 2009), reptiles (Glor et al. 2001), amphibians (Gallmetzer & Schulze, 2015; Scriven et al., 2018), fish (Giam et al., 2015), birds (Azhar et al. 2011), small mammals (Bernard et al.

2009), bats (Shafie et al. 2011; Struebig et al., 2011), ungulates and other herbivores (Azhar et al., 2014), primates (Danielsen & Heegaard, 1995, Foster et al., 2011), mammalian carnivores (Hearn et al., 2018; Jennings et al., 2015; Wearn et al., 2017), and megaherbivores (Estes et al., 2012; Yue et al., 2015). Compared to alternate tropical agricultural crops (rubber, coffee, cocoa and acacia), oil palm plantations contain significantly less biodiversity, both in richness indices and species abundance counts (Fitzherbert et al., 2008; Foster et al., 2011; Koh & Wilcove, 2008). Across all studies reviewed in Fitzherbert et al. (2008), a mean 85% of all faunal species found in primary forest were absent in oil palm plantations, and those species lost were generally of highest conservation concern. Species absent after conversion are generally forest specialists with restricted dietary niches or behaviours that otherwise rely on forest habitat features, resulting in a shifting and often simplification of the biotic community in a region (Butchart et al., 2004; Fitzherbert et al., 2008; Foster et al., 2011; Koh & Wilcove, 2008; Pardo et al., 2019). As such, species that do persist in the monoculture are often generalists (be it in dietary or habitat terms), pests, or invasives (Danielson & Heegaard, 1995; Rembold et al., 2017; Wearn et al., 2017; Yue et al., 2015). Beyond the forest loss by the plantation establishment, any remnant forests persisting beyond or within the agriculture are often severely degraded, the scope of which is often secondarily exacerbated by the agricultural establishment. As an example, Luskin et al. (2017) recorded what they dubbed a ‘cross-boundary subsidy cascade’, whereby forests flanking plantations were significantly degraded following localised population explosions of wild pigs; increases in pig reproductive success was facilitated by the consistent availability of a high-quality diet of oil palm kernels. Overall, over 400 records of species listed as threatened by the IUCN contain reference to oil palm as a direct threat to their survival (Meijaard et al., 2018).

The drivers of biodiversity loss by the establishment and maintenance of oil palm plantations are manifold. In a broad review, Dislich et al. (2017) found oil palm plantations had a functional decrease in over 78% of the studied ecosystem functions present in natural tropical forests. The structural simplification of a tropical rainforest down to a monoculture matrix is an unsurprisingly dramatic and detrimental change to those species residing in the area. The microclimates of oil palm plantations, although varied with age of crop, are substantially hotter and drier from natural forest patches (Hardwick et al., 2015; Luskin & Potts, 2011; Meijide et al., 2018). Soil degradation is documented under oil palm cultivation (Guillaume et al., 2016; Lee-Cruz et al., 2013). Hydrological and erosion regimes are altered and degraded by the forest clearing and establishment of oil palm monoculture, often with dramatic social impacts (Chellaiah & Yule, 2018; Horton et al., 2017; Luke et al., 2017; Merten et al., 2016). Indeed, Tulloch et al. (2016) simulated the risks of oil palm plantation establishment to marine ecosystems via runoff and sedimentation effects, and found over 60% of relevant coastal ecosystems were to be degraded under the worst-case development scenarios. The conversion of natural ecosystems such as tropical rainforests and peat swamps to oil palm carries extensive implications for global carbon stocks, creating potential feedback loops with respect to greenhouse gas emissions and climate change (Danielsen et al., 2009; Fargione et al., 2008; van Straaten et al., 2015). Furthermore, some plantations conduct open burning to facilitate ground clearing for both initial establishment and the 20-year replanting cycles (Comte et al., 2012; Meijaard et al., 2018). Oil palm plantations can foster and incubate anthropogenic risks to wildlife beyond those directly associated with the extensive land use changes, as hunting, road accidents, conflict with domestic animals, and the potential for disease transmission are increased within and near the agricultural matrix (Azhar et al., 2013; Corlett, 2007; Laurance & Arrea, 2017; Milner-Gulland et al., 2003; Nájera et al., 2013). Palm oil production is linked with the application of fertilisers, pesticides, and other agrochemicals, and species persisting within the matrix and in the surrounding forests can be deleteriously impacted, both directly through acute events like poisonings, and indirectly through the repercussions of living in contact with polluted water, soil, and/or vegetation (Dislich et al., 2017; Kurniawan, 2016; Naim et al., 2011; Salim et al., 2014a; Salim et al., 2014b; Sulai et al. 2015). With regards to the environmental threats of agrochemicals, rigorously peer-reviewed studies exploring the impacts of such applications on surrounding biodiversity are both limited– not wholly unsurprising given the complex systems in question– and critical, given the scope and scale of concerns, particularly for human health implications (Ali & Shaari, 2015; Bessou et al., 2017; Donald, 2004; Foster et al., 2011; Meijaard et al., 2018).

As such, there exist a variety of proposals to best balance the global demand for oil palm and its products with the sustaining and conservation of biodiversity (Luskin et al. 2018; Phalan et al. 2011; Tscharntke et al. 2012). Two main branches of thought divide the debate arena: those hailing land-sparing agricultural practices, whereby forests are preserved, and agriculture and wilderness are effectively segregated (Edwards et al. 2013; Gibson et al. 2011; Grass et al., 2019; Nantha & Tisdell 2009; Yue et al. 2015); and those striving for the design and adoption of effective land-sharing, whereby native lands are conserved, as possible, within and around the monoculture, and wildlife-friendly, or at least less detrimental, practices adopted and integrated by the agricultural sector (Abram et al., 2014; Ashraf et al., 2018; Bhagwat et al., 2008; Foster et al., 2011; Gérard et al., 2017; Gray et al., 2016; Koh, 2008; Mitchell et al., 2018; Perfecto & Vandermeer, 2008; Perfecto & Vandermeer, 2010). Depending on the scale of inquiry, these conservation methods need not necessarily be mutually exclusive, and when paired with economic underpinnings, can indeed be proposed for the conservation of biodiversity (Clough et al., 2011; Grass et al., 2019), or certain flagship charismatic species, such as the Bornean orang-utan (Davies et al., 2017; Nantha & Tisdell, 2009) or the Bornean elephant (Evans et al., 2017b; Evans et al., 2018; Runting et al., 2015). Complimentary agricultural strategies are developing alongside the biodiversity debate, such as efforts to increase the productivity yields in established crops to offset further expansion (Basiron, 2007; Kushairi et al., 2018; Pretty, 2018; Varkkey et al., 2018). Assessments evaluating the best initial land use allocation parameters prior to further plantation establishment are similarly in development (Asner et al., 2018; Dinerstein et al., 2015; Law et al., 2015; Meijaard et al., 2018). Lastly, studies are beginning to assign economic value to natural ecosystems and associated biodiversity in terms of directly augmenting oil palm revenue via decreasing pest-mediated losses, improving riparian soil stability, nutrient transference, and carbon stock value (Bessou et al., 2017; Dislich et al., 2017; Edwards et al. 2014; Gray & Lewis, 2014; Horton et al. 2018; Nurdiansyah et al. 2016; Silmi et al. 2013). Efforts both nationally (e.g. MSPO Malaysian Sustainable Palm Oil certification) and internationally (e.g. RSPO Roundtable for Sustainable Palm Oil) to design and implement 'sustainable' palm oil industry guidelines and certification schemes exist (Gatti et al., 2019; Meijaard et al., 2018; Tan et al., 2009; Yaap et al., 2010). Corporate companies are publically declaring no-deforestation commitments —although these are often without the necessary teeth to create tangible change (Curtis et al., 2018)— and largely western consumers express a willingness to purchase goods containing palm oil produced in conditions less detrimental to biodiversity (Bateman et al., 2010; Meijaard et al., 2018). For any of these strategies to succeed, however, enthusiastic and participatory support from local administrations and enforcement agencies are critical and often staggeringly complicated to obtain (Gatti et al., 2019).

Untangling mechanisms facilitating the persistence of biodiversity near and possibly within oil palm plantations is particularly crucial as international outcry against palm oil and the resultant economic pressures intensify. Global food demand has tripled in the past 50 years (Pretty, 2018), and is projected to double between 2005–2050, a demand which will drive the increased conversion of natural spaces into agriculture (Ehrlich & Harte, 2015; Tilman et al., 2011; Tilman et al., 2002). Over 570 million ha of forests in Southeast Asia, Latin America, and Africa are considered suitable for oil palm establishment, and the number of new oil palm concessions is increasing in Papua New Guinea, the Amazon, and Madagascar (Butler et al., 2009; Butler & Laurance, 2009; Pirker et al., 2016; Strona et al., 2018; Varkkey et al., 2018). Contained within these potential expansion zones are 270 million hectares of areas considered biodiversity hotspots, and conversion of these regions would impact 39% of all globally threatened amphibians, 64% of all threatened birds, and 54% of all threatened mammals (Meijaard et al., 2018). Paired with the impending expansion of the biofuel market (Fargione et al., 2010; Phalan, 2009), the palm oil industry will continue to grow; there is thus a scientific impetus to mitigate unnecessary biodiversity losses and develop sound management advice (Lucey et al., 2017).

1.5.2 Sabah, Malaysian Borneo

The island of Borneo is highlighted as a biodiversity hotspot (De Bruyn et al., 2014; Myers et al., 2000), yet it is experiencing one of the highest deforestation rates in the world due to the logging, rubber and, most notably, palm oil industries (Gaveau et al., 2014; Gaveau et al., 2016; Gaveau et al., 2019; Rautner et al., 2005). Between 2005 and 2015, Meijaard et al. (2018) estimate 50% of the deforestation on the island was due to oil palm expansion. In simulations pairing land-use cover change rates in Borneo with climatic projections, Struebig et al. (2015) estimate that up to 49% of Bornean mammal species will experience a significant loss of suitable habitat in the imminent future. Comprised of three governmental jurisdictions, the island is divided into two Malaysian states, five Indonesian provinces (Kalimantan), and the country of Brunei Darussalam. This study was conducted in the East Malaysian state of Sabah.

Borneo's tumultuous environmental history is reflected in Sabah's history (Gaveau et al., 2014). Controlled by the British in 1882, Sabah began experiencing large-scale forest loss with the colonial exploitation of natural resources. The establishment of tobacco and rubber plantations began between 1890-1930, and this loss occurred in conjunction with the commencement of selective logging for economically viable trees under the colonial administration of the British North Borneo Chartered Company (McMorrow & Talip, 2001). The rate of forest loss intensified in the 1950s to the extent that in less than 30 years, Sabah's forest cover decreased by nearly 30% (McMorrow & Talip, 2001; Reynolds et al., 2011). Gaveau et al. (2014) estimate that from 1973–2010, over 39% (22,865 km^2) of Sabah's forested areas were cleared. With the development of various governmental restrictions on timber harvest yields and the establishment of semi-structured monitoring programs, widespread clear-cut logging slowed in Sabah, although selective logging continues under the jurisdiction of the Sabah Forestry Department (McMorrow & Talip, 2001). Although this study does not focus on the impacts of logging on Sabah's biodiversity, it is important to note that due to its aggressive logging history, many of Sabah's forests are considered significantly degraded, both directly and indirectly, by the timber extraction process (McMorrow & Talip, 2001). The creation of large amounts of disturbed forests has allowed the surreptitious growth of the agricultural sector; under Native Customary Land Rights, secondary 'disturbed' forests not allocated to private ownership can be cleared for agricultural development; this technical loophole has been used by many plantations to claim a zero forest clearance policy (Gaveau et al., 2016; McMorrow & Talip, 2001). This allowance created an underestimation of the costs of agricultural expansion at the expense of forested land, and has been recently publicly criticised by Gatti et al. (2019).

The diversification from logging to industrial agriculture was relatively abrupt following the introduction of the oil palm sector in Peninsular Malaysia. With the first commercial plantation established in Peninsular Malaysia in 1910, the industry exploded until there was little suitable land remaining, and the sector shifted focused towards the East Malaysian states of Sabah and Sarawak (Sheil et al., 2009). The first oil palm estate was established in Sabah in the 1980s, and the expansion rates were rapid (Hai et al., 2001; Norwana Dayang et al., 2011). During 1973–2015, nearly 1.05 million hectares of forested areas in Sabah — equating to 18% of the state's forests—were converted to industrial oil palm plantations (Gaveau et al., 2016). Koh and Wilcove (2008) estimate that a proportion of this loss stemmed from degraded forests specifically degazetted for oil palm cultivation. As of 2017, 1.55 million hectares, representing over 21% of Sabah's entire terrestrial area, were officially classified and reported as active palm oil plantations (MPOB, 2017). The majority of plantations in Malaysia are private estates, principally dominated by large industrial companies and conglomerates, such as Sime Darby Berhad or IOI Corporation Berhad, although smallholder and government-supported plantation schemes do exist (MPOB, 2017).

Malaysia is the world's second largest producer of palm oil, and the state of Sabah is the largest contributor to this figure (MPOB, 2018; Norwana Dayang et al., 2011). In 2017, Sabah produced 5.2 million tons of crude palm oil, representing over 26% of Malaysia's entire crude oil production (MPOB, 2018). During the same reporting period, Sabah produced approximately 24% of Malaysian palm kernel (total production volume of just under 1.6 million tons; MPOB, 2018). Sabahan 2017 crude palm kernel oil production figures were of similar relative percentage of Malaysian production to that of kernel production, with over 500,000 tons produced in the state (MPOB, 2018). Lastly, over 600,000 tons of palm kernel cake were produced in Sabah in 2017, translating to 24% of total Malaysian production (MPOB, 2018). As of most recent figures, Malaysia contains a total oil palm planted area of over 5.81 million hectares, and the industry generated more than RM 77 billion (~£14 billion) in export revenue in 2017 (MPOB, 2017; Varkkey et al. 2018). The Sabahan palm oil industry will continue to expand, and with a stated total goal of 2.1 million hectares of plantations active in the state (Runting et al., 2015), will undoubtedly lead to more forest loss, despite governmental proclamations to protect 50% of forested lands in the state (Abram et al., 2014; MPOB, 2017; Varkkey et al. 2018).

1.5.3 Study Site: the Lower Kinabatangan

The extent of the oil palm industry's explosive growth may be most poignantly evident in the Lower Kinabatangan floodplain of eastern Sabah (Figure 1.1). The Kinabatangan River is Sabah's largest and longest river, stretching over 560 km and encompassing a total catchment area of 16,800 km^2 (Harun et al., 2015a). The river supports the largest wetlands and freshwater fisheries in the state and is the main water supply for the urban areas of eastern Sabah (Hai et al., 2001; Harun et al., 2015b). The river originates in the interior mountains of the Maliau Basin and passes through the relatively large forest blocks of central Sabah before descending to the eastern lowlands. Here, the main river channel measures an average of 112.7 m wide (Horton et al., 2017), and freely meanders across a largely alluvial plain; it is fed by several permanent tributaries, and at least 20 oxbow lakes are located in this region (Boonratana, 2000). The river mouth culminates in a mangrove-covered estuary the drains into the Sulu Sea; this site is currently protected as Sabah's first Ramsar Site, the Lower Kinabatangan-Segama Wetlands.

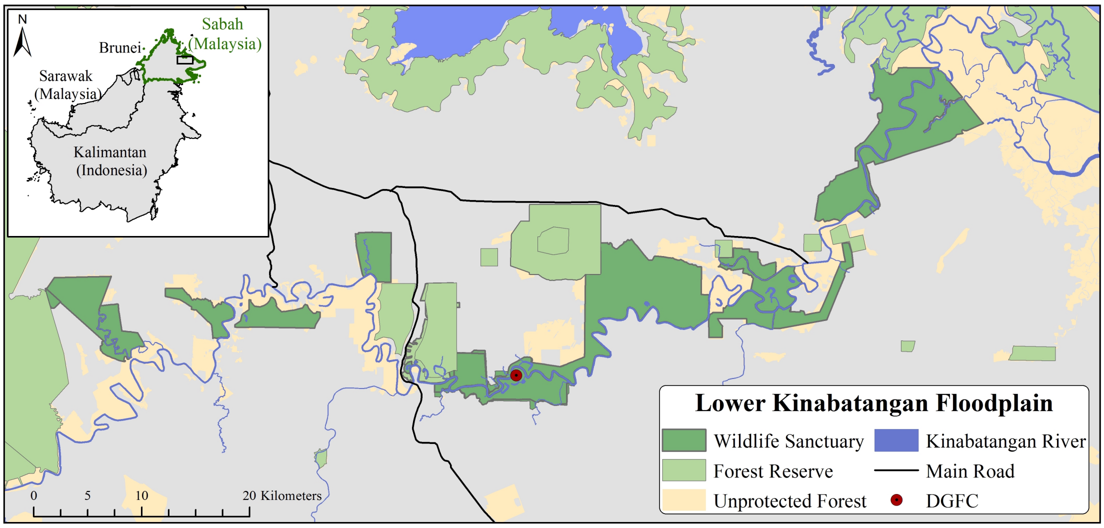

Figure 1.1. Study site map of the Lower Kinabatangan Floodplain showing the protected areas and field centre (DGFC) in Sabah, Malaysian Borneo. The grey areas in the main map denote non-forested land classes dominated by oil palm plantations and small settlements.

The floodplain began agricultural conversion in the 1800s with the introduction of small-scale rubber and tobacco crops (Hai et al., 2001; McMorrow & Talip, 2001). Selective logging for economically viable trees began in the 1950s and marked the beginning of the region's large-scale forest degradation (Hai et al., 2001; Lackman-Ancrenaz et al., 2001; McMorrow & Talip, 2001). The floodplain's wet tropical climate and alluvial soils are highly suitable for oil palm cultivation (Pirker et al., 2016). The conversion of the floodplain to large-scale agriculture began in the 1980s, and the oil palm estates of the Kinabatangan now account for 28% of Sabah's total cultivation area (Abram et al., 2014; Estes et al., 2012). Currently, over half of the floodplain has been converted into agricultural or other non-forest land usage (Abram et al., 2014); conversion is still occurring and is often unregulated (Stark et al., 2017), particularly in terms of the maintenance of riparian buffers of native vegetation (Horton et al., 2017). The remaining natural habitat patches flanking the Kinabatangan River consist of dry lowland forests, semi-inundated forests, small grasslands, and areas of swamp forest (Abram et al., 2014; Estes et al., 2012).

Within this forest and agricultural matrix exists the 270 km^2 Lower Kinabatangan Wildlife Sanctuary (hereafter LKWS), established in 2005 by the Sabah Wildlife Department. Comprised of 10 forest lots of varying degrees of disturbance history, the sanctuary is physically connected to seven additional fragments of Virgin Forest Reserves, protected areas managed by the Sabah Forestry Department. This network of protected areas equates to approximately 450 km^2 along 150 km of the lower reaches of the river (Figure 1.1; Ancrenaz et al., 2004; Estes et al., 2012; Goossens et al., 2005). An estimated additional 30,000 ha of forests persist outside of protected areas on private lands (Abram et al., 2014).

Despite the extensive habitat fragmentation and degradation, the Sanctuary's corridors of riparian forests support extraordinarily high biodiversity, including populations of endemic Bornean orang-utan (Goossens et al., 2005), Bornean elephant (Othman, 2017; Evans et al., 2017b), proboscis monkey (*Nasalis larvatus,* Stark, 2018), estuarine crocodiles (*Crocodylus porosus,* Evans, 2016), anuran species (Gillespie et al., 2012; Scriven et al., 2018), Sunda clouded leopard (Hearn et al., 2018), flat-headed cat (*Prionailurus planiceps*, Hearn et al., 2010), and Malayan sun bear (Guharajan et al., 2018). In addition to these charismatic megafauna, the sanctuary supports 15 confirmed small carnivore species from five families (Appendix I; Evans et al., 2016b). By rapid survey estimates, the LKWS supports 33 amphibians, over 200 bird species, 196 butterflies, and over 1,100 identified plants (Azmi, 1998; Boonratana & Sharma, 1997; Mohamed et al., 2003). New natural history discoveries from the region are frequent, particularly regarding invertebrate ecology (e.g. Miller et al., 2014; Miller et al., 2018; Symondson et al., 2014). The LKWS is therefore an ideal natural laboratory to evaluate the impacts of oil palm agriculture on native wildlife.

1.5.4 Study species: Bornean carnivores as landscape sentinels

With the context of this dynamic landscape persists a diverse guild of mammalian carnivores. A total of 25 small- to medium-sized carnivore species are found in Sabah, with seven scientific families represented. Eight civet species (Viverridae), five cat species (Felidae), one linsang species (Prionodontidae), one bear species (Ursidae), two mongoose species (Herpestidae), one skunk species (Mephitidae), and seven mustelid species have been documented in the state of Sabah (Phillipps, 2016; Ross et al., 2017; Wilting et al., 2016). This community is one of the richest co-existing extant mammalian carnivore guilds in the world

(Ross et al., 2017), and comprises an incredibly high concentration of species endemic to the island, globally second only to Madagascar (Belant & Wilting, 2013). Indeed, Borneo has been highlighted as a region of carnivore conservation priority (Dalerum et al., 2009; Di Minin et al., 2016; Dobrovolski et al., 2013; Schreiber et al., 1989; Schipper et al., 2008). Effective management of this guild, however, is hindered by a paucity of knowledge regarding the ecology and behaviours of these species, particularly in terms of evidence-based responses to anthropogenic disturbances (Brooke, 2014; Mathai et al., 2016; Shepherd et al., 2011). The difficulties researching tropical carnivores are manifold—most are wary of humans, nocturnal, semi-arboreal, and occur at naturally low densities (Belant et al., 2013). Multiple tools have been developed to uncover the secret lives of these elusive species (e.g. radio-collaring Gitzen et al., 2013; non-invasive genetics Goossens & Salgado-Lynn, 2013; transect surveys Mathai et al., 2013; live trapping McCarthy et al., 2013; interviews Mohd. Azlan et al., 2013; camera trapping Sunarto et al., 2013). Most of these techniques have been deployed, at least to some extent, in the study of Bornean carnivores, but very little research has been applied to anthropogenically-disturbed regions.

This research thus selected two small carnivore species to act as landscape sentinel models within the natural and agricultural mosaic of the Lower Kinabatangan: the Malay civet (*Viverra tangalunga*) and the common palm civet (*Paradoxurus hermaphroditus;* but see Veron et al., 2015 for suggested alternative systematic nomenclature). These small carnivores are two of the 34 currently recognised global species in the Viverridae family (Jennings et al., 2009). The taxonomy of the family has undergone extensive revisions following systematic molecular evaluations (e.g. Gaubert & Veron, 2003; Nyakatura & Bininda-Emonds, 2012; Patou et al., 2008; Patou et al., 2010; Veron et al., 2014; Veron et al., 2015). Malay civets belong to the Viverrinae subfamily with five other largely ground-dwelling species of Asian and African civets (Jennings & Veron, 2009). Common palm civets belong to the Paradoxurinae subfamily with six other Asian species (Jennings & Veron, 2009). Indeed, there is genetic evidence for the separation of the common palm civet species into three distinct species (Veron et al., 2015), yet this is not yet widely reiterated within the publishing community (Duckworth et al., 2016b).

Malay civets are the second largest viverrid in Borneo, weighing approximately 3–7 kg (Phillipps, 2016). Each animal bears a striking pelage patterned with individually unique spots and stripes. The species is predominantly solitary, ground-dwelling, and nocturnal, creating day nesting sites in areas with adequate cover, such as logs or vine tangles (Azlan, 2005; Colón, 2002; Davis, 1962; Jennings et al., 2006; Jennings et al., 2010; Ross et al., 2017). Malay civets are considered dietary generalists, ingesting a wide range of items such as insects, amphibians, reptiles, small mammals, and fruit (Colón & Sugau, 2012; Joscelyne, unpublished data; Macdonald & Wise, 1979). The species is found throughout the Sundaic region of Southeast Asia, including Peninsular Malaysia, Singapore, the Philippines, Borneo, and Indonesia, and has been documented in elevations ranging from sea level to 1,200 m (Duckworth et al., 2016a; Jennings & Veron, 2011; Payne & Francis, 1985; Ross et al., 2016). Malay civets have been recorded in a variety of habitats, including primary lowland, secondary lowland, montane, and mossy forests (Duckworth et al., 2016a). The species shows evidence of adaptation in disturbed habitats, with sightings reported in and around agricultural areas and human settlements (Duckworth et al., 2016a; Payne & Francis, 1985). Despite this apparent persistence in anthropogenically-impacted habitats, population densities are reported to be lower in disturbed landscapes. Colón (2002) reported a lower density of Malay civets in logged compared to unlogged forests in Danum Valley, Sabah, and suggested this was due to reduced fruit availability in the disturbed habitat. Heydon and Bulloh (1996) found similar results with line transect surveys in Ulu Segama Forest Reserve in Sabah, Malaysia, and noted a decreased presence of predominantly carnivorous civets in logged forest compared to unlogged forests. There are indications, however, that the species may have limits to their persistence within anthropogenically-disturbed landscapes (Jailan et al., 2018; Jennings et al., 2015; Ross et al., 2016; Twining et al., 2017). Very little is known regarding the species' utilisation of oil palm agriculture; most authors suggest the species will utilise the landscape for nocturnal foraging, yet there are no reports of the species' persistence solely within the crop (Bernard et al., 2014; Jennings et al., 2010; Jennings et al., 2015; Verwilghen, 2015; Yue et al., 2015).

The Malay civet is classified as 'Least Concern' with a stable population trend by the IUCN, and is unlisted on CITES (Duckworth et al., 2016a). In Sabah, it is listed as a Schedule 2, Part 1 Protected Animal under the Wildlife Conservation Enactment (Sabah Wildlife Department, 1997), meaning it can be hunted with a governmentally issued license. Despite their apparent persistence in a variety of habitats, threats to *V. tangalunga* include hunting, persecution due to its reputation as a poultry-raiding pest, secondary poisoning, and the expansion of the perfume industry (Duckworth et al., 2016a; Jennings, pers. comm.; Murphy, 2007; Shepherd & Shepherd, 2010). There is evidence the species is commonly consumed by local communities (Murphy, 2007; Shepherd & Shepherd, 2010); a raid of an open-air market in Nabawan, Sabah resulted in the seizure of two Malay civet carcasses illegally sold for bushmeat (Goossens, pers. comm.). This species does not readily appear to be targeted for international wildlife trade; however, the industry still poses a threat due to the largely non-selective capture methodologies, such as snares, utilised in the search for economically-valuable target species (Gray et al., 2018; Harrison et al., 2016). There are reports of secondary poisoning of small carnivores by anticoagulant rodenticides utilised in agricultural landscapes (Jennings & Veron, 2009; Jennings, pers. comm.; Naim, 2011; Rattner et al., 2014), yet the true extent of this risk is unknown. Malay civets have a perineal scent gland that produces a pungent secretion containing the macrocyclic compound, civetone (Sack, 1915). Civetone has been harvested from wild-captured civets in Africa and parts of Asia for use in the perfume industry (Jennings & Veron, 2009); possible future expansion of this market may pose a threat to Malay civets.

Common palm civets are considerably smaller than Malay civets, weighing approximately 1–4 kg, although there is morphological variation across the species' extant range (Jennings & Veron, 2009). Common palm civets are semi-arboreal, nocturnal, and solitary outside of breeding periods (Joshi et al., 1995; Grassman, 1998; Nakashima et al., 2013; Rabinowitz, 1991). One of the most frugivorous of all carnivore species, *P. hermaphroditus* has been documented consuming a wide variety of fruits, to the extent that it is considered an important seed disperser throughout its range (Chakravarthy & Ratnam, 2015; Grassman, 1998; Nakashima & Sukor, 2010; Nakashima et al., 2010a; Nakashima et al., 2010b). Individuals have also been documented consuming small mammals, amphibians, and some insects (Jothish, 2011). Common palm civets are considered one of the most common viverrid carnivores across Asia, and are naturally found throughout South and Southeast Asia (Duckworth et al., 2016b; Nakabayashi et al., 2016). There are reports of common palm civet occurrence in Sulawesi (Indonesia), Japan, and several New Guinean islands; these populations are considered introduced (Duckworth et al., 2016b). The species has been recorded at elevations ranging from sea-level to 2,400 m (Duckworth et al., 2016b). Population densities of common palm civets are currently unknown, but considered high in most areas (Duckworth et al., 2016b). These civets have been observed in a wide variety of habitat types, including evergreen and deciduous forests, scrubland, agricultural plantations, and forest fragments of varying sizes (Azlan, 2003; Nakabayashi et al., 2017; Nakabayashi et al., 2016). Common palm civets appear to be adaptable to anthropogenic land uses; the species persists in the heavily urbanized environment of Singapore (Chua et al., 2012), and there are reports of individuals adapting to human infrastructure in less developed areas (Nakabayashi et al., 2014; Spaan et al., 2014). Indeed, Nakashima et al. (2013) documented the suitability of logged forests as common palm civet habitat if fruit productivity was adequate. Common palm civets have been documented within oil palm agriculture, although little is known regarding their behaviours in such landscapes (Jennings et al., 2015; Nakashima et al., 2013; Verwilghen, 2015; Wahyudi & Stuebing, 2013; Yue et al., 2015).

Common palm civets are listed on CITES Appendix III in India and ‘Least Concern’ with a decreasing population trend by the IUCN (Duckworth et al., 2016b). Within Malaysian Borneo, common palm civets share the same protection status as Malay civets. Threats to common palm civets include habitat loss and fragmentation, hunting, secondary poisoning, *kopi luwak* production, and the pet trade (Duckworth et al., 2016b). In many countries, common palm civets are persecuted as a pest species for raiding fruit orchards and chicken coops (e.g. Su, 2005). As with Malay civets, the species is eaten as a wild meat source throughout its range (Abdullah, 2019; Gupta, 2004; Jennings & Veron, 2009). Further, Shepherd (2012) determined the growth of the *kopi luwak* trade was the main driver of increased occurrences of common palm civets in Jakarta wildlife markets. *Kopi luwak*, or civet coffee, is a delicacy where civets are fed coffee cherries and the excreted beans are made into one of the most expensive coffees in the world (D'Cruze et al., 2014). Due to its high economic return and increased demands for 'wild' civet coffee, the industry is a burgeoning threat to wild civet populations (Carder et al., 2016; D'Cruze et al., 2014). Lastly, both local and international pet trade threatens wild common palm civets; there are numerous reports of the species kept as pets (Roberts, 2019; Shepherd, 2001; Shepherd, 2012), and evidence of a growing international demand and trade (Abdullah, 2019; Nijman et al., 2014; Roberts, 2019).

1.6 Thesis overview & aims

Overall, this research aimed to evaluate the ecology of two model small carnivore species, the Malay civet and the common palm civet, at the interface between degraded tropical forests and oil palm plantations. Through the use of diverse analytical techniques, this work sought to weave a narrative assessing the price of persistence for wildlife sentinels surviving within heavily human-modified landscapes.

Chapter 1 has provided a contextualising review of the impacts of anthropogenic land use changes on biodiversity, with specific focus on the role of oil palm agriculture in carnivore research and conservation. Appendix I presents the published results of a long-term biodiversity assessment using camera traps and opportunistic sightings of small carnivores within the highly degraded and fragmented landscape of the LKWS (Evans et al., 2016b). **Chapter 2** sought to explore the health of two civet species within the LKWS. Over 100 small carnivores were live-trapped over the course of five years, resulting in the collection of morphometric measurements, reproductive observations, parasite samples, and the most extensive collection of haematology and serum biochemistry parameters recorded for Bornean civets to date. In addition to providing important natural history information on both civet species, the possible deleterious effects of oil palm plantation landscapes on these health indices were evaluated. **Chapter 3** presents preliminary results from the first known GPS-collaring of a Viverridae species, with discussions emphasising the scientific value of the resultant high quality spatio-temporal data collected from the species. Technical methodological considerations were assessed, including experimental determination of the locational accuracy and precisions of these research tools. A version of Chapter 3 has been published in Ecological Research (Evans et al., 2016a). **Chapter 4** presents the spatial ecology of 16 Malay and four common palm civet males tracked with GPS-collars within the forests and oil palm plantations of the Lower Kinabatangan. By intensely studying the home ranges, sleeping site selections, spatial interactions, and nocturnal movement behaviours of these individuals, this chapter aimed to present insights into how the two species utilise the heterogeneous LKWS landscape. **Chapter 5** examined a little-studied impact of civet ecology on the edge of oil palm plantations by using a non-lethal biomarker to explore if civets were exposed to heavy metal pollutants within the Lower Kinabatangan. **Chapter 6** combined the data streams from the previous chapters to synthesise the multi-facetted pressures faced by civets across the modified LKWS landscape, and aimed to effectively link observed patterns to ecological processes. Given the diversity of topics covered in this thesis, study limitations and further research recommendations were discussed within each chapter. Finally, **Chapter 7** discussed the conservation recommendations and implications of the research within the context of additional threats faced by Sabahan carnivores.

APPENDIX I

IUCN/SSC
Small Carnivore
Specialist Group

ORIGINAL ARTICLE

Small Carnivores of the Lower Kinabatangan Wildlife Sanctuary, Sabah, Borneo, including a new locality for the Otter Civet *Cynogale bennettii*

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Abstract.

The tropical rainforest biodiversity of Sabah, Borneo is threatened by large-scale agricultural development, logging, and increasing hunting pressures. From 2010—2015, an extensive camera-trapping study in the Lower Kinabatangan Wildlife Sanctuary (LKWS) monitored wildlife utilisation of a lowland riparian forest corridor. This effort, culminating in nearly 600,000 images, was the longest running camera-trapping study in the Sanctuary, and documented 11 small carnivore species over 24,506 trap nights. The Malay Civet *Viverra tangalunga* was the most frequently detected species, followed by the Malay Badger *Mydaus javanensis* and the Common Palm Civet *Paradoxurus hermaphroditus*. The survey also collected the first photographic record of an Otter Civet *Cynogale bennettii* in the LKWS, which represents a new locality for this little-known Southeast Asian species. Opportunistic sightings of five additional species, including the Endangered Flat-headed Cat *Prionailurus planiceps*, increased the total count of small carnivores persisting in the LKWS to 16. Given the highly degraded and fragmented status of the LKWS, this study highlights the importance of riparian lowland forest fragments in sustaining carnivore diversity, and also emphasizes the importance of continued, long-term monitoring efforts.

Keywords: Viverridae, Mustelidae, fragmented lowland rainforest, camera-trapping, Borneo, palm oil plantation

Introduction

Habitat destruction and degradation by the anthropogenic conversion of natural ecosystems is currently the leading threat to global biodiversity (Schipper *et al*. 2008, Crooks *et al*. 2011). Agricultural development alone has resulted in the destruction of over 400 million hectares of tropical forests between 1995 and 2007, and currently threatens at least 40% of all terrestrial vertebrates (Visconti *et al*. 2011). With burgeoning human populations and rising global food demand, the maintenance of biodiversity in increasingly human-dominated landscapes will require specific knowledge of species' ecological responses to fragmented habitats.

The Southeast Asian island of Borneo is undergoing one of the highest rates of deforestation in the world, and is projected to lose an estimated 75% of its remaining native landscapes within the century if land conversion practices persist (Sodhi *et al*. 2004, Rautner *et al*. 2005). The main drivers of the forest loss and fragmentation are the expansions of agricultural oil palm (*Elaeis guineensis*) and logging industries, which are considered the greatest threats to Southeast Asian biodiversity (Wilcove & Koh 2010). Coincidently, the region is identified as a global 'biodiversity hotspot' given the extraordinarily high numbers of endemic species paired with the highest global proportion of threatened species, excluding amphibians, of any region (Myers *et al*. 2000, Brooks *et al*. 2002, Sodhi *et al*. 2010).

In the face of these pressures, Borneo's tropical forests continue to sustain a high diversity of carnivore species (Corbet & Hill 1992). Eight civet species (Viverridae), five cat species (Felidae), one linsang (Prionodontidae), one bear (Ursidae), two mongooses (Herpestidae) and seven confirmed mustelid species have been documented across the island (IUCN 2015). The ecological importance of small carnivore species is well known, with the guild acting as regulatory predators, seed dispersers, and model species for landscape-level conservation research (Colón 2002, Mudappa *et al*. 2007,; Nakashima *et al*. 2010). Borneo has therefore been highlighted as a critically important priority region for small carnivore conservation (Schreiber *et al*. 1989).

As is the case with many small carnivores, there exists a substantial paucity of information regarding even basic ecological parameters of Bornean species (Schipper *et al*. 2008). However, opportunistic sightings (Boonratana & Sharma 1997, Bennett 2014), a handful of targeted research projects (Colón 2002, Nakashima *et al*. 2013) and a growing number of systematic camera-trapping surveys (*e.g*., Wells *et al*. 2004, Belden *et al*. 2007, Cheyne *et al*. 2010, Mathai *et al*. 2010, Wilting *et al*. 2010a, Brodie & Giordano 2011, Matsubayashi *et al*. 2011) have begun to fill in the information gaps concerning the guild. Attempts at modelling species distributions at a coarse geographic scale are developing (e.g. Jennings & Veron 2011, Cheyne *et al*. in prep, Samejima *et al*. in prep), but progress is slow and based on accurate species presence records, data that are still being accumulated in many regions.

Therefore, this study aimed to provide an inventory of the small carnivore species persisting in a highly fragmented lowland tropical forest in Sabah, Malaysian Borneo. Here, the results from both opportunistic sightings and the first systematic and longest-running camera trapping survey of the Lower Kinabatangan Wildlife Sanctuary in eastern Sabah are reported.

Materials and methods

Study areas

The study was conducted within the Lower Kinabatangan Floodplain (approximate range 5°18'N to 5°24'N and 117°54'E to 118°33'E) in eastern Sabah, Malaysian Borneo. The Kinabatangan River is the longest river in Borneo and sustains some of the richest fisheries in the state (Hai *et al*. 2001, Röper *et al*. 2014). The climate of the area is considered humid tropical, with temperatures ranging from 21°–34° C (Ancrenaz *et al*. 2004). Mean annual rainfall measures 3,000 mm, with wetter months occurring between October-May (Estes *et al*. 2012). The floodplain is subject to intermittent flooding events of varying severity and occasional drought (Estes *et al*. 2012). Nearly 50% of the floodplain has been converted to oil palm plantations, and patches of both private and protected secondary riverine forest persist within the agricultural matrix (Abram *et al*. 2014).

The camera-trapping survey occurred in the riparian lowland forests of the Lower Kinabatangan Wildlife Sanctuary (LKWS), a 279 km^2 area of degraded habitat flanking the Kinabatangan River surrounded by large oil palm plantation estates. Comprised of 10 lots of varying degrees of disturbance history and isolation, the sanctuary is connected to seven additional fragments of Virgin Forest Reserves, managed by the Sabah Forestry Department, increasing the size of protected area to 450 km^2 (Ancrenaz *et al*. 2004, Goossens *et al*. 2005). The sanctuary contains a mixture of dry lowland, semi-inundated, and swamp forests interspersed with small grasslands (Abram *et al*. 2014). Despite the extensive anthropogenic habitat fragmentation, the LKWS supports many endemic Bornean species (Goossens *et al*. 2005, Sha *et al*. 2008, Goossens *et al*. 2016), and serves as the sole forest corridor bridging the coastal mangroves to the east and the large continuous tracts of rainforest in central Sabah.

Camera-trapping

Camera traps were deployed within the LKWS from 12 November 2010 through 9 May 2015. Active camera trap sites varied from nine to 25 stations throughout this period due to logistical constraints (*i.e*., wildlife damage, theft, battery failure). Sites were stationed at least 1 km apart within the thin (~100-1200 m) forest corridor of the LKWS Lots 5 and 7, forest blocks on the north bank of the river (Figure 1). At each site, one or two Reconyx HyperFire Professional Infrared (IR) passive camera traps (Model HC500 or PC800, Reconyx, Holmen, USA) were deployed and protected by armour casing. Traps were tree-mounted and set 0.5 m from the forest floor on naturally occurring riverine trails. Once cameras detected a moving heat source, a series of three photos at 1-second intervals were recorded. In lowlight conditions, an IR flash was triggered to illuminate the subject while minimizing animal disturbance. When two cameras were mounted at a site, units were placed facing each other but slightly offset to avoid night-time image washout from the opposing camera's IR flash. Sites were checked biweekly or monthly, based on battery performance, and riverine trails were cleared of excess foliage to reduce camera misfires.

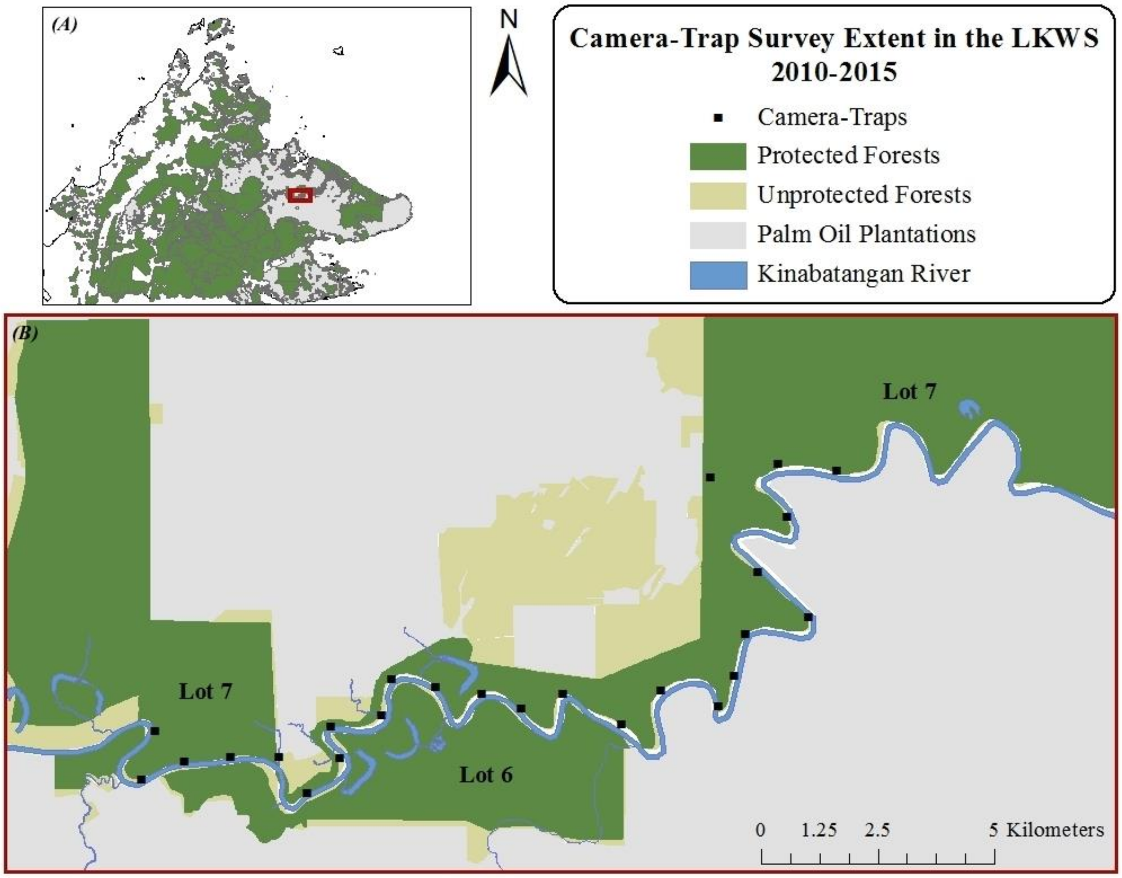

Figure 1. Map of camera-trap survey stations within Lots 5 and 7 in the Lower Kinabatangan Wildlife Sanctuary from 2010—2015.

Data handling

Once SD cards were collected, metadata were extracted from the images using ExifTool 9.6.8.0. Each photo was individually examined for the presence of an animal and, if a confident identification could be recorded, was classified based on the species present. If no positive identification could be made, the photo was excluded from future analyses. Each burst of three images was considered a single capture. Captures were then further grouped into unique events, whereby photos of the same species >30 minutes apart were classified as independent events, per Yasuda & Tsuyuki (2012), in order to avoid pseudoreplication. Survey effort was quantified by calculating total potential camera-trap nights (active calendar nights x number of active camera-traps).

Results

Throughout the 48 non-consecutive month survey, camera-traps accumulated 24,506 total potential trap nights and captured a total of 596,240 images. Of these, 419,528 photos recorded the presence of wildlife, with the remaining images consisting of humans or false trigger events. Species could not be identified in 1,254 images, and as such, were excluded from analyses.

Overall, 13 species of Bornean Carnivora were detected in 21,715 images across 2,327 unique events. This count includes multiple captures of the Sunda Clouded Leopard *Neofelis diardi* and the Malayan Sun Bear *Helarctos malayanus*, which, per Mathai *et al.* (2011), are excluded from these results. After the removal of these species, 11 small carnivore species were detected in 2,030 unique capture events throughout the survey (Table 1). Small carnivores detected on the camera traps comprised of five Viverridae species, one Prionodontidae species, three Mustelidae species, one Felidae species, and either one or two Herpestidae species. In most cases, low photo quality made distinguishing between the Bornean mongooses (Collared Mongoose *Herpestes semitorquatus* and the Short-tailed Mongoose *Herpestes brachyurus*) difficult, and as such we did not differentiate between the two in this survey.

Table 1. Small carnivore results from November 2010—May 2015 camera-trapping survey within Lots 5 and 7 of the Lower Kinabatangan Wildlife Sanctuary.

Species	Scientific name	No. of Capture events	No. of camera-trap stations detected	No. of trap nights until first detection	2015 IUCN Red List Status
Malay Civet	*Viverra tangalunga*	1,108	24	21	Least Concern
Common Palm Civet	*Paradoxurus hermaphroditus*	179	20	21	Least Concern
Banded Palm Civet	*Hemigalus derbyanus*	62	12	208	Vulnerable
Otter Civet	*Cynogale bennettii*	1	1	208	Endangered
Binturong	*Arctictis binturong*	2	1	19,321	Vulnerable
Banded Linsang	*Prionodon linsang*	1	1	12,211	Least Concern
Malay Badger	*Mydaus javanensis*	470	18	188	Least Concern
Smooth-coated Otter	*Lutrogale perspicillata*	140	12	166	Vulnerable
Yellow-throated Marten	*Martes flavigula*	11	6	565	Least Concern
Mongoose sp.	*Herpestes* sp.	28	11	628	Least Concern
Leopard Cat	*Prionailurus bengalensis*	28	11	48	Least Concern

The greatest abundance of captures occurred for Malay Civets, followed by the Malay Badger and the Common Palm Civet, all of which were documented across the greatest number of camera-trap stations. Only a handful of unique capture events were recorded for the Binturong, Banded Linsang and Otter Civet, and each were documented at one station only. Seven of these photo-captured species are listed as Least Concern, three as Vulnerable, and one as Endangered on the IUCN Red List (IUCN 2015).

Of special note, the first reported camera-trap image of the Endangered Otter Civet in the LKWS was taken on 27 November 2010 at 04h58 (5°25’N, 118° 04’E; Figure 2).

The camera-trap station was located in Lot 5 of the LKWS approximately 50 m from the riverbank and 530 m from the nearest oil palm plantation.

Figure 2. Camera-trap photo of an Otter Civet *Cynogale bennettii* within Lot 5 of the Lower Kinabatangan Wildlife Sanctuary (DGFC/SWD).

Opportunistic Sightings

Additionally, five small carnivore species were opportunistically sighted but not recorded on camera-traps, raising the total number of documented species to 16. Multiple records of the Small-toothed Palm Civet *Arctogalidia trivirgata* were reported throughout the LKWS (Figure 3A). The Malay Weasel *Mustela nudipes* was documented in several unique events within Lot 6 of the LKWS. The Endangered Flat-headed Cat *Prionailurus planiceps* was sighted and photographed by researchers along both sides of the riverbanks on multiple occasions (Figure 3B). The Asian Small-clawed Otter *Aonyx cinereus* was documented on a separate research camera-trap in the study area, and signs of the species have been recorded along the oxbow lakes in the LKWS (Evans unpublished data). A single non-related camera-trap recorded the presence of a Marbled Cat *Pardofelis marmorata* at the eastern edge of this study's survey extent. Lastly, in addition to the camera-trap photo of the Otter Civet, opportunistic sightings were made within Lot 6 of the LKWS in three separate occurrences. In the early evening of 25 July 2013, a solitary individual was documented close to an oxbow lake in close proximity to Danau Girang Field Centre (~5°24'N, 118°02'E). In mid-August 2013, an individual was seen crossing the concrete main path of the Field Centre (~5°25'N, 118°02'E). Lastly, on 8 February 2015, several research assistants observed an adult Otter Civet accompanied by two offspring once again crossing the concrete path, confirming the presence of a breeding unit of *C. bennettii* in the area.

Figure 3. Photos of (A) a Small-toothed Palm Civet *Arctogalidia trivirgata* and (B) Flat-headed Cat *Prionailurus planiceps* imaged within Lot 6 of the Lower Kinabatangan Wildlife Sanctuary by researcher S. H. Vickers on 7 June 2015 at 20h12 and 6 May 2015, 21h47.

Discussion

The results from this long-term monitoring survey of small carnivores within a degraded and fragmented riverine habitat demonstrate the importance of the Lower Kinabatangan Wildlife Sanctuary for small carnivore persistence. Overall, the sanctuary appears to support species diversity comparable to less disturbed forests throughout Borneo, with generalist species such as the Malay Civet and the Common Palm Civet documented routinely (e.g. Belden *et al.* 2007, Wilting *et al.* 2010a, Brodie & Giordani 2011, Mathai *et al.* 2010, Matsubayashi *et al.* 2011). Species with low capture rates are those species displaying behavioural traits nonconductive to capture by trail-based camera-traps, such as the arboreal Binturong (Wilting *et al.* 2010a) or the dense understory-preferring Banded Linsang (Cheyne *et al.* 2010). It is of interest, however, to note the relatively low number of photographic capture events of Leopard Cats, given that many authors suggest the species may thrive in disturbed areas, especially in regions containing oil palm plantations (Azlan & Sharma 2006, Rajaratnam *et al.* 2007, Jennings *et al.* 2015).

The importance of supporting camera-trapping surveys with researcher presence within a study area is highlighted by the results of this survey, as five additional species would have been otherwise undocumented. The Small-toothed Palm Civet is highly arboreal, making terrestrial detection improbable (Walston & Duckworth 2003), while Asian Small-clawed Otters and Flat-headed Cats reside in close proximity to shallow pools and tributaries, areas not targeted by this survey (Wilting *et al.* 2010b, Hussain *et al.* 2011). It has been suggested that historically low photographic detection rates of Malay Weasels might be attributable to a behavioural preference of hunting in dense undergrowth (Duckworth *et al.* 2006, Ross *et al.* 2013). When attempting to document the carnivore species within an area, species' specific behavioural ecology should be taken into consideration during survey design and planning (Sunarto *et al.* 2013).

Of the remaining Bornean Carnivora species, five species were neither photographed nor observed throughout the five-year monitoring survey of the LKWS. Neither the Masked Palm Civet *Paguma larvata* nor the Hose's Civet *Diplogale hosei* were detected, results not entirely surprising, as it has been suggested these species do not occur in lowland forests (Wilting *et al.* 2010a, Matsubayashi *et al.* 2011). Neither the Hairy-nosed Otter *Lutra sumatrana* nor the Bay Cat *Catopuma badia* were detected in the lower floodplains, despite both being documented in Deramakot Forest Reserve within the Kinabatangan, approximately 75 km upriver from the current survey site (Mohamed *et al.* 2009, Wilting *et al.* 2010a). Finally, despite apparent observations of the Bornean Ferret Badger *Melogale everetti* approximately 45 km downriver from this study area in the early 1990's (Boonratana 2010), this survey did not detect the species during over four years of monitoring.

This study confirms a new locality for the Endangered Otter Civet, an elusive and significantly understudied Southeast Asian civet species (Veron *et al.* 2006). This nocturnal animal is believed to reside in swampy areas and lowland primary forest streams, although some observations have been made in secondary forests (Heydon & Ghaffar 1997, Veron *et al.* 2006, Cheyne *et al.* in prep). However, this documentation of *C. bennettii* in a significantly degraded and fragmented environment suggests that the species may persist in a broader range of habitats than originally believed. Alternatively, the presence of a breeding unit could suggest the LKWS forest patches are of sufficient ecological health to act as species reservoirs, offsetting the immediate detriments to species residing in close proximity to oil palm plantations. These preliminary records demand more targeted research efforts to determine the population status of *C. bennettii* within the floodplain. Regardless, the confirmed presence of this incredibly rare species in the LKWS strikes a strong case for the importance of these forest lots, and should play a substantial role in spearheading the extension of legal protective measures to the 30,173 ha of unprotected forests persisting within the floodplain (Abram *et al.* 2014).

Although these preliminary results demonstrating the presence of both common and rare small carnivores in the LKWS are undoubtedly positive, this inventory itself should be taken with caution, as several of these occurrences were marked by a single photo across over four years of continuous monitoring. Species residing in fragmented habitats are faced with a multitude of threats and survival pressures (Laurance 2008, Gerber *et al.* 2012), such that it is possible the LKWS small carnivore guild is not yet at equilibrium. Specifically, the authors would like to emphasize the threat of increased illegal hunting activities, which are exacerbated in habitat fragments due to the relative ease of accessing the forest (Cullen *et al.* 2000, Milner-Gulland *et al.* 2003). Throughout this survey period, multiple photos documented illegal encroachment and evidence of hunting within the LKWS. In order to preserve the tenuously rich biodiversity persisting in the protected regions, significant effort must be invested to curb these illegal activities (Shepherd & Shepherd 2010). In face of these threats, more detailed and rigorous population and density estimates for the small carnivores from this region are required, which will, in turn, provide researchers a greater understanding of the conservation importance of degraded and fragmented riverine habitats. It is suggested that research efforts pair survey transects with both trail-based and arboreal camera trapping efforts, as by Oliveira-Santos *et al.* (2008), to maximize the probability of cataloguing all potential small carnivore species, regardless of behavioural traits. As the agricultural sector continues to expand and pristine rainforests are encroached upon all over the globe, it will be critical for the conservation community to understand the mechanisms by which forest fragments may benefit biodiversity.

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Chapter 2. Health of small carnivores in the fragmented landscape of the Lower Kinabatangan

2.1 Introduction

Habitat loss, degradation, and fragmentation pose significant threats to global biodiversity, and species' extinction rates are at an all-time high (Ceballos et al., 2017; IUCN, 2018). Species face both global and local suites of stressors from human activities, which combine to undermine the survival capability of many wildlife populations (Chapter 1). Determining the explicit mechanisms of species' loss following anthropogenic change is complicated yet critical for the design and execution of effective conservation strategies (Laurance et al., 2012; Ripple et al., 2017).

Conservation physiology aims to link individual physiological fitness to anthropogenically-mediated population declines, often (and ideally) prior to the manifestation of measurable losses (Cooke et al., 2013; Ellis et al., 2012; Wikelski & Cooke, 2006). Some species display an apparently greater ecological resistance to anthropogenic pressures, at least when assessed by more traditional ecological metrics such as species' presence or localised abundance counts (Appendix I; Caruso et al., 2016; Miller et al., 2015; Ramiadantsoa et al., 2018; Sih, 2013). Individuals, and by extension, populations, surviving within fragmented and degraded habitats can however be chronically stressed (Johnstone et al., 2011), malnourished (Birnie-Gauvin et al., 2017), immunosuppressed (Messina et al., 2018), at elevated risk of pathogen or parasite exposure (Murray et al., 2015; Wells et al., 2007), or fail to successfully reproduce (Banks et al., 2007). It is therefore critical to assess the physiological health of individuals, and by extension, species, persisting along and within the edges of natural and anthropogenic landscapes. Such assessments will in turn enable effective conservation plans to be crafted through the identification of otherwise cryptic threats to a population's survival (e.g. Cooke et al., 2012; Madliger et al., 2017).

The determination of wildlife health is a philosophically complex and developing field (Hanisch et al., 2012; Kindig & Stoddart, 2003; Raubenheimer et al., 2012;

Stephen, 2014), and multiple metrics have evaluated a species' physiological response to life in a changing world (Ellis et al., 2012; Homyack, 2010; Johnstone et al., 2017; Madliger et al., 2018). Firstly, evidence of reproduction can serve as an indication of relative metapopulation functionality (Holland & Bennett, 2010); for the majority of mammalian species, reproduction only occurs successfully given the presence and contact of two sexually healthy adult individuals. The lack of both accessible and viable mates in disturbed habitats can carry grave implications for species' survival, poignantly demonstrated in the case of the now locally extinct Sumatran rhinoceros (*Dicerorhinus sumatrensis*, Goossens et al., 2013; Havmøller et al., 2016). Further, reproduction is an energetically demanding process that occurs only if basic survival needs such as access to food, water, and breeding areas are met (Banks et al., 2007; Josserand et al., 2017; Keith et al., 1993). Unfortunately, the reproductive biology of many wildlife species remains poorly understood (Andrews et al., 2019; Wildt & Wemmer, 1999).

Indices of an animal's body condition are common metrics assessed in conservation physiology (Homyack, 2010). Variation in a species' body mass can belay insights into individual nutrition status, particularly lipid stores (Stevenson & Woods, 2006). Body mass and condition can impact immune system function (Cabezas et al., 2006), rates of reproductive success (Atkinson & Ramsay, 1995), and long-term survival (Bender et al., 2007). Species persisting in degraded and fragmented habitats often display overall poorer body conditions than those in less disturbed landscapes (e.g. diademed sifaka *Propithecus diadema*, Irwin et al., 2019; Bornean banteng *Bos javanicus lowi*, Prosser et al., 2016; cottontail *Sylvilagus transitionalis,* Villafuerte et al., 1997). The opposing trend has also been documented, however, particularly for those species displaying behavioural adaptations, such as crop raiding, to the fragmenting matrix (e.g. roe deer *Capreolus capreolus,* Hewison et al., 2009; bearded pig *Sus barbatus,* Love et al., 2017; review by Oro et al., 2013). Thus, monitoring species' morphometrics can provide important insights into wildlife responses to anthropogenic habitat loss and degradation.

Perhaps some of the most informative, albeit complicated, metrics utilised to evaluate the health of wild species are haematology and serum biochemistry profiles (Table A2.1–A2.2). Mammalian blood is a highly dynamic and reactive fluid composed of erythrocytes, leukocytes, thrombocytes, and a suite of circulating pathophysiological markers such as minerals and hormones; all of these components can react to and reflect the overall status of an individual (Kerr, 2002). Natural variation in the absolute quantification of blood parameters collected from healthy individuals exists (Friedrichs et al., 2012), and reference ranges often depend upon intrinsic factors such as an individual's sex, age, and reproductive status (Keohane et al., 2016). Clinically, changes in blood parameters away from relatively normal baselines can be indicative of disease, malnutrition, toxicant exposure, or chronic stress (Davis & Maney, 2018; Johnstone et al., 2017; Maceda-Veiga et al., 2015). The evaluation of blood parameters such as erythrocyte characteristics, white blood cell counts, stress indices, and lipid profiles of species persisting in fragmented and degraded habitats have elucidated some of the physiological prices of persistence (e.g. howler monkey *Alouatta pigra*, García-Feria et al., 2017; sifaka, Irwin et al., 2010; agile antechinus *Antechinus agilis*, Johnstone et al., 2012; maned wolf *Chrysocyon brachyurus*, May-Júnior et al., 2009). However, blood profiles are still severely lacking for most wildlife species (Deem et al., 2001), due at least in part to the invasive nature of sample collection and processing (Maceda-Veiga et al., 2015). Given these factors, the collection and assessment of baseline blood profiles of wild species is both warranted and crucial.

The loss and degradation of Bornean lowland tropical rainforests via the establishment of oil palm plantations poses a threat to the region's rich faunal diversity (Meijaard et al., 2018). Purported generalist species, such as long-tailed macaques (*Macaca fascicularis*), wild pigs, Asian water monitor lizards (*Varanus salvator*), and civets (Viverridae spp.) are observed in both forested fragments and within the agricultural matrix; some researchers go so far as to postulate these species may be thriving (Guerrero-Sanchez, 2019; Luskin et al., 2017; Twining et al., 2017; Wearn et al., 2017; Yue et al., 2015). There are, however, scant, if any, studies specifically evaluating the physiological health status of the species within anthropogenically-modified landscapes. Indeed, very little is known concerning some basic ecological parameters of Bornean generalists, particularly the enigmatic small carnivores (Mathai et al., 2016; Schreiber et al., 1989).

This study aimed to assess and evaluate the health of common palm (*Paradoxurus hermaphroditus*) and Malay civets (*Viverra tangalunga*) in the agriculturally fragmented landscape of the Lower Kinabatangan Wildlife Sanctuary (LKWS). Through the deployment of a multi-year trapping and sampling campaign, this study sought to i) report baseline natural history information regarding these little-studied species, including evidence of population demographics, reproduction, and parasitic infections. Further, this work strove to ii) evaluate variations in observed morphometric measurements of the two species. The collection of wild blood samples allowed this study to describe, for the first time, the haematological and serum biochemistry parameters for wild Bornean viverrids. This study further aimed to iii) evaluate how variations in civet blood parameters were related to landscape and seasonal factors, while controlling for the identification of natural physiological variation due to an animal's age and sex.

2.2 Methods

2.2.1 Study site

This study occurred in eastern Sabah, Malaysian Borneo (approximate range: 5°18'N to 5°42'N and 117°54'E to 118°33'E). The climate of the area is considered humid tropical; daily temperatures ranged from 22°–34°C from 2012–2017 (Figure 2.1). Mean annual rainfall measured 2680 ± 210.5 mm (mean ± S.E) and fell aseasonally, with the wetter annual months usually occurring from October through March. The floodplain is subject to flooding events of varying severity and occasional drought (Davison, 2006).

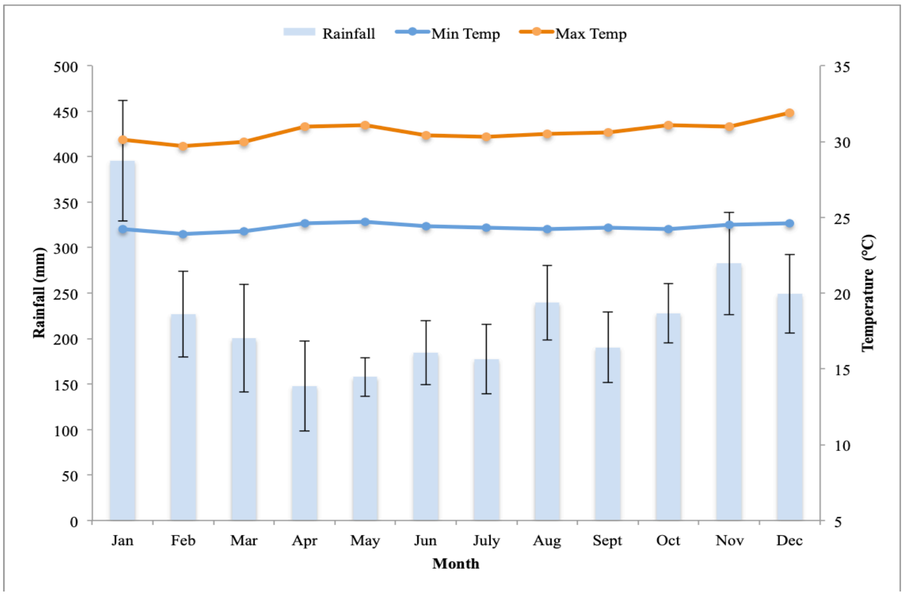


Figure 2.1. Mean monthly rainfall, minimum, and maximum temperatures recorded from DGFC in Lot 6 of the LKWS from 2012–2017. Standard error bars represent the variation in average monthly rainfall across the six included years.

This study was based in the Lower Kinabatangan Wildlife Sanctuary (LKWS), a 270 km^2 area of protected albeit degraded forest flanking the Kinabatangan River, and the surrounding oil palm matrix landscape (Figure 1.1). Comprised of 10 forest lots of varying degrees of disturbance history, the Sabah Wildlife Department maintains jurisdiction over the protected area. The Sanctuary is connected to seven additional fragments of Virgin Forest Reserves, managed by the Sabah Forestry Department, increasing the size of politically protected area to 450 km^2 along 150 km of river (Ancrenaz et al., 2004, Estes et al., 2012; Goossens et al., 2005). These remaining patches of riparian forests are a mixture of dry lowland, semi-inundated, and swamp forests interspersed with grasslands (Abram et al., 2014). Outside of these protected areas, over 50% of the floodplain has been converted into agricultural (dominated by oil palm plantations) or other non-forested land classes (Abram et al., 2014; Estes et al., 2012).

2.2.2 Trapping and anaesthesia

Trapping periods for wild small carnivores spanned March 2013 to January 2018. Small carnivores were live-trapped using either custom-built box traps or commercial spring-loaded traps. Box trap dimensions averaged 110 cm x 35 cm x 40 cm and were activated by a treadle mechanism, while spring traps measured 91 cm x 30 cm x 30 cm. Whenever possible, traps were placed 300–500 m apart within the riparian border of the LKWS or along the edges of oil palm plantations.

Trap sites were selected based on adequate canopy cover to protect from sun and rain, high dry ground, proximity to fruiting trees and animal trails, and civet signs such as footprints, scat, or potential day bed sites. The trap floor was covered with soil and ground vegetation to minimize detection and stabilize the set. Each trap was covered with foliage to provide additional shade and shelter. Traps were set by 18:30 h with a variety of lures, including motion decoys, sound makers (Lucky Duck^{TM}, Baldwin, USA), scent attractants, and used cooking oil. Traps were checked between 07:00 h and 08:00 h and closed during the day to avoid diurnal captures of non-target species. A passive infrared camera-trap (Reconyx PC500, Reconyx, Inc., Holmen, Wisconsin) was set at each site to monitor the effectiveness of the trap set.

Upon identification of a capture, the animal's weight was visually estimated and the appropriate anaesthesia dosage loaded into a handheld 3.0 ml syringe. Animals were subdued towards the back of the trap with the aid of a purpose-built wooden squeeze door, whereupon a qualified veterinarian administered anesthesia via intramuscular injection. Animals were either sedated with 5 mg kg^{-1} Tiletamine/Zolazepam (Zoletil^{TM}, Virbac Laboratories, Carros, France), or a mixture of equal parts 1.5 mg kg^{-1} Ketamine (Narketan^{TM}, Vétoquinol UK Limited, Buckingham, UK), Xylazine (Ilium Xylazil^{TM}, Troy Laboratories PTY Limited, Glendenning, Australia), and Tiletamine/Zolazepam. In the case of the latter drug combination, the reversal agent Yohimbine (Reverzine^{TM}, Bomac Pty Limited, Hornsby, Australia) was administered (1:1–1:3 anaesthetic volume: reversal volume ratio) once the animal was safely placed in a pet carrier to recover. Personal protection equipment included nitrile gloves, N95 or N100 respirators (3M, Minnesota, USA), and over-clothes designated to sampling activities. Following process completion, all sampling materials were sprayed with absolute ethanol and materials thoroughly washed with a virucidal agent (Virucidal Extra, AVS manufacturing & Marketing, Holywood, Northern Ireland).

Upon complete anesthesia induction, the animal was removed from the trap and moved to a prepared sampling area. Sterile eye lubrication was administered and a blindfold placed to minimise external stimulation. The animal's vital signs (respiration rate, heart rate, rectal temperature, and peripheral oxygen saturation [SpO_2]) were monitored in 5–10 min increments throughout sampling. Rectal temperature (°C) was recorded with a digital thermometer. Respiration rate (breaths/min) was visually measured by thoracic elevations for 1 min. Heart rate (beats/min) and SpO_2 were recorded by a portable field pulse oximeter (Rad-57, Masimo Corporation, California, USA) fitted with a small tongue-clip attachment. If SpO_2 readings dropped below 85% or breathing was determined shallow or erratic, 1-2 mg kg^{-1} of doxapram hydrochloride (Dopram-V^{TM}, 20mg/ml, USA) was administered intramuscularly. An RFID (radio-frequency identification) microchip was subcutaneously implanted between the shoulder blades of each anaesthetised individual (Trovan Ltd., UK).

After the animal was deemed stable, a complete physical exam was conducted, and weight, sex, age, and reproductive status were evaluated. Age was scored by a combination of tooth condition, body size, and signs of reproductive activity (females: nipple wear, lactation, or visible pregnancy; males: testicular descent). Pregnancy status was determined by abdominal palpation by an experienced veterinarian; it is important to note that only females in mid- to late stages of pregnancy could be positively identified by these methods. Age categories were assigned as juvenile (small in size, presence of milk teeth), subadult (small in size, transitional teeth phases), adult (large body size, signs of active reproduction, good teeth), and old (slight body condition despite large size, poor or worn teeth). For statistical analyses, individuals were further binned into a classification scheme of immature (juvenile + subadult) and mature (adult + old). All assessments were made by the same observer (M. Evans).

Morphometric measurements were collected for each individual and included the following: circumference of head, neck, and thoracic cavity; head length; front and hindfoot length and width; height at shoulder; total body length (nose to tail tip); body length (nose to base of tail [sacrum/caudal vertebrae junction]); and tail length with a measuring tape. Photographic records of distinctive neck markings and any additionally unique features were collected for each individual. Ectoparasites (e.g. ticks, fleas) were manually collected following a full body search, with specific attention to forelimbs, ears, feet, and axilla. Parasites were removed and stored in 95% ethanol for eventual identification.

All trapping, handling, and sampling protocols followed the guidelines of the American Society of Mammalogists (Sikes et al., 2016), and were approved by the Sabah Biodiversity Centre and the Sabah Wildlife Department (Licence ref.no: JKM/MBS.1000-2/2 JLD.6[8]).

2.2.3. Sample collection and laboratory analyses

Approximately 1–1.5 mg kg^{-1} of blood was attempted to be collected from each individual via cephalic, brachial, jugular, or femoral venipuncture (23-gauge/3-cc syringe or 25-gauge/1-cc syringe). Blood was immediately stored in both empty (red) and EDTA (ethylenediaminetetraacetic acid)-containing vacutainer tubes and placed in a cooler box while field sampling continued. Whole blood was centrifuged approximately 4 h post-collection at 1000 rpm for 15 min (model EBA 21, Hettich Instruments, Tuttlingen, Germany). The serum was separated from the clot and frozen. The sample stored within EDTA was kept cool (~3–5 °C) until sample transfer. Both the frozen serum sample and the cool EDTA tubes were sent to Gribbles Pathology Laboratory Sdn Bhd (Sandakan, Sabah, Malaysia) within 24–48 h from collection for serum biochemistry and haematology analyses. This fully MS ISO 15189 accredited analytical laboratory is the leading local authority in handling biological samples and supplies reliable results to the hospitals and veterinarian clinics in the region. A total of 16 haematology and 23 biochemistry parameters were analyzed from civet blood samples (Tables A2.1–A2.2). As these animals were wild-caught, fasting and hydration statuses were unknown.

2.2.4 Data analysis

Analyses were performed using R 3.5.0 (R Core Team, 2018). Sexual dimorphism in both species was evaluated using first capture measurements from mature individuals. Morphometric data were tested for normality with the Shapiro-Wilks test, and when data were normally distributed, dataset variances were evaluated with Fisher exact tests. Morphometrics were compared between sexes using either two-tailed t-tests or Mann-Whitney U (MWU) tests. Regarding the removal of outliers, two Malay civet females and one common palm civet female were excluded from the total body length and tail measurements as portions of their tails were missing.

Differences between the weights of adult LKWS civets and those reported in the literature were evaluated with Kruskall-Wallis tests, and significant differences determined by Tukey post-hoc pairwise comparisons. Additional comparisons between morphometrics were not conducted, as the small samples sizes paired with the human error intrinsic with field measurements were deemed too significant to warrant rigorous statistical investigation.

The establishment of so-called veterinarian reference intervals (Friedrichs et al., 2012) from civet haematology and serum biochemistry data was not conducted as it was deemed inappropriate; it is erroneous to presume the measurements from the LKWS are indicative of healthy or 'normal' civets from which deviations might be measured or contrasted against. Common palm civet blood profiles were summarised by both sex and age category; due to the small sample size, complex statistical modeling was not conducted. The influence of sex on adult common palm civet haematology and biochemistry values was evaluated by either a two-sample t-test or a MWU test. To acknowledge the potential influence of age on haematology profiles, common palm civet values were pooled regardless of sex, and differences between immature and mature profiles examined by MWU tests. There was not a sufficient sample size to evaluate the effect of age on serum biochemistry profiles. Common palm values were compared to those previously reported in small studies; there are insufficient global data for Species360 reference intervals to be established for either species.

The effects of age category, sex, sampling season, and distance to oil palm plantation on Malay civet blood parameters were assessed with generalised linear modeling (GLM). All individuals were visibly healthy (in good body condition with no clinically apparent symptoms of illness); for individuals with multiple capture events, only blood parameters from the first successful capture were included in modeling processes. The specific blood parameter data type determined each model family, and link functions were selected based on AIC minimisation and best normalisation of model residual plots (Table A2.6). Count data were first modeled with Poisson families; all were found to be over-dispersed (over-dispersion statistic > 20); final models were thus fit with negative binomial model structures using the package *MASS* (Venables & Ripley, 2002). Proportional data (PCV, RDW) were modeled using binomial generalised linear models fitted with 'logit' link functions (Thomas et al., 2017). Lastly, due to reported values below detection limits for uric acid, bilirubin, and GGT, these data were binned into binomial classes (0/1); models thus evaluated the factors influencing normal versus elevated concentrations of these parameters within the sample population.

The most parsimonious models for each blood parameter were determined by multi-model inference, whereby candidate model structures were generated and small-sample size corrected Akaike's Information Criteria (AICc) values compared using the 'dredge' function in the *MuMIN* package (Bartón, 2018). The top models were selected as those with a ΔAICc <2, and were averaged using the natural average method (Burnham & Anderson, 2002). All independent variables were standardised such that the dataset mean equaled 0 and the standard deviation 0.5 prior to model averaging to allow for direct comparison between terms (Grueber et al., 2011). The same algorithm was applied to the exploration of the factors influencing adult Malay civet weight, whereby capture year, sex, and distance to oil palm plantation were included as potential model parameters.

2.3 Results

2.3.1 Trapping

A total of 1657 trap nights (calendar night x number of active traps) were conducted throughout the LKWS, resulting in 121 total small carnivore anaesthesia procedures on 96 unique individuals (7.3% trapping success rate [includes repeat anaesthesia sampling efforts but excludes repeat captures of recently sampled individuals that did not result in anaesthesia induction]; Figure 2.2; Table 2.1). An additional 11 opportunistic hair samples were collected; these were from unsuccessful anaesthesia induction procedures or opportunistic carcasses. The sex ratio of captured civets was balanced for both species (common palm civets: 10 ♀, 10 ♂; Malay civets: 44 ♀, 35 ♂).

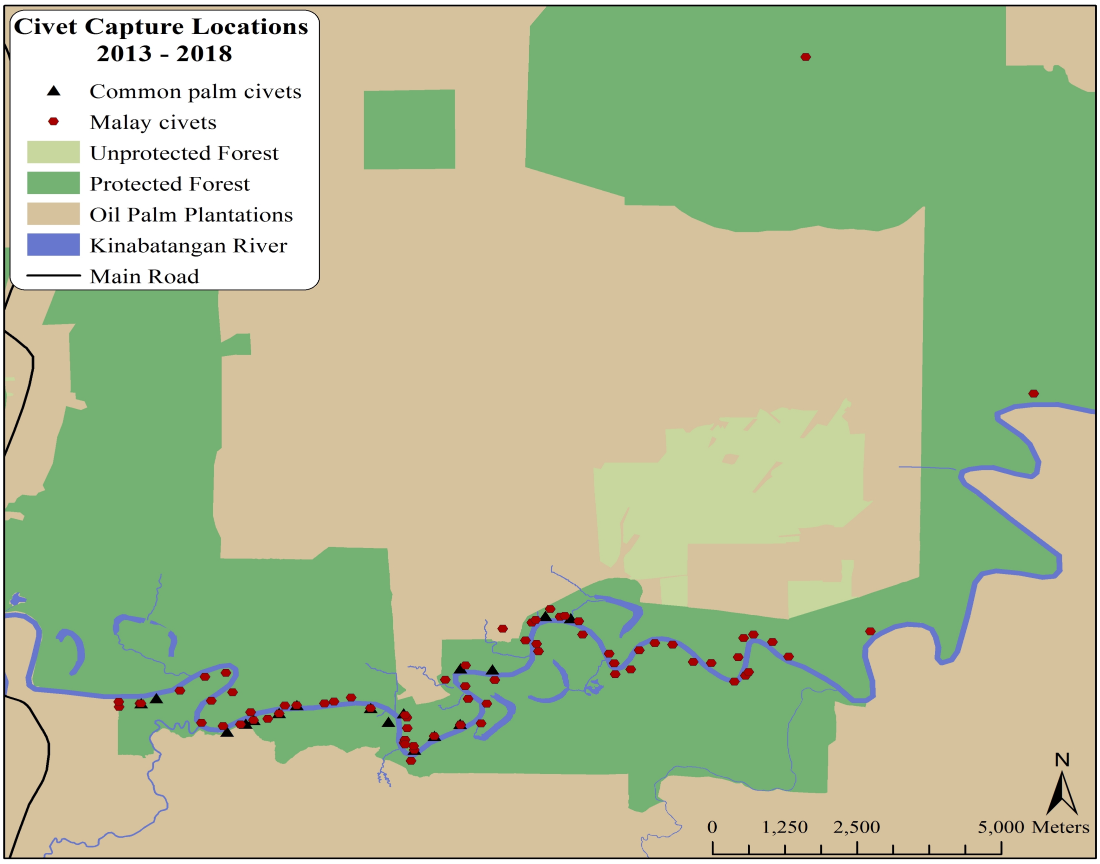


Figure 2.2. Civet capture sites in the LKWS, 2013–2018.

Table 2.1: Summary of sampled small carnivore individuals from the LKWS and surrounding oil palm plantations in Sabah, Malaysia 2012– 2018.

Species	Unique Individuals
Malay civet (*Viverra tangalunga*)	81
Common palm civet (*Paradoxurus hermaphroditus*)	21
Leopard cat (*Prionailurus bengalensis*)	2
Short-tailed mongoose (*Herpestes brachyurus*)	1
Sunda stink-badger (*Mydaus javanesnsis*)	1

2.3.2 Reproductive activity

There were no readily apparent temporal patterns in live-trapped female reproductive status for either civet species (Figure 2.3).

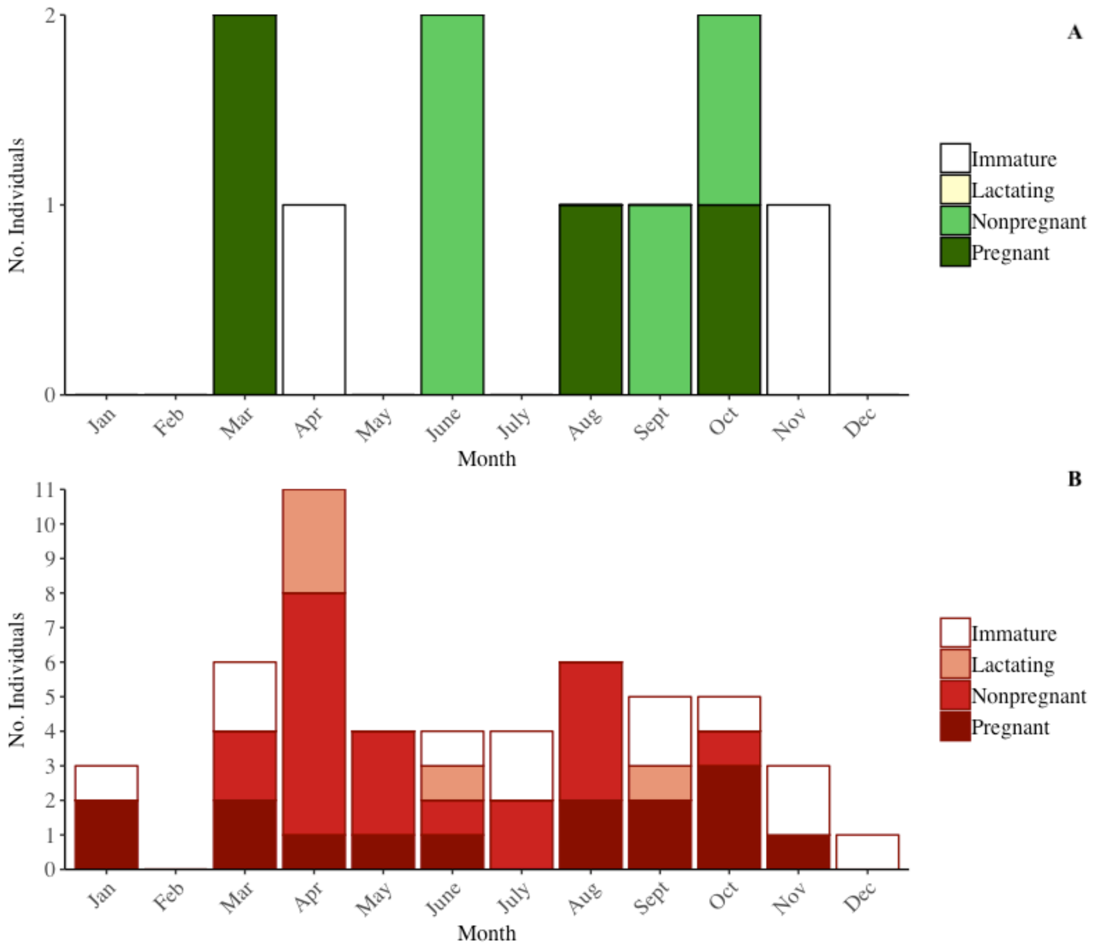


Figure 2.3. Reproductive demographics of female A) common palm and B) Malay civets captured within the LKWS, displayed by calendar month.

2.3.3 Parasites

The presence of microfilaria in blood films was noted from one adult male and one adult female Malay civet. These individuals (MC F17, MC M26) were captured on opposite sides of the river; the female was captured near oil palm plantation in Lot 5 and the male in the larger forest block of Lot 6. The female had a tick located on her abdomen when she was first sampled; she was otherwise observably healthy and reproductively active. MC M26 was an older male with several physical maladies, including one blind eye and potential limb deformation.

Ticks were observed on six Malay civets (three males, three females), one female common palm civet, one short-tailed mongoose, and one Sunda stink-badger. Most observations were of a single tick attached to the forelimbs or feet of an animal. One additional male Malay civet appeared to have arthropod eggs deposited within its alar fold (Figure A2.1). Neither fleas nor lice were detected on trapped small carnivores.

2.3.4 Morphology

Mature common palm civets did not present statistically significant sexual dimorphism for any morphometrics; summary measurements are thus presented for the sampled mature population (Table 2.2). Significant differences between adult common palm civet weights were recorded between study sites ($\chi^2 = 14.52$, df = 5, $p < 0.02$, Figure 2.4). Adult common palm civets caught in the LKWS did not differ from those civets sampled at other Bornean sites, but were significantly lighter than those caught in Thailand (Grassman, 1998, $p < 0.0001$; Rabinowitz, 1991, $p < 0.0001$). Capture records from Sum (2011) reported a mean common palm civet weight of 2.4 kg (n = 4) in Bintulu, Sarawak, which is similar to those caught in the LKWS and other Bornean sites.

Table 2.2: Summary morphometrics of mature common palm civets captured in the LKWS from 2013–2018. All non-weight measurements are reported in cm. Total = total body length (nose to end of tail); HB = head to body length; Tail = tail length; Thorax Circ = thoracic circumference; Hind L/W = hindfoot length and width; Fore L/W = forefoot length and width; Shoulder = height at shoulder; Neck Circ = neck circumference; Head Circ = head circumference; Head L = head length.

	n	Mean	SD	Min – Max
Weight (kg)	15	2.04	0.24	1.5 – 2.8
Total	10	90.1	3.2	85.3 – 96.0
HB	13	49.9	2.7	43.0 – 53.7
Tail	12	39.7	2.4	36.0 – 42.9
Thorax Circ	13	22.7	2.6	19.5 – 27.5
Hind L	13	5.9	0.8	4.4 – 7.5
Hind W	11	3.0	0.2	2.6 – 3.4
Fore L	11	4.4	0.6	3.5 – 5.6
Fore W	11	3.1	0.4	2.5 – 3.7
Shoulder	12	23.1	2.3	18.3 – 26.0
Neck Circ	11	14.6	1.0	13.3 – 16.5
Head Circ	11	17.6	1.4	15.5 – 19.8
Head L	11	11.9	0.6	10.3 – 12.6

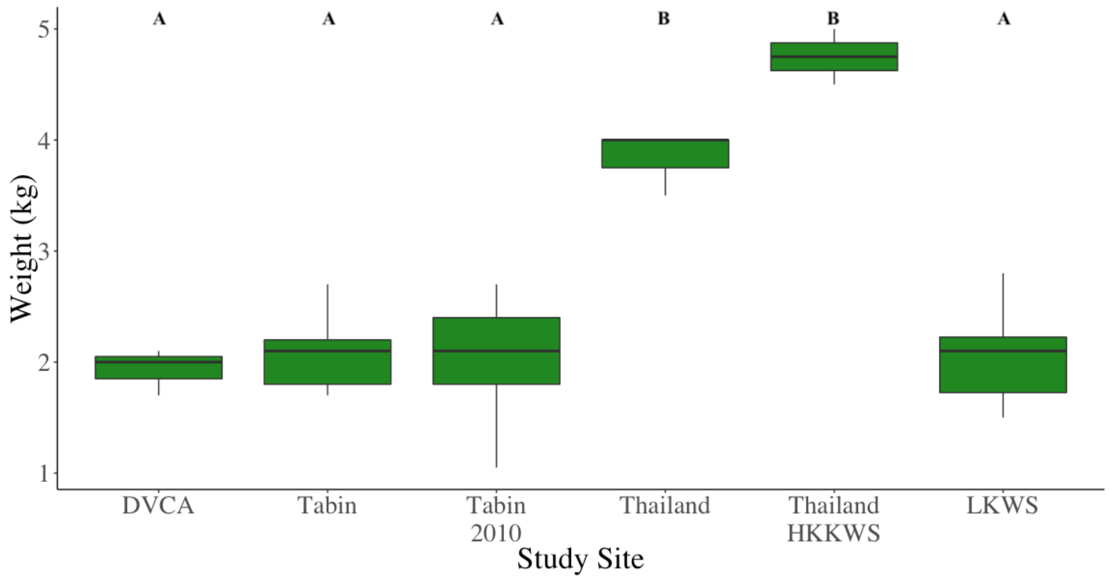


Figure 2.4. Weights of wild adult common palm civets sampled across multiple study sites. Capital letters (A,B) denote statistically significant differences groups between study sites ($p < 0.05$). DVCA = Danum Valley Conservation Area, Sabah (Nakabayashi et al., 2017; n = 3); Tabin = Tabin Wildlife Reserve, Sabah (Nakashima et al., 2013; n = 12); Tabin 2010 = Tabin Wildlife Reserve, Sabah (Nakabayashi et al., 2014; n = 25); Thailand = Kaeng Krachan National Park (Grassman, 1998; n = 3); Thailand HKKWS = Huai Kha Khaeng Wildlife Sanctuary (Rabinowitz, 1991; n = 2); LKWS = Lower Kinabatangan Wildlife Sanctuary (current study, n = 15). Boxplots visually summarise civet weights from each study; the central line is the median, while the boxplot boundaries denote the 1st and 3rd dataset quartiles. Whiskers extend to the maximum/minimum weight within 1.5 times the interquartile range of the dataset.

In contrast, mature Malay civets demonstrated sexual dimorphism for some morphometrics, with male measurements larger than female (Table 2.3). Male Malay civets were significantly longer than females (t = -3.05, df = 45, $p < 0.005$), and had larger thoracic circumferences (t = -2.92, df = 52, $p < 0.01$). Males had longer and wider hindfeet (respectively: W = 204, $p < 0.0005$; W = 304, $p < 0.05$), although only forefoot width varied by sex (W = 294, $p < 0.05$). Lastly, males had greater neck and head circumferences than females (respectively: W = 275, $p < 0.05$; t = -2.89, df = 54, $p < 0.01$).

Table 2.3: Summary morphological data from mature Malay civets captured in the LKWS 2013–2018. All non-weight measurements are reported in cm. Bold text describes directionality of significance, with bolded text indicating the larger values. Shorthand notations match those provided in Table 2.2.

	All civets				Female				Male			
	n	Median	IQR	Min – Max	n	Median	IQR	Min – Max	n	Median	IQR	Min – Max
Weight (kg)	60	4.50	0.75	3.5 – 6	-	-	-	-	-	-	-	-
Total^**	-	-	-	-	25	97.2	3.5	91.3 – 105	22	**100.1**	3.2	94.6 – 106
HB	57	67.1	4.5	50.5 – 73.5	-	-	-	-	-	-	-	-
Tail^	57	32.5	2.2	27.8 – 38.4	-	-	-	-	-	-	-	-
Thorax Circ^**	-	-	-	-	29	29.9	2.3	25.7 –34	25	**31.9**	2.8	28.0 – 37.6
Hind L***	-	-	-	-	31	3.3	0.6	2.9 – 4.7	28	**3.7**	0.5	3.0 – 4.4
Hind W*	-	-	-	-	31	3.0	0.5	2.4 – 5	28	**3.3**	0.6	2.3 – 4.1
Fore L	59	3.7	0.6	3.0 – 5.1	-	-	-	-	-	-	-	-
Fore W*	-	-	-	-	31	3.5	0.4	2.8 – 4.5	28	**3.7**	0.5	3.2 – 5.0
Shoulder	58	31.6	4.0	21.5 – 37.2	-	-	-	-	-	-	-	-
Neck Circ*	-	-	-	-	30	18.3	2.2	16.2 – 21.4	28	**19.5**	2.3	17.1 – 26.4
Head Circ^**	-	-	-	-	29	19.4	1.2	17.5 – 22.0	27	**20.6**	1.7	18.0 – 24.8
Head L^	53	14.5	0.9	12.0 – 16.6	-	-	-	-	-	-	-	-

^denotes datasets were normally distributed, so summary results are instead group mean and standard deviation
**denotes statistical significance related to $p < 0.05$; **$p < 0.01$; ***$p < 0.001$*

Adult Malay civet weight was not significantly influenced by sex or proximity to oil palm plantation but did vary based on capture year (Table A2.3). Adult civets caught in 2016 ($p < 0.0002$) and 2017 ($p < 0.001$) were significantly lighter than those captured in other sampling years; adults captured in 2016 were an average of 230 g lighter than those captured in 2013.

Malay civet weights varied significantly between geographic sampling sites (χ^2= 65.57, df = 5, $p < 0.0001$, Figure 2.5). Adult Malay civets caught in the LKWS were significantly heavier than those in Danum Valley Conservation Area (Colón, 2002; $p < 0.0001$) and both males and females in Sulawesi (Jennings et al., 2006; $p < 0.01$ and $p < 0.0001$, respectively). Capture records from Sum (2011) reported a mean Malay civet weight of 3.6 kg (n = 21) in Bintulu, Sarawak, which is lighter than the average weight of 4.6 kg for those caught in the LKWS. In contrast, LKWS civets were an average of 2.02 kg lighter than male and 1.15 kg lighter than female civets from Peninsular Malaysia (Jennings et al., 2010; $p < 0.0001$ for both).

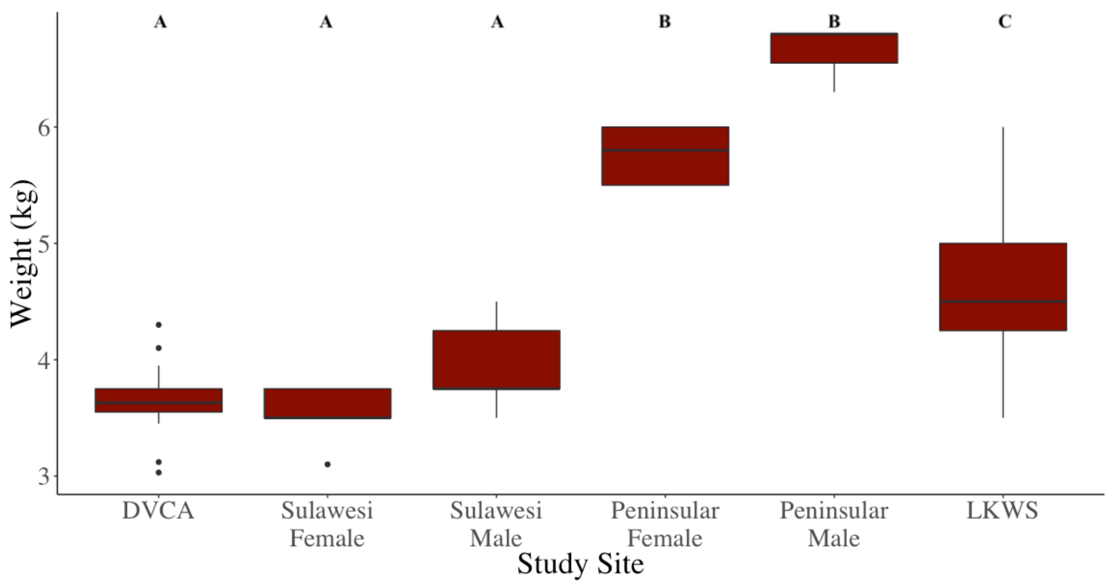


Figure 2.5. Weights of wild adult Malay civets sampled across multiple geographic study sites. Capital letters (A-C) denote statistically significant differences between study sites ($p < 0.05$). DVCA = Danum Valley Conservation Area, Sabah (Colón, 2002, n = 22); Sulawesi = Buton Island, Indonesia (Jennings et al., 2006, n = 9 females, n = 10 males); Peninsular = Krau Wildlife Preserve, Peninsular Malaysia (Jennings et al., 2010; n = 5 females, n = 3 males); LKWS = Lower Kinabatangan Wildlife Sanctuary, Sabah (current study, n = 60). Boxplots visually summarise civet weights from each study; the central line is the median, while the boxplot boundaries denote the 1st and 3rd dataset quartiles. Whiskers extend to the maximum/minimum weight within 1.5 times the interquartile range of the dataset. Dots denote individual statistical outliers outside the whiskers within each subset.

2.3.5 Common palm civet blood parameters

Not every anaesthesia procedure resulted in a fully successful venipuncture, particularly those involving common palm civets. Haematology profiles were successfully established for 12 unique common palm civets (nine males, six females). One additional sample was unable to be assessed due to premature clotting following collection. Serum biochemistry panels were successfully determined for nine unique common palm civets (five males, four females); one additional sample was unable to be assessed due to laboratory error. Of the nine successfully analysed serum samples, one individual's potassium, corrected calcium, and alkaline phosphatase values were removed due to suspected contamination with K-EDTA (per Bowen & Remaley, 2014).

Due to low sample size, the differences between female and male common palm civet haematology profiles were evaluated for only mature individuals (Table 2.4). Mature female common palm civets had significantly higher white blood cell (t = 2.82, df = 4.08, $p < 0.05$) and neutrophil counts (t = 3.14, df = 6, $p < 0.05$) than males. No other parameters significantly differed by sex.

Table 2.4: Summary haematology profiles for wild mature common palm civets sampled within the LKWS 2013–2018. Bold text denotes the directionality of significance, such that the bolded values represent the sex with the statistically greater values. Shorthand notation for haematology parameters matches those provided in Table A2.1.

		All Civets				Female				Male			
Parameter	**Unit**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**
Haem	g/L	9	116	14.2	98.0 – 136	–	–	–	–	–	–	–	–
RBC	x 10^{12}/L	9	8.10	1.13	6.44 – 9.35	–	–	–	–	–	–	–	–
PCV	L/L	9	0.43	0.05	0.36 – 0.49	–	–	–	–	–	–	–	–
MCV	fL	9	51.1	2.84	46.0 – 57.0	–	–	–	–	–	–	–	–
MCH^	pg	9	14.0	0.0	13.0 – 15.0	–	–	–	–	–	–	–	–
MCHC	g/L	9	273	16.9	251 – 310	–	–	–	–	–	–	–	–
RDW	%	9	21.1	1.96	17.9 – 24.4	–	–	–	–	–	–	–	–
WBC*	x 10^9/L	–	–	–	–	5	**7.98**	2.76	4.30 – 11.0	4	4.48	0.25	4.20 – 4.80
Neut*	x 10^9/L	–	–	–	–	4	**6.95**	2.27	4.10 – 9.60	4	3.15	0.85	2.10 – 4.10
Lymp	x 10^9/L	8	1.33	0.53	0.50 – 2.00	–	–	–	–	–	–	–	–
Mono	x 10^9/L	8	0.28	0.18	0.00 – 0.60	–	–	–	–	–	–	–	–
Eos^	x 10^9/L	4	0.10	0.03	0.10 – 0.20	–	–	–	–	–	–	–	–
N:L	-	8	4.56	2.98	1.05 – 9.60	–	–	–	–	–	–	–	–
Plat	x 10^9/L	9	300	167	136 – 625	–	–	–	–	–	–	–	–
Gluc	mmol/L	7	5.0	1.4	2.7 – 6.8	–	–	–	–	–	–	–	–

^denotes summary statistics presented are median and IQR, as the dataset was non-normally distributed

**denotes statistical significance related to $p < 0.05$*

To explore the effect of age on common palm haematology profiles, values were binned into sexually immature or mature categories, regardless of sex. Only mean corpuscular volume (MCV) significantly differed between age categories; immature civets expressed readings an average of 7.2 fL greater than mature common palm civets (W = 26, $p < 0.05$; Table A2.4).

The differences between female and male serum biochemistry profiles were assessed for mature individuals only due to small sample size (Table 2.5). Mature female common palm civets had significantly lower low-density lipoprotein (LDL; t = -3.61, df = 6, $p < 0.02$) and creatinine levels (t = -3.02, df = 5, $p < 0.05$) than males. No other parameters differed by animal sex; the role of age category could not be assessed as only one sample was successfully collected from an immature animal. The majority of sampled adult common palm civets did not display elevated levels of uric acid, bilirubin, or gamma-glutamyl transpeptidase (GGT; Table 2.6).

Table 2.5: Summary biochemistry profiles for wild mature common palm civets sampled within the LKWS from 2013–2018. Bold text denotes the directionality of significance, such that the bolded values represent the sex with the statistically greater values. Shorthand notation for biochemistry parameters matches those provided in Table A2.2.

		All Civets				Female				Male			
Parameter	**Unit**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**
Tchol	mmol/L	8	3.5	0.88	2.1 – 5.1	–	–	–	–	–	–	–	–
Tri	mmol/L	8	0.83	0.23	0.51 – 1.26	–	–	–	–	–	–	–	–
HDL^	mmol/L	8	1.59	0.75	1.36 – 3.02	–	–	–	–	–	–	–	–
LDL**	mmol/L	–	–	–	–	4	0.857	0.32	0.42 – 1.16	4	**1.56**	0.23	1.23 – 1.74
Ratio	-	8	1.9	0.40	1.4 – 2.6	–	–	–	–	–	–	–	–
Na	mmol/L	8	146	4.90	140 – 156	–	–	–	–	–	–	–	–
K	mmol/L	7	4.2	0.30	3.7 – 4.6	–	–	–	–	–	–	–	–
Cl^	mmol/L	8	110.5	5.00	94.0 – 115.0	–	–	–	–	–	–	–	–
Ur	mmol/L	7	6.5	2.7	2.90 – 13.4	–	–	–	–	–	–	–	–
Creat*	umol/L	–	–	–	–	3	33	5.6	28 – 39	4	**42**	2.2	39 – 44
Ca	mmol/L	6	2.15	0.18	1.88 – 2.35	–	–	–	–	–	–	–	–
Co_Ca	mmol/L	6	2.55	0.30	2.28 – 2.95	–	–	–	–	–	–	–	–
P	mmol/L	8	1.40	0.37	0.95 – 2.12	–	–	–	–	–	–	–	–
TotProt	g/L	8	82.5	8.33	72.0 – 95.0	–	–	–	–	–	–	–	–
Alb	g/L	5	26.8	8.76	12.0 – 35.0	–	–	–	–	–	–	–	–
Glob	g/L	5	51.8	13.2	37.0 – 73.0	–	–	–	–	–	–	–	–
AlbGloRatio	-	5	0.57	0.25	0.20 – 0.90	–	–	–	–	–	–	–	–
AlkPho	U/L	7	29.9	9.08	14.0 – 42.0	–	–	–	–	–	–	–	–
AST^	U/L	8	364	319	299 – 1067	–	–	–	–	–	–	–	–
ALT	U/L	8	289.2	150.2	116 – 508	–	–	–	–	–	–	–	–

^denotes data were non-normally distributed and thus summary statistics presented are median and IQR

*denotes statistical significance related to $p < 0.05$; **$p < 0.02$

Table 2.6: Description of wild mature common palm civet blood parameters treated as a binomial classification scheme of below the limit of detection (‘L.D.’) and elevated relative to the limit of detection (‘Elevated’). Shorthand notation for biochemistry parameters matches those provided in Table A2.2.

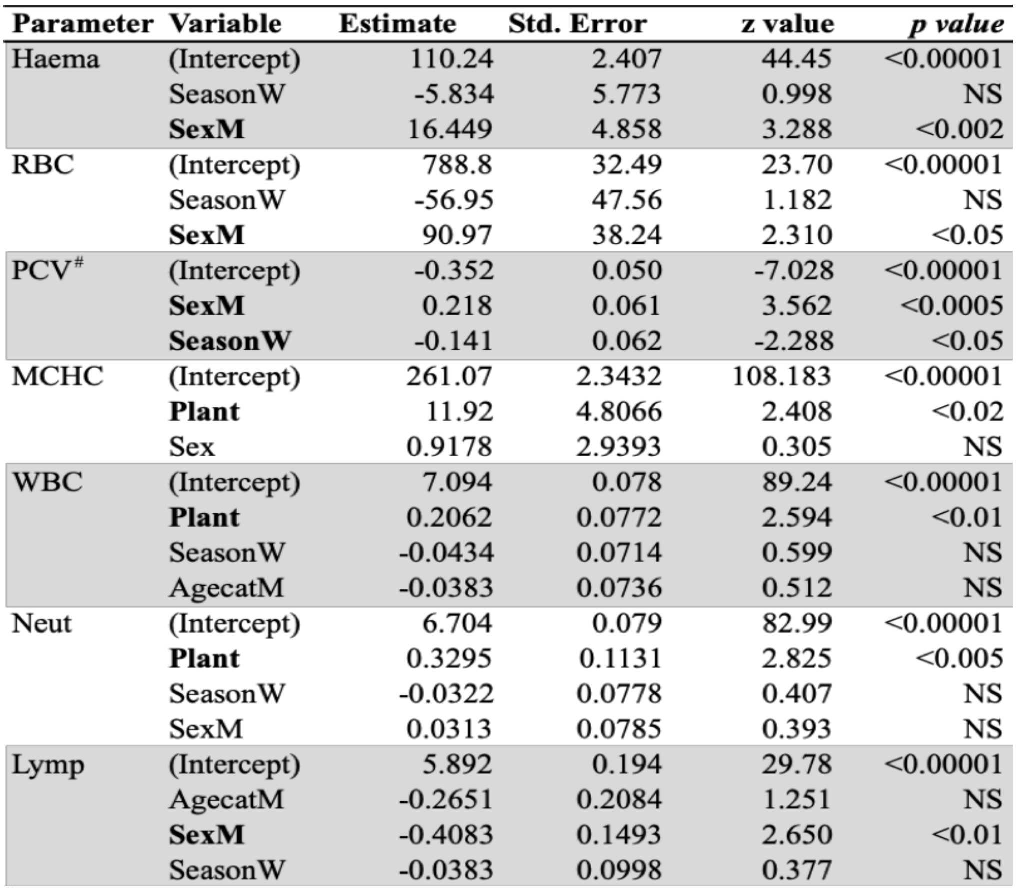
		No. of civets		
Parameter	**L.D.**	**< L.D.**	**Elevated**	**Elevated Values**
UA	0.01 mmol/L	5	1	0.02 mmol/L
Bili	2 umol/L	4	2	6 umol/L
GGT	3 U/L	8	0	–

2.3.6 Malay civet blood parameters

Haematology profiles were successfully established for 46 unique Malay civets (22 males, 24 females). An additional nine collected samples were unable to be assessed due to haemolysis, premature clotting, or insufficient sample volume. Serum biochemistry panels were successfully evaluated for 51 unique Malay civets (22 males, 29 females). Of these, 17 samples had to be removed from potassium, calcium, and alkaline phosphatase due to suspected contamination with K-EDTA (Bowen & Remaley, 2014). Two additional biochemistry samples were unable to be assessed due to insufficient sample volume or laboratory error. The two Malay civet individuals with circulating microfilariae were removed from the modeling datasets (Table A2.5).

Several Malay civet haematology parameters were influenced by sex, proximity to oil palm plantation, and sampling season (Table 2.7; Tables A2.7–2.8). Summary descriptors of blood parameters within the sampled population, partitioned as appropriate given these GLM results, can be found in Table A2.9. Haemoglobin concentration and total red blood cell count were significantly elevated in male Malay civets compared to females. Females, in contrast, had significantly elevated lymphocyte counts compared to males. Civet packed cell volume (PCV) was elevated in males compared to females and in animals trapped in the dry compared to the wet season. Malay civets captured in closer proximity to oil palm plantations expressed significantly depressed mean corpuscular haemoglobin concentration (MCHC), white blood cell (WBC) counts, and neutrophil counts.

Table 2.7: Standardised parameter estimates for statistically significant averaged models describing Malay civet haematology profiles. NS denotes statistically non-significant ($p > 0.05$) terms. Bold terms indicate statistically significant variables. SeasonW = wet season; SexM = male; Plant = distance to oil palm plantation; AgecatM = mature civets. Intercept = standardised reference level for factorised predictor variables (ex: female, dry season). Shorthand notation for response variables matches those provided in Table A2.1.



Parameter	Variable	Estimate	Std. Error	z value	*p value*
Haema	(Intercept)	110.24	2.407	44.45	<0.00001
	SeasonW	-5.834	5.773	0.998	NS
	SexM	16.449	4.858	3.288	<0.002
RBC	(Intercept)	788.8	32.49	23.70	<0.00001
	SeasonW	-56.95	47.56	1.182	NS
	SexM	90.97	38.24	2.310	<0.05
PCV$^{\#}$	(Intercept)	-0.352	0.050	-7.028	<0.00001
	SexM	0.218	0.061	3.562	<0.0005
	SeasonW	-0.141	0.062	-2.288	<0.05
MCHC	(Intercept)	261.07	2.3432	108.183	<0.00001
	Plant	11.92	4.8066	2.408	<0.02
	Sex	0.9178	2.9393	0.305	NS
WBC	(Intercept)	7.094	0.078	89.24	<0.00001
	Plant	0.2062	0.0772	2.594	<0.01
	SeasonW	-0.0434	0.0714	0.599	NS
	AgecatM	-0.0383	0.0736	0.512	NS
Neut	(Intercept)	6.704	0.079	82.99	<0.00001
	Plant	0.3295	0.1131	2.825	<0.005
	SeasonW	-0.0322	0.0778	0.407	NS
	SexM	0.0313	0.0785	0.393	NS
Lymp	(Intercept)	5.892	0.194	29.78	<0.00001
	AgecatM	-0.2651	0.2084	1.251	NS
	SexM	-0.4083	0.1493	2.650	<0.01
	SeasonW	-0.0383	0.0998	0.377	NS

$^{\#}$*denotes a non-averaged final model [i.e. there were 0 models whereby ΔAICc < 2]*

Generalised linear modeling determined the importance of Malay civet age and distance to oil palm plantation in serum biochemistry profiles of the trapped population (Table 2.8; Tables A2.10–A2.11). Malay civet profiles for uric acid, bilirubin, and GGT measures were more varied than those collected from common palm civets (Table 2.9). Summary descriptors of these parameters within this sampled population, partitioned as appropriate given GLM results, can be found in Table A2.12.

Phosphate and alkaline phosphatase measures were significantly elevated in immature Malay civets compared to mature individuals. Mature civets, in contrast, expressed significantly higher total protein and globulin measures compared to immature civets. Bilirubin was elevated in mature compared to immature individuals and in animals trapped nearer to oil palm plantations. Measured civet HDL decreased as the distance from the capture site to oil palm plantation increased. In contrast, Malay civets captured farther from oil palm plantations had elevated LDL, total cholesterol to high density lipoprotein (HDL) ratio, and urea values relative to those sampled nearer to agriculture.

Table 2.8: Model-averaged standardised estimates for statistically significant models describing Malay civet serum biochemistry parameters. NS denotes statistically non-significant (*p* > 0.05) term. Bold terms indicate statistically significant. SeasonW = wet season; SexM = male; Plant = distance to oil palm plantation; AgecatM = mature civets. Intercept = standardised reference level for factorised predictor variables (ex: female, dry season). Shorthand notation for response variables matches those provided in Table A2.2.

Parameter	Variable	Estimate	Std. Error	z value	*p value*
HDL	(Intercept)	0.7505	0.02996	24.395	<0.0001
	Plant	-0.14327	0.06277	2.225	<0.05
	SexM	-0.04649	0.06385	0.719	NS
	AgecatM	0.04053	0.06368	0.628	NS
LDL	(Intercept)	0.93432	0.03005	30.289	<0.0001
	Plant	0.15995	0.06147	2.535	<0.02
	SeasonW	0.02354	0.04867	0.477	NS
Ratio	(Intercept)	0.459962	0.018138	24.693	<0.0001
	SeasonW	0.052898	0.044337	1.177	NS
	Plant	0.120363	0.036981	3.17	<0.002
	SexM	0.005378	0.01999	0.264	NS
Ur	(Intercept)	8.10705	0.30766	25.65	<0.0001
	Plant	2.16648	0.64364	3.278	<0.002
	SexM	0.28442	0.53764	0.522	NS
	SeasonW	-0.07368	0.29705	0.243	NS
P	(Intercept)	0.43634	0.03568	11.907	<0.0001
	AgecatM	-0.31563	0.08359	3.68	<0.0005
	SeasonW	-0.06615	0.08114	0.805	NS
	Plant	-0.04145	0.06625	0.617	NS
TotProt	(Intercept)	79.3888	1.0175	75.967	<0.0001
	AgecatM	6.4601	2.2529	2.793	<0.01
	Plant	2.128	2.352	0.893	NS
	SeasonW	0.6281	1.5043	0.411	NS
	SexM	-0.1973	0.9099	0.213	NS
Glo	(Intercept)	50.29	1.082	45.147	<0.0001
	AgecatM	6.086	2.29	2.584	<0.01
	SexM	-1.943	2.436	0.788	NS
	Plant	2.222	2.582	0.85	NS
AlkPho	(Intercept)	5.6895	0.3881	13.973	<0.0001
	AgecatM	-2.5542	1.0914	2.231	<0.05
	SexM	0.149	0.4608	0.312	NS
Bili	(Intercept)	-1.0642	0.3436	3.013	<0.005
	AgecatM	2.1862	1.0281	2.068	<0.05
	SexM	0.6235	0.6318	0.975	NS
	Plant	-1.2697	0.5829	2.123	<0.05

[#] *denotes a non-averaged final model [i.e. there were 0 models whereby ΔAICc < 2].*

Table 2.9: Description of wild Malay civet blood parameters described by a binomial classification scheme of below the limit of detection ('L.D.') and elevated relative to the limit of detection ('Elevated'). Shorthand notation for biochemistry parameters matches those provided in Table A2.2.

		No. of civets			**No. of immature civets**			**No. of mature civets**		
Parameter	**L.D.**	**<LD**	**Elevated**	**Min – Max (elevated)**	**<LD**	**Elevated**	**Min – Max (elevated)**	**<LD**	**Elevated**	**Min – Max (elevated)**
UA	0.01 mmol/L	41	7	0.01 – 0.02	–	–	–	–	–	–
Bili*#	2 umol/L	–	–	–	**12**	1	3	18	**17**	2 – 256
GGT	3 U/L	18	30	3 – 195	–	–	–	–	–	–

**denotes statistical significance related to $p < 0.05$*

#parameter significantly varied with distance from capture site to oil palm plantation

2.4 Discussion

This study reports insights into the health status of small carnivores persisting within the agriculturally-fragmented LKWS. By utilising a suite of natural history observations and physiological metrics derived from the longest running field study of these species to date, a multi-facetted narrative regarding the risks and possible rewards of civet persistence in the LKWS landscape can be discussed. This study is the first to report haematology and serum biochemistry profiles for Malay civets and common palm civets; the establishment of these values, although not to be directly interpreted as healthy reference intervals in the clinical sense, will provide future studies a foundation upon which to contextualise their findings. Kinabatangan civet blood parameters were influenced by sex, age, sampling season, and distance to oil palm plantation; some are biologically explainable, while others suggest civets may be at risk.

2.4.1 Pregnancy

This study significantly enriches the known natural history of wild civet species by demonstrating a lack of temporal predictability in reproductive cycles. Previous research (Colón, 1999; Davis, 1962; Jennings et al., 2006; Wade, 1958) attempted to divine breeding seasonality from the capture of specific civet age classes or reproductive groups (i.e. juveniles, lactating females), which, although descriptive, carries substantial analytical interpretation risks (i.e. no acknowledgment of capture effort, skewed or non-continuous sampling periods, etc.). Although this study's results are similarly descriptive, they are derived from the most continuous and longest running trapping effort reported to date, and do at least acknowledge non-pregnant female capture rates. In agreement with our findings, captive Malay civets are not known to demonstrate seasonal breeding (Jaffar, pers. comm.). Regardless of seasonality, the documentation of reproductively active civet females, young adults, and recaptured individuals within the LKWS stands as tangible evidence of breeding and at least some multi-year survival within the population. These observations support the notion that civet individuals persisting in the LKWS have access to adequate reproductive resources, both in terms of abiotic requirements and available mates (Banks et al., 2007). There is evidence of generalist species adapting, reproductively, to anthropogenically-impacted landscapes. Luskin et al. (2017) found wild boar (*Sus scrofa*) fecundity and population sizes increased due to the accessible proximity of supplemental food stocks from oil palm plantations in Sumatra; perhaps small carnivores in the LKWS similarly benefit from the agriculture, and are thus uncoupled from seasonally-modulated reproduction cycles in the purely forested DVCA postulated by Colón (1999). Excessively optimistic interpretations of these results should be avoided, as true reproductive success is not evaluated by the simple detection of pregnancies within a given population. Future research into infant survival rates and dispersal success is warranted to more fully elucidate the population dynamics of these species within fragmented ecosystems (Keith et al., 1993; Robinson et al., 2014). Such efforts would be further enhanced with the inclusion of molecular research techniques, as little is known regarding the genetic status and thus health of the LKWS civet populations; carnivores persisting in highly fragmented landscapes can be threatened by inbreeding (Banks et al., 2007; Comizzoli et al., 2010). Lastly, the most straightforward caveat to these findings relates to the relatively simplistic pregnancy detection method– palpitation can only detect late phase pregnancies, thus our dataset most likely contains false negatives.

2.4.2 Parasites

The documentation of microfilaria in the blood smears of two Malay civet individuals is the first known record for the species and warrants further research. Microfilariae are immature parasitic nematodes from the family Onchocercidae, and are normally transmitted by intermediate mosquito vectors (Ballweber, 2001). There are records of Onchocercidae detection in common palm civets in Kalimantan (*Dirofilaria* sp., Masbar et al., 1981) and Malaysia (*Brugia malayi* (subperiodic) & *B. pahangi,* Edeson & Wilson, 1964); the microfilariae detected in the LKWS could be one of these species, as none are host-specific. This study was unable to identify the specific microfilariae; the implications of final identification could carry significant weight in terms of both wildlife and human health in the region. *Dirofilaria* sp., specifically *D. immitis* (commonly known as canine heartworm), can be transmitted from the definitive canine hosts to wild species (Simón et al., 2012) and to humans (Pampiglione et al., 2009). *B. malayi* can similarly be zoonotic, and can cause lymphatic elephantitis in chronically infected humans, while wildlife hosts are minimally affected (Simonsen et al., 2014). Human infection with *B. pahangi* can cause an allergic reaction; this particular nematode has already been identified in domestic dogs and cats in Peninsular Malaysia (Mak et al., 1980).

Interestingly, if the blood profiles of these parasitised animals were compared with those from the total LKWS Malay civet population, the parameters from these individuals do not represent statistically significant outliers (>2 standard deviations from the mean). Male 26 had the highest reported PCV, the second highest haemoglobin concentration and erythrocyte count, and the second lowest cholesterol value of the civets; regardless, none of these values were statistically extreme relative to the sampled population. Female 17 expressed a measurable concentration of uric acid, but this was also not considered a statistically extreme or clinically significant finding. One possible explanation is the total Malay civet population is more heavily parasitized than indicated by these two cases of positive blood smears. Blood smear microfilariae detection can generate false negatives for a multitude of reasons, such as temporal periodicity of microfilariae circulation contrasting with time of sample collection (Edeson & Wilson, 1964; Simonsen et al., 2014); host immune responses destroying microfilariae while adult nematodes persist out of circulation (Simón & Genchi, 2000); or latency periods between contraction of the parasite and peripheral circulation (Ballweber, 2001; Hoch & Strickland, 2008). The usage of antigen- or antibody-based parasite assays or PCR-based assessments to support microscopy detection would more rigorously evaluate nematode infections in small carnivores within the LKWS and oil palm landscape (Chansiri et al., 2002; Little et al., 2018).

Very few ticks and no fleas were detected on the sampled carnivores in this study, which was an unexpected finding considering the array of arthropods collected from civets throughout Southeast Asia (Wicker et al., 2017). In terms of parasitism intensity, Colón (1999) collected 76 ticks from 10 Malay civets, which is a significantly elevated tick prevalence and individual parasite load than the average detection of 1–2 ticks on a parasitised LKWS civet. Common palm civets have been documented hosts for *Ixodes* sp. (Aroon et al., 2009; Tanskul et al., 1983), *Haemaphysalis* sp. (Aroon et al., 2009; Hoogstraal & Trapido, 1966), *Dermacentor* sp. (Hoogstraal & Wassef, 1985), and *Amblyomma* sp. (Aroon et al., 2009) across their range. Malay civets have been documented hosts for *Ixodes granulatus* (Razali et al., 2018), *Haemaphysalis* sp. (Colón, 1999; Hoogstraal, 1962), and *Amblyomma* sp. (Colón, 1999). Parasitism by these genera is most likely occurring in the LKWS; efforts are currently underway to identify the arthropods in collaboration with an epidemiological team. These genera are vectors of zoonotic pathogens such as *Rickettsia* and *Borrelia* spp., which can seriously impact both wildlife and human populations. Indeed, in Sabah, the near-fatal infection of a field researcher with a spotted fever group rickettsiae, a bacteria spread by arthropod vectors, highlights the importance (and clinical difficulty) of multi-facetted epidemiology research in disturbed ecosystems (i.e. 'One Health'; Destoumieux-Garzón et al., 2018; Salgado Lynn et al., 2018).

Further research into the prevalence and epidemiology of diseases within civets persisting in fragmented ecosystems is heavily warranted, particularly given the potential of Viverridae species to host and spread zoonotic pathogens such as rabies (Susetya et al., 2008), SARS coronavirus (Bell et al., 2004), influenza (Roberton et al., 2006), *Toxoplasma gondii*, and a suite of protozoans, platyhelminths, and nematodes (Wicker et al., 2017). Indeed, explicit epidemiological studies focusing on Viverridae have uncovered new viruses with zoonotic potential, such as a novel ikoma lyssavirus documented in an African civet (*Civettictis civetta*, Marston et al., 2012). Further, records of common palm civets infected with diseases commonly associated with domestic animals, such as canine distemper virus (Techangamsuwan et al., 2015), canine parvovirus (Mendenhall et al., 2016), and feline parvovirus (Demeter et al., 2009) sets both a potentially dangerous precedent and a valid line of inquiry regarding the effects of habitat fragmentation on wild carnivore populations in the LKWS. Domestic animals (plantation dogs and cats, hunting dogs) have been documented within the protected forest lots of the LKWS, and there is very little known regarding the risks and transmission dynamics of these potentially devastating pathogens to wild Bornean carnivores. Further research is thus strongly recommended.

2.4.3 Morphology

The lack of significant sexual dimorphism for LKWS common palm civets agrees with previous research (Nakashima et al., 2013). Overall, common palm civets sampled in the LKWS were within the reported range of body weights from other Bornean sites (Nakabayashi et al., 2014; Nakashima et al., 2013; Sum, 2011). Bornean common palm civets were, however, lighter than those sampled in Thailand (Grassman, 1998; Rabinowitz, 1991). Although the influence of the small sample sizes from these studies (n = 3 and n = 4, respectively) should be acknowledged, the average civet weight captured in Thailand was double that of any other Bornean studies, and thus most likely reflects a genuine geographic distinction. Indeed, genetic research by Veron et al. (2015) suggests the common palm civet *P. hermaphroditus* should be split into three geographically distinct species: *P. hermaphroditus* (India and Indochinese regions), *P. musangus* (Indochinese and Sundaic regions), and *P. philippinensis* (Mentawai Islands, Borneo, and the Philippines). By these delineations, the lighter common palm civets sampled in Borneo would be genetically distinct from those heavier civets in Thailand, which could explain this measured geographic variation in body mass (as suggested by findings of Meiri et al., 2009).

In contrast to the common palm civet data, adult Malay civets displayed some expected measures of sexual dimorphism, with males larger than females for those parameters. Similar differences were recorded from Malay civets in DVCA (Colón, 2002), Sulawesi (Jennings et al., 2006), Peninsular Malaysia (Jennings et al., 2010), and Sarawak (Sum, 2011); this study is, however, the first to report the role of sex influencing civet total length. Further, the males and females in the LKWS did not significantly differ in weight, which contrasts the findings in Sulawesi and Peninsular Malaysia (Jennings et al., 2006; 2010). Instead, adult LKWS Malay civet body weight significantly varied with sampling year when statistically controlling for sex and proximity of capture site to oil palm plantation. Specifically, Malay civets captured in 2016 and 2017 were lighter than those caught in 2013 through 2015 and 2018. Interestingly, this may suggest ENSO (El Niño-Southern Oscillation) events negatively impact Malay civet body mass in degraded forests. A medium-strength ENSO event occurred in 2015 in the LKWS, with rainfall significantly diminishing throughout the year relative to previous and following years (Chen et al., 2016). In undisturbed dipterocarp forests, ENSO phases are believed to impact primary productivity positively due to the triggering of synchronised fruit production, called masting events (Appanah, 1985; Curran & Leighton, 2000). In degraded lowland forests, such as the LKWS, however, very few dipterocarp species remain, and the impacts of ENSO events on these landscapes are less clear (Fredriksson et al., 2007; Stark, 2018). Interestingly, Seymour et al. (2017) reported male Malay civet body weight significantly increased during ENSO years in Sulawesi, in direct contrast to what was documented in LKWS civets. In both Sarawak and East Kalimantan, *Ficus* spp. mortality rates increased and syconia production significantly decreased during the severe droughts of the 1997–1998 ENSO event and for at least the following year (Fredriksson et al., 2007; Harrison, 2001). It is possible that such a decreased productivity from the LKWS *Ficus* spp. led to a food shortage for the generalist Malay civets, resulting in the decrease in body mass for the two years following the 2015 droughts. Seymour et al. (2017) similarly recorded the lowest mean civet body weight in the year following the ENSO, with several trapped individuals described as emaciated. Similar post-ENSO famine occurrences have been described across the region, whereby the body conditions of fruit predators such as Malayan sun bear (*Helarctos malayanus*), bearded pigs, and Bornean orang-utans (*Pongo pygmaeus*) markedly reduce following droughts affiliated with ENSO events (Fredriksson et al., 2006; Knott, 1998; Wong et al., 2005; Wright et al., 1999). This finding stresses the importance of long-term monitoring of wildlife populations to uncover temporal fluxes in body condition.

This study adds to the recorded geographic variations in adult Malay civet size. Discussions evaluating geographic differences in intraspecific body size consider the influence of cryptic genetic factors, conspecific guild composition, and specific habitat suitability (Heaney, 1978; Hillaert et al., 2018; Meiri et al., 2005). First, research by Veron et al. (2014) reported Malay civet haplotypes collected across the species' extant range to be poorly geographically structured. Their research further suggests the ancestral population originated in Borneo and naturally dispersed to Peninsular Malaysia in the Pleistocene; they also provide genetic evidence supporting human-mediated dispersal of the species to Sulawesi and the Philippines. These detectable genetic differences could, at least partially, assist in explaining the large size of civets from Peninsular Malaysia relative to other sampling sites. Alternatively, the sampling sites contain significantly differing carnivore communities, which could in turn influence the body size of this species. The Malay civet is one of 10 viverrids in Peninsular Malaysia (Ratnayeke et al., 2018); one of eight viverrids in Borneo (Chapter 1); and one of three terrestrial carnivores in Sulawesi (Jennings et al., 2006). This spectrum of competition pressures could drive the evolution of varied body forms in the species by competitive release, as reported by Dayan and Simberloff (1994) in their examination of morphological differences of mustelids across the British Isles. Concurrently, predation pressures significantly varied between assessed sites; Bornean civets are believed to be predated upon by Sunda clouded leopards (*Neofelis diardi*), while Peninsular Malaysian civets share habitat with the significantly larger Indochinese leopards (*Panthera pardus delacouri*) and Malayan tigers (*Panthera tigris jacksoni*, Laidlaw, 2000). Body size and morphology of individuals can be influenced by predation risks and might further explain this geographic plasticity of Malay civet body mass (Magnhagen & Heibo, 2004; Relyea, 2001; Woodward et al., 2005).

Lastly, these morphological differences could be related to the specific suitability of these sites as Malay civet habitat (Ellis et al., 2012). Interestingly, when considering the same relative geographic location of northeastern Borneo, Malay civets in the agriculturally fragmented LKWS were substantially heavier than those sampled in the contiguous forests of DVCA (Colón, 1999) and acacia forests in Sarawak (Sum, 2011). The agriculturally fragmented and degraded lowland forests of the LKWS may be more suitable for this generalist species in terms of food quality or availability, facilitating the marked increase in adult mass. Oil palm plantations may themselves provide a supplemental food source for Malay civets, be it via direct consumption of fruit kernels or of the affiliated rodents and small mammals (Guharajan et al., 2017; Joscelyne et al., unpublished data; Rajaratnam et al., 2007). Guharajan et al. (2018) suggested sun bears may be persisting in the forest fragments of the LKWS due, at least in part, to crop raiding opportunities; similar strategies are documented for other generalist tropical species such as primates and pigs (Hockings et al., 2009; Love et al., 2018; Luskin et al., 2017). It is important to reinforce that this elevation in average civet body mass does not necessarily translate to an overall healthier population (Ishigame et al., 2006). To determine this, blood parameters, particularly lipid profiles, should be contrasted from civets persisting in such vastly different landscapes to determine if bigger is indeed better.

2.4.4 Blood parameters

Overall, this study is the first to report wild civet blood profiles in the agriculturally fragmented and degraded LKWS landscape. Within the sampled population, some blood parameters expressed large individual variation, with extreme values documented on an individual scale. Factors such as age, sex, capture season, and proximity to oil palm plantations influenced the measured values of these some of these parameters.

Common palm civet haematology- factors

In this study, both white blood cell and neutrophil counts were significantly elevated in female adult common palm civets relative to males; similar trends have been documented in black howler monkeys (García-Feria et al., 2017) and Tasmanian devils (*Sarcophilus harrisii*, Hope & Peck, 2016). This is the first reported sexual variation in haematology profiles for this species; for those few other studies evaluating common palm civet haematology profiles, no statistical differences were determined between sexes (Ahmad, pers. comm.), largely suspected due to small ($n < 2$) sample size (Salakij et al., 2007; Satyaningtijas et al., 2014; Ulfa et al., 2018). There is evidence that mammalian immunology naturally varies between males and females (Roved et al., 2017; Klein & Flanagan, 2016). Lowered male neutrophil counts may be due to the suppression of neutrophil activity by androgens (male sex hormones; Folstad & Karter, 1992; Roved et al., 2017;). Alternatively, this may be related to reproduction; indeed, as early-term pregnancy was unable to be determined for sampled civets, there could be a cryptic exacerbating effect of pregnancy on female neutrophil counts. Neutrophilia has been documented in pregnant dogs (Dimço et al., 2013), sows (Schalk et al., 2019), and humans (Odhiambo et al., 2017). It is thus recommended that researchers evaluate, or at least account for, these sex effects when interpreting common palm civet blood profiles.

The only difference in haematology profiles relative to civet age was that of elevated MCV values in immature common palm civets; this finding agrees with profiles of rescued civets in Singapore (Ahmad et al., 2017). Mean corpuscular volume decreases with age in an array of species; physiologically, the relatively high number of circulating young, and thus large, erythrocytes (reticulocytes) in growing individuals will inflate MCV measurements (Gamaldo et al., 2011; Hernández & Margalida, 2010; Hoffmann et al., 2015). It is thus also recommended that age be accounted for in evaluations of civet blood profiles.

Common palm civet haematology- compared to species literature

No landscape effects were evaluated for common palm civets due to low sample size, but comparisons with reported common palm civet blood profiles from other studies (Figure A2.2–A2.3; Ahmad et al., 2017; Salakij et al., 2007; Satyaningtijas et al., 2014; Ulfa et al., 2018) can be discussed. Unfortunately, neither of the sampled LKWS civet species have internationally-recognized Species360 blood reference intervals derived from healthy captive animals (Cozijn, pers. comm.), so these other studies provide the only directly comparable species' values to best contextualise LKWS civet blood profiles. There remain a few important caveats to consider prior to comparison, however. Any documented differences could very well be due to the effect of sample sizes, particularly considering the studies of Salakij et al. (n = 4; 2007) and Ulfa et al. (n = 6; 2018). Further, the statuses of assessed animals intrinsically differed across these studies, and blood profiles should not necessarily be interpreted as healthy baselines from any of the studies. Other common palm civet blood values come from wild but rescued individuals from Singapore (Ahmad et al., 2017); animals kept for *kopi luwak* production in West Java (Ulfa et al., 2018); captive individuals sourced from Jakarta wildlife markets (Satyuaningtijas et al., 2014);

and captive display animals at a zoological park in Thailand (Salakij et al., 2007). Reported blood parameters in a given species can be directly affected by diet (Wiesel et al., 2018), housing type (Fox et al., 2009), capture and sampling protocols (Santos et al., 2015; Crooks et al., 2013), and, more broadly, wild vs. captive status (Constable et al., 1998; Couch et al., 2017; Maceda-Veiga et al., 2015). Thus, this broad spectrum of life histories could just as likely explain the variation in reported blood profiles between these studies, so overly forceful or pointed comparison should be undertaken critically and clinical diagnoses only suggested.

Adult common palm civets in the LKWS had the lowest mean haemoglobin concentration, MCHC values, glucose concentration, red blood cell distribution, red blood cell and platelet counts reported for the species. Concurrently, LKWS civets had the largest reported mean values for MCV, mean corpuscular haemoglobin (MCH), and PCV values (Figure A2.2). Lower platelet counts and glucose concentrations were determined to not be of clinical concern; thrombocytopenia is considered functional and not indicative of physiological problems (Kerr, 2002), while blood glucose is largely influenced by fasting status, which could not be controlled for in the wild population. Following a systematic evaluation of red blood cell morphology and oxygen-carrying capacity descriptors (Johnstone et al., 2017; Keohane et al., 2016), the profiles of the wild LKWS population may indicate macrocytic and hypochromic anaemia relative to the other sample groups (Maceda-Veiga et al., 2015). This could be a result of chronic stressors experienced by the wild population; following blood loss (via parasitism, injury, etc.) or elevation of circulating stress hormones, the increased release of reticulocytes (immature erythrocytes) from the bone marrow generates what is known as regenerative anaemia (Johnstone et al., 2011). Unfortunately, reticulocyte profiles were not directly established for sampled civets. Reticulocytes are, however, both larger and less capable of producing haemoglobin than fully mature erythrocytes, which could explain the macrocytic and hypochromic characteristics described in the LKWS population (Doig, 2016; Fisher & Crook, 1962; Keohane et al., 2016). Similar findings of anaemia triggered by stress or parasite infections have been documented in wild species (agile antechinus, Johnstone et al., 2012; hedgehog *Erinaceus europaeus*, Pfäffle et al., 2009; Brazilian carnivores, Santos et al., 2018); further research is warranted, particularly evaluating if the scale of measured differences is indicative of physiological detriment such as diminished reproductive success or dispersal survival (e.g. Vitousek et al., 2014).

In terms of the leukocyte profiles of common palm civets, adults from the LKWS expressed the lowest lymphocyte counts, some of the highest neutrophil counts, and the highest neutrophil to lymphocyte ratios across the examined studies (Figure A2.3). Changes to the white blood profiles of wild animals are difficult to interpret (Davis et al., 2008; Maceda-Veiga et al., 2015), but broad physiological patterns can be useful in discussing the interpretation of these values. Neutrophils are the primary reactive unit of the innate immune system, thus this documented elevation in the wild population suggests civets may be experiencing increased exposure to pathogens or sources of inflammation (Keohane et al., 2016). Indeed, neutrophilia in wild conspecifics is often expected due to the cryptic effects of pathogen exposure and functional immune readiness (Kerr, 2002). Alternatively, the neutrophil to lymphocyte ratio can reflect an individual's stress levels, particularly when the traditional stress biomarker, glucocorticoid, is not assessed (Davis & Maney, 2018; Davis et al., 2008). Stressors, particularly those that are chronic in nature, alter an organism's leukocyte balance in a predictable manner, such that stress increases circulating neutrophil counts and decreases the circulation of lymphocytes (Davis et al., 2008). Laboratory experiments have determined this ratio scales directly with the magnitude of the stressor and positively relates to the levels of circulating glucocorticoids (Davis et al., 2008). Environmentally-catalysed neutrophilia and lymphopenia has been documented in agile antechinus (Johnstone et al., 2012), indri (*Indri indri,* Junge et al., 2011), and multiple species of bats (Seltmann et al., 2017) persisting in disturbed environments. Given the relative neutrophilia and lymphopenia in wild common palm civets, it is suggested the LKWS civets experience elevated stress levels relative to the other sampled animals, a finding which can carry significantly negative consequences for the population's long-term health (Davis et al., 2008). It is important to re-emphasise the LKWS animals were captured with box traps prior to blood sampling, a process that does intensify acute stress experienced by an individual. The rate of change to leukocyte profiles in response to stressors varies by taxon (Davis et al., 2008; Davis & Maney, 2018), but is less temporally sensitive than traditional hormone biomarkers, particularly when considering chronic stressors. Temporal assessments of leukocyte ratios following capture of green sea turtles (*Chelonia mydas*) and hellbenders (*Cryptobranchus alleganiensis*) found an elevation of this ratio only 24 and 28 hours following capture, respectively (Aguirre et al., 1995; DuRant et al., 2015). Nonetheless, this effect should not be completely excluded from consideration, as the specific leukocyte response kinetics are unknown in the species.

Common palm civet biochemistry- factors

Creatinine and LDL concentrations for adult male common palm civets were significantly elevated relative to female values. The increased creatinine in male common palm civets could be due to differing muscle mass between the sexes, as creatinine is directly produced in muscle tissue; although no sexual dimorphism was recorded in the weights of LKWS civets, perhaps males were more muscular than females (Delanaye et al., 2017; Kerr, 2002). This sex-dependency has been documented in other small carnivores (Tasmanian devil, Hope & Peck, 2016; feral cat *Felis catus*, Hwang et al., 2015). Elevated male LDL cholesterol measurements are most likely due to sexual variation in civet foraging behaviours, as the circulating quantity of this lipoprotein most often responds to an individual's diet (Constable et al., 1998; Schmidt et al., 2006); additional behavioural research into the possible sexual variation in prey selection of common palm civets is warranted.

Common palm civet biochemistry- compared to species literature

There is only one other published description of common palm civet biochemistry profiles (Ahmad et al., 2017); the values of the two studies largely appear similar in terms of the population's parameter mean and standard deviation. Adult LKWS civets demonstrated markedly lower bilirubin and creatinine levels than those from Singapore (Figure A2.4). As elevation of these two parameters indicates clinical harm, particularly regarding renal and hepatocellular systems, this trend indicates reduced physiological damage may be occurring in the LKWS population, and is most likely an observational artifact from within the Singapore population. This study reports the first lipid, chloride, uric acid, GGT, and aspartate aminotransferase (AST) profiles for the species; these values are briefly contrasted with domestic animal reference intervals below.

Malay civet haematology- factors

In contrast to common palm civets, Malay civet haematology parameters did not vary with an animal's age, instead differing with sex, season, and landscape parameters. Male Malay civets had elevated haemoglobin levels, red blood cell counts, and PCV values compared to females. These parameters are frequently naturally elevated in male mammals (Iberian lynx *Lynx pardinus*, Beltrán et al., 1990; grizzly bear *Ursus arctos*, Brannon, 1985; Tasmanian devil, Hope & Peck, 2016; see reviews by Kerr, 2002; Murphy, 2014); this is largely attested to the effects of sex hormones, specifically androgens, on red blood cell production (Kerr, 2002; Zitzmann & Nieschlag, 2004). Packed cell volume was further influenced by capture season, whereby individuals sampled in the dry season expressed elevated PCV values relative to those captured in the wetter season. This likely suggests civet hydration status decreased during the dry season, as PCV measurements are clinically elevated in dehydrated individuals (Kerr, 2002; Nayak et al., 2012). Interestingly, this was the only parameter for the species to vary with season, in contrast to other studies evaluating seasonal effects on carnivore blood profiles (Eastern quoll *Dasyurus viverrinus*, Fancourt & Nicol, 2019; Tasmanian devil, Stannard et al., 2016; brown hyena *Parahyaena brunnea*, Wiesel et al., 2018). This could be due to the lack of apparent breeding season in Malay civets, or evidence for the species demonstrating flexibility to any seasonal pulses in resource availability.

Mean corpuscular haemoglobin concentration (MCHC) was the only erythrocyte parameter that significantly varied in relation to landscape structure; civets captured closer to oil palm plantations expressed significantly lower MCHC compared to those sampled farther from agriculture. As an individual's MCHC value directly relates to the oxygen transport potential of blood, a relative decrease of this index clinically indicates hypochromic anaemia (Johnstone et al., 2017). A decrease in an individual's MCHC can relate to difficulties in haemoglobin synthesis, which is most often attributed to insufficient iron levels (Keohane et al., 2016); indeed, iron deficiencies in wild carnivores persisting in degraded habitats have been documented (grey wolf *Canis lupus*, DelGiudice et al., 1991; howler monkey, García-Feriea et al., 2017; maned wolf, May-Júnior et al., 2009). Normally, anaemia resulting from an iron deficiency generates both hypochromic and microcytic (reduced MCV) red blood cell profiles; Malay civet MCV values, however, did not vary with proximity of oil palm plantation. Additional research into the specific iron status of wild civets within the fragmented landscape is thus warranted to determine if iron deficiencies are occurring. Alternatively, exposure to certain toxins can result in anaemia related to haemoglobin concentrations (Katavolos et al., 2007; Levengood et al., 2000; Serieys et al., 2018); it is possible Malay civets nearer to oil palm are being exposed to such a pollution source. Specific serum iron assessments, transferrin levels, and ferritin concentrations could be assessed in future research aiming to evaluate civet erythrocyte parameters and indices (Hoffbrand et al., 2006).

With respect to immune system parameters, female Malay civet lymphocyte counts were elevated compared to males. As previously discussed, sex hormones have been reported to modulate immune responses in mammals (Roved et al., 2017); testosterone levels of male civets may suppress lymphocyte production rates relative to those of female civets (Foo et al., 2017). Alternatively, circulating oestrogen and progesterone could biochemically enhance female civets' adaptive immune responses (Foo et al., 2017; Klein, 2000). Lower male lymphocyte counts have been similarly recorded in Tasmanian devils (Hope & Peck, 2016), and is thus important to account for when evaluating wild civet leukocyte profiles.

Malay civet leukocyte profiles were significantly correlated by proximity to oil palm plantations, with individuals captured closer to the agriculture expressing lower neutrophil and total white blood cell counts than those sampled farther away. Given the lack of species-specific reference intervals for normal or baseline leukocyte counts, this variation can be interpreted in two ways (Salvante, 2006): 1) those individuals farther from oil palm were actively responding to elevated infections, and thus the lower leukocyte values in civets sampled near oil palm represent normal immune system baselines; or 2) those individuals sampled farther from oil palm are of optimal immune condition, and thus the lower leukocyte values near oil palm are indicative of immune impairment. Relative leukopenia and neutropenia have been documented in other species exposed to various disturbances; these studies all concluded anthropogenic activities depress the immunological status of persisting species (bat spp., Allen et al., 2009 & Seltmann et al., 2017; sifaka, Irwin et al., 2010; agile antechinus, Johnstone et al., 2012; bobcat *Lynx rufus*, Serieys et al., 2018; review by Messina et al., 2018). The suggested biochemical mechanisms for this reactive immunosuppression remain largely hypothetical; the physiological upkeep of a functional innate cellular immune system is metabolically costly, so decreases in circulating neutrophils may be a (mal)adaptive response to other energetic demands associated with persistence in degraded landscapes (Pfeifer et al., 2017). Exposure to immunosuppressing chemicals, such as pesticides or heavy metals, is also often elevated in disturbed habitats (Repetto & Baliga, 1997; Selgrade, 2007; Serieys et al., 2018). The results from this study suggests Malay civets captured nearer to agriculture express lowered innate immune functionality than those in less agriculturally-disturbed areas, which may carry significant implications for these individuals' susceptibility to pathogens.

Malay civet haematology- compared to species literature

As previously stated, there are no certified reference intervals for Malay civet blood profiles of what constitutes a normal value, and, in contrast to the few studies on common palm civets, there are no peer-reviewed reports describing Malay civet haematology. In order to best contextualise the profiles collected from the LKWS population, a report by Salakij et al. (2009) summarised the haematology profiles of four captive large Indian civets (*Viverra zibetha*) in Thailand. Large Indian civets are the closest phylogenetic relation to Malay civets (Nyakatura & Bininda-Emonds, 2012); the same caveats previously described regarding overly powerful comparisons between opportunistically collected datasets hold. In terms of erythrocyte profiles and metrics, adult LKWS Malay civets expressed markedly lower mean haemoglobin concentration, MCHC values, red blood cell counts, and red blood cell distribution values compared to adult large Indian civets; Malay civets also had comparatively elevated MCV measurements (Figure A2.5). These trends match the patterns observed in the LKWS common palm civet erythrocyte profiles, and similarly suggest the wild civet population may be experiencing regenerative anaemia. When paired with the positive relationship between Malay civet MCHC values and distance from oil palm plantation, these profiles suggest the agriculture may be negatively impacting the overall fitness of the persisting individuals.

In terms of leukocyte profiles, wild Malay civets had lower lymphocyte counts paired with higher neutrophil counts and neutrophil to lymphocyte ratios than captive large Indian civets (Figure A2.6). These profiles also match the differences documented between wild LKWS common palm civets and conspecific outgroups, and physiologically indicate the wild populations may be persisting in more stressful environments. For a more rigorous assessment of the stress levels of small carnivores residing in disturbed ecosystems, a targeted study of glucocorticoid levels could be conducted. Direct assays of circulating blood stress hormones would be inappropriate, as the trapping process required to obtain said sample would inflate hormone concentrations (Sheriff et al., 2011). The use of non-invasive or less temporally sensitive sample techniques, however, such as faecal glucocorticoid metabolite or hair cortisol assessments, could provide further insights into the functionality of the endocrine systems of LKWS small carnivores (Busch & Hayward, 2009). Indeed, these methods have uncovered elevated stress profiles in mammals persisting in fragmented and degraded landscapes worldwide (collared brown lemur *Eulemur collaris*, Balestri et al., 2014; tiger, Bhattacharjee et al., 2015; howler monkey, Martínez-Mota et al., 2007; grizzly bear, Wasser et al., 2004).

Malay civet biochemistry- factors

Malay civet serum biochemistry values did not vary by sex; instead, age category and landscape characteristics had the strongest effect on these parameters. The elevation of phosphate and alkaline phosphatase concentrations in immature Malay civets compared to adults was not unexpected, and can be explained by physiological growth processes. Both the mineral and enzyme increase in circulation during bone growth and development processes occurring in young individuals (Fernandez & Kidney, 2007; Shapiro & Heaney, 2003; Taylor et al., 1994). This age effect has been documented in mammalian carnivores (common palm civet, Ahmad et al., 2017; grizzly bear, Brannon, 1985; Florida panther *Puma concolor coryi*, Dunbar et al., 1997; lynx, García et al., 2010; Tasmanian devil, Hope & Peck, 2016; Peck et al., 2015; Culpeo fox *Lycalopex culpaeus*, Rubio et al., 2014; grey wolf, Seal et al., 1975; brown hyena, Wiesel et al., 2018). Further, lower globulin, bilirubin, and total protein measurements in immature relative to mature individuals is most likely due to the development of immune responses and hepatic systems of maturing animals (Kerr, 2002). This trend is similarly in agreement with records in other carnivore species (Amur leopard *Panthera pardus orientalis*, Bodgener & Lewis, 2017; red panda *Ailurus fulgens*, Burrel et al., 2018; grizzly bear, Brannon, 1985; Tasmanian devil, Hope & Peck, 2016; Peck et al., 2015; Stannard et al., 2016; Indian leopard *P.p. fusca*, Shanmugam et al., 2017; and brown hyena, Wiesel et al., 2018).

Malay civet lipid profiles varied with proximity to oil palm plantations, suggesting civet diet may vary throughout the landscape. Lipid profiles respond to an animal's diet, be it via changes in the selection of specific food items or changes to the nutritional quality of food, particularly regarding fat and carbohydrate content (Shanmugam et al., 2011; Wiesel et al., 2018). Surprisingly, LDL-cholesterol and the ratio of total cholesterol to HDL-cholesterol levels were lower, and HDL-cholesterol higher, in civets captured nearer to oil palm plantations; such a lipoprotein balance is clinically indicative of a reduced risk of cardiovascular disease in mammals (Bruss, 2002; Millán et al., 2009b). Interestingly, nutritional research claims consumption of oil palm products reduces LDL-cholesterol (Basiron & Weng, 2004; Edem, 2002; but see contrasting findings of Sun et al., 2015) and increases HDL-cholesterol in both humans and laboratory rats (Dauqan et al., 2011; Karaji-Bani et al., 2006). Indeed, this is often a significant selling point of marketing campaigns lauding oil palm as a 'healthy' oil product (Kushairi et al., 2018). Malay civets have been observed ingesting both oil palm fruits and small mammals within oil palm plantations (Joscelyne et al., unpublished data; Guharajan et al., 2017); this opportunistic dietary plasticity may impart cardiovascular benefits to LKWS civets. Alternatively, there is evidence that circulating HDL-cholesterol can be increased by elevated cardiovascular exercise (e.g. Gustavsen et al., 2016; Kraus et al., 2002). It is possible those civets persisting nearer to the agriculture demonstrate a more active lifestyle than those individuals from deeper forest, perhaps as a response to difficulties accessing required resources within the agricultural matrix.

Malay civet dietary flexibility across the LKWS landscape is also indicated by the positive relationship between blood urea concentration and distance from capture site to oil palm plantation. Serum urea is traditionally measured as part of a renal function panel, whereby elevation indicates dysfunction (Kerr, 2002). Civet creatinine levels, however, did not predictably respond to the proximity of an oil palm plantation. Creatinine is the clinically more specific marker used in the diagnosis of renal dysfunction (Braun & Lefevre, 2008), thus the spatial variation in civet urea is most likely due to a factor not directly related to renal function. An increase in protein consumption can elevate circulating urea levels, as urea is a waste product of amino acid breakdown (Kerr, 2002). This suggests Malay civets captured closer to oil palm plantations may have diets lower in protein relative to those captured deeper in the forest. Depressed blood urea values measured from wildlife in fragmented and degraded landscapes have been attributed to deficiencies in dietary protein intake (maned wolf, Curi et al., 2015; howler monkey, García-Ferier et al., 2017; sifaka, Irwin et al., 2010; bobcat, Serieys et al., 2018). Further, diets high in animal protein, particularly red meat, are linked to increased LDL-cholesterol levels in humans (Li et al., 1999; McAfee et al., 2010). Further targeted research into Malay civet dietary habits relative to landscape composition is strongly required to untangle these findings; genetic assessments of civet faeces (e.g. Cancio et al., 2017; Symondson, 2002) or stable isotope analyses could evaluate the degree of omnivory in the LKWS civets relative to landscape composition (Kurle, 2009; Newsome et al., 2015; Philips, 2012). Further, evaluation of lipid profiles of Malay civets in less disturbed forests such as DVCA would provide a comparative reference dataset devoid of oil palm effects.

Malay civets captured nearer to oil palm plantations had a significantly greater probability of expressing elevated bilirubin concentrations. Given the evidence of regenerative anaemia occurring within the population, elevated bilirubin circulation could be indicative of a higher erythrocyte destruction rate in those individuals captured nearer to oil palm plantations, as bilirubin is a byproduct of haeme breakdown (Tennant & Center, 2008; Rostal et al., 2013). Alternatively, elevated bilirubin concentrations can indicate liver malfunction, particularly in cholestatic complications such as obstructive biliary disease (Giannini, 2005; Kerr, 2002; Musana, 2008). Liver damage has been recorded in wildlife persisting in degraded habitats (indri, Junge et al., 2011), thus it is possible some biliary damage may be occurring in Malay civets closer to oil palm plantations. However, none of the liver enzymes (ALT, AST, GGT) more traditionally indicative and sensitive of hepatocellular damage varied with capture proximity to oil palm plantation, further complicating the story.

The lack of spatial trends in the relative measurements of these enzymes could, however, be due to the fact that the LKWS population as a whole displays elevated enzyme profiles indicative of liver damage, regardless of distance to oil palm. Unfortunately, there are no published biochemistry profiles of Malay civets or closely related phylogenetic proxies against which to contextualise these results. Comparisons can instead be conducted between healthy reference intervals from domestic cats and dogs (Kaneko et al., 2008) in an attempt to discuss the relative magnitude of civet parameters in the LKWS. Both sampled civet species displayed significantly elevated liver enzyme profiles compared to the reference intervals of domestic carnivores, suggesting the LKWS animals may be experiencing population-wide hepatocellular damage, regardless of an individual's age, sex, or proximity to oil palm plantation (Figure A2.7). These findings further highlight the importance, and difficulty, of determining species-specific reference intervals.

2.4.5 Limitations

Overall, several logistical considerations were unable to be controlled, and may influence the reported blood profiles for both civet species. As previously mentioned with respect to leukocyte stress profiles, it is important to reiterate these animals were captured in box traps at a remote field site. There is evidence that wild animal blood profiles can be influenced by trapping and anaesthetic methodologies (Brockman, 1981; Crooks et al., 2003; Santos et al., 2015), so any future comparative studies should bear this study’s methodologies in mind. Further, little is known about the most recent meal of a wild-trapped animal; an individual’s glucose and lipid profiles can differ based on fasting status (Nigam, 2011; Schmidt et al., 2006; Ulfa et al., 2018). Lastly, although utmost care was taken to minimise sample degradation due to improper storage temperatures or delays in clinical assessment, this study was conducted at a remote location without access to stable cold storage options such as continuously running freezers or liquid nitrogen, so some samples may cryptically be of subpar quality.

Despite these considerations, this study has provided evidence of active breeding, demonstrated variations in biogeographic morphology, and highlighted possible indications of anaemia, immunosuppression, dietary variation, and liver damage in the civet populations of the LKWS landscape. The evaluation of civet health metrics has provided a powerful toolkit for rapid assessment of the physiological status of the two civet species living in this fragmented ecosystem; perhaps more importantly, this study has sought to evaluate the possible risks posed by such landscapes to the future viability of persisting populations. Further analyses into the specific spatial behaviours of these species will tease apart the potential landscape-level drivers of these results. Further captive and geographic sampling efforts will be required to establish baseline levels for these species, and as discussed earlier, to discriminate potential causes of documented variations in civet health data, ideally to link specific threats, such as toxin or disease exposure, to mitigate any anthropogenic threats to the species.

Appendix II. Supplementary information for health analyses

Table A2.1: Haematology parameters and descriptors evaluated for wild civet blood samples analysed by Gribbles Pathology Laboratory.

Group	Parameter, Shorthand	Unit	Description	Source
Erythrocyte (Red Blood Cell, RBC) Parameters	Haemoglobin, Haem	g/L	Globular protein within erythrocytes used to transport O_2 from lungs to tissues & CO_2 from tissues to lungs; indicator of physiological status and anaemias	Keohane, 2016
	Red blood cell count, RBC	/L	Total count of circulating erythrocytes (RBC) within a volume of whole blood	Clark & Hippel, 2016
	Packed cell volume, PCV	L/L	Volume of packed red blood cells within a volume of whole blood. Also called haematocrit; can indicate anaemia	Clark & Hippel, 2016
	Mean corpuscular volume, MCV	fL	Erythrocyte index equates to average volume of an erythrocyte. Mathematically equals PCV/RBC. Aids in classification of anaemias	Clark & Hippel, 2016
	Mean corpuscular haemoglobin, MCH	pg	Erythrocyte index equates to average weight of haemoglobin per erythrocyte. Mathematically equals Haem/RBC.	Clark & Hippel, 2016
	Mean corpuscular haemoglobin concentration, MCHC	g/L	Erythrocyte index equates to average concentration of haemoglobin per erythrocyte. Mathematically equals Haem/PCV.	Clark & Hippel, 2016
	Red cell distribution width, RDW	%	Quantitative assessment of the degree of variation in size of circulating erythrocytes. Assists in classification of anaemias and changes in erythrocyte morphology	Longanbach & Miers, 2016
Leukocyte (White Blood Cells, WBC) Parameters	Total, WBC	/L	Total circulating white blood cells (leukocytes) in 1 L of blood; general assessment of immune functioning	Roquiz et al., 2016
	Neutrophil count, Neut	/L	Granular leukocyte acts as primary phagocytic cell responding to infection, inflammation, and stress. Generally most abundant in circulation	Davis et al., 2008
	Lymphocyte count, Lymp	/L	Agranular leukocyte involved in various immune functions, including modulation of immune system and immunoglobulin production	Davis et al., 2008
	Monocyte count, Mono	/L	Agranular & long-lived phagocyte associated with defense against infections and bacteria. Usually low circulating numbers	Roquiz et al., 2016
	Eosinophil count, Eos	/L	Granular leukocyte responds to inflammation and defence against helminth parasites. Usually low circulating numbers	Roquiz et al., 2016
	Basophil count, Baso	/L	Granular leukocyte; functionality less understood; involved in allergies and inflammation. Usually low circulating numbers or absent	Roquiz et al., 2016
	Neutrophil:Lymphocyte ratio, N:L	-	Marker of stress responses in mammalian species, scales directly with stressor magnitiude and gluccocorticoid levels	Davis et al., 2008
Clotting	Platelet count, Plat	/L	Nonnucleated circulating blood cell that responds to blood vessel damage and commences clotting process	Fritsma, 2016
Glucose	Glucose, Gluc	mmol/L	Sugar monomer in blood from ingested carbohydrates; strongly influenced by fasting status, diseases like diabetets, and some relation to stress	McCowen et al., 2001

Table A2.2: Serum biochemistry parameters and descriptors evaluated for wild civet blood samples analysed by Gribbles Pathology Laboratory.

Group	Parameter, Shorthand	Unit	Description	Source
Lipids	Total cholesterol, Tchol	mmol/L	Lipid essential for normal function of cells, including cell membrane formation and hormone development. Transported within body by HDL and LDL. Excess can cause vascular disease.	Ishigame et al., 2006
	Triglyceride, Tri	mmol/L	Lipid circulating in blood and main component of fat tissue. Transported by very low-density lipoproteins. High levels associated with cardiovascular disease and dietary intake.	Kalinski et al., 2017
	High-density lipoprotein, HDL	mmol/L	Lipoprotein that binds cholesterol in circulation and carries to liver for disposal. Low values relate to increased risk of vascular disease.	Kerr, 2002
	Low-density lipoprotein, LDL	mmol/L	Lipoprotein that binds circulating cholesterol, but via deposition of excess cholesterol in blood vessel walls. High values relate to increased risk of vascular disease.	Kerr, 2002
	Total cholesterol:HDL ratio, Ratio	-	Ratio used to evaluate lipid balance in organism.	Kerr, 2002
Electrolytes	Sodium, Na	mmol/L	Electrolyte required for fluid retention, nerve, and muscle functions. Dependent on hydration status, body salt and water balances.	Kerr, 2002
	Potassium, K	mmol/L	Electrolyte required for cell metabolism, nerve stimulation, and muscle function.	Kerr, 2002
	Chloride, Cl	mmol/L	Electrolyte required for fluid retention and acid-base balance. Generally trends with Na except when acid-base imbalance occurs.	Kerr, 2002
Renal Function	Urea, Ur	mmol/L	Waste product produced in liver during protein breakdown, filtered from blood by kidneys. Can relate to liver and/or kidney functionality.	Kerr, 2002
	Creatinine, Creat	umol/L	Waste product produced by muscle usage, filtered from blood by kidneys. Relates to kidney functions, particularly glomerular filtration rates.	Kerr, 2002
	Uric acid, UA	mmol/L	Waste produced in purine breakdown and end product of protein metabolism processeses; removed from blood by kidneys. Relates to diet and kidney function.	Kerr, 2002
	Calcium, Ca	mmol/L	Most prevalent mineral in body with multiple functions including muscular and cardiac processes, signaling, bone & teeth health, and blood clotting. Circulating levels strongly regulated by homeostatic feedback loops.	Goltzman, 2018
	Corrected calcium, Co_Ca	mmol/L	Second measure of calcium that accounts for protein- bound Ca; this reports 'free' & metabolically active circulating Ca. Preferred diagnostic.	Goltzman, 2018
	Phosphate, P	mmol/L	Mineral required for muscle and nerve function, and bone and teeth development. Absorbed in intestines and excreted by kidneys. Alternative reporting names: Phosphorus.	Kerr, 2002
Liver Function	Total protein, TotProt	g/L	Summary of circulating proteins in blood (equates to sum of albumin and globulins). Interpretation depends on albumin and immunoglobulins relations.	Kerr, 2002
	Albumin, Alb	g/L	Protein produced by liver with multiple functions; responds to liver disease, hydration, and dietary status.	Kerr, 2002
	Globulin, Glo	g/L	Group of proteins (enzymes, antibodies, hormones, etc.) generated by liver and immune system; strongly related to inflammation.	Kerr, 2002
	Albumin:Globulin Ratio, AlbGloRatio	-	Generally >1 in humans. Can be indicator of recent disease exposure or system imbalances.	Couch et al., 2017
	Alkaline phosphatase, AlkPho (ALP)	U/L	Enzyme concentrated in liver and bone tissues. Elevation indicates diseases of these systems, although young organisms can have greater circulating concentrations due to skeletal growth.	Kerr, 2002
	Total bilirubin, Bili	umol/L	Orange-yellow pigment that is the waste product of heme breakdown. Processed by the liver, and elevation indicates poor liver function.	Kerr, 2002
	Gamma-glutamyl transpeptidase, GGT	U/L	Enzyme produced in liver with multiple functions; elevation indicates liver damage, particularly as relates to bile duct functionality and biliary disease. Quick response but non specific; best diagnostically used in conjunction with ALP.	Kerr, 2002
	Aspartate aminotransferase, AST	U/L	Enzyme produced in liver and muscle tissue with multiple functions. Circulatory levels routinely low, but will respond to liver or muscle damage (non-specific). Best diagnostically used in conjunction with ALT.	Kerr, 2002
	Alanine transaminase, ALT	U/L	Enzyme found in liver and some kidney cells, it breaks down proteins. Circulatory levels routinely low, but will elevate following liver damage. More specific for hepatocellular damage than AST.	Kerr, 2002

Figure A2.1. Photograph of suspected tick eggs deposited within the alar fold of male Malay civet sampled within the LKWS on 2-May-2013.

Table A2.3: Averaged top model structures (Gamma family, square root link function) and model averaged standardised parameters evaluating adult Malay civet weight with respect to an individual's sex, capture year, and distance from capture site to nearest accessible oil palm plantation. Included are log-likelihood(Log*L*), Akaike's Information Criterion with the small sample bias adjustment(AICc), and Akaike weights (*wi*) for predicting associations between standardised independent variables and Malay civet weight. Sex = factor male; Plant = distance to oil palm plantation NS denotes non-significant term ($p < 0.05$).

Candidate Model	**df**	**Log*L***	**AICc**	**ΔAIC**	***wi***
Year	7	-41.51	99.30	0	0.5
Sex + Year	8	-40.67	100.44	1.14	0.3
Year + Plantation	8	-41.10	101.21	1.90	0.19

Response	**Parameter**	**Estimate**	**Std. Error**	**z value**	***p value***
Weight	(Intercept)	2.255	0.03928	56.05	<0.0001
	Year-2014	-0.06776	0.05940	1.113	NS
	Year-2015	-0.07013	0.05950	1.151	NS
	Year-2016	-0.23004	0.05913	3.798	<0.0002
	Year-2017	-0.16432	0.04690	3.420	<0.001
	Year-2018	-0.07334	0.13302	0.538	NS
	Sex	0.01235	0.02626	0.465	NS
	Plant	-0.00570	0.01901	0.295	NS

Table A2.4: Summary haematology profiles for wild immature common palm civets sampled within the LKWS 2013–2018. Bold text denotes the directionality of significance, such that the bolded values represent a parameter with a statistically greater measurement in the immature group compared to mature common palm civets. Shorthand notation for haematology parameters matches those provided in Table A2.1.

		Immature common palm civets			
Parameter	**Unit**	**n**	**Mean**	**SD**	**Min – Max**
Haem	g/L	3	98.7	5.77	92.0 – 102
RBC	x 10^{12}/L	3	6.45	0.94	5.44 – 7.29
PCV	L/L	3	0.38	0.05	0.32 – 0.41
MCV*	fL	3	**58.3**	2.08	56.0 – 60.0
MCH	pg	3	15.3	1.53	14.0 – 17.0
MCHC	g/L	3	264	19.9	250 – 287
RDW	%	3	21.2	1.63	19.4 – 22.5
WBC	x 10^{9}/L	3	5.57	1.59	4.60 – 7.40
Neut	x 10^{9}/L	2	3.15	0.21	3.00 – 3.30
Lymp	x 10^{9}/L	3	3.20	3.30	1.10 – 7.00
Mono	x 10^{9}/L	3	0.23	0.15	0.10 – 0.40
Eos	x 10^{9}/L	1	0.00	-	-
N:L	-	2	2.50	0.707	2.0 – 3.0
Plat	x 10^{9}/L	3	196	219	29.0 – 444
Gluc	mmol/L	1	7.9	-	-

**denotes statistical significance related to $p < 0.05$ relative to mature common palm civet blood profiles*

Table A2.5: Blood profiles for the two microfilaria-infected Malay civets. If included in the total Malay civet dataset, parameters from these individuals would not be considered statistical outliers (> 2 SD from the dataset mean) for any of the parameters. Refer to Tables A2.1-A2.2 for parameter shorthand reference.

Parameter	**Unit**	**MC F17**	**MC M26**
Haem	g/L	118	148
RBC	x 10^{12}/L	9.35	10.3
PCV	L/L	0.46	0.58
MCV	fL	49	56
MCH	pg	13	14
MCHC	g/L	258	256
RDW	%	20.6	21.1
WBC	x 10^{9}/L	15.3	7.10
Neut	x 10^{9}/L	13.2	5.80
Lymp	x 10^{9}/L	1.10	1.10
Mono	x 10^{9}/L	0.80	0.20
Eos	x 10^{9}/L	0.30	0.10
N:L	-	12	5.27
Plat	x 10^{9}/L	199	300
Gluc	mmol/L	8.1	6.8
Tchol	mmol/L	3.3	2.6
Tri	mmol/L	0.69	0.73
HDL	mmol/L	2.43	1.67
LDL	mmol/L	0.55	0.59
Ratio	-	1.4	1.6
Na	mmol/L	151	144
K	mmol/L	3.9	3.8
Cl	mmol/L	120	114
Ur	mmol/L	9.5	13.3
Creat	umol/L	65	84
Co_Ca	mmol/L	2.25	2.36
P	mmol/L	1.57	1.36
TotProt	g/L	79	75
Alb	g/L	27	23
Glob	g/L	52	52
AlbGloRatio	-	0.5	0.4
AlkPho	U/L	9	14
AST	U/L	155	104
ALT	U/L	178	87
Bili	umol/L	3	< L.D.
GGT	U/L	5	7
UA	mmol/L	0.01	< L.D.

Table A2.6: Final global model structures for Malay civet blood parameter generalised modeling. Refer to Tables A2.1-A2.2 for parameter shorthand reference.

Parameter	Model Family	Link Function
Haem	Gamma	Identity
RBC	Negative Binomial	Identity
PCV	Binomial	Logit
MCV	Gamma	Log
MCH	Gamma	Log
MCHC	Gamma	Identity
RDW	Binomial	Logit
WBC	Negative Binomial	Log
Neut	Negative Binomial	Log
Lymp	Negative Binomial	Log
Mono	Negative Binomial	Identity
N:L	Gamma	Sqrt
Plat	Negative Binomial	Identity
Gluc	Gamma	Log
Tchol	Gamma	Log
Tri	Gamma	Log
HDL	Gamma	Log
LDL	Gamma	Sqrt
Ratio	Gamma	Log
Na	Gamma	Log
K	Gamma	Identity
Cl	Gamma	Identity
Ur	Gamma	Identity
Creat	Gamma	Log
UA	Binomial	Cauchit
Co_Ca	Gamma	Identity
P	Gamma	Log
TotProt	Gamma	Identity
Alb	Gamma	Log
Glo	Gamma	Identity
AlbGloRatio	Gamma	Log
AlkPho	Gamma	Sqrt
Bili	Binomial	Cloglog
GGT	Binomial	Cauchit
AST	Gamma	Identity
ALT	Gamma	Log

Table A2.7: Top candidate (ΔAICc < 2) model structures included in model averaging, log-likelihood(Log*L*), Akaike's Information Criterion with the small sample bias adjustment(AICc), and Akaike weights (*wi*) for predicting associations between standardised independent biological and spatial variables and Malay civet haematology parameters. Season= dry or wet capture season; sex= male or female civet; agecat= immature or mature civets; plant= Euclidean distance from capture site to nearest accessible oil palm plantation. Refer to Table A2.1 for parameter shorthand reference.

Parameter	**Candidate Model**	**df**	**Log*L***	**AICc**	**ΔAICc**	***wi***
Haema*	Season + Sex	4	-183.45	375.45	0	0.64
	Sex	3	-185.23	377.05	1.13	0.36
RBC*	Season + Sex	4	-274.05	557.13	0	0.72
	Sex	3	-276.19	558.99	1.86	0.28
PCV[#*]	Season + Sex	3	-140.24	286.48	0	1
MCV	(Null)	2	-129.91	264.11	0	0.52
	Agecat	3	-129.34	265.29	1.18	0.29
	Sex	3	-129.71	266.01	1.91	0.20
MCH	Agecat + Sex	4	-54.26	117.54	0	0.13
	Agecat + Plant	4	-54.38	117.79	0.26	0.12
	Sex	3	-55.67	117.95	0.41	0.11
	Agecat + Sex + Plant	5	-53.21	118.00	0.47	0.11
	Plant	4	-55.83	118.26	0.72	0.09
	Sex + Plant	4	-54.64	118.3	0.76	0.09
	Agecat	3	-55.87	118.34	0.81	0.09
	Agecat + Season + Plant	5	-53.62	118.81	1.28	0.07
	(Null)	2	-57.31	118.92	1.38	0.07
	Agecat + Season + Sex	5	-53.71	118.99	1.46	0.06
	Agecat + Season + Sex + Plant	6	-52.51	119.28	1.74	0.06
MCHC*	Plant	3	-181.65	369.91	0	0.72
	Sex + Plant	4	-181.40	371.82	1.92	0.28
WBC*	Plant	3	-311.47	629.54	0	0.38
	Plant + Season	4	-310.70	630.43	0.89	0.25
	Agecat + Plant	4	-310.92	630.87	1.33	0.20
	Agecat + Plant + Season	5	-309.80	631.17	1.63	0.17
Neut*	Plant	3	-296.23	599.09	0	0.48
	Plant + Season	4	-295.62	600.32	1.23	0.26
	Plant + Sex	4	-295.64	600.37	1.28	0.25
N:L	Agecat + Sex + Plant	5	-98.38	208.43	0	0.31
	Sex + Plant	4	-99.88	208.85	0.42	0.25
	Sex	3	-101.25	209.14	0.71	0.22
	Agecat + Sex	4	-100.05	209.18	0.75	0.22
Lymp*	Agecat + Sex	4	-255.54	520.16	0	0.52
	Agecat + Season + Sex	5	-255.00	521.67	1.50	0.24
	Sex	3	-257.56	521.74	1.58	0.24
Mono	Agecat	3	-197.32	401.29	0	0.27
	Agecat + Plant	4	-196.20	401.51	0.22	0.24
	(Null)	2	-198.67	401.65	0.36	0.22
	Season	3	-197.96	402.58	1.29	0.14
	Plant	3	-198.04	402.72	1.44	0.13
Plat	(Null)	2	-264.99	534.28	0	0.46
	Agecat	3	-264.16	534.93	0.65	0.34
	Sex	3	-264.68	535.97	1.68	0.20
Gluc	(Null)	2	-74.76	153.83	0	0.48
	Sex	3	-73.99	154.63	0.80	0.32
	Season	3	-74.51	155.67	1.84	0.19

**denotes parameters with final averaged structures containing statistically significant terms (p < 0.05)*

[#] *denotes parameter with singular and final model structure (no models within 2 AICc of top model)*

Table A2.8: Model-averaged standardised estimates of statistically non-significant top-models of Malay civet haematology parameters. NS denotes statistically non-significant (*p* > 0.05) term. Table A2.1 for parameter shorthand reference; variable shorthand match those of Table 2.7.

Parameter	Variable	Estimate	Std. Error	z value	*p value*
MCV	(Intercept)	3.965	0.01356	284.16	<0.00001
	AgecatM	0.009271	0.02219	0.411	NS
	SexM	0.003339	0.01391	0.235	NS
MCH	(Intercept)	2.621	0.009436	269.58	<0.00001
	AgecatM	0.02418	0.0252	0.945	NS
	SexM	0.01759	0.02118	0.819	NS
	Plant	0.01639	0.02086	0.775	NS
	SeasonW	0.0041	0.0119	0.34	NS
RDW	(Intercept)	-1.293	0.03668	34.26	<0.00001
	AgecatM	-0.01761	0.05325	0.324	NS
N:L	(Intercept)	2.168	0.142	14.8	<0.00001
	AgecatM	0.2126	0.2852	0.733	NS
	SexM	0.5558	0.293	1.84	NS
	Plant	0.2038	0.2803	0.713	NS
Mono	(Intercept)	63.73	13.79	4.543	<0.00001
	AgecatM	-11.34	15.05	0.742	NS
	Plant	5.777	10.08	0.565	NS
	SeasonW	1.824	6.115	0.294	NS
Plat	(Intercept)	305.7	36.69	8.177	<0.00001
	AgecatM	-18.79	37.42	0.495	NS
	SexM	5.878	20.3	0.284	NS
Gluc	(Intercept)	1.711	0.04029	41.16	<0.00001
	SexM	0.03456	0.06733	0.506	NS
	SeasonW	-0.01165	0.04313	0.264	NS

Table A2.9: Summary haematology profiles for wild Malay civets sampled within the LKWS from 2013–2018. Bold text denotes the directionality of significance, such that the bolded values represent the sex with the statistically greater values ($p < 0.05$). Refer to Table A2.1 for parameter shorthand reference.

		All civets				Female				Male			
Parameter	**Unit**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**
Haem**	g/L	44	–	–	–	23	103	15.1	73.0 – 131	21	**119**	17.7	73.0 – 149
RBC*	x 10^{12}/L	44	–	–	–	23	7.66	1.24	4.98 – 10.5	21	**8.51**	1.31	4.72 – 10.7
PCV*$^{@}$	L/L	44	–	–	–	23	0.40	0.05	0.30 – 0.50	21	**0.45**	0.07	0.31 – 0.58
MCV	fL	44	52.7	4.74	44.0 – 66.0	–	–	–	–	–	–	–	–
MCH	pg	44	13.8	0.89	11.0 – 16.0	–	–	–	–	–	–	–	–
MCHC #	g/L	44	261	16.5	233 – 304	–	–	–	–	–	–	–	–
RDW	%	44	21.5	1.69	17.6 – 25.6	–	–	–	–	–	–	–	–
WBC #	x 10^{9}/L	44	11.5	3.43	5.70 – 23.3	–	–	–	–	–	–	–	–
Neut #	x 10^{9}/L	42	8.28	3.41	3.10 – 17.3	–	–	–	–	–	–	–	–
Lymp**	x 10^{9}/L	42	–	–	–	22	**2.96**	1.60	0.60 – 6.90	20	1.96	0.99	0.60 – 4.20
N:L	-	42	4.8	4.08	0.78 – 17.8	–	–	–	–	–	–	–	–
Mono	x 10^{9}/L	42	0.55	0.38	0.00 – 1.80	–	–	–	–	–	–	–	–
Eos	x 10^{9}/L	24	0.52	0.50	0.00 – 1.80	–	–	–	–	–	–	–	–
Baso	x 10^{9}/L	5	0.16	0.31	0.00 – 0.70	–	–	–	–	–	–	–	–
Plat	x 10^{9}/L	43	295	116	88.0 – 568	–	–	–	–	–	–	–	–
Gluc	mmol/L	41	5.5	1.4	1.5 – 8.9	–	–	–	–	–	–	–	–

**denotes significance values for sex differences such that model parameter's p value < 0.05; **p value < 0.01*

#denotes parameter significantly varies with distance from capture site to oil palm plantation

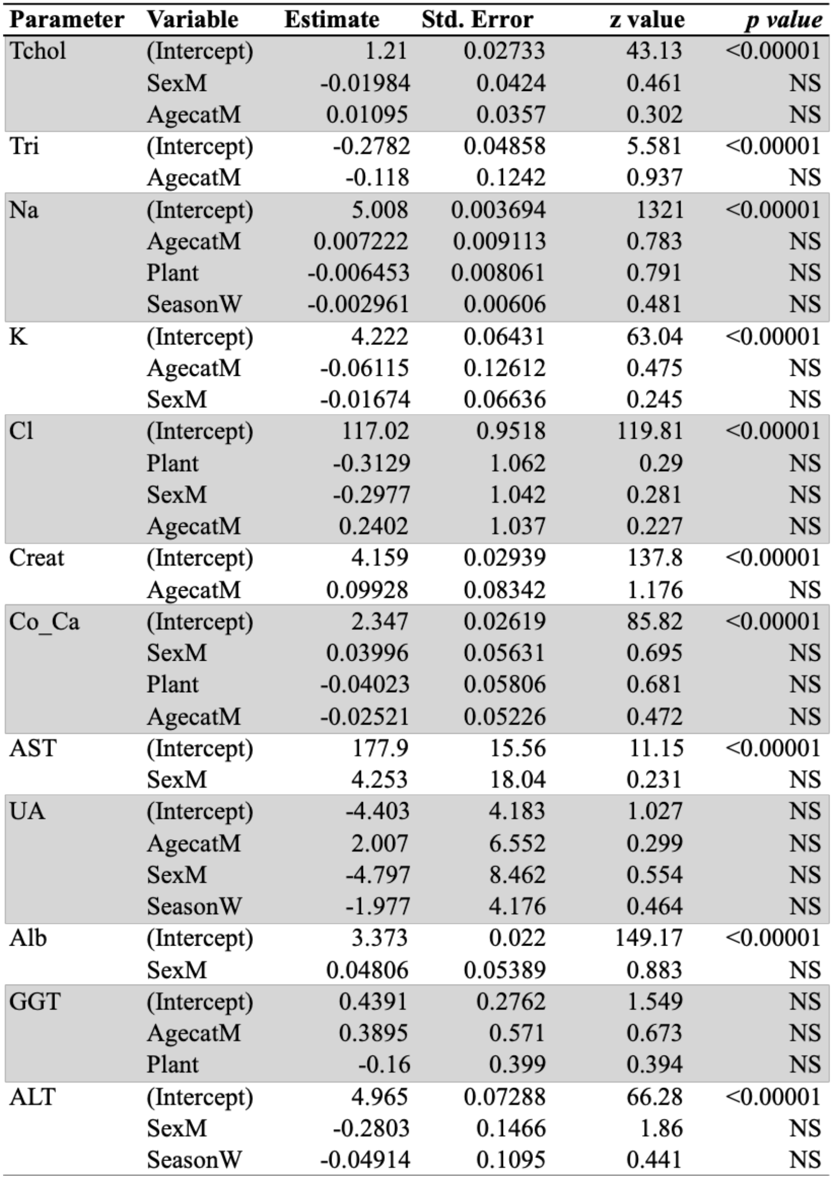
$^{@}$*denotes parameter significantly varies with capture season*

Table A2.10: Top candidate (ΔAICc<2) model structures included in model averaging, log-likelihood(Log*L*), Akaike's Information Criterion with the small sample bias adjustment(AICc), and Akaike weights (*wi*) for predicting associations between standardised independent biological and spatial variables and Malay civet serum biochemistry parameters. Refer to Table A2.2 for parameter shorthand reference; variable shorthand match those in Table A2.7.

Parameter	Candidate Model	df	Log*L*	AICc	ΔAICc	*wi*
Tchol	(Null)	2	-43.96	92.19	0	0.47
	Sex	3	-43.22	92.97	0.78	0.32
	Agecat	3	-43.59	93.71	1.52	0.22
Tri	Agecat	3	3.38	-0.23	0	0.64
	(Null)	2	1.68	0.90	1.14	0.36
HDL*	Plant	3	-27.31	61.16	0	0.28
	Sex + Plant	4	-26.14	61.18	0.02	0.28
	Agecat + Sex + Plant	5	-25.1	61.59	0.43	0.23
	Agecat + Plant	4	-26.36	61.63	0.47	0.22
LDL*	Plant	3	-26.07	58.66	0	0.66
	Season + Plant	4	-25.56	60.03	1.36	0.34
Ratio*	Season + Plant	4	10.29	-11.67	0	0.54
	Plant	3	8.37	-10.22	1.46	0.26
	Season + Sex + Plant	5	10.55	-9.71	1.96	0.20
Na	Agecat + Plant	4	-133.34	275.59	0	0.20
	Agecat	3	-134.73	275.98	0.40	0.17
	Plant	3	-134.87	276.28	0.69	0.14
	(Null)	2	-136.11	276.48	0.89	0.13
	Season + Plant	4	-134.01	276.93	1.34	0.10
	Agecat + Season + Plant	5	-132.87	277.13	1.54	0.09
	Season	3	-135.36	277.24	1.66	0.09
	Agecat + Season	4	-134.32	277.55	1.97	0.08
K	(Null)	2	-12.5	29.41	0	0.49
	Agecat	3	-11.71	30.28	0.87	0.32
	Sex	3	-12.25	31.36	1.95	0.19
Cl	(Null)	2	-162	328.26	0	0.44
	Plant	3	-161.65	329.84	1.58	0.20
	Sex	3	-161.67	329.88	1.62	0.19
	Agecat	3	-161.79	330.10	1.85	0.17
Ur*	Plant	3	-100.28	207.10	0	0.46
	Sex + Plant	4	-99.34	207.62	0.51	0.36
	Season + Plant	4	-100.02	208.98	1.88	0.18
Creat	Agecat	3	-190.42	387.39	0	0.72
	(Null)	2	-192.5	389.26	1.87	0.28
UA	Agecat + Sex	3	-16.75	40.05	0	0.24
	Season + Sex	3	-16.81	40.16	0.12	0.23
	Season	2	-18.32	40.91	0.86	0.16
	Sex	2	-18.32	40.91	0.86	0.16
	Agecat + Season + Sex	4	-16.17	41.27	1.23	0.13
	(Null)	1	-19.94	41.97	1.92	0.09
Co_Ca	(Null)	2	15.78	-27.14	0	0.21
	Sex + Plant	4	18.26	-26.98	0.15	0.19
	Plant	3	16.78	-26.66	0.47	0.17
	Agecat	3	16.53	-26.18	0.96	0.13
	Sex	3	16.4	-25.92	1.22	0.11
	Agecat + Sex	4	17.55	-25.57	1.57	0.10
	Agecat + Sex +Plant	5	18.93	-25.47	1.67	0.09
P*	Agecat + Season	4	-19.10	47.11	0	0.31
	Agecat	3	-20.48	47.50	0.38	0.25
	Agecat + Sex +Plant	5	-18.07	47.54	0.42	0.25
	Agecat + Plant	4	-19.57	48.05	0.93	0.19
TotProt*	Agecat + Plant	4	-164.18	337.27	0	0.32
	Agecat	3	-165.58	337.70	0.43	0.26
	Agecat + Season + Plant	5	-163.64	338.67	1.40	0.16
	Agecat + Season	4	-165.06	339.04	1.77	0.13
	Agecat + Sex + Plant	5	-163.89	339.17	1.90	0.12
AST	(Null)	2	-287.96	580.17	0	0.73
	Sex	3	-287.8	582.13	1.96	0.27
Alb	Sex	3	-138.91	284.40	0	0.56
	(Null)	2	-140.3	284.87	0.47	0.44
Glo*	Agecat + Sex +Plant	5	-152.04	315.59	0	0.36
	Agecat	3	-154.9	316.37	0.78	0.24
	Agecat + Plant	4	-153.83	316.64	1.05	0.21
	Agecat + Sex	4	-154.01	317.00	1.41	0.18
AlbGloRatio	(Null)	2	20.69	-37.11	0	0.26
	Sex	3	21.46	-36.34	0.76	0.18
	Agecat	3	21.31	-36.04	1.07	0.15
	Sex + Plant	4	22.50	-36.03	1.08	0.15
	Plant	3	21.28	-36.00	1.11	0.15
	Agecat + Sex	4	22.21	-35.45	1.65	0.11
AlkPho*	Agecat	3	-118.63	244.26	0	0.73
	Agecat + Sex	4	-118.26	246.25	1.99	0.27
Bili*	Agecat + Sex + Plant	4	-24.09	57.11	0	0.63
	Agecat + Plant	3	-25.83	58.21	1.1	0.37
GGT	(Null)	1	-31.76	65.60	0	0.35
	Agecat	2	-30.76	65.79	0.19	0.32
	Plant	2	-31.43	67.13	1.53	0.16
	Agecat + Plant	3	-30.32	67.18	1.58	0.16
ALT	Sex	3	-258.84	524.23	0	0.65
	Season + Sex	4	-258.26	525.47	1.24	0.35

**denotes blood parameters with final averaged structures containing statistically significant terms ($p < 0.05$)*

Table A2.11: Model-averaged standardised estimates of statistically non-significant top-models of Malay civet serum biochemistry parameters. NS denotes statistically non-significant (*p* > 0.05) term. Refer to Table A2.2 for parameter shorthand reference; variable shorthand match those provided in Table 2.7.



Parameter	Variable	Estimate	Std. Error	z value	*p value*
Tchol	(Intercept)	1.21	0.02733	43.13	<0.00001
	SexM	-0.01984	0.0424	0.461	NS
	AgecatM	0.01095	0.0357	0.302	NS
Tri	(Intercept)	-0.2782	0.04858	5.581	<0.00001
	AgecatM	-0.118	0.1242	0.937	NS
Na	(Intercept)	5.008	0.003694	1321	<0.00001
	AgecatM	0.007222	0.009113	0.783	NS
	Plant	-0.006453	0.008061	0.791	NS
	SeasonW	-0.002961	0.00606	0.481	NS
K	(Intercept)	4.222	0.06431	63.04	<0.00001
	AgecatM	-0.06115	0.12612	0.475	NS
	SexM	-0.01674	0.06636	0.245	NS
Cl	(Intercept)	117.02	0.9518	119.81	<0.00001
	Plant	-0.3129	1.062	0.29	NS
	SexM	-0.2977	1.042	0.281	NS
	AgecatM	0.2402	1.037	0.227	NS
Creat	(Intercept)	4.159	0.02939	137.8	<0.00001
	AgecatM	0.09928	0.08342	1.176	NS
Co_Ca	(Intercept)	2.347	0.02619	85.82	<0.00001
	SexM	0.03996	0.05631	0.695	NS
	Plant	-0.04023	0.05806	0.681	NS
	AgecatM	-0.02521	0.05226	0.472	NS
AST	(Intercept)	177.9	15.56	11.15	<0.00001
	SexM	4.253	18.04	0.231	NS
UA	(Intercept)	-4.403	4.183	1.027	NS
	AgecatM	2.007	6.552	0.299	NS
	SexM	-4.797	8.462	0.554	NS
	SeasonW	-1.977	4.176	0.464	NS
Alb	(Intercept)	3.373	0.022	149.17	<0.00001
	SexM	0.04806	0.05389	0.883	NS
GGT	(Intercept)	0.4391	0.2762	1.549	NS
	AgecatM	0.3895	0.571	0.673	NS
	Plant	-0.16	0.399	0.394	NS
ALT	(Intercept)	4.965	0.07288	66.28	<0.00001
	SexM	-0.2803	0.1466	1.86	NS
	SeasonW	-0.04914	0.1095	0.441	NS

Table A2.12: Summary serum biochemistry profiles for wild Malay civets sampled within the LKWS from 2013–2018. Bold text denotes the directionality of significance, such that the bolded values represent the sex with the statistically greater values. Refer to Table A2.2 for parameter shorthand reference.

		All Civets				Immature				Mature			
Parameter	**Unit**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**	**n**	**Mean**	**SD**	**Min – Max**
Tchol	mmol/L	49	3.4	0.64	2.5 – 5.6	–	–	–	–	–	–	–	–
Tri	mmol/L	49	0.76	0.26	0.37 – 1.67	–	–	–	–	–	–	–	–
HDL #	mmol/L	49	2.13	0.48	1.39 – 3.25	–	–	–	–	–	–	–	–
LDL #	mmol/L	49	0.879	0.40	0.03 – 1.95	–	–	–	–	–	–	–	–
Ratio #	-	49	1.6	0.22	1.1 – 2.0	–	–	–	–	–	–	–	–
Na	mmol/L	49	150	3.94	141 – 159	–	–	–	–	–	–	–	–
K	mmol/L	32	4.2	0.37	3.5 – 5.0	–	–	–	–	–	–	–	–
Cl	mmol/L	49	117	6.64	103 – 131	–	–	–	–	–	–	–	–
Ur #	mmol/L	48	8.1	2.3	3.30 – 14.2	–	–	–	–	–	–	–	–
Creat	umol/L	48	64	13	37 – 89	–	–	–	–	–	–	–	–
Co_Ca	mmol/L	31	2.35	0.15	2.03 – 2.78	–	–	–	–	–	–	–	–
P***	mmol/L	–	–	–	–	13	**1.93**	0.69	0.99 – 3.68	36	1.43	0.29	0.92 – 2.13
TotProt**	g/L	–	–	–	–	13	74.8	8.88	61.0 – 86.0	36	**81.1**	6.36	67.0 – 92.0
Alb	g/L	46	29.2	4.40	10.0 – 37.0	–	–	–	–	–	–	–	–
Glob**	g/L	–	–	–	–	13	46.1	8.11	32.0 – 59.0	33	**51.9**	7.06	39.0 – 82.0
AlbGloRatio	-	46	0.60	0.13	0.10 – 0.90	–	–	–	–	–	–	–	–
AlkPho*	U/L	–	–	–	–	7	**57.4**	33.3	22.0 – 127	21	25.6	19	7.0 – 71
AST	U/L	49	177.9	108.9	17.0 – 559	–	–	–	–	–	–	–	–
ALT	U/L	47	144.8	77.5	48.0 – 395	–	–	–	–	–	–	–	–

*denotes significance values for sex differences such that model parameter's $p < 0.05$; **$p < 0.01$; ***$p < 0.001$

#denotes parameter significantly varies with distance from capture site to oil palm plantation

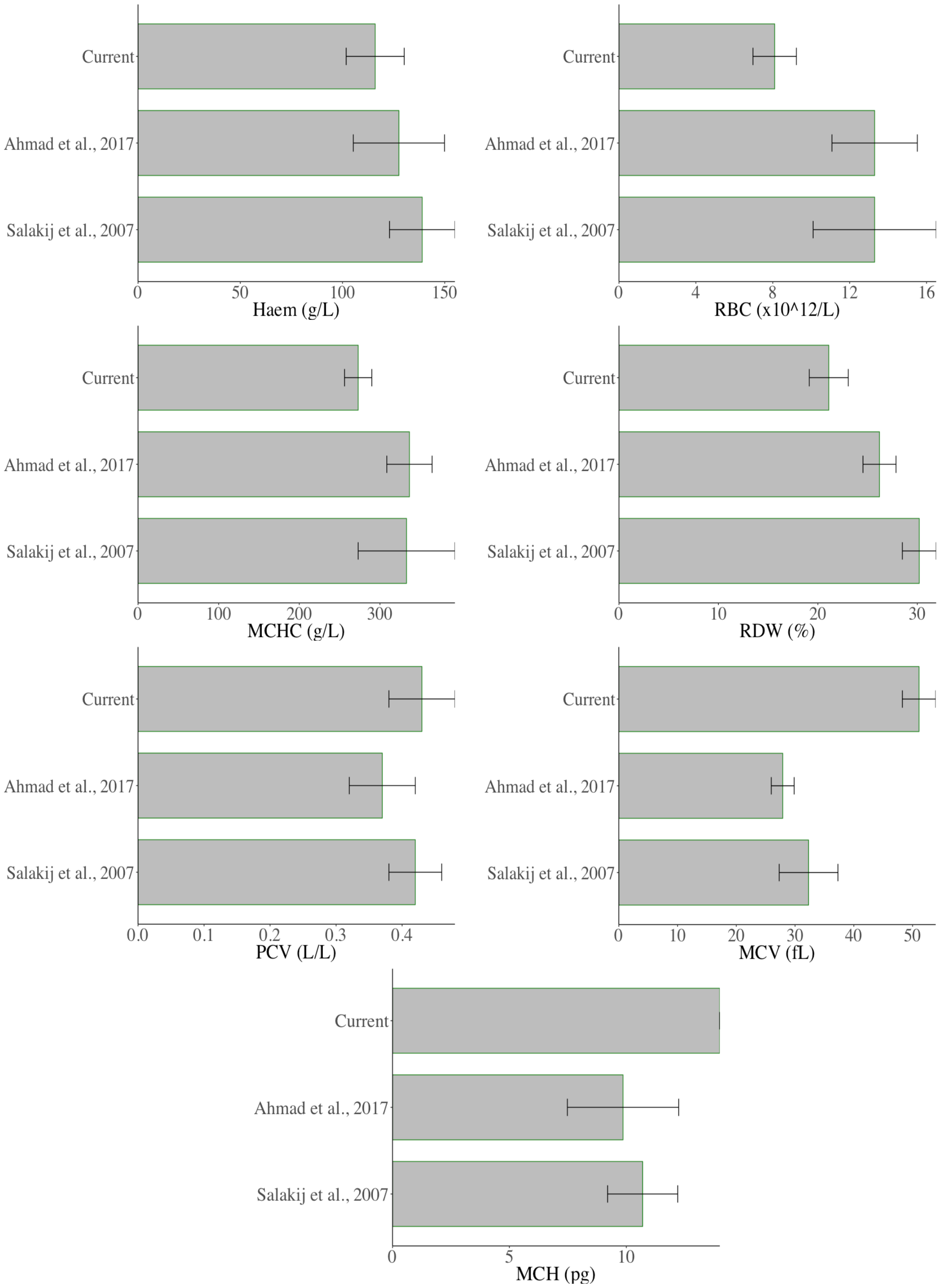


Figure A2.2. Bar plots displaying LKWS common palm civet blood haematology parameters indicative of anaemia relative to other sampled civet blood profiles. Bars represent each study's mean value and error bars the standard deviation of each dataset. Refer to Table A2.1 for parameter shorthand reference.

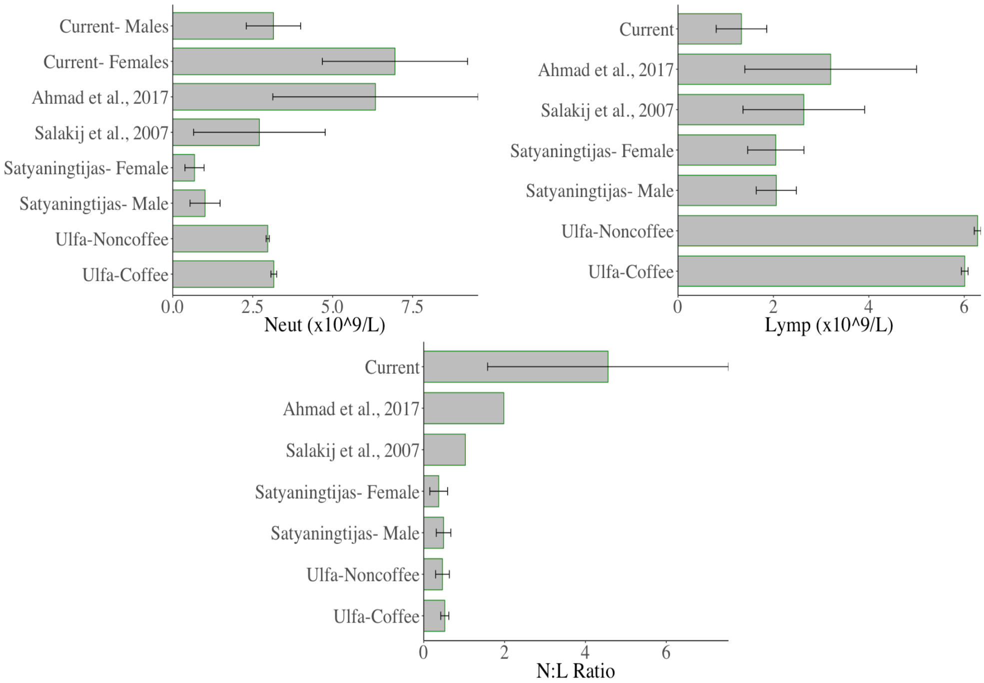


Figure A2.3. Bar plots displaying LKWS common palm civet blood haematology parameters indicative of altered leukocyte profiles relative to other sampled civet blood values. Bars represent each study's mean value and error bars the standard deviation of each dataset. Refer to Table A2.1 for parameter shorthand reference.

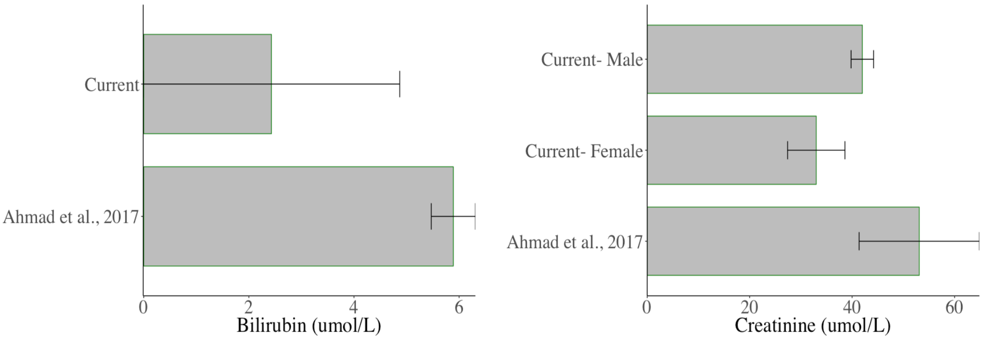


Figure A2.4. Bar plots displaying common palm civet blood biochemistry parameters whereby the LKWS civets have the markedly lowest reported mean measurements. Bars represent each study's mean value and error bars the standard deviation of each dataset. Refer Table A2.2 for parameter shorthand reference.

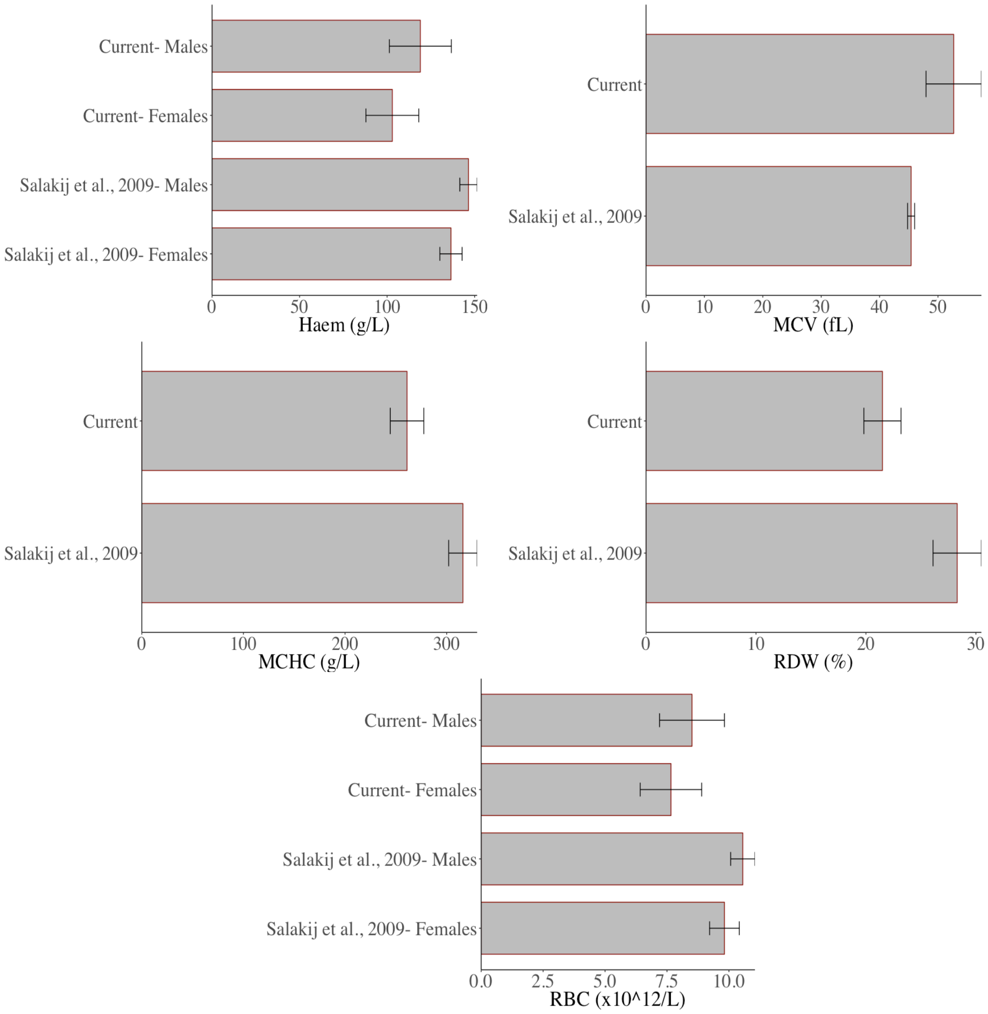


Figure A2.5. Bar plots displaying Malay civet blood haematology parameters indicative of anaemia relative to captive Large Indian civet blood profiles. Bars represent each study's mean value and error bars the standard deviation of each dataset. Refer to Table A2.1 for parameter shorthand reference.

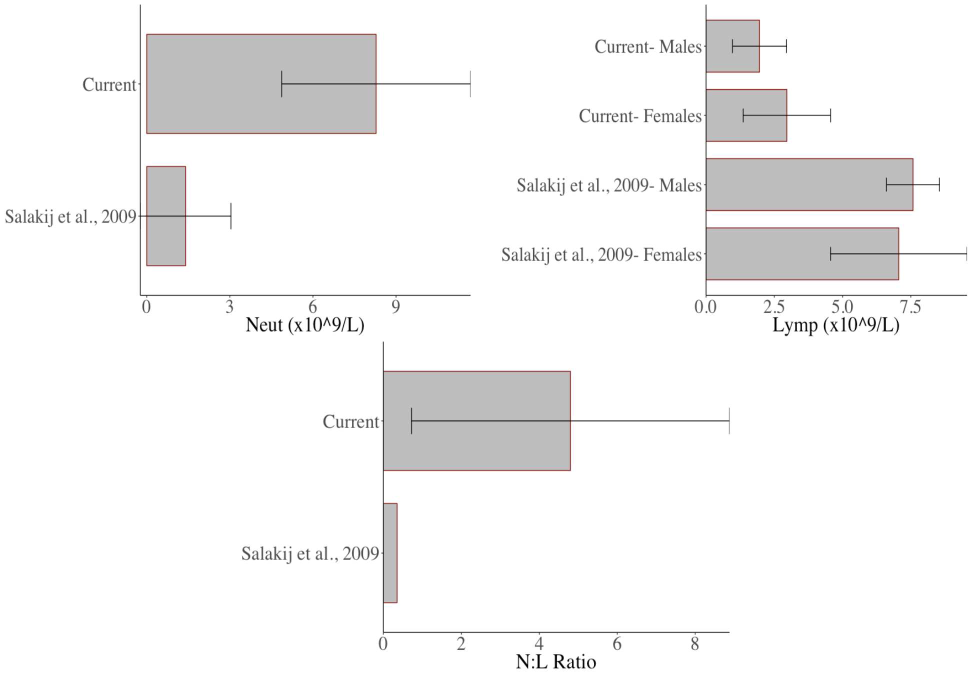


Figure A2.6. Bar plots displaying LKWS Malay civet blood haematology parameters indicative of altered leukocyte profiles relative to captive Large Indian civet blood values. Bars represent each study's mean value and error bars the standard deviation of each dataset. Refer to Table A2.1 for parameter shorthand reference.

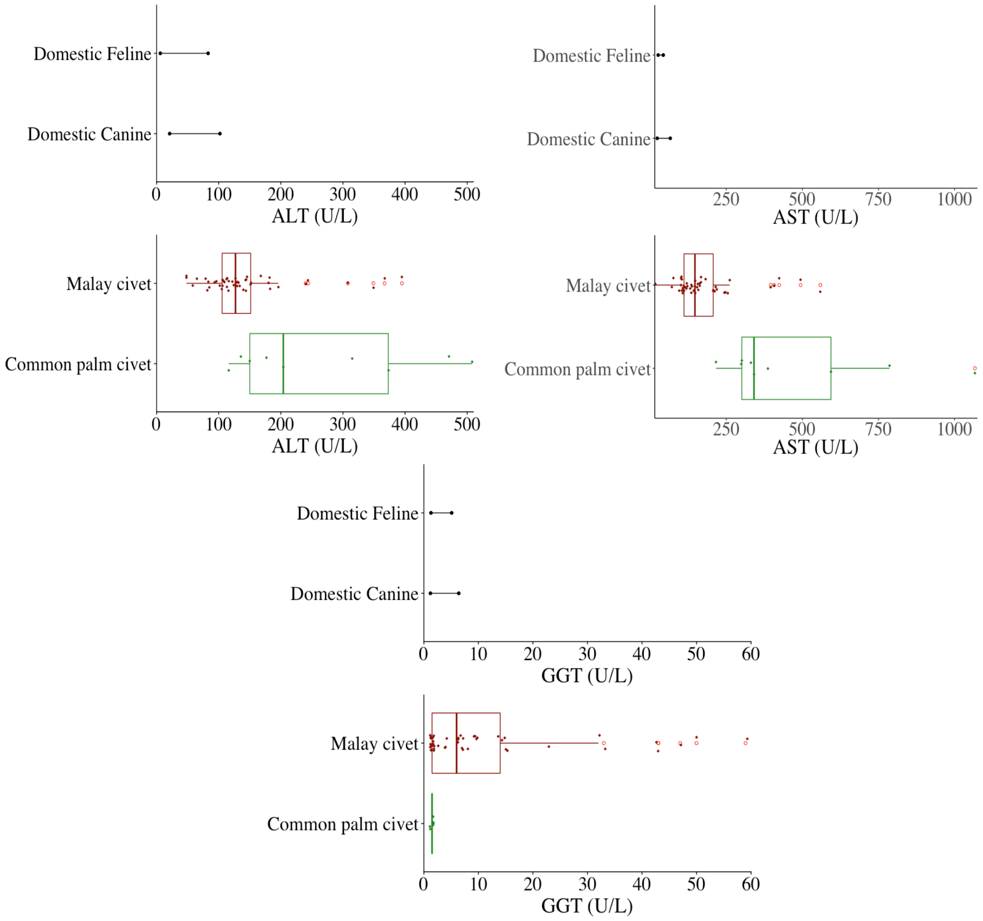


Figure A2.7. Liver enzyme (ALT, AST, and GGT) profiles of LKWS civets compared with certified reference intervals of healthy domestic animals (from Kaneko, 2008). Red circles denote statistical outliers relative to the population's summary values (> 2 SD from the mean). Refer to Table A2.2 for parameter shorthand reference. When reported values of GGT were < L.D., a numeric placeholder equal to ½ L.D. was included; one extreme female Malay civet outlier (195 U/L) was not displayed on the GGT plot.

Chapter 3. First known satellite collaring of a viverrid: results and implications of GPS-collaring Malay civets (*Viverra tangalunga*)#

#This chapter is an adaptation of a manuscript published in the peer-reviewed journal Ecological Research, Evans et al., 2016a.

3.1 Introduction

Global biodiversity loss is progressing at increasingly alarming rates (Barnosky et al., 2011; Ceballos et al., 2015; Ripple et al., 2015; Schipper et al., 2008). To mitigate further loss, effective conservation management plans are critical, which in turn require in-depth understandings of species' biological requirements (Chetkiewicz et al., 2006; Cooke, 2008; Margules & Pressey, 2000). Documenting and quantifying factors crucial to species survival are the central aims of applied wildlife research, and the design of innovative research tools facilitates the achievement of these goals.

Remote tracking technologies in wildlife studies have revolutionized scientific understanding of animal behavioural patterns and processes (Cooke et al., 2004; Fuller & Fuller, 2012; Ropert-Coudert & Wilson, 2005). The application of radio telemetry as very high frequency (VHF) collar transmitters allowed for the first remote documentation of animal movements in the 1960s (Craighead et al., 1963). While revolutionary, VHF tracking often requires significant field effort for sparse and relatively inaccurate data (Gitzen et al., 2013; Recio et al., 2011a). Furthermore, the collection, applicability, and quality of VHF data are limited by intrinsic biases such as observer presence, site remoteness, weather, and specific animal behaviours (Fuller et al., 2005; Recio et al., 2011b).

In response to these limitations, satellite-based tracking technologies, such as the Global Positioning System (GPS), were first applied to wildlife in the 1970s (Craighead et al., 1972). This development meant the collection of larger, more consistent, fine-scaled and accurate datasets (Kochanny et al., 2002; Rodgers, 2001). Satellite tracking minimizes logistical effort and eliminates the influence of observer presence on recorded behavioural patterns, generating datasets otherwise unobtainable by VHF tracking and more relevant to conservation actions (Hebblewhite & Haydon, 2010). Satellite collars have established habitat utilisation and preferences for wary and remote species (Amstrup et al., 2004; Simcharoen et al., 2014), uncovered areas of previously unknown reproductive significance in widely migrating species (Hays et al., 2014; Lindsell et al., 2009; Schofield et al., 2009), and discovered novel cryptic behaviours (Bandeira de Melo et al., 2007; Davis et al., 1999; Lührs & Kappeler, 2013).

The universal application of GPS to wildlife tracking is, however, still limited by technological constraints, as historically, both transmitters and batteries have been bulky and large (> 400 g, some up to 2.2 kg) (Rodgers, 2001). Most terrestrial GPS studies have focused on mammals > 7 kg, so spatial research on small and medium-sized species relies on VHF transmitters (Blackie, 2010; Cagnacci et al., 2010). Owing to recent advancements in both battery longevity and the miniaturization of GPS component design, long-term satellite technologies are being applied to increasingly smaller mammalian species, such as the ocelot (*Leopardus pardalis*, Haines et al., 2006), European hedgehog (*Erinaceus europaeus*, Recio et al., 2011c), fossa (*Cryptoprocta ferox,* Lührs & Kappeler, 2013), fisher (*Martes pennant*, Brown et al., 2012), and brushtail possum (*Trichosurus vulpecula,* Blackie, 2010; Dennis et al., 2010).

The Viverridae family (Order Carnivora) comprises 34 species in 14 genera, the majority of which weigh < 8 kg (Jennings & Veron, 2009). There exists a significant paucity of data concerning even basic ecological information of this family (Schreiber et al., 1989), and five viverrid species are not yet represented in peer-reviewed literature (Brooke et al., 2014*).* What studies do occur are dominated by camera-trap deployments (Jennings et al., 2015; Wilting et al., 2010b), survey transects (Heydon & Bulloh, 1996; Iseborn et al., 2010), and a handful of VHF studies (Berhanu et al., 2013; Camps & Alldredge, 2013; Grassman, 1998; Grassman et al., 2005a; Joshi et al., 1995; Nakashima et al., 2013). Viverrids are threatened by habitat loss and hunting, but also by lack of scientific information regarding rudimentary survival parameters (Brooke et al., 2014; Schipper et al., 2008). This knowledge gap poses a substantial threat to the effective conservation and management of these species. Therefore, this study sought to demonstrate the applicability, performance, and value of satellite tracking a model viverrid, the Malay civet (*Viverra tangalunga*). Weighing between 3–7 kg, *V. tangalunga* is a predominantly solitary and terrestrial small carnivore found throughout the Sundaic region of Southeast Asia (Chapter 1; Payne & Francis, 1985). Although several VHF studies have evaluated the spatial ecology of *V. tangalunga* (Colón, 2002; Jennings et al., 2006; Jennings et al., 2010; Nozaki et al., 1994), this study represents the first known application of GPS collars to the Viverridae family, and ultimately aimed to demonstrate the scientific and conservation value of GPS technology deployments on small carnivores.

3.2 Methods

3.2.1 Study site

The Lower Kinabatangan Floodplain is located in eastern Sabah, Malaysian Borneo (approximate range: 5°18’N to 5°42’N and 117°54’E to 118°33’E). The climate is humid tropical with temperatures ranging from 21°– 34°C (Ancrenaz et al., 2004). This study was based in the Lower Kinabatangan Wildlife Sanctuary (LKWS), a 270 km^2 area of protected secondary forest flanking the Kinabatangan River (Ancrenaz et al., 2004; Goossens et al., 2005). Comprised of ten riparian lots of varying degrees of disturbance history, the sanctuary contains a mixture of dry lowland, semi-inundated, and swamp forests interspersed with small grasslands (Abram et al., 2014).

3.2.2 Trapping and immobilisation

Trapping periods spanned October 2013 through August 2015. Small carnivores were trapped using locally constructed, specially designed box treadle traps (110 cm x 35 cm x 40 cm). Traps were set by 18:00 h, checked between 07:00 h and 08:00 h, and closed during the day to avoid non-target diurnal captures.

Upon capture, animals were administered anesthesia by a qualified veterinarian. Animals were either sedated with Tiletamine/Zolazepam (Zoletil^{TM}, Virbac Laboratories, Carros, France), or a mixture of Ketamine (Narketan^{TM}, Vétoquinol UK Limited, Buckingham, UK), Xylazine (Ilium Xylazil^{TM}, Troy Laboratories PTY Limited, Glendenning, Australia) and Tiletamine/Zolazepam. In the case of the latter drug combination, the reversal agent Yohimbine (Reverzine^{TM}, Bomac Pty Limited, Hornsby, Australia) was administered once sampling was complete.

3.2.3. GPS-collaring and tracking

GPS collars (Collar 1A and second-generation Collar 1A, e-obs GmbH, Grünwald, Germany) weighed 65–70 g, or between 1.3–1.4% of average adult civet body weight, well within the restrictions of the American Mammal Society for the ethical collaring of animals (Sikes et al., 2016). Each tag contained a GPS microchip, either a 2300 mAh or 2500 mAh battery, UHF radiotransmitter, a tri-axial accelerometer, and an antenna. The collar was constructed to degrade through a thin section of leather near the fastening, and efforts were made to retrieve the collar following the cessation of data collection.

Civets are nocturnal and utilize day bed resting sites in dense forest or grassy areas (Colón, 2002; Jennings et al., 2006). To conserve tag battery life and obtain the highest resolution of relevant GPS fixes, collars were set to record 13 hourly GPS points from 1800h until 0600h. Collars were programmed with a 150 s 'GPS timeout,' whereby the unit would cease searching for available satellites if no successful fix was acquired within this limit. For each successful GPS point, the collar recorded longitude, latitude, date, time, time to first fix, battery voltage, temperature, speed estimate, and heading.

Due to the small size of the tags, a remote ultra-high frequency (UHF) download was required to access GPS and activity sensor data. A hand-held device (BaseStation II, e-obs GmbH) needed to be within transmittable range of a tagged individual, following which a high-speed wireless radio-link would be established and logged data downloaded to the BaseStation.

Collars emitted a UHF radio signal for two and a half hours daily to allow for tracking. Collared individuals were tracked using a UHF 7E 868MHz Yagiantenna (e-obs GmbH), an AOR AR8200 handscanner radio receiver (AOR Ltd, Tokyo, Japan), and the BaseStation. For most data download events, animals were tracked via the UHF pinger until adequate tag proximity (~50–150 m) was reached for data download to commence.

Data extraction occurred through the use of DataDecoder software v5_1s6 and v7_1 (e-obs GmbH), which converted encrypted BaseStation data into a desired file format. These were imported into MS Excel and ArcGIS 10.1 for subsequent analysis.

3.2.4 Collar stationary performance

Prior to deployment, three first-generation and four second-generation collars were tested at a stationary reference point under semi-closed canopy for a 13 h nocturnal period. Collar performance was determined by proportion of successful fix attempts. Accuracy was measured as Euclidean distance between collar fixes and the unit's true location, as recorded by a GPSmap 62 GPS (Garmin Ltd., Kansas, USA). The precision of fixes was evaluated by measuring the Euclidean inter-point distances between each collar's hourly fixes. Each collar's maximum linear error was determined as the greatest inter-point distance, representing effective point spread, collected throughout this trial period.

3.2.5 Data analysis

All spatial analyses were carried out with ArcGIS software (Version 10.1, ESRI, Inc., Redlands, CA). In stationary accuracy tests, data were log transformed for normality, and a pooled, two-tailed, two-sample t-test was used to evaluate if linear error differed by collar generation. A Mann-Whitney U test determined whether linear inter-point differences differed by collar generation. Maximum inter-point distances between generations were tested by a pooled, two-tailed, two-sample t-test. For field-deployed collar data, in-field performance values were pooled regardless of collar generation. To quantify tracking data resolution per collaring effort, a mean value of location fixes per active collaring day was calculated for this study and other viverrid VHF research. The total number of successfully recorded locations was divided by the maximum active collaring days for each animal in each study, and a two-tailed, two-sample t-test compared the log-transformed mean fix values between GPS and VHF studies.

3.3 Results

3.3.1 Trapping

From October 2013 through August 2015, 731 trap nights (night x number of active traps) were conducted throughout the LKWS, resulting in 43 small carnivore captures (5.9% trapping success rate). Of these, 27 unique Malay civets were captured, and nine of these individuals collared (eight males, one female).

3.3.2 Collar stationary performance

Of the collars tested, fix success was high and location error slight, with second-generation collars outperforming first in most parameters. First-generation units demonstrated a mean (±SE) fix success of 87.2 ± 5.13% (n = 39), while second-generation collars obtained all attempted fixes (n = 50).

In terms of collar accuracy, mean (± SE) Euclidean distance error between GPS fixes and true location was 21.0 ± 2.60 m for first-generation units (n = 34). Second-generation collars displayed a significantly lower mean horizontal distance error of 12.3 ± 1.87 m, nearly half as large as that of the first-generation units (n = 50) (t = 3.9225, df = 82, $p < 0.001$). Collar precision improved between first- (n = 177) and second- (n = 288) generation units, with each collecting median inter-point distances of 19.65 m and 12.67 m, respectively (U = 33749, $p < 0.0001$). The mean (± SE) maximum linear point spread of first-generation collars [75.9 ± 17.7 m (n = 3)] did not, however, significantly vary from that recorded by second-generation units [53.3 ± 14.7 m (n = 4); t = 0.9926, df = 5, $p = 0.367$].

3.3.3 Collar field performance

From October 2013 through August 2015, nine Malay civets (eight males and one female) were fitted with GPS collars. Data were successfully retrieved from seven of these nine individuals (Table 3.1).

Table 3.1. Collaring details and performance indices for seven male Malay civets tracked in the Lower Kinabatangan Wildlife Sanctuary in 2013–2015.

ID	Mass (kg)	Collaring date	Collar generation	Total nights tracked	Total successful GPS fixes	Fix success (%)
Male 1	5.5	27 October 2013	1	187	1990	81.9
Male 2	4.5	3 November 2013	1	37	329	68.3
Male 3	4.3	5 April 2014	1	130	438	26.0
Male 4	5.3	7 April 2014	1	119	339	22.0
Male 6	5.3	6 April 2015	2	27	310	88.3
Male 7	5.0	5 August 2015	2	77[#]	747[#]	74.5[#]
Male 8	4.3	8 August 2015	2	74[#]	758[#]	78.7[#]

[#] *as of October 2015*

Four animals were recaptured following completion of the data collection period, and no change was documented in body condition or weight, although minor hair loss was noted.

In total, 8,450 GPS fixes were attempted by all collars, with 4,906 successfully obtaining latitude and longitude, a total fix success of 58.1%, with individual collar performances ranging from 22.0% to 88.3%. Collar longevity reached a maximum of 187 days before battery exhaustion. The shortest complete deployment occurred when a collar was prematurely shed after 27 nights of data collection.

Collars collected a mean (±SE) 8.1 (± 1.7) fix locations per active collaring day, representing a significantly greater maximum data resolution than of that collected by VHF studies on Asian viverrids (Table 3.2; $t = 11.604$, $df = 36$, $p < 0.0001$).

Table 3.2. Collar performance and data value [mean ± standard error (SE) of locations per collaring day] of Asian viverrid spatial ecology studies.

Species	**Collar Type**	**No. successfully collared animals**	**Mean (±SE) locations per collaring day**	**Minmax tracking duration (days)**	**Study**
Viverra tangalunga	GPS/UHF	7*	8.1 ± 1.7*	27*–187	Current
Viverra tangalunga	VHF	12	0.4 ± 0.09	138–410	Colón, 2002
Viverra tangalunga	VHF	7	0.3 ± 0.07	6–59	Jennings et al., 2010
Paradoxurus hermaphroditus	VHF	12	0.6 ± 0.08	133–670	Nakashima et al., 2013

**as of October 2015*

3.3.4 Phase II collar testing and deployment

Since the publication of the above results, an additional 15 GPS/UHF collars underwent stationary testing and were deployed on 12 additional wild civets in the LKWS.

Phase II collar stationary performance

The mean testing fix success of the 15 additional collars was 98.0 ± 1.06% (n = 264 fixes). In terms of collar accuracy of these additional units, the mean (± SE) Euclidean distance error between GPS fixes and the true location was 17.4 ± 1.03 m (n = 264 total points; median = 12.3 m). Collar precision for these additional units was fair, with units collecting a median inter-point distance of 18.2 m (n = 1,938 points; mean = 24.0 m). The mean maximum linear point spread for these units was 79.7 ± 9.19 m (n = 15).

Therefore, in terms of the study's overall stationary collar tests (Phase I and Phase II), GPS-collars recorded location with an average accuracy of 17.0 ± 0.86 m (median = 12.2 m; n = 348 points), and median precision of 17.5 m (mean = 24.1 ± 0.43 m; n = 2403 points). The combined stationary tests reported a mean maximum linear point spread of 74.4 ± 7.27 m (median = 67.6 m, n = 22).

Collar field performance- Malay civets

In total, 12,139 GPS fixes were attempted by the 11 additional collars deployed on eight Malay civet individuals, with 9,622 successfully obtaining coordinates. This represents a total fix success of 79.3%, with individual collar performances ranging from 66.9% to 94.3%. Collar longevity reached a maximum of 246 days before battery exhaustion was documented. The shortest deployment occurred when a collar prematurely failed after seven nights of data collection. This additional collaring phase did include elevated failure rates compared to those reported in the manuscript: three units prematurely failed most likely due to water damage, and those individual civets were re-fitted with new units.

In total, 20,589 GPS fixes were attempted by all the GPS-collars deployed on Malay civets in both data collection phases, of which 14,528 were successfully established, representing an overall study fix success of 70.6%.

Collar field performance- Common palm civets

In total, 10,271 GPS fixes were attempted by collars deployed on four common palm civets, with 9,243 fixes successfully obtaining coordinates. This represents a total fix success of 90.0%, with individual collar performances ranging from 64.2% to 98.0%. Common palm civet collar longevity reached a maximum of 353 days before battery exhaustion was documented. The shortest complete deployment occurred when a collar was prematurely shed after 73 nights of data collection.

The phase II Malay civet collars collected a mean (±SE) 10.4 (± 0.5) fix locations per active collaring night, while common palm civet collars collected a mean (±SE) 11.3 (± 1.0) fix locations per active collaring night (Table 3.3).

Table 3.3: Updated GPS-collar performance and data value of units deployed since publication of the manuscript.

Species	Collar Type	No. successfully collared animals	Mean (±SE) locations per collaring night	Min–max tracking duration (night)	Study
Viverra tangalunga	GPS/UHF	8	10.4 ± 0.5	7–246	Current
Paradoxurus hermaphroditus	GPS/UHF	4	11.3 ± 1.0	73–353	Current

3.4 Discussion

The recent downsizing of satellite tracking technologies has allowed a greater diversity of species to be collared with the aim of providing accurate and high-resolution spatiotemporal data. This study demonstrated the successful preliminary performance of small satellite collars, both in stationary tests and deployed upon a novel small carnivore, the Malay civet.

Stationary test performance parameters of both first- and second-generation collars were comparable to the high fix success rates, accuracy, and precision values of other small satellite unit performance studies (Cain et al., 2005; Dennis et al., 2010; Jiang et al., 2008; LaPoint et al., 2013). The error associated with

triangulation-based VHF tracking can be upwards of 200 m, so this slight GPS error is of little comparative consequence (Bartolommei et al., 2012; Grassman et al., 2005b; Nakashima et al., 2013). These stationary trials demonstrate the much higher quality of GPS compared to VHF data in small carnivore research.
This study reports the first known satellite collaring of a Viverridae species. Overall fix success rate was similar to the performances of other small, field-deployed GPS units (Blackie, 2010; Brown et al., 2012; Haines et al., 2006; Recio et al., 2010). Large variability of GPS fix success rates between tracked individuals (22.0–88.3%) is a commonly documented trend in satellite tracking, and could be attributed to the specific behaviours of collared animals (Blackie, 2010; Mattisson et al., 2010; Recio et al., 2011a). Collar-bearing civets utilised a range of microhabitat types, with some individuals (Males 3, 4, 6–8) residing in areas of greater undergrowth and canopy densities than others (Males 1, 2). These environmental factors can influence fix success rates and should be taken into consideration when designing and analyzing studies on tropical terrestrial species (Gitzen et al., 2013; Mattisson et al., 2010; Rempel et al., 1995).

The volume and fine-scale spatiotemporal resolution of data collected by satellite collars exceeded that of Asian VHF-based Viverridae studies, with satellite units collecting, on average, more than 16-times more locations per sampling day than traditional radio-telemetry methods. This increased data resolution allows for more biologically rigorous questions to be answered on wary and cryptic species in demanding field conditions, without the negative effects of VHF observer bias, and for significantly less effort per resultant fix. Positive results from this first civet GPS collaring, along with the high quality and resolution of stationary trial data, confirms this method as a strong alternative to traditional VHF telemetry tracking for small carnivore research.

Despite these successful first deployments, it is of value to note a design limitation with this brand of satellite units. There is currently no standardized internal calibration value of GPS fix quality in these collars, such as a dilution of precision (DOP), a common component of most unit design. These values facilitate the development of post-hoc data screening protocols to increase the biological relevancy of acquired GPS data (Frair et al., 2010; Lewis et al., 2007).

Study designs must carefully consider the objectives of their research before deciding upon the deployment of satellite units, as several shortcomings must be overcome before the technology becomes a standard method in small carnivore research (Cooke, 2008). While collars utilised in this study are currently the smallest known mammalian long-term GPS units, 65 g is still much too large for certain species. For those species large enough to bear a tag, battery life can be an issue, such that long-term behavioural patterns are unable to be determined. The balance between data resolution and study longevity must be considered when planning studies (Kochanny et al., 2002; Land et al., 2006; Tomkiewicz et al., 2010*)*.

Furthermore, GPS hardware is currently more expensive than VHF transmitters (Rodgers, 2001). This high initial cost can pose a logistical barrier to projects, and researchers must not sacrifice statistical power in the blind pursuit of advanced techniques. Many scientists discuss that for certain research questions, analytical rigor is strengthened more so by an increase in the number of individuals tracked than by the number of locations per animal (Hebblewhite & Haydon, 2010). Researchers must then carefully consider their specific study aims, budget, focal species, and working conditions to strike a balance between the deployment of several expensive GPS units vs. a larger number of VHF collars, as this study demonstrated. Additionally, when GPS collar failures do occur, they are considerably more costly in both value and relative data loss than VHF failures. A large amount of GPS collar failures have been documented in field-deployed scenarios (Blackie, 2010; Blake et al., 2001; Gau et al., 2004; Hebblewhite et al., 2007; Johnson et al., 2002). In this study alone, 22% (n = 2) of deployed GPS collars failed. Research must then be further prepared to accommodate the costs, both monetary and scientific, of such occurrences with robust study designs.

Despite these considerations, the resolution and quality of GPS data remain irrefutable advantages of the technology. This study highlights the value of GPS collars for small carnivore research due to the data accuracy, quantity and quality otherwise unobtainable in this study area with alternative methods such as VHF or camera trap surveys. The successful application of GPS collars to *V.*

tangalunga generated a large dataset of fine-scale spatiotemporal information useful for identifying landscape features important for the persistence of small tropical carnivores. This information can begin to fill the knowledge gaps currently afflicting the guild, such that informed and effective conservation management plans might be drafted. Given a well-crafted study and sufficient funds, small carnivore scientists can utilize satellite technologies to explore the next frontier in understanding and conserving this unique guild.

Chapter 4. Spatial ecology of small carnivores in the fragmented Lower Kinabatangan landscape

4.1 Introduction

The anthropogenic destruction, degradation, and fragmentation of natural ecosystems pose the greatest risks to the persistence of global biodiversity (Crooks et al., 2011; Newbold et al., 2015; Schipper et al., 2008). With a growing human population matched with increasing demands for land, food, and limited natural resources, so-called 'pristine' natural areas are becoming increasingly scarce, and those which do remain are becoming more accessible to humans (Ceballos et al., 2015; Goswami & Vasudev, 2017). Wildlife species residing within such rapidly evolving landscapes face a suite of threats, and ultimately, are either extirpated by or adapt to the new order (Chapter 1). Carnivores, with their high trophic positions, large energetic demands, and potential for human-wildlife conflict are often particularly sensitive to the loss and degradation of native habitats (Crooks, 2002; Dickman, 2010; Di Minin et al., 2016; Ryall & Fahrig, 2006). Research evaluating the effects of the expansion of human-dominated landscapes on carnivores depicts a largely deleterious relationship (Chapter 1). However, the ecological flexibility of a carnivore species dictates its ability to persist within habitat fragments and anthropogenic matrices, and some species have adapted, even appearing to flourish in some select instances, across the gradient of human disturbance (leopards *Panthera pardus* and hyenas *Hyaena hyaena*, Athreya et al., 2013; urban carnivores, Bateman & Fleming, 2012; Eurasian lynx *Lynx lynx*, Bouyer et al., 2014; tigers *Panthera tigris*, Carter et al., 2012; caracal *Caracal caracal*, Ramesh et al., 2017; temperate mesocarnivores, Sálek et al., 2015; mesocarnivores, Verdade et al., 2011). Understanding the ecology and behaviours of carnivores within disturbed landscapes is crucial for crafting effective and research-informed conservation actions for the mitigation of widespread biodiversity loss (Macdonald, 2016).

A fundamental ecological parameter of wildlife research is the concept of species' spatial ecology. The primary lens through which researchers evaluate the spatial ecology of wild individuals is the concept of a home range. First formally defined by Burt (1943), a home range is the area an individual non-randomly utilises to access resources required for survival, such as food, water, and mates. A home range is classically considered an area that is used routinely and with a tangible measure of site-fidelity; Burt (1943) stated that occasional or sporadic movements outside of the spatial extent of the norm are not to be formally classified as within the home range. The establishment of a home range occurs from the interplay between an individual's internal state and external (both biotic and abiotic) factors (Huxley, 1934; Nathan et al., 2008). An individual's body mass, diet, sex, age, and reproductive status define its survival requirements, and as such, set the necessary parameters for the establishment and usage of a defined home range (Clutton-Brock & Harvey, 1978; Gittleman & Harvey, 1982; Swihart et al., 1988). Concurrently, resource distribution and predictability, habitat patchiness, weather patterns, and both inter- and intraspecific interactions describe the external environment within which an individual actively responds (Allen et al., 2016; Börger et al., 2008; McLoughlin & Ferguson, 2000; Powell & Mitchell, 2012). By these concepts, an individual's home range may shift in size, shape, or location through an alteration in any of these defining mechanisms (Bengsen et al., 2016; Potts & Lewis, 2014). Theoretically, carnivore home range size is negatively related to habitat suitability, a term that encompasses resource quality, stability, and predictability at the scale of an individual's perception (Aronsson et al., 2016; Bengsen et al., 2016; Duncan et al., 2015; Macdonald, 1983; Mortelliti & Boitani, 2008; Walton et al., 2017).

Habitat fragmentation directly alters the conditions within which carnivore populations seek to access required resources (Chapter 1); as such, changes to the size and composition of carnivore home ranges have been documented following anthropogenic disturbances (golden jackal *Canis aureus*, Admasu et al., 2004; coyotes *Canis latrans*, Atwood & Weeks, 2003; European wildcat *Felis silvestris,* Jerosch et al., 2017; bobcat *Lynx rufus*, Poessel et al., 2014; red foxes, Walton et al., 2017). Primarily, if the anthropogenic conversion of a natural landscape produces native habitat fragments that are too small to meet the biological requirements (and thus contain a given home range) of a carnivore and the surrounding anthropogenic matrix is functionally impermeable, a species' occupancy and long-term persistence is unlikely (Keinath et al., 2017; Kuefler et al., 2010). Indeed, this has been the main driver in many localised large carnivore extinctions across the globe (reviewed by Crooks et al., 2011; Woodroffe & Ginsberg, 1998). However, if remnant habitat fragments are of adequate size, composition, or configuration to facilitate a carnivore's access to necessary resources, a population has the opportunity to persist (Carter et al., 2012; Caryl et al., 2012; Moreira-Arce et al., 2015; Vieira et al., 2009; Wintle et al., 2019). This persistence is further facilitated by the degree of functional impedance posed by the anthropogenic land use; if the new matrix is permeable to, or can be successfully utilised by a species, a population's survival probability further increases (Debinski, 2006; Evans et al., 2017a; Tigas et al., 2002; Smith et al., 2019). Examples of high adaptability to anthropogenic landscapes include carnivores thriving within urbanised areas (e.g. Bateman & Fleming, 2012; Newsome et al., 2015; Sálek et al., 2015) or agricultural regions (e.g. Ferreira et al., 2018; Jerosch et al., 2017; Humphries et al., 2016). Thus, evaluating an individual's home range within altered landscapes can provide holistic insights into the driving mechanisms of carnivore occurrence, tolerance, survival, and persistence within disturbed habitats (Fieberg & Börger, 2012; Nilsen et al., 2005), which in turn can be crafted into informed conservation actions (e.g. Tracey et al. 2014).

Spatial ecology also refers to the organisation of neighbouring conspecifics within a landscape, and species can be classified as behaviourally territorial or non-territorial. As an adaption of the home range definition, a territory is defined as a ranging area held by an individual actively defended against conspecific intrusion (Grant et al., 1992). In the event of a lack of explicit territoriality, whereby conspecific home ranges spatially overlap, the potential for intraspecific interactions exists. These can take on a variety of forms in carnivores, ranging from otherwise solitary individuals (e.g. foxes *Vulpes vulpes*) solely coming in contact for mating episodes, to the formation of complex, hierarchical social groups, such as Eurasian badgers (*Meles meles,* Banks et al., 2007; Clutton-Brock & Harvey, 1978; Macdonald, 1983). As in the case with an individual's home range, the occurrence and extent of intraspecific interactions within a localised population are influenced by both behavioural factors and environmental context (McLoughlin et al., 2000; Nathan et al., 2008). As such, habitat fragmentation can drastically impact the extent and frequency of species interactions, particularly when two species compete for similar resources (review by Banks et al., 2007). The nature and degree of inter- and intraspecific interactions, in turn, can have significant ecological implications, as contacts between individuals can impact hunting performance (African wild dogs *Lycaon pictus,* Creel & Creel, 1995), reproductive success (cheetah *Acinonyx jubatus,* Caro, 1994), and disease transmission (Channel Island fox *Urocyon littoralis,* Sanchez & Hudgens, 2015) of carnivores worldwide.

The patterns of home range establishment and configuration within a landscape are functions of the process of fine-scale movements an individual makes as it seeks to obtain required resources (Jeltsch et al., 2013; Van Moorter et al., 2016). Animal movement, like home ranging, results from the interplay between an individual's internal state, physical ability to move, and external pressures, and thus is both informative of and reactive to environmental change (Doherty & Driscoll, 2018; Fahrig, 2007; Nathan et al., 2008; van Moorter et al., 2013). Based on Optimal Foraging Theory, individuals will move less in environments with high resource productivity, as they are able to obtain their required resources successfully at low energetic expenditure (Mueller et al., 2011). Habitat fragmentation can however alter the distribution and predictability of resources (Chapter 1), which in turn, obliges animals to alter their movement behaviours. If a species is restricted to remnant habitat patches following fragmentation, overall movement paths may decrease in length or become highly tortuous (Haddad et al., 2015; Tucker et al., 2018). Alternatively, if anthropogenic land uses provide animals with spatially clustered, predictable resources, movement can similarly decrease, as exemplified in waste raiding behaviours of urbanised raccoons (*Procyon lotor*, Prange et al., 2004). Increases in carnivore movements within fragmented landscapes have also been documented, particularly when anthropogenic land use presents a perceived risk (foxes, Phillips et al., 2004; brown bears *Ursus arctos,* Martin et al., 2013). The implications of altered animal movement patterns in fragmented habitats goes beyond an individual's survival, as movement capabilities across a landscape will ultimately dictate population growth patterns via altered rates of successful mate contact, infant dispersal patterns, and population gene flow (Allan et al., 2003). Further, the movement of individual organisms drives landscape-level ecosystem functions such as seed dispersal, predator-prey interactions, nutrient cycling, and disease transmission patterns (Bauer & Hoye, 2014). Thus, by examining responses of a species to landscape alterations in terms of specific movement parameters, the processes behind alterations to spatial ecology patterns in fragmented environments become apparent (Nathan et al., 2008), which can then be applied to crafting effective conservation actions (Allen & Singh, 2016).

In Southeast Asia, Borneo has undergone large-scale conversion and degradation of natural landscapes by oil palm agriculture and logging (Chapter 1; Gaveau et al., 2014; Gaveau et al., 2016). Persisting within this dynamic landscape is a high diversity of small carnivore species, including the Malay civet (*Viverra tangalunga*)*,* and the common palm civet (*Paradoxurus hermaphroditus*, Appendix I; Evans et al., 2016b; Mathai et al., 2016; Yue et al., 2015). Small carnivores are some of the most understudied species in the world, yet can act as valuable ecosystem indicators, seed dispersers, and readily-accessible models for evaluating carnivore responses to habitat alterations such as degradation and fragmentation (Chapter 1; Brooke et al., 2014; Wan, 2009; Mudappa et al., 2007; Nakashima et al., 2010). To date, little is known about the ecology of Bornean viverrid species, particularly regarding their spatial ecology in anthropogenically-degraded habitats (Mathai et al., 2016; Meijaard et al., 2016). Anecdotal and local accounts suggest some small carnivores have adapted to patchwork landscapes of degraded forests and oil palm plantations, while others report a more limited flexibility to land use changes (Azhar et al., 2014; Azlan & Sharma, 2006; Bernard et al., 2014; Heydon & Bulloh, 1996; Jennings et al., 2015; Nakabayashi et al. 2016; Ross et al., 2016; Twining et al., 2017). With recent advancements in remote-tracking technologies, an unprecedented quantity and quality of spatiotemporal data can now be collected from civet species (Chapter 3; Cagnacci et al., 2010; Evans et al., 2016a; Hebblewhite & Haydon, 2010; Kays et al. 2015). As data collection technologies have advanced, so too have data analysis methods, facilitating even deeper and informative understanding of species behaviours (Börger et al., 2008; Long et al., 2015; Moorcroft, 2012; Seidel et al., 2018).

This research aimed to apply advanced tracking techniques to explore the spatial ecology of two model small carnivore species, the Malay civet and the common palm civet, within the degraded and fragmented lowland forests and oil palm plantations of northeastern Borneo. This study sought to: i) identify whether civets entered oil palm plantations, and if so, how and to what extent; ii) critically determine civet home ranges within the Lower Kinabatangan Wildlife Sanctuary and surrounding oil palm plantations; iii) quantify the inter- and intraspecific spatial organisation of male civets throughout the fragmented landscape; and iv) characterize fine-scale ranging behaviours through the landscape and evaluate the potential factors influencing nightly movements.

4.2 Methods

4.2.1 Trapping and GPS-collaring civets

Trapping periods began in March 2013 and completed January 2018. Details of small carnivore trapping and collaring protocols can be found in Chapters 2 and 3. Capture site, health condition, reproductive status, and adequate body size were the main determinants of GPS-collaring suitability. Male civets were the primary targets for collaring due to their larger head and neck circumferences (Chapter 2), which also served to increase the statistical power of the study. One female Malay civet was experimentally fitted with a GPS unit, yet no data were collected; it was suspected the unit prematurely dropped due to the species' sexual dimorphism in head circumference (Chapter 2). For details of technical tag specifications, pre-deployment collar testing, data collection schedules, and tracking protocols, refer to Chapter 3.

4.2.2 Home range analyses

Two different home range estimators were utilised in this study: i) minimum convex polygons (MCP), and ii) biased random bridges (BRB). The minimum convex polygon is a widely utilised, non-parametric, point-based home range estimator. A computationally simple 2-dimensional model, a MCP is the smallest polygon encompassing an individual's locations in which no internal angle exceeds 180 degrees (Mohr, 1947). By disregarding the distribution of point locations within the polygon, MCPs acts as an indicator of the total possible area utilised by an individual within a tracking period (Pebsworth et al., 2012). Despite their ease of calculation, MCPs hold little biological relevancy, as they are highly sensitive to both sample size and outliers (such as those 'exploratory movements' mentioned in Burt's (1943) home range definition), and generally overestimate an individual's range through the inclusion of areas never actually accessed by the individual (Burgman & Fox, 2003; Stark et al., 2017). Therefore, most recent studies employing MCPs do so for purely comparative purposes. MCP range contours were calculated for each civet using 100% and 95% of an individual's GPS points, thus producing home range estimates comparable to previous civet radio-tracking literature (Table A3.1). All data points from each individual were included in MCP construction, and if an individual was GPS-collared twice, the two datasets were combined. For the 95% range estimates, points were included based on distance to the data's centroid, such that points farthest from the point cloud's spatial center were excluded (Calenge, 2006). To determine the minimum number of GPS locations required for home range stabilization, the packages *adehabitatHR* (Calenge, 2006) and *lattice* (Sarkar, 2008) were used to generate cumulative plots of 95% MCP range size from a sliding data window every 20 consecutive GPS points for each animal. If an asymptote was reached but shifted substantially due to either a range contraction or expansion, the individual's dataset was split and treated as two distinct home ranges for all resultant analyses.

As an improvement on MCP estimators, the BRB method was developed to provide a 3-dimensional utilisation distribution estimator of civet range usage. The BRB estimator is a movement-based home range model that accounts for the spatial and temporal information of input tracking data in the construction of utilisation distributions (Benhamou, 2011; Benhamou & Cornélis, 2010). Remote-tracking data are a collection of related locations in both space and time, and as such, are serially autocorrelated (Otis & White, 1999). Point-based estimator methods, such as MCPs, do not encompass this aspect of the input data, but movement-based estimators incorporate it to produce highly biologically relevant 3-D space use maps, whereby the animal's probability of utilising a given area is produced (utilisation distribution). The BRB method creates this utilisation distribution by determining measures of space use based on movement paths, not point clouds (Benhamou, 2011; Benhamou & Riotte-Lambert, 2012; Cornélis et al., 2011; Horne et al., 2007). BRB utilisation distribution contours were calculated for both total (90%) and core (50%) home ranges, as recommended per Börger et al. (2006). To account for the spatial pseudo-replication of diurnal sleeping sites within the data structure, all 18:00 h fixes were removed prior to analyses; thus, home range estimates represent 'active' nocturnal civet ranges. For those individuals that were collared twice, the data from the longest running collar deployment were used in the estimation of home range utilisation distributions.

For the calculation of BRBs, the selection and optimisation of three parameters (T_{max}, L_{min}, and h_{min}) was required. The same values were applied to all individuals in the study and accounted for the serial autocorrelation structure intrinsic in GPS-tracking data along with the locational errors from GPS units. The maximum time threshold, T_{max}, is the longest time period within which sequential GPS fixes are considered temporally related. This value informs the model of the number of locations to include in utilisation distribution construction. The autocorrelation structure of each individual's dataset was determined by semivariogram analysis using the acfdist.ltraj function in the package *adehabitatLT* (Calenge, 2006). T_{max} was set to 7,800 sec (2 h plus 10 min of tolerance to account for differences in GPS fix time) for all civet BRBs, which was appropriately greater than the hourly GPS fix schedule. The minimum step length, L_{min}, allowed BRB home range models to account for imperfect locational accuracy intrinsic to GPS collars; this value defines the maximum segment length below which an animal is to be considered stationary, thus reducing model noise (Benhamou & Riotte-Lambert, 2012). L_{min} was set to 17 m for all civet BRB models based on the results of stationary collar accuracy tests (Chapter 3). Lastly, the minimum smoothing parameter, h_{min}, which embodies the standard deviation in the relocation uncertainty for a civet, was set to 40 m for both species. This value must be larger than the standard deviation of GPS collar accuracy (16 m, Chapter 3) and smaller than half the mean distance travelled by a civet in time T_{max} (100 m for Malay civets; 60 m for common palm civets; Benhamou, 2011; Benhamou & Cornélis, 2010). To determine the most suitable final h_{min} value, per suggestions by Benhamou (2004), calculation of the population's mean cosine of relative turning angles provided a quantified indication of the unpredictability of civet movements. Values for Malay and common palm civet trajectories were close to 0, suggesting a larger h_{min} value would more appropriately capture the high levels of directional uncertainty in civet movements. Finally, BRB models interpolated civet locations every 300 sec (5 min).

The factors influencing the size of Malay civet total (90%) and core (50%) home ranges were evaluated using general linear models (GLM). Civet weight and the proportion of oil palm contained within the range contour were included as independent variables in the global models. To account for repeated measures, only the first home range contours for Malay civet male 7 (7.1) were included in the modelling. The global models were refined by stepwise deletion of insignificant terms using the drop1 function. Models were fitted with a Gaussian error distribution and identity link function, and model assumptions checked by optimising the standardised residual plots.

Range estimates were calculated utilising the statistical software R 3.5.0 (R Core Development Team, 2018) and the additional packages *adehabitatHS* (Calenge, 2006), *rgdal* (Bivand et al., 2018), *rgeos* (Bivand & Rundel, 2017), *sp* (Pebesma & Bivand, 2005), *gpclib* (Peng et al., 2007), and *shapefiles* (Stabler, 2013). Resultant home range contours were exported as shapefiles using the packages *maptools* (Bivand & Lewin-Koh, 2018) and *PBSmapping* (Schnute et al., 2018) and imported into ArcGIS 10.1 (ESRI, 2011) for spatial analyses.

4.2.3 Home range overlap

Home range overlaps were evaluated for pairs of civets simultaneously GPS-collared and residing in close proximity, referred to hereafter as dyads. Home range overlaps were estimated for each dyad as the index of the volume of intersection (VI) of the 90% BRB utilisation distributions (Fieberg & Kochanny, 2005; Millspaugh et al., 2000; Seidel, 1992). This index ranges from 0 (no overlap) to 1 (identical UDs). Following Method 5 of Fieberg and Kochanny (2005), the volume of intersection index was determined by the integration of overlapping utilisation distribution raster surfaces, clipped at 90%, of the two individuals in a given dyad (UD_1 and UD_2) in *adehabitatHR*:

$$VI = \iint_{-\infty}^{\infty} \min[UD_1(x,y), UD_2(x,y)]dxdy$$

4.2.4 Movement parameters

Only those nightly movement tracks containing a minimum of seven GPS fixes were retained. Although this may have slightly biased the tracking datasets for more open areas, it was important that tracks containing low fix successes were not utilised in determining movement properties; seven points a night was the most data conservative value given the population's total fix success of 65% (equating to just over six fixes a night). The number of fixes per night was included as a factor in the final model to control for these differences. Nightly path lengths (NPL) were calculated for each individual in ArcGIS as the cumulative sum of distances between hourly fixes. Average nightly speed (m/h) and nightly relative turning angles (TA, in radians) were determined for each individual in the package *adehabitatLT*. The absolute values of the hourly relative turning angles were calculated prior to the calculation of mean nightly turning angle; thus, paths with high TA values were considered tortuous while those with low TA values were straight.

Lunar phase (radians) for each tracking night was determined with the package *lunar* (Lazaridis, 2014), whereby a full moon was represented by π, and a new moon as 0 and 2π. For data collected after October 2015, nightly temperature was reported as the average of hourly nocturnal temperature readings collected by an automated weather station data logger located at Danau Girang Field Centre (5°24'49" N, 118°2'15" E). For data preceding October 2015, the minimum daily temperature was used as a proxy for nightly temperature, as all daily minimum temperatures recorded by the data logger occurred during nocturnal hours. A rain index was generated for each tracking night by taking the summed volume of rain measured on the dates of a given track night and the following calendar day, dividing this value by 48 to generate a rough estimation of mean hourly rainfall, and finally multiplying by 12 to represent an index of nocturnal rain. Finally, the proportion of the nightly movement track contained within oil palm was determined in ArcGIS (ESRI, 2011).

The influences of environmental and habitat parameters on nocturnal movement were evaluated by general additive mixed models (GAMM) using the package *mgcv* (Wood, 2006). GAMMs allowed for the detection of both linear and non-linear relationships between nightly movement parameters and predictor variables, which is well suited for ecological datasets (Wood, 2006). Civet ID was included as a random factor to account for the repeated movement measures per individual. Global models contained the effects of lunar phase, nightly temperature, rain index, the proportion of the nightly path contained within oil palm, and the number of successful GPS fixes, treated as a factor. To account for the circular structure of moon phase data, the variable was fitted with a cyclic cubic spline smoother. The remaining continuous predictor variables were fitted with thin plate regression spline smoothers, optimised within the *mgcv* package using cross-validation. If linear relationships were determined by GAMM outputs (edf = 1), the model was refitted to include the effect of the variable with the smoothing removed. Malay civet nightly path lengths were square root transformed, while common palm civet nightly path lengths were log transformed to best meet modelling assumptions of data normality. Nightly turning angles were not transformed prior to analysis. Model selection was achieved by stepwise comparison of Akaike Information Criterion (AIC) values. Final model structure was selected once the removal of a term did not change the model’s AIC by more than 2; this process was essentially a manual dredge function conducted by the *MuMIn* package (Bartón, 2018), which does not currently run with GAMM models (Burnham & Anderson, 2002). Model validation was conducted by the graphic evaluation of the normality of model residuals using the gam.check function. Model effect plots were generated using the package *gratia* (Simpson, 2019).

4.3 Results

4.3.1 GPS-collaring

A total of 24 GPS collars were deployed within the LKWS landscape on 16 Malay civet individuals and four common palm civet individuals (Figure 4.1);

three Malay civets were collared twice due to prematurely lost or malfunctioning units. All collared individuals were male, with the exception the one experimental unit deployment on a female Malay civet. Field performance varied between individual units, and high quality data were collected from 19 of the collared individuals (Chapter 3, Table 4.1).

Overall, seven Malay and two common palm civets did not enter oil palm plantations during the collaring period, while ten individuals (eight Malay civets, two common palm civets) utilised both agriculture and forest (Table 4.2). The utilisation of oil palm agriculture varied between the collared individuals and was non-normally distributed; the median proportion of common palm civet GPS fixes occurring in oil palm was 15.5% (range: 0–47.7%, n = 4 individuals), while the median proportion of Malay civet's fixes occurring within oil palm was 0% (range: 0–68.5%; n = 17 individuals).

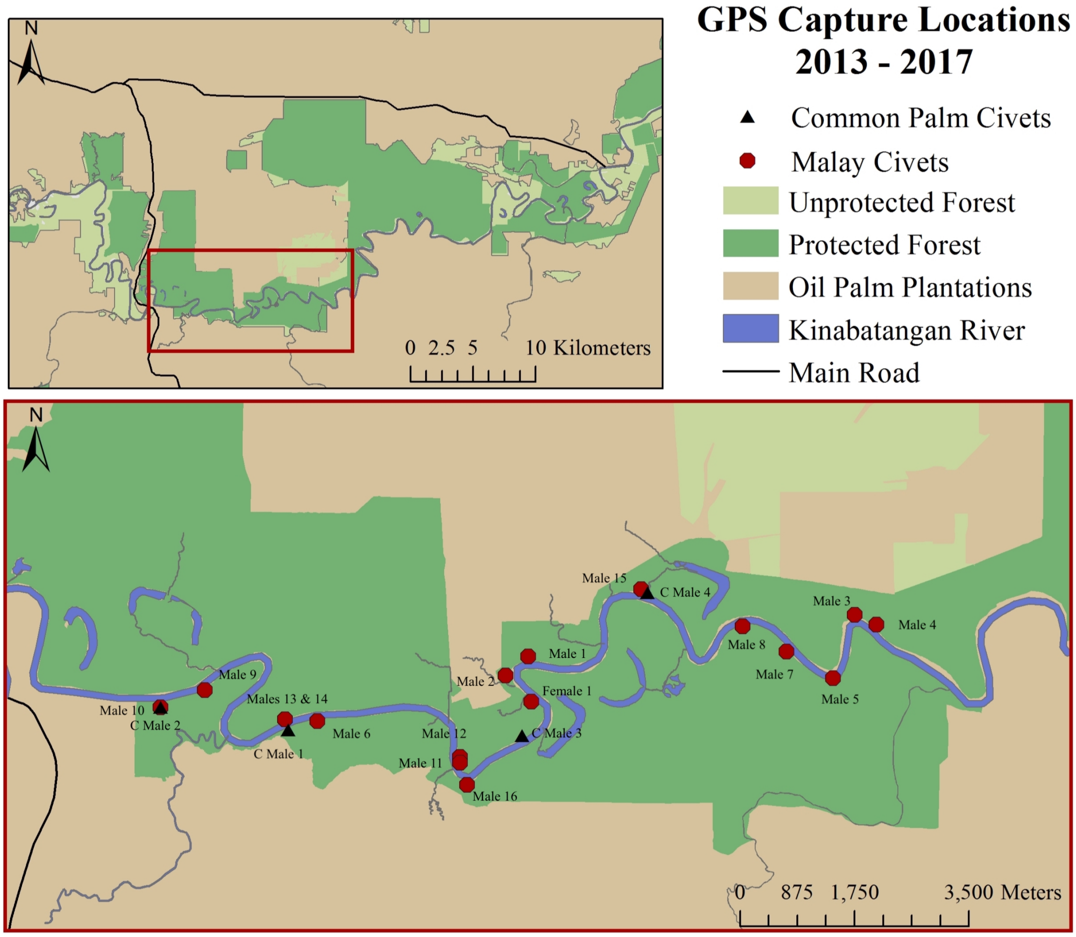


Figure 4.1 Locations of GPS-collar deployment on Malay (●) and common palm (▲) civets within the LKWS, Sabah, Malaysia. Coordinates shown represent the first capture for each individual.

Table 4.1: Collaring details of civets GPS-tracked in the LKWS from 2013–2018. #denotes individuals that were collared twice following premature unit failure or loss. The values presented in the table are the union of the two data collection periods.

	ID	Collaring Date	Weight (kg)	Track Nights	Successful GPS Fixes	Fix Success (%)	% of Fixes in Plantation
Common palm civet	C Male 1	2015-04-04	2.65	153	1277	64.2	47.7
	C Male 2	2016-06-13	2.20	73	871	92.4	0.0
	C Male 3	2017-01-28	2.80	212	2603	94.4	31.0
	C Male 4	2017-06-25	1.51	353	4492	98.0	0.0
Malay civet	Male 1	2013-10-27	5.50	187	1990	81.4	66.1
	Male 2	2013-11-03	4.50	37	329	68.3	53.2
	Female 1	2013-11-11	3.80	1	2	13.3	0.0
	Male 3	2014-04-05	4.27	130	437	26.0	0.0
	Male 4	2014-04-07	5.30	119	339	22.0	0.0
	Male 5	2014-06-11	4.50	6	8	10.1	0.0
	Male 6	2015-04-06	5.25	28	318	88.6	14.8
	Male 7	2015-08-05	5.00	192	1630	65.5	0.0
	Male 8	2015-08-08	4.25	83	857	79.6	0.0
	Male 9	2016-03-30	4.25	100	942	73.1	0.0
	Male 10	2016-06-20	4.50	63	669	81.9	58.4
	Male 11#	2017-01-25	4.25	101	1108	84.8	23.5
	Male 12#	2017-02-02	4.00	65	784	92.7	13.1
	Male 13#	2017-03-22	4.50	159	1537	74.3	0.0
	Male 14	2017-03-23	4.50	246	2301	71.9	0.0
	Male 15	2017-06-24	4.75	150	1837	94.2	68.5
	Male 16	2017-10-27	5.50	52	444	68.9	33.8

Diurnal sleeping site locations varied between individuals of both species, with some individuals sleeping solely in forest, and others in both oil palm agriculture and forest (Table 4.2). As with nocturnal utilisation of agriculture, sleeping site data were heavily skewed. The median percentage of common palm civet diurnal sleeping sites contained in oil palm was 5.0% (range: 0–34.2%; n = 5 datasets), while the median percentage of Malay civet sleeping sites in agriculture was 0% (range: 0–84.1%; n = 16 datasets). For those common palm civet individuals that slept within the agriculture, the mean percentage of sleeping sites located in oil palm was 15.9% (range: 5.0–34.2%). The total percentage of sleeping sites in oil palm for those Malay civets that slept in the agriculture was greater than common palm civets (mean: 37.8%, range: 3.4–84.1%).

Table 4.2: Descriptive summary of diurnal sleeping sites (SS) for GPS-collared civets in the LKWS. Sleeping sites were defined as successful 06:00 h GPS fixes.

	ID	n	% of SS in Plantation
Common palm civet	C Male 1.1	38	34.2
	C Male 1.2	47	8.5
	C Male 2	66	0.0
	C Male 3	201	5.0
	C Male 4	348	0.0
Malay civet	Male 1	146	58.2
	Male 2	26	30.8
	Male 3	23	0.0
	Male 4	8	0.0
	Male 6	24	0.0
	Male 7.1	49	0.0
	Male 7.2	38	0.0
	Male 8	58	0.0
	Male 9	76	0.0
	Male 10	44	84.1
	Male 11	76	5.3
	Male 12	59	3.4
	Male 13	107	0.0
	Male 14	160	0.0
	Male 15	136	74.3
	Male 16	23	8.7

4.3.2 Home ranges

The collection of 200 fixes was sufficient to reach a stable 95% MCP home range area asymptote for both civet species (Figures A3.1–A3.2), thus individuals with fewer fixes were excluded from further spatial analyses (n = 2). Common palm civet Male 1 displayed a home range expansion after 52 tracking nights; this coincided with the clearance of the mature oil palm trees within his home range (Figure A3.3). As such, this individual's dataset was split and spatial analyses conducted for each period (denoted as C Male 1.1 and 1.2). Malay civet Male 7 displayed a similarly marked range shift after the collection of 800 GPS fixes; his tracking data was similarly divided and analysed as two separate datasets (denoted as Male 7.1 and 7.2).

Both MCP and BRB home range estimates were generated for 19 GPS-collared civets (Table 4.3; Figures 4.2–4.3). As expected, MCP home range estimates were larger than BRB estimates for both species.

Table 4.3: Home range estimates for GPS-collared common palm and Malay civets in the LKWS, Sabah, Malaysia. n = number of GPS points collected during the sampling period used in estimator development. MCP = minimum convex polygon estimator. BRB = biased random bridges estimator.

	ID	**MCP (ha)**			**BRB (ha)**		
		n	**100%**	**95%**	**n**	**90%**	**50%**
Common palm civet	C Male 1.1	472	44.2	27.1	442	27.7	7.06
	C Male 1.2	772	44.9	41.1	744	40.7	10.1
	C Male 2	871	42.1	17.6	806	24.2	8.36
	C Male 3	2603	124.9	107.2	2404	90.6	21.8
	C Male 4	4492	36.9	6.75	4147	7.63	2.15
	Mean (±SE)	**2311 (815.5)**	**63.2 (20.7)**	**43.7 (22.5)**	**2144 (749)**	**38.2 (14.1)**	**9.90 (3.26)**
Malay civet	Male 1	1990	526.8	267.3	1866	210.5	59.3
	Male 2	329	244.4	228.5	317	184.7	65.3
	Male 3	438	65.5	42.8	383	45.9	13.6
	Male 4	339	103.6	75.6	291	65.0	20.6
	Male 6	318	256.5	247.5	293	214.9	75.3
	Male 7.1	786	73.4	70.0	741	65.0	19.9
	Male 7.2	844	510.6	250.3	793	241.4	90.0
	Male 8	857	238.5	191.6	803	108.7	21.3
	Male 9	942	95.8	92.8	890	96.0	35.5
	Male 10	669	135.7	119.2	645	104.0	31.6
	Male 11	1108	117.2	103.3	799	89.8	22.9
	Male 12	784	107.2	101.1	652	85.3	28.4
	Male 13	1537	64.0	56.8	1321	45.9	12.3
	Male 14	2301	71.4	53.4	2193	49.4	12.5
	Male 15	1837	311.2	231.0	1714	186.0	65.5
	Male 16	444	193.5	151.8	416	141.1	44.4
	Mean (±SE)	**970 (20.1)**	**194.7 (37.1)**	**142.7 (20.1)**	**882 (147)**	**120.9 (16.6)**	**38.7 (6.21)**

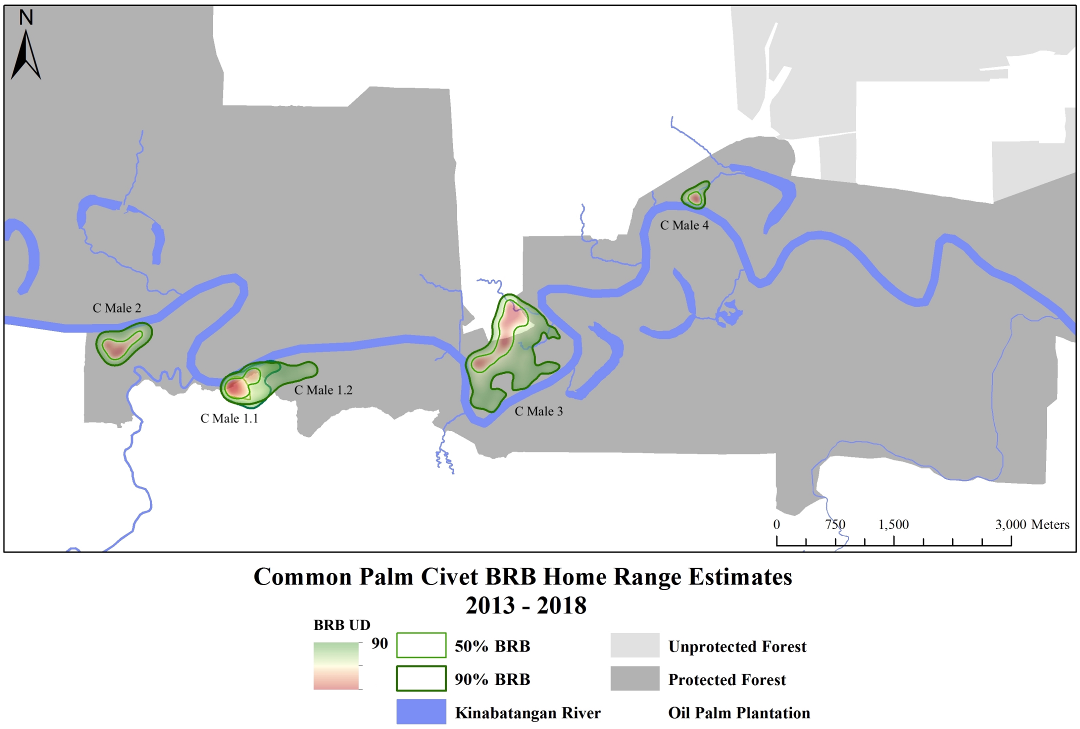


Figure 4.2. Male common palm civet biased random bridges (BRB) home range estimates in the LKWS, generated from hourly nocturnal GPS fixes. Maps show each individual's home range utilisation distribution surfaces clipped at 90%, and each raster surface is overlaid with contour outlines for total (90%) and core (50%) BRB range estimates.

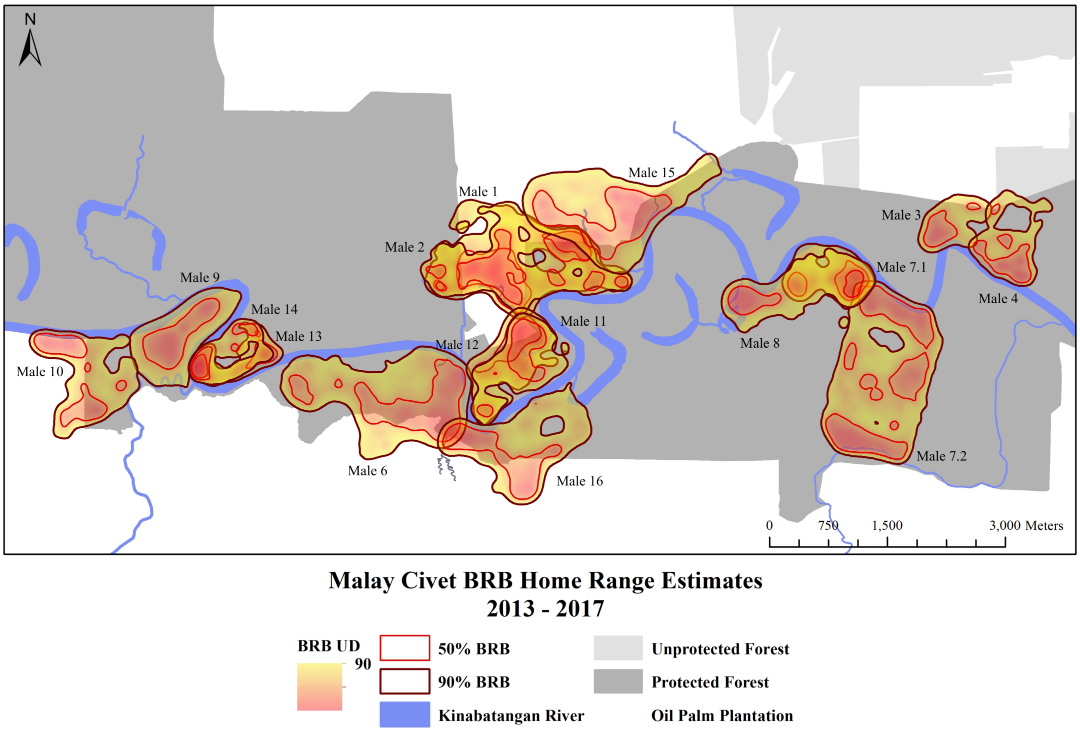


Figure 4.3. Male Malay civet biased random bridges (BRB) home range estimates in the LKWS, generated from hourly nocturnal GPS fixes. Maps show each individual's home range utilisation distribution surfaces clipped at 90%, and each raster is overlaid with contour outlines for total (90%) and core (50%) BRB range estimates.

Common palm civets

Total (90% BRB) home ranges for male common palm civets varied from 7.63–90.6 ha, resulting in a mean (±SE) total range size of 38.2 ± 14.1 ha. The utilisation of oil palm agriculture within the total home range varied between the collared individuals; the median proportion of total range comprising oil palm was 21.3% (range: 0–63.7%; Figure 4.2). For those individuals that accessed oil palm, the mean proportion of their total ranges encompassing agriculture was 42.0% (range: 21.3–63.7%). Those individuals that stayed in the forest held smaller total ranges compared to those that accessed oil palm (mean (±SE) total range: 15.9 ± 8.29 ha; 53.0 ± 19.2 ha, respectively); given the small sample size, however, the statistical significance of this difference was not evaluated. The heaviest male (C Male 3) had the largest total home range, while the lightest male (C Male 4) held the smallest; given the small sample size, the significance of this observation could not be rigorously assessed.

Common palm civet core home ranges (50% BRB) varied in size from 2.15–21.8 ha (mean ±SE: 9.90 ± 3.26 ha; Figure 4.2). The utilisation of oil palm agriculture within the core ranges varied between the collared individuals; the median proportion of core range comprising oil palm was 52.4% (range: 0–77.7%). When individuals did access oil palm in their core ranging behaviours, the mean percent of the range composed of agriculture was 67.4% (range: 52.4–77.7%). As with total home range sizes, common palm civet core ranges were larger for those individuals that utilised the oil palm than those that lived strictly in the forest (mean ±SE: 13.0 ± 4.49 ha; 5.26 ± 3.11 ha, respectively).

Malay civets

Malay civets held larger total ranges (90% BRB) than common palm civets (mean ±SE total home range: 120.9 ± 16.6 ha; range: 45.9–241.4 ha). The presence of agriculture within civet total ranges varied across the population; the median proportion of total range containing oil palm was 5.0% (range: 0–67.8%; Figure 4.3). For those individuals that did utilise oil palm, the mean proportion of their total ranges encompassing the agriculture was 36.1% (range: 9.9–67.8%). There was a significant positive relationship between the percentage of the total home range containing oil palm and the overall range size ($F_{1,13} = 21.83$, $p <$

0.0005, Adj. $R^2 = 0.598$; Figure 4.4). A 10% increase in the proportion of oil palm within an individual's total range resulted in an overall increase of range size by 20.2 ± 4.32 ha ($t = 4.672$, $p < 0.0005$). There was no significant association between civet weight and total home range size.

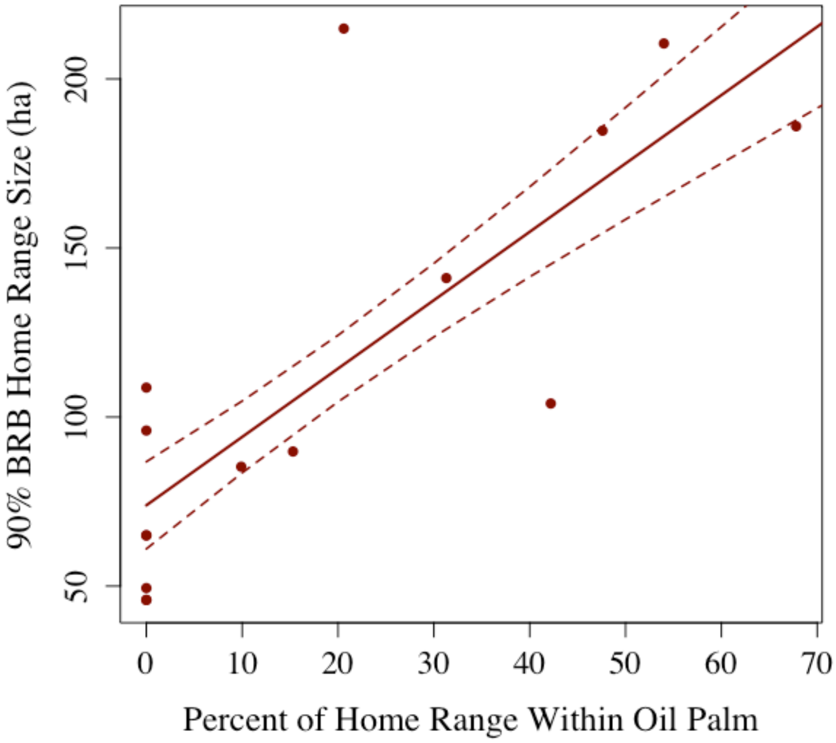


Figure 4.4. Predicted relationship between Malay civet total home range size (90% BRB) and percent of home range containing oil palm agriculture. Points are the recorded values from the 15 Malay civet males. Solid lines indicate model estimates while the dashed lines represent the model's standard error.

Malay civet males similarly held larger core ranges than common palm civet males. The mean (±SE) Malay civet core home range size was 38.7 ± 6.21 ha (range: 12.3–90.0 ha; Figure 4.3). As with the total range, the presence of agriculture within civet core ranges was unevenly distributed; the population's median proportion of core range comprised of oil palm was 8.6% (range: 0–79.8%). When an individual accessed oil palm, the mean proportion of core range comprising agriculture was 51.1% (range: 17.2–79.8%). As with the total home range size, there was a significant positive relationship between the proportion of the core range containing oil palm and the overall size of the core range ($F_{1,13} = 10.53$, $p < 0.01$; Adj. $R^2 = 0.405$; Figure 4.5). A 10% increase in the proportion of oil palm within a civet's core range resulted in the core range increasing by 4.6 ± 1.4 ha in size (t = 3.24, $p < 0.01$). There was no significant association between a male civet's weight and core home range size.

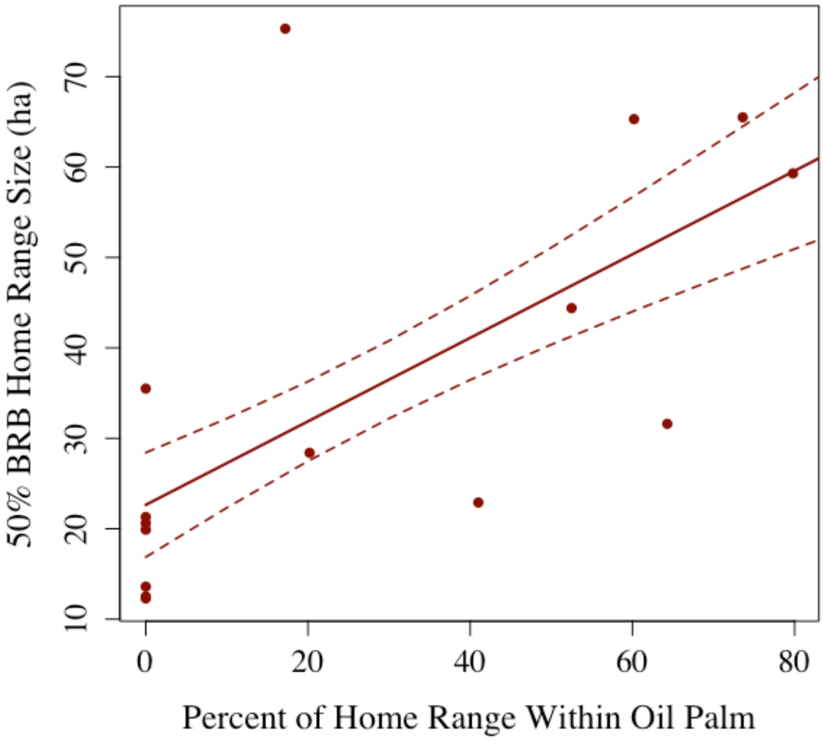


Figure 4.5. Predicted relationship between the size of Malay civet core range (50% BRB) and percent of the core range containing oil palm agriculture. Points are the recorded values from the 15 Malay civet males. Solid lines indicate model estimates while the dashed lines represent the model's standard error.

4.3.3 Home range overlap

The opportunity for simultaneous spatial overlap between civet home ranges was documented for 14 unique dyads. Seven dyads were between Malay civet males (intraspecific), while the remaining seven consisted of a common palm civet and a Malay civet (interspecific). The spatial overlap of civet home ranges varied considerably from complete exclusion to a maximum volume of intersection index (VI) value of 0.65 (Table 4.4, Figures 4.2–4.3). The highest intraspecific VI values were recorded when both civet ranges contained oil palm and the area of home range overlap contained oil palm. This relationship was not consistently predictable, however, as the home ranges of the forest-only males 13 and 14 highly overlapped (VI = 0.52).

Interspecific civet dyads displayed skewed overlap values, with most dyads presenting close to exclusive VI values. The mean interspecific overlap value (0.17) was lower than that of dyads containing only Malay civets (VI = 0.30). As with intraspecific dyads, however, the highest VI values occurred when the region of home range overlap contained oil palm.

Table 4.4: Volume of intersection index (VI) values for male civet dyads GPS-tracked within the LKWS. VI values range from 0 (explicitly unique ranges) to 1 (exactly equivalent home ranges).

	Dyad ID	**Volume of Intersection Index (VI)**	**Percent of 90% BRB in oil palm (Male A)**	**Percent of 90% BRB in oil palm (Male B)**	**Percent of Oil Palm in Overlap**
Intraspecific Interactions	Male 1 : Male 2	0.65	54.0	47.6	50.1
	Male 3 : Male 4	0.01	0.0	0.0	0.0
	Male 7.1 : Male 8	0.33	0.0	0.0	0.0
	Male 7.2 : Male 8	0.02	0.0	0.0	0.0
	Male 9 : Male 10	0.00	0.0	42.2	0.0
	Male 11 : Male 12	0.57	15.3	9.9	12.1
	Male 13 : Male 14	0.52	0.0	0.0	0.0
Mean Intraspecific VI (±SE)		**0.30 (0.11)**	-	-	-
Interspecific Interactions	C Male 1.1 : Male 6	0.00	63.7	20.6	0.0
	C Male 1.2 : Male 6	0.04	41.2	20.6	0.0
	C Male 2 : Male 9	0.06	0.0	0.0	0.0
	C Male 2 : Male 10	0.04	0.0	42.2	0.0
	C Male 3 : Male 11	0.64	21.3	15.3	18.0
	C Male 3 : Male 12	0.44	21.3	9.9	12.4
	C Male 4 : Male 15	0.00	0.0	67.8	0.0
Mean Interspecific VI (±SE)		**0.17 (0.10)**	-	-	-

4.3.4 Movement parameters

Movement parameters varied by civet individual for both species (Figure A3.4). Common palm civets demonstrated variable nocturnal movements, with individuals moving between a mean of 628.8 m to 1880.2 m per night (Table 4.5). Malay civets conducted longer nightly ranging patterns than common palm civets, with individuals moving between a mean of 1035.5 m to 3803.6 m per night. Common palm civet mean nightly speed ranged from 52.9 m/h to 156.4 m/h, while Malay civets moved more quickly (range of individual nightly average speed: 119.3 to 333.3 meters per hour). Common palm civet nightly paths contained mean nightly turning angles ranging from 76.0° to 110.4°, while Malay civet nightly paths were overall less tortuous, with individual turning angle means ranging from 68.1° to 91.9°.

Table 4.5: Summary characteristics of nocturnal movements of GPS-collared civet species in the LKWS from 2013–2018. n: count of nocturnal paths with greater than 7 GPS fixes; |TA|: the nightly mean of absolute values of turning angles conducted along a nocturnal movement path.

	ID	n	Nocturnal Path Length (m)		Speed (m/h)		|TA| (°)	
			Mean	SE	Mean	SE	Mean	SE
Common palm civet	C Male 1.1	48	1456.4	80.7	132.8	6.6	87.6	2.99
	C Male 1.2	78	1572.6	65.4	165.6	5.7	81.4	2.31
	C Male 2	72	1478.8	61.1	127.9	5.4	90.9	2.12
	C Male 3	212	1880.2	41.1	156.4	3.5	76.0	1.23
	C Male 4	353	628.8	11.1	52.9	0.9	100.4	0.86
Malay civet	Male 1	179	2176.8	66.5	196.0	6.0	73.4	1.51
	Male 2	33	2016.1	134.0	192.3	12.3	68.3	3.58
	Male 3	9	1301.2	201.4	150.3	24.9	94.7	7.24
	Male 4	10	1680.0	158.5	173.1	14.3	74.1	6.56
	Male 6	27	3803.6	250.4	333.3	19.2	68.1	3.42
	Male 7.1	71	1755.9	82.4	166.4	7.4	96.4	2.49
	Male 7.2	78	3023.1	113.0	293.7	11.3	71.2	2.63
	Male 8	79	2035.0	99.5	187.0	8.4	87.8	2.17
	Male 9	88	3373.9	114.8	321.7	9.2	88.0	2.06
	Male 10	61	1953.0	112.5	184.0	10.2	74.2	2.48
	Male 11	97	2073.0	74.7	185.0	6.1	86.9	2.14
	Male 12	65	1900.1	75.5	162.3	6.1	82.2	2.69
	Male 13	138	1271.9	47.9	119.3	4.3	91.0	1.99
	Male 14	208	1035.5	36.6	101.3	3.6	91.9	1.66
	Male 15	150	2318.3	100.7	200.1	8.6	80.4	1.84
	Male 16	42	2120.0	153.3	213.1	13.8	78.2	3.40

Common palm civets

Common civet nightly path length (NPL) was significantly associated with lunar phase, the number of GPS fixes, and the proportion of the path contained within oil palm (Adj. R^2= 0.126, scale estimate = 0.105, AIC = 508.2, Table 4.6). Specifically, common palm civet NPL increased during the full moon and generally as GPS fix success increased (Figure 4.6). Nocturnal path lengths peaked when civets travelled in both forest and oil palm agriculture within a night; nightly movement paths were shorter when civets exclusively used either forest or oil palm (Figure 4.6). There were no significant effects of nightly temperature or rain on common civet NPL.

Table 4.6: Final general additive mixed model (GAMM) evaluating associations between log-transformed common palm civet nightly path lengths and smoothed and linear predictive variables. Model coefficients are presented on log scale and are not back transformed. edf = effective degrees of freedom; Ref.df = reference degree of freedom; Lunar = lunar phase, in radians, fitted as a circular smoother. PropOp = proportion of nightly path contained within oil palm plantation.

Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Lunar)	3.87	8.00	6.84	<0.0001
s(PropOp)	4.69	4.69	24.85	<0.0001
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	6.91	0.18	38.01	<0.0001
Fixes.8	0.15	0.08	1.75	<0.10
Fixes.9	0.26	0.09	2.95	<0.005
Fixes.10	0.33	0.09	3.64	<0.0005
Fixes.11	0.19	0.09	2.15	<0.05
Fixes.12	0.26	0.09	2.97	<0.005
Fixes.13	0.24	0.09	2.69	<0.01

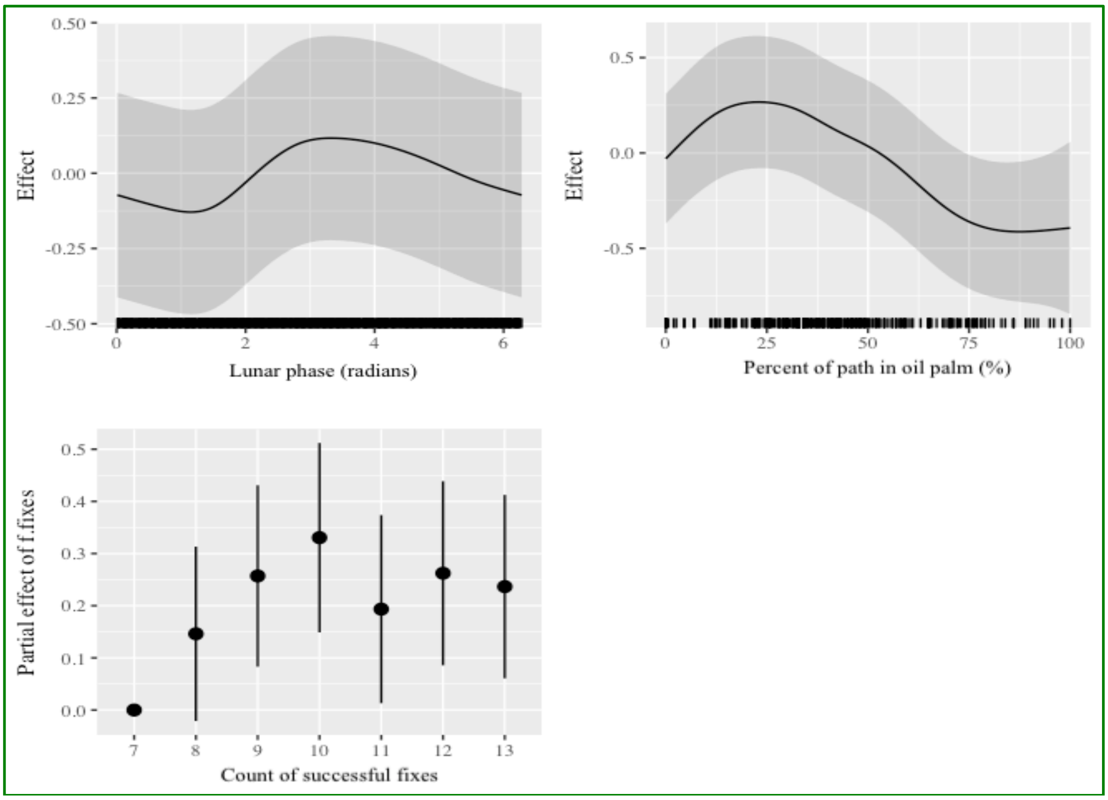
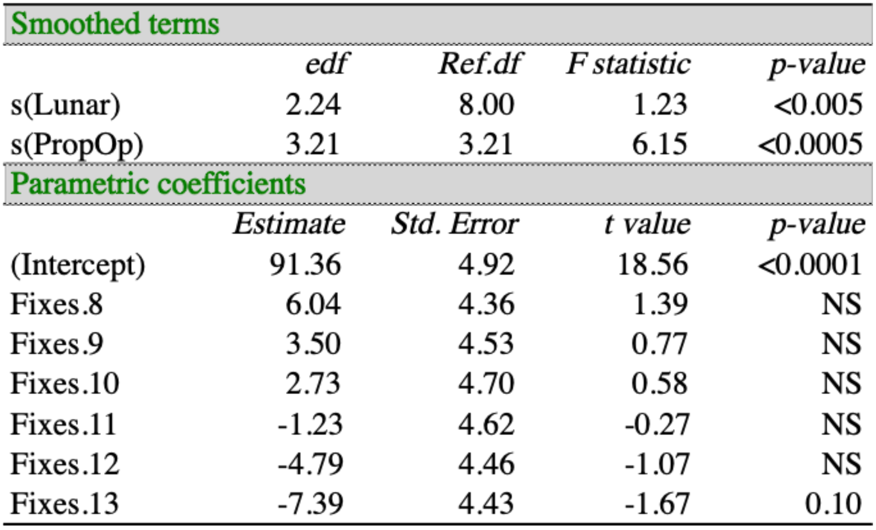


Figure 4.6. General additive mixed model plots displaying the non-linear smoothed effects of lunar phase (presented in radians as a circular smoother, such that a full moon occurs at π, and a new moon at 0 and 2π) and proportion of track within oil palm on log-transformed nightly path length for male common palm civets. Also shown are the partial parametric effects of GPS fix success (f.fixes) on log-transformed civet nightly path length. Shaded regions represent the confidence intervals of the effects. Civet ID was included in model structure as a random effect.

Common palm civet mean nightly turning angles (TA) were similarly related to lunar phase and proportion of oil palm utilised (Adj. $R^2 = 0.133$, scale estimate = 290.17, n = 741); the inclusion of GPS fix success in the final model improved overall model power, despite the effect being largely statistically insignificant (Table 4.7). Common palm civet movement was the most directed (lowest TA) during the new moon and when the animal spent ~ 25% of its nightly path in oil palm (Figure 4.7). There were no significant associations between rainfall or temperature and common palm civet mean nightly TA.

Table 4.7: Final general additive mixed model (GAMM) evaluating associations between common palm civet nightly turning angles and smoothed and linear predictive variables. edf = effective degrees of freedom; Ref.df = reference degree of freedom; Lunar = lunar phase, in radians, fitted as a circular smoother; PropOp = proportion of nightly path contained within oil palm plantation. NS= non-significant term ($p < 0.10$; per Wood, 2006; Zuur et al., 2009).



Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Lunar)	2.24	8.00	1.23	<0.005
s(PropOp)	3.21	3.21	6.15	<0.0005
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	91.36	4.92	18.56	<0.0001
Fixes.8	6.04	4.36	1.39	NS
Fixes.9	3.50	4.53	0.77	NS
Fixes.10	2.73	4.70	0.58	NS
Fixes.11	-1.23	4.62	-0.27	NS
Fixes.12	-4.79	4.46	-1.07	NS
Fixes.13	-7.39	4.43	-1.67	0.10

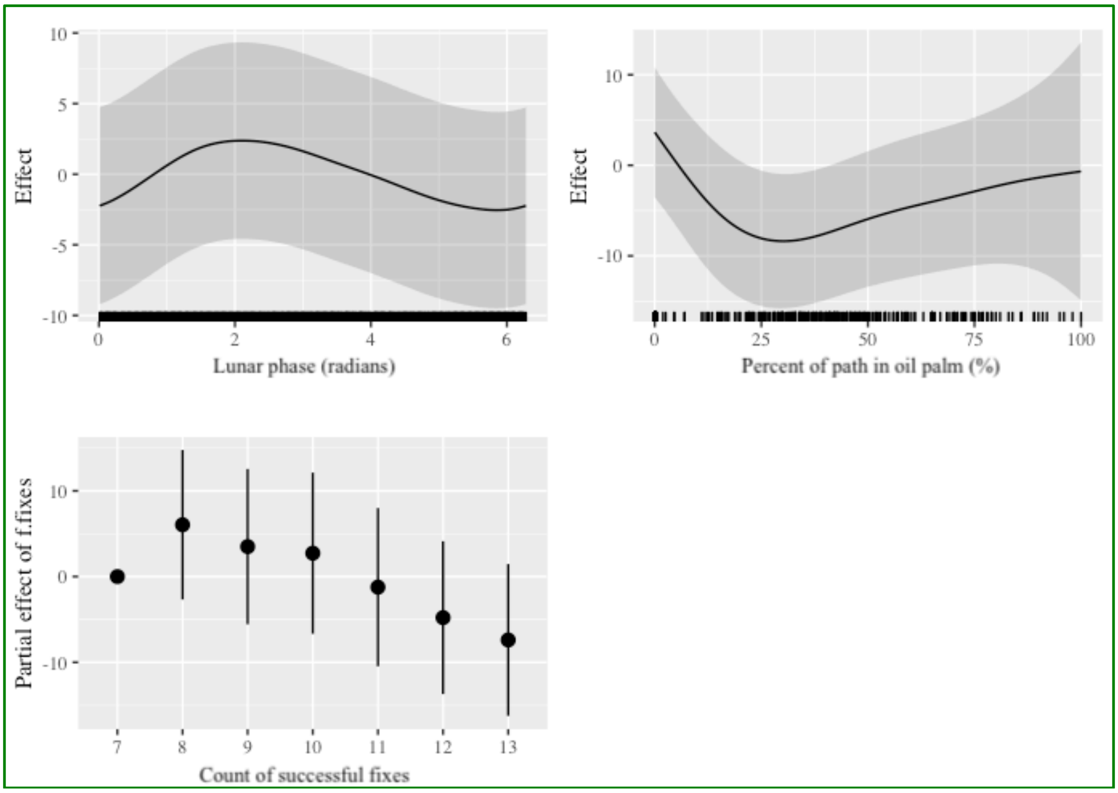


Figure 4.7. General additive mixed model plots representing the non-linear smoothed effects of lunar phase (presented in radians as a circular smoother, such that a full moon occurs at π, and a new moon at 0 and 2π) and proportion of track within oil palm on nightly turning angles for male common palm civets. Also shown are the largely non-significant parametric linear effects of GPS fix success (f.fixes) on civet nightly turning angles. Shaded regions and error bars represent the confidence intervals of the effects Tick marks on the x-axis represent raw data points. Civet ID was included in model structure as a random effect.

Malay civets

Malay civet nightly path length was significantly associated with rain, lunar phase, the number of GPS fixes, and the proportion of the path contained within oil palm (Adj. $R^2 = 0.127$, scale estimate = 77.28, AIC = 9311, Table 4.8). Specifically, Malay civet NPL increased during nights preceding the full moon (waxing gibbous), on nights with little rainfall, and as GPS fix success increased (Figure 4.8). Malay civet NPL peaked when civets used both forest and oil palm agriculture; nightly movement paths were shorter when civets exclusively used either forest or oil palm (Figure 4.8). There was no significant association between nightly temperature and Malay civet NPL.

Table 5.8: Final general additive mixed model (GAMM) evaluating associations between square root-transformed Malay civet nightly path lengths and smoothed and linear predictive variables. Model coefficients are presented on square root scale and are not back transformed. edf = effective degrees of freedom; Ref.df = reference degree of freedom; Lunar = lunar phase, in radians, fitted as a circular smoother. PropOp = proportion of nightly path contained within oil palm plantation. RainInd = rain index. NS = non-significant term ($p < 0.10$; per Wood, 2006; Zuur et al., 2009).

Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Lunar)	1.70	8.00	0.67	<0.05
s(PropOp)	5.72	5.72	27.49	<0.0001
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	39.80	2.07	19.20	<0.0001
RainInd	-0.13	0.06	-2.30	<0.05
Fixes.8	0.16	1.29	0.12	NS
Fixes.9	3.02	1.12	2.52	<0.02
Fixes.10	5.46	1.15	4.75	<0.0001
Fixes.11	5.86	1.14	5.14	<0.0001
Fixes.12	7.61	1.12	6.81	<0.0001
Fixes.13	7.98	1.20	6.67	<0.0001

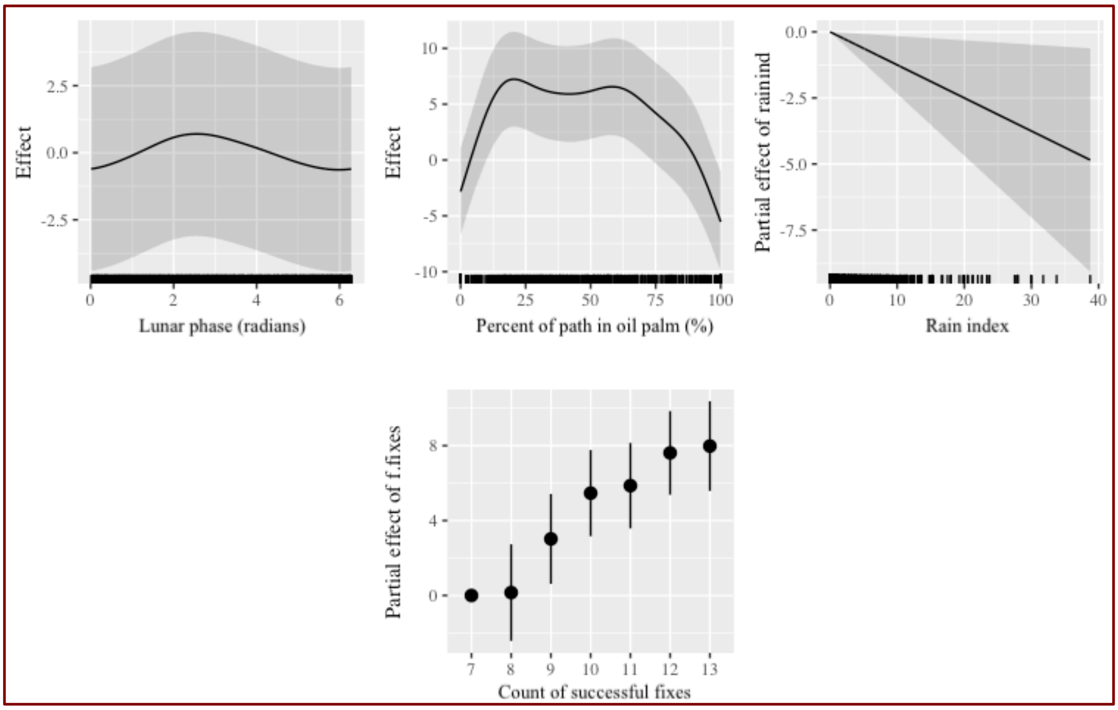


Figure 4.8. General additive mixed model plots representing the non-linear smoothed effects of lunar phase (presented in radians as a circular smoother, such that a full moon occurs at π, and a new moon at 0 and 2π) and proportion of oil palm on square root-transformed nightly path length for Malay civets. Also shown are the partial linear effects of rain (rainind) and GPS fix success (f.fixes) on square root-transformed civet nightly path length. Shaded regions represent the confidence intervals of the effects. Civet ID was included in model structure as a random effect.

Malay civet nightly mean turning angle (TA) was significantly associated with rain and the proportion of the path contained within oil palm (Adj. $R^2 = 0.095$, scale estimate = 450.9, AIC = 11527, Table 4.9). Specifically, Malay civet mean nightly TA was lowest on nights with low rainfall and when civets used both forest and oil palm agriculture (minimum TA reached at ~ 30% and ~ 65% oil palm); mean nightly TA were higher when civets exclusively used forest or oil palm (Figure 4.9). There were no significant associations between nightly temperature, lunar phase, or GPS fix success and Malay civet mean nightly TA.

Table 4.9: Final general additive mixed model (GAMM) evaluating associations between Malay civet nightly turning angles and smoothed and linear predictive variables. edf = effective degrees of freedom; Ref.df = reference degree of freedom; PropOp = proportion of nightly path contained within oil palm plantation. RainInd = rain index.

Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(RainInd)	3.74	3.74	4.41	<0.002
s(PropOp)	3.63	3.63	8.62	<0.0001
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	82.03	1.76	46.53	<0.0001

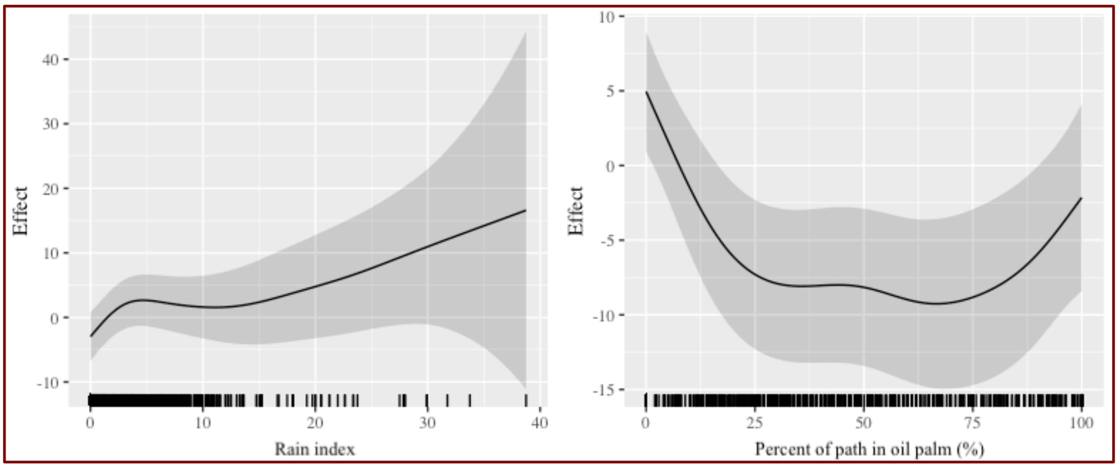


Figure 4.9. General additive mixed model plots representing the non-linear smoothed effects of rain and proportion of oil palm on nightly turning angles for male Malay civets. Shaded regions represent the confidence intervals of the effects. Tick marks on the x-axis represent raw data points. Civet ID was included in model structure as a random effect.

4.4 Discussion

This study presents the first insights into the spatial ecology of civet species persisting in a patchwork landscape of degraded tropical forests and oil palm agriculture. Through this first deployment of GPS technology on viverrids, the most extensive spatiotemporal dataset for these species has been collected, and has positively confirmed that both civets utilise forest and oil palm plantations, not only for nocturnal foraging, but also as diurnal sleeping sites. These results suggest oil palm agriculture does not act as a definitive barrier to civet movements, but may represent a less suitable habitat than remnant forests. Malay civet home range size positively correlated with the relative proportion of oil palm agriculture accessed by individuals, suggesting that despite some individual's intense usage of the agriculture, it may pose sub-optimal habitat in terms of resource accessibility. The variation in both inter- and intra-specific home range overlaps indicates these species are not spatially territorial, but preliminary observations suggest the degree of small carnivore range overlap may be modulated by the presence of oil palm. This first detailed analysis of fine-scale nightly movements of these species provides valuable insights into the factors influencing small carnivore movement patterns in anthropogenically-modified landscapes.

4.4.1 Comparison with previously reported MCP home ranges

The mean 100% MCP home range estimate for male common palm civets in the LKWS was significantly smaller than those from Thailand (Table A3.1; Grassman, 1998; Rabinowitz, 1991), but larger than that of individuals tracked in Nepal (Joshi et al., 1995). 100% MCP estimates are highly sensitive to outliers and overestimate home ranging behaviours of focal individuals (Burgman & Fox, 2003), so interpretation of this result should be taken with care (particularly considering Rabinowitz's documentation of fire-mediated dispersion by one collared male). Considering that the common palm civets sampled in Thailand were significantly heavier than those in the LKWS (Chapter 2), it is however possible this difference in ranging behaviours may reflect a genuine geographic distinction in the ecology of these groups. Indeed, as previously discussed in Chapter 2, there is evidence of genetic differences between the widespread populations of common palm civets (Veron et al., 2015; Wozencraft, 2005), which could further explain this variation in individual home range size. When common palm civet home ranges are compared with 95% MCP estimates from other sites in Sabah, the mean home range of LKWS males was larger than those recorded in DVCA (Nakabayashi et al., 2017), but smaller than those in Tabin

Wildlife Reserve (Nakashima et al., 2013). This variation may be due to differences in site productivity; as largely frugivorous omnivores, common palm civet home ranges have been documented responding to changes in local phenology and seasonality (Joshi et al., 1995; Nakashima et al., 2013). The primary forests of DVCA could represent highly productive common palm civet habitat, thus explaining the smaller observed home ranges (Nakabayashi et al., 2017), while the mixture of agriculture and degraded landscapes of Tabin and the LKWS could facilitate the establishment of larger home ranges. Given the small sample size of the current study, the effect of fruiting season on common palm civet spatial ecology in the LKWS was not assessed, so future research is warranted. Interestingly, Nakashima et al. (2017) reported home ranges of common palm civets that accessed oil palm plantations were smaller than those that remained solely in the forests; although our sample size was small, the results suggest the inverse relationship may be occurring in the LKWS.

Malay civet MCP home range estimates were some of the largest reported in the literature, with Male 1's 100% MCP the largest reported for the species to date (526.8 ha; Colón, 2002; Jennings et al., 2006; Jennings et al., 2010; Macdonald & Wise, 1979; Nozaki et al., 1994). This variation in range sizes could be partially explained by morphometric differences between individuals (Chapter 2; Swihart et al. 1998); indeed, the largest civets were tracked in Peninsular Malaysia and held larger ranges than the significantly smaller animals in Indonesia and previous studies in Malaysian Borneo. However, the LKWS Malay civets, which are smaller than those from Peninsular Malaysia (Chapter 2), held similar sized home ranges, suggesting there is another reason for the geographic variation in the species' spatial ecology. The size of a solitary male carnivore's home range is theoretically inversely related to resource abundance and predictability, entailing both food sources and reproductively active females (Duncan et al., 2015; McLoughlin et al., 2000; Nilsen et al., 2005; Sandell, 1989; Walton et al., 2017). This geographic variation in home range size could thus provide insights into habitat suitability for the species. The large range sizes in the LKWS, particularly those of individuals that accessed oil palm, could imply the landscape represents lower habitat productivity, and thus suitability, for

Malay civets compared to those sites in Sulawesi and more contiguous forests in eastern Sabah.

4.4.2 BRB home ranges

This study reports the first application of an advanced home range model to civet spatiotemporal data. One limitation of model performance was the overestimation of civet home range UDs beyond the hard barrier posed by the Kinabatangan River (Figures 4.2–4.3). Due to the sinuousity of the river paired with high levels of civet activity along the riverbank, the boundary function within the BRB model was not able to be consistently or repeatably applied in the estimation of each individual's home range UD. The standardisation of a constant hmin value in the study facilitated consistent overestimation error within the population; indeed, individual home range models overlapped the river only slightly. However, in future studies evaluating civet resource utilisation, more active efforts to delineate and exclude regions of null utilisation probability from civet BRB models should be explored (e.g. methodologies of Jay et al., 2012).

Individuals of both species of civets had both total and core home ranges encompassing degraded forest and oil palm plantations, supporting the postulation that these species display some spatial plasticity to anthropogenic land uses. Despite this apparent flexibility, the positive correlation between oil palm usage and Malay civet home range size, regardless of contour level, suggests agriculture is of overall lower suitability than those forested habitats in the LKWS (Macdonald, 1983; McLoughlin & Ferguson, 2000; Nilsen et al., 2005). Similarly, common palm civet males that utilised oil palm plantation tended to hold larger home ranges than those individuals that stayed within the protected forests. Negative relationships between anthropogenic landscapes and carnivore home range sizes have been documented in bobcats (Poessel et al., 2014; Riley et al., 2003), caracals (Ramesh et al., 2017), and black-backed jackals (*Canis mesomelas*, Ferguson et al., 1983). It is possible that oil palm plantations provide resources of insufficient quality or predictability; indeed, given the spatial variation in Malay civet serum biochemistry markers reported in Chapter 2, civet protein intake may be negatively impacted by oil palm landscapes. It is of importance to note all home ranges of GPS-tracked civets in this study contained, at least in some degree, natural forest. Efforts were made to capture small carnivores in areas with small (< 20 m) forested riparian buffers, yet despite the deployment of over 110 trap nights, no individuals were trapped, and only one female Malay civet was recorded on the camera traps. Camera trapping by Jennings et al. (2015) reported Malay civet occupancy rates within oil palm plantations were strongly influenced by the proximity of native habitat cover, with a very low probability of recording Malay civets deep in the interior of oil palm plantations. However, our findings preliminarily agree with the suggestion that Malay civet presence within agriculture may be positively related to access to native vegetation, at least to some degree, as the maximum distance a Malay civet individual was recorded from natural forest was 980 m (Male 1). Future efforts to capture and GPS-collar civets deep (> 2 km) in the interior of oil palm plantations are warranted, as this project did not attempt such trapping protocols.

This study's wide range of individual variation in both the probability of utilisation and the specific intensity of utilisation of oil palm plantations poses further lines of inquiry regarding the ecology of these species in anthropogenically-modified landscapes. Newsome et al. (2015) documented similarly large individual variations in the spatial behaviours of urban coyotes, and suggested this flexibility exemplified the successful adaptation of the species to anthropogenic landscapes. Future research should include a thorough evaluation of civet habitat selection processes within both remnant forests and oil palm plantations, with the goal of untangling factors that may influence a given civet to access oil palm agriculture. The mere size of the native forested area available to an individual did not appear to necessarily dictate an individual's entrance into or intensity of utilisation of oil palm agriculture, as would be expected in a sort of making the best out of a bad situation process. It is possible civets are demonstrating modulated habitat selection responses to specific riparian forest qualities beyond patch size; perhaps civets utilise oil palm more readily when available riparian forests are more susceptible to flooding or have sparse understory vegetation, regardless of the total area of forest. Therefore, an examination of the specific forest characteristics (both in terms of structure i.e.

Moreira-Arce et al., 2016, and productivity, i.e. Nathan et al., 2008) within civet home ranges, and across the entirety of the LKWS landscape, would provide insights into the habitat selection preferences of these species.

Complementarily, core ranges of those individuals using both habitat types were largely composed of oil palm, with variation between individuals. It is therefore dually important to quantify the characteristics of the oil palm plantations that correlate with preferential utilisation by civets, particularly if conservation outcomes are desired (i.e. Perfecto & Vandermeer, 2010). Given the lack of individuals with home ranges contained entirely within agriculture, there is currently little empirical evidence of oil palm being a highly preferred landscape for civets (i.e. as a sort of 'magnet effect', such as those posed by dumps to American black bears (Beckmann & Berger, 2003) or European wolves (*Canis lupus*; Bateman & Fleming, 2012)). The region's oil palm plantations are owned and operated by different companies exercising their own crop management schemes, however; plantations differ in crop age, harvesting protocols, maintenance of understory vegetation, pest management strategies, presence of domestic animals such as dogs or chickens, and the extent of human activity (both legal and illegal– hunting is widespread in the region). Any of these factors may play a thus unidentified role in determining to what extent a civet utilises agriculture, and future research is strongly warranted.

4.4.3 Sleeping sites

The successful deployment of GPS collars on these species uncovered similarly high degrees of individual variation in civet diurnal sleeping site behaviours, with special emphasis placed on the documentation of some individuals spending the majority of their diurnal resting sites within oil palm agriculture. Previous research examining characteristics of civet diurnal resting sites in forested habitats describe the importance of dense understory vegetation and vine tangles (Chutipong et al., 2015; Colón, 2002; Jennings et al., 2006; Jennings et al., 2010; Joshi et al., 1995; Mudappa, 2006; Nakashima et al., 2013; Sum, 2011), yet this study is the first to report substantial evidence of Malay civet tolerance to sleeping in oil palm plantations. Nakashima et al. (2013) observed common palm civets occasionally utilising heavily foliaged oil palm trees in Tabin Wildlife

Reserve, yet reported individuals preferentially slept in forests. Indeed, research by Jennings et al. (2010, 2015) has repeatedly suggested Malay civets strongly depend on natural forests for diurnal resting sites, yet these results from the LKWS suggest the species is more flexible than previously reported. Observationally, some of the sleeping sites within oil palm plantations occurred in regions of low crop productivity, including small patches left to fallow, suggesting civets may exhibit preferences for 'forest-like' characteristics in their sleeping site selection process. Evaluating the specific characteristics of these sleeping sites, both within the agriculture and across the LKWS landscape as a whole (in terms of use vs. availability, such as work on orang-utan [*Pongo pygmaeus*] nest selection by Davies et al., 2019), would provide further insights into the specific mechanisms of small carnivore adaptability within oil palm agriculture. These findings pose a particularly intriguing conservation opportunity, as these behaviours suggest civet persistence within agricultural landscapes may be facilitated by the maintenance of small patches of remnant forest within the oil palm matrix. A multitude of studies (Chapter 1; Edwards et al., 2010; Koh, 2008; Yue et al., 2015) present sobering cases of oil palm plantations being completely destructive to biodiversity, despite all efforts to improve hospitability through the establishment of riparian buffers, strategically-placed remnant forest patches, and diverse flowering plants. The results from this study would be one of the first positive cases of fostering biodiversity persistence within Malaysian oil palm.

4.4.4 Home range overlap

In terms of the spatial configuration of the LKWS small carnivores, variable but overall low levels of intra- and interspecific home range overlaps were documented between collared individuals. To the best of our knowledge, there were no apparent physical boundaries, such as tributaries, electric fences, or drainage ditches separating the ranges of assessed dyads, yet nearly half the Malay civet dyads and over half the interspecific dyads exhibited near exclusive home ranges. Contrastingly, the remaining dyads demonstrated high levels of range overlap, and the VI index values for both dyad types were highest when the zone of overlapping home ranges contained oil palm. Previous estimates of Malay civet home range overlaps vary, with most research suggesting the species does not exhibit territorial behaviours (Colón, 2002; Jennings et al., 2006; Jennings et al., 2010), which largely agrees with the findings reported here. These preliminary observations however suggest the degree of intraspecific home range overlap may be modulated by the specific quality of the shared habitat. Sandell (1989) proposed that in solitary male carnivores, exclusive home ranges occur when dietary and reproductive resources (i.e. females) are both stable and evenly distributed within the landscape. By the resource distribution hypothesis, overlapping male home ranges take place when one of two environments occur: 1) resources are extremely limited, clumped, or unstable (lowest habitat suitability), or 2) resources are exceedingly abundant (high habitat suitability; Sandell, 1989). In the first instance, exclusive home ranges are not established as the high cost of defending an area outweighs the benefits of exclusive resource control (McLoughlin et al., 2000). Moreover, exclusive home ranges do not occur in the upper thresholds of habitat productivity, as animals do not benefit from additional resources by actively excluding intruders (McLoughlin et al., 2000). The theoretical interplay between home range size and spatial overlap, succinctly summarized by Figure 1 in McLoughlin et al. (2000), suggests Malay civets in the LKWS persist across the spectrum of habitat quality; with the largest and overlapping home ranges occurring in oil palm, and both intermediate, exclusive ranges and small, overlapping ranges occurring in forests of increasing quality. This pattern does not agree with the findings of Colón (2002), who found the degree of Malay civet home range overlap increased in non-disturbed forests relative to logged forests. Further research should aim to identify home range- and landscape-scale indices of habitat quality, particularly focusing on zones of extensive intraspecific overlap and regions of exclusive range establishment. Assessing the spatial configuration of female civets across the landscape would provide more contextualising details for evaluating male civet ranges. Concurrently, female carnivore home ranges are often more reactive to measures of habitat and resource quality (e.g. bobcats, Ferguson et al., 2009; raccoons Gehrt & Fritzell, 1998; bears, McLoughlin et al., 2000; theory by Sandell, 1989), warranting future research into the spatial ecology of female civets. Lastly, the organisation of male carnivore ranges can be structured by genetic relatedness, with some species displaying elevated tolerance of home range sharing with their kin (European pine marten *Martes*

martes, Bartolommei et al., 2016; white-nosed coati *Nasau narica*, Gompper et al., 1998; swift foxes *Vulpes velox*, Kitchen et al., 2005). The identification of the degree of relatedness between collared individuals would therefore provide an alternative hypothesis regarding the observed variation in home range overlap within the population.

The low spatial overlap between the home ranges of male Malay and common palm civets may provide evidence of niche partitioning between the mesocarnivores, whereby co-existence in the LKWS occurs due to the lack of spatial competition at the home range scale. As both Malay and common palm civets are omnivorous dietary generalists (Colón & Sugau, 2012; Joshi et al., 1995), interspecific competition will most likely occur in zones of range overlap. By the Competitive Exclusion Principle, actively competing yet successfully co-existing carnivore species must exhibit diversified behaviours on at least one axis of resource selection, be it spatial, temporal, or dietary (Gause, 1934; Schoener, 1974). These preliminary insights suggest Malay civets and common palm civets may be offsetting direct competition through spatial avoidance at the home range scale, perhaps via the active selection of differing habitats (i.e. forest structure, specific tree types, etc.). Further examination into the habitat parameters actively selected for by both species in their nocturnal range establishment would further elucidate the mechanisms of mesocarnivore co-existence, while providing guidelines for conservation planning.

It is important to note that the true extent of inter- and intraspecific home range overlap within the LKWS is likely underestimated, given that not every animal was necessarily captured, let alone GPS-collared, across the landscape. Thus, these results are only presented as insights into the spatial organisation of these species within the region. During live-trapping efforts, the aim was to deploy at least two GPS units within a trapping set; once this goal was achieved, traps (and associated bait) were immediately removed from the region to avoid influencing the movements of collared animals. Future work could conduct live-trapping grids specifically oriented towards mark-recapture methodologies (e.g. Efford, 2004; Krebs et al., 2011), which would provide more robust indications of small carnivore demographics within the landscape. Indeed, given the unique pelage patterns of Malay civets, localised population densities could be estimated with camera traps and spatially explicit capture-recapture models (Borchers & Efford, 2008; Royle et al., 2014). As habitat fragmentation can affect localised carnivore densities (Chapter 1; reviewed by Debinski & Holt, 2000; Sunda clouded leopards *Neofelis diardi*, Hearn et al., 2017; hedgehogs *Erinaceus europeaus,* Hubert et al., 2011; urban carnivore spp., Sálek et al., 2015), determining the interplay between civet density, home range size, and degree of range overlap across the LKWS would provide further insights into the responses of small carnivores to oil palm agriculture. Indeed, Heydon & Bulloh (1996) reported the density of civets in logged forests was lower than that in unlogged forests, while results from Colón's (2002) VHF-tracking study suggested similar decreases in Malay civet densities following disturbance; our preliminary variations in male range size and overlap within these disturbed habitats suggests there may be a similar negative impact of oil palm on civet densities.

4.4.5 Movement parameters

The focused analysis of nightly movement parameters demonstrates both species of civets respond on a fine scale to environmental and landscape-level factors. Environmentally, common palm civets responded to variations in lunar phase, while Malay civet movement varied in response to both lunar phase and rainfall. Variations in carnivore nocturnal activity has been linked to lunar phase, and responses are broadly considered a balance between target prey visibility/wariness, and an avoidance of elevated predation risk by higher order carnivores (cheetahs and African wild dogs, Cozzi et al., 2012; foxes and lynx, Penteriani et al., 2013; Prugh & Golden, 2014; bobcats, Rockhill et al., 2013; leopards, Van Cleave et al., 2018). Common palm civets moved most during the full moon, suggesting hunting success may be lower on brighter nights; small prey species such as tree shrews (Tupaiidae spp.) or rats may be more aware of nocturnal predators during the full moon (e.g. old field mice, *Peromyscas polionotus,* Wolfe & Summerlin, 1989; yellow-necked mice *Apodemus flavicollis* and bank voles *Myodes glareolus*, Wróbel & Bogdziewicz, 2015). The less straightforward relationship between Malay civet NPL and moon phase may be attributed to the fact that the species is terrestrial, and structural factors such as canopy cover or understory density may modulate the illumination provided by a given lunar phase. Alternatively, civet species may alter their nightly movements in response to the threat of predation by Sunda clouded leopards, owls, pythons (*Malayopython reticulatus*), or estuarine crocodiles (*Crocodylus porosus*). Interestingly and in direct contrast to this study's findings, Joshi et al. (1995) reported VHF-tracked common palm civets significantly decreased their nocturnal activity during the full moon. This difference is most likely a reflection of the elevated predation risk faced by common palm civets in Nepal compared to in the LKWS; higher order predators killed several of Joshi et al.'s tracked individuals during the study, and the research group determined civet spatial ecology was most responsive to predation threats. The lunar-philic behaviour of LKWS civets may thus indicate top-down predation pressure does not play as strong of a role in determining civet nocturnal activity in the floodplain, and individuals instead scale their behaviours in response to foraging efficiency. Malay civet nocturnal movements responded negatively to rainfall, with shorter and more angular nightly paths occurring during heavy rain. Similar responses have been documented in lions (*Panthera leo,* Elliot et al., 2014), domestic cats (Haspel & Calhoon, 1993), hyena (Stratford & Stratford, 2011), foxes (Doncaster, 1985), and wolves (Theuerkauf et al., 2003), and could reflect the species' increased hunting success during rainy nights, or simply the species' tendency to seek shelter and maintain body heat. Interestingly, neither of the LKWS species altered their nocturnal movements based on nightly temperature, despite ambient temperature influencing activity patterns of other carnivores (wolves, Theuerkauf, 2009). This, however, may be due to the minimal fluctuations in nightly temperature in the lowland forests of eastern Sabah.

In addition to these responses to nightly environmental conditions, civet movement varied strongly with land cover type. Nightly movement tracks for both species contained at least partially within oil palm plantations were longer than those contained within the forest, suggesting that even though civets are able to utilise plantations in the general spatial sense of a home range and foraging ground, this may come with a steep energetic price tag. For carnivores, the length of movement pathways is generally associated with low availability of dietary resources (Gittleman & Harvey, 1982). Therefore, these longer and more directed nocturnal paths travelled by civets partially within the plantation could reflect patchy distribution of resources, paired perhaps with spatial avoidance of perceived threats such as dogs or humans. In contrast, short and tortuous nightly path lengths were most likely to occur when an individual spent the entire night in the forest or agriculture, which would indicate successful foraging behaviours. Phillips et al. (2004) similarly documented directed and swift movements of foxes in open grassland habitats, while Moriarty et al. (2016) reported Pacific martens (*Martes caurina*) moved quickly and linearly across open logging stands. Alternatively, it is possible the highly linear road structures paired with irrigation ditches within oil palm plantations could be influencing civet movement patterns; similar behaviours were recorded in Tasmanian devils and spotted-tailed quolls (*Dasyurus maculatus*) along roads in Australia (Andersen et al., 2017). More detailed, mechanistic evaluations of civet movements within oil palm, such as integrated step selection functions (e.g. Carvalho et al., 2016; Smith et al., 2019), could provide greater insights into the driving processes behind these variations in fine-scale civet behaviours across and within agricultural landscapes.

In conclusion, both species of civets appear to persist in both heavily degraded forest and oil palm plantations within the Lower Kinabatangan, although at varied energetic costs. However positive these results may seem in terms of the persistence of small carnivore species, special attention must be given to the additional pressures these animals may be experiencing due to such close associations with oil palm plantations. Civets may experience elevated probabilities of persecution if they enter oil palm plantations; Kinabatangan villagers and oil palm staff express frustration with civets predating upon domestic chickens. Hunting pressure is greater in and around plantations; domestic animals such as plantation dogs or cats may spread diseases or parasites, along with increasing the predation risk; and animals can be exposed to a suite of pollutants and agrochemicals, particularly rodenticides (Cullen et al., 2000). It is thus possible that despite their spatial adaptability to oil palm plantations as both a foraging and diurnal resting resource, the agriculture may still represent an ecological trap for the LKWS civets.

Appendix III. Supplementary information for spatial analyses

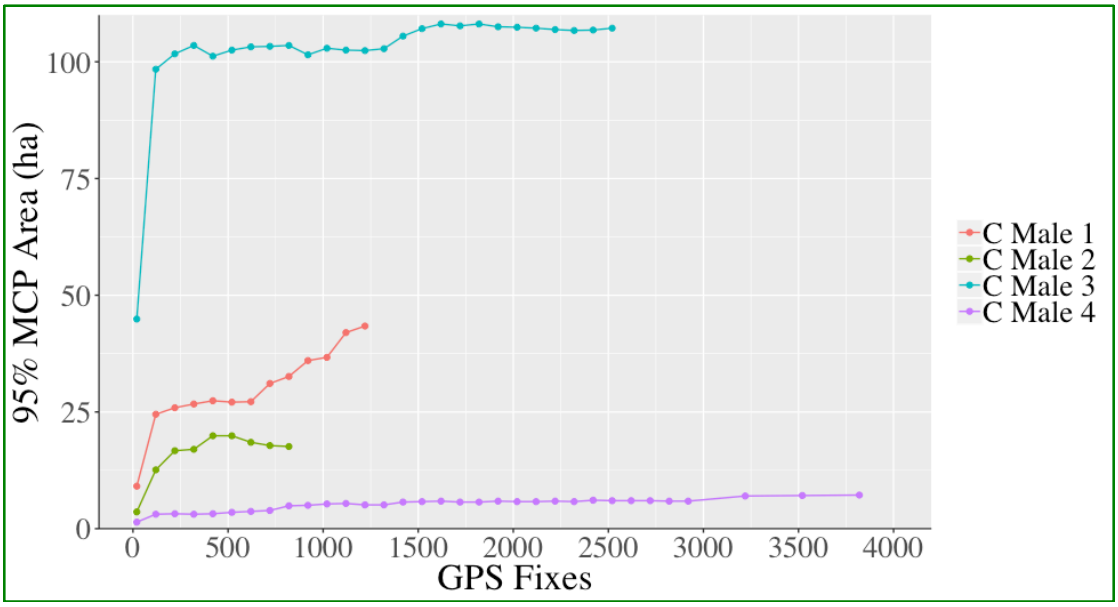


Figure A3.1. Cumulative plot of 95% minimum convex polygon (MCP) home range area per successful GPS fixes collected by collared male common palm civets in the LKWS, Sabah, Malaysia. Note the home range expansion of C Male 1 following the collection of 520 GPS fixes, which corresponded to the clearance of the mature oil palm trees within the individual's range.

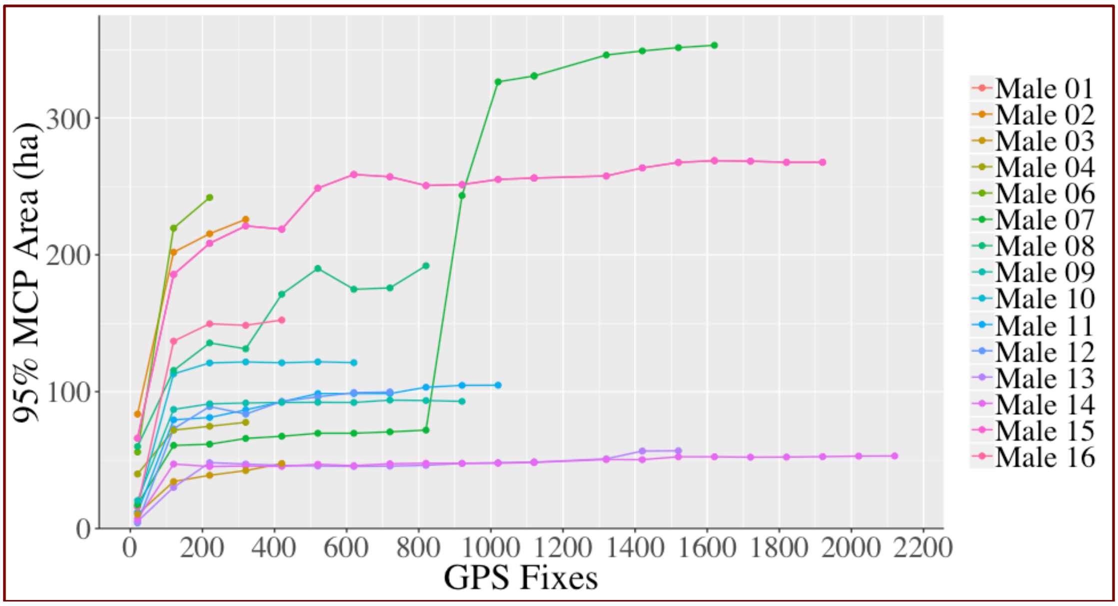


Figure A3.2. Cumulative plot of 95% minimum convex polygon (MCP) home range area per successful GPS fixes collected by collared male Malay civets in the LKWS, Sabah, Malaysia. Note the home range shift and expansion of Male 7 following the collection of 800 GPS fixes.

Figure A3.3. The clearance of mature oil palm within common palm civet Male 1's range during GPS tracking. A widespread practice in oil palm cultivation, mature trees are either manually (top left photo) or chemically felled and replanted with young trees every 15–20 years (Yaap et al., 2010). The reasoning behind the practice is twofold: 1) it is exceedingly difficult to collect palm kernel bunches from tall oil palm trees, and 2) mature trees have a slightly lower kernel production rate than younger trees. In this particular case, once the trees were felled, the area was burnt (bottom photo); this is illegal in Malaysia.

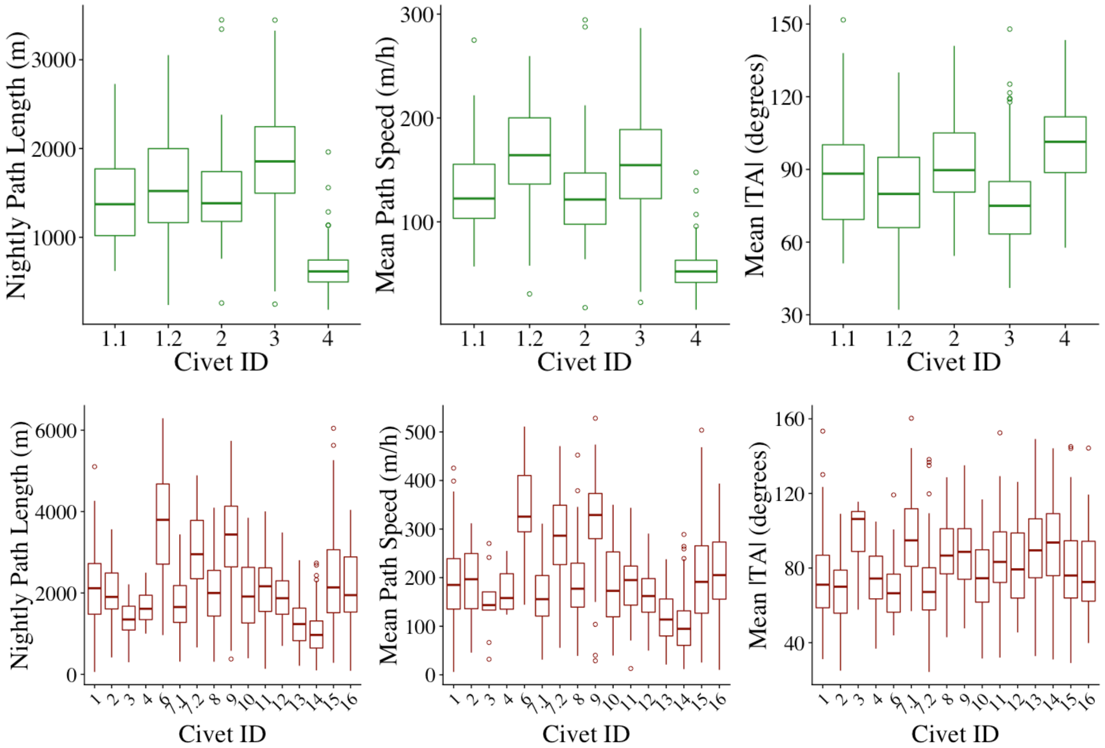


Figure A3.4. Summary of nightly movement parameters for each GPS-collared civet. |TA| denotes mean nightly turning angle. The green panels display male common palm civet data, while the red panels correspond to the male Malay civet data. Boxplots visually summarise civet movement parameters from each individual; the central line is the median, while the boxplot boundaries denote each dataset's 1st and 3rd quartiles. Whiskers extend to the maximum or minimum data point within 1.5 times the interquartile range (IQR) from the median. Open circles denote individual statistical outliers (> 1.5 IQR from the median) within each subset.

Table A3.1: Previously reported Malay and common palm civet minimum convex polygon (MCP) home range estimates derived from VHF-tracking.

	Study	Site		100% MCP (ha)		95% MCP (ha)		Comments
			n	**Mean**	**Min – Max**	**Mean**	**Min – Max**	
Common palm civet	Nakabayshi et al., 2017	Danum Valley Conservation Area, Sabah Malaysia	3	–	–	28.4	23.5 – 35.9	
	Nakashima et al., 2013	Tabin Wildlife Reserve, Sabah Malaysia	6	–	–	79.2	19.7 – 176.7	Male ranges larger than female ranges
	Nakashima et al., 2013	Tabin Wildlife Reserve, Sabah Malaysia	6	–	–	29.6	10.5 – 54.8	Female ranges smaller than male ranges
	Rabinowitz, 1991	Huai Kha Khaeng Wildlife Sanctuary, Thailand	2	1063	425 – 1700	–	–	Maximum range included large dispersal event
	Grassman, 1998	Kaeng Krachan National Park, Thailand	3	196.7	110 – 340	–	–	
	Joshi et al., 1995	Royal Chitwan National Park, Nepal	5	14.1	6.1 – 19.6	–	–	
Malay civet	Colón, 2002	Danum Valley Conservation Area, Sabah Malaysia	12	135.4	69 – 329	110.3	56 – 283	Male range size equal to female range size
	Jennings et al., 2006	Buton Island, Sulawesi, Indonesia	7	82.4	28 – 197	70.7	24 – 189	Male range size equal to female range size
	Jennings et al., 2010	Krau Wildlife Reserve, Peninsular Malaysia	5	195.6	112 – 377	142.6	78 – 185	Male range size equal to female range size
	Macdonald & Wise, 1979	Gunung Mulu National Park, Sarawak Malaysia	1	50	–	–	–	
	Nozaki, 1994	Kutai National Park, Kalimantan, Indonesia	4	71	27 – 120	–	–	

Chapter 5. Landscape sentinels: metal biomonitoring with model small carnivores in a fragmented ecosystem

5.1 Introduction

Habitat fragmentation poses a direct threat to the persistence of global biodiversity (Crooks et al., 2017; Laurance, 2008; Schipper et al., 2008). In addition to the suite of stressors associated with the loss and degradation of natural habitat (Chapter 1), species residing within fragmented landscapes face an increased risk of exposure to potentially dangerous pollutants such as pesticides, heavy metals, or endocrine-disrupters (Barbosa et al., 2003; Newbold et al., 2015; Nogeire et al. 2015; Weathers et al., 2001). Human land uses such as agriculture (O'Sullivan et al., 1993), roadways (Marcheselli et al., 2010; Trombulak & Frissell, 2000), industrial factories (Beernaert et al., 2007), urban zones (Perugini et al., 2011), and mining operations (Pereira et al., 2006) all represent significant pollution hotspots. Forest fragment edges can act as concentrators of deleterious agents (Weathers et al., 2001); as such, habitat fragmentation and degradation pose risks to wildlife persisting both within the directly treated matrices and along remnant habitat edges. Pollutants can negatively affect biodiversity by causing immediate death (Salim et al., 2014a; Sánchez-Barbudo et al., 2012), decimating food sources (Devine & Furlong, 2007), precipitating immune suppression (Bocharova et al., 2013; Selgrade, 2007), causing reproductive sterility (Dauwe et al., 2004; Sonne, 2010), altering gene expression (Harley et al., 2016), bioaccumulating and biomagnifying within ecosystems (Marcheselli et al., 2010; Ohlendorf et al., 1990), and ultimately triggering population collapses (Desforges et al., 2018).

Pollutants can be broadly organized into two distinct categories: inorganic or organic; this work focuses specifically on inorganic pollution. Metals and metalloids naturally occur throughout the biosphere, including the soil, atmosphere, and hydrosphere, and do not degrade over time (Mandal & Suzuki, 2002). Natural processes such as erosion, forest fires and volcanic eruptions shape the mobility of metals and metalloids across the planet, and natural geographic variations in geological mineral formations, and thus metal concentrations, exist (Pacyna & Pacyna, 2002). Human activities, however, alter these movement cycles; the extent of this effect can be quantified by an anthropogenic enrichment factor (Nriagu, 1996; Pacyna & Pacyna, 2001; Walker et al., 2012). Industrial activities, mining, the combustion of fossil fuels, waste disposal, and agricultural processes and practices can all alter normal cycling regimes and thus localised concentrations of metals (Atafar et al. 2010; Gibbs et al., 2009; Hanson & Trout, 2001; Moore et al., 2011; Walker et al., 2012).

Metals and metalloids can either be essential or nonessential for living organisms. Essential elements, by definition, are required at a certain species-specific threshold in order for biological processes to occur and result in normal growth and reproduction. In total, 12 metallic elements are considered essential for organisms at trace or ultra-trace concentrations: iron, copper, manganese, zinc, cobalt, molybdenum, selenium, chromium, nickel, vanadium, silicon, and arsenic (Walker et al., 2012). There exists some debate on the inclusion of some elements, such as arsenic, nickel, and chromium, into the essential classification, and the contention most often revolves around the focal biotic taxon (Di Bona et al., 2011; Nielsen, 1991; Uthus, 1992). Other metallic elements, such as lead, cadmium, or mercury, are classically considered nonessential and are most often toxic to biological systems (Walker et al., 2012). Despite the nomenclature, both essential and nonessential metals can harm organisms. The therapeutic window for essential elements is species-specific and can be very narrow, such that deviations towards either excess or deficiency can result in serious health ramifications (Cempel & Nikel, 2006; Mandal & Suzuki, 2002; Wang et al., 2006). In contrast, the exposure of an organism to a nonessential metal past a tolerance threshold is deleterious and can be described by classic dose-response relationships, whereby the severity of effect is scaled by the dosage of exposure (Walker et al., 2012). Indirectly, nonessential and essential metals can interact, such that exposure to an excess of nonessential metals can hinder an organism’s uptake of essential metals, resulting in detrimental deficiencies (Goyer, 1997).

Metals can negatively act on all levels of biological organization. On the cellular level, metals affect osmoregulation, disturb cellular communication pathways, and can generate cellular oxidative stress (Basu et al., 2005; Cempel & Nikel, 2006; Espín et al., 2014a,b). Exposure can affect gene expression with often-detrimental repercussions (Beyersmann, 2002; Chanda et al., 2006; Harley et al., 2016). The accumulation of metals within organs can lead to organ damage and eventual breakdown; for example, the storage of cadmium in mammalian livers and kidneys results in proteinuria (Sarkar et al., 2013). Both cellular and organismal growth and development rates are retarded by many metals (Dietz et al., 2013; Wang et al., 2006). Metallically-facilitated neurophysiological damage can lead to behavioural modifications such as decreased foraging, learning, and memory retention in exposed organisms (Basu et al., 2005; Kalisinska et al., 2016). Metallic pollutants can significantly impact the reproductive capabilities, and thus population growth rates, of many organisms (sea bass *Lateolabrax japonicus*, Abascal et al., 2007; blue tits *Parus caeruleus,* Dauwe et al., 2004; humans, Gennart et al., 1992). Lastly, heavy metals, particularly mercury, can be biomagnified within the food chain, which carries costly implications for entire biological communities (Janssen et al., 1993; Mann et al., 2011).

The scope of metallic accumulation and associated toxicity in wildlife is dependent upon several abiotic and biotic factors. First, the toxicity of a metal is target species-specific; some organisms are particularly sensitive to metallic pollutants, while others have evolved adaptations to elevated metal exposure (van der Ent et al., 2013; Heikens et al., 2001; Morgan et al., 2007; Wang et al., 2006). The severity of a metallic pollutant's biological effect varies by the mode of uptake; for example, the physiological effects following topical arsenic exposure differ from those following ingestion (Mandal & Suzuki, 2002). Ecologically, an individual's host characteristics, such as sex, age, or reproductive status, can influence both its exposure probability and vulnerability to metallic pollutants (Burger et al., 2003; Ferrario et al., 2016; Lazarus et al., 2018; Noël et al., 2016; Peakall & Burger, 2003; Wani et al., 2015). Lastly, the severity of a metal's effect on an individual occurs within the larger context of the animal's environment; additional stressors such as drought, food scarcity, or disease can increase the exposure to and physiological impact of a pollutant on an individual (e.g. Marcogliese & Pietrock, 2011).

Given these considerations, it is important to study the presence and movement of metallic elements within the biosphere, particularly those areas directly impacted by large-scale land use changes. In Asia, rapid urbanisation, agricultural intensification, surges in both industrial and mining activities, ineffective waste treatment, and poor regulatory oversight systems have significantly altered local and regional metal concentrations (Hungspreugs, 1988; Islam et al., 2015; Li et al., 2009; Zhao et al., 2006). In particular, the expansion of the palm oil industry poses a viable pollution threat to the health of those wildlife species managing to survive the associated extensive landscape alterations (Fernandez & Joshi, 2002; Fitzherbert et al., 2008; Meijaard et al., 2018).

The establishment and maintenance of oil palm plantations can alter metallic cycling through both agricultural processes and practices (Olafisoye et al., 2017; Zarcinas et al., 2004). Open burning to clear native vegetation prior to plantation establishment is common, despite the illegality of the practice (Comte et al., 2012; Fargione et al., 2008; Kim et al., 2015). The combustion of forest vegetation increases atmospheric and soil concentrations of metals such as aluminum, mercury, copper, and zinc (Pereira & Úbeda, 2010; Yamasoe et al., 2000). Oil palm plantation establishment and maintenance is accompanied with marked increases in soil erosion rates (Guillaume et al., 2015; Meijaard et al., 2018), which in turn, alter localised soil metal distributions and concentrations. In synchrony, high sedimentation loading–which includes associated metals– into native hydrological systems occurs in oil palm plantation landscapes due to increased surface run off, decreased vegetative ground cover, and failure of plantations to maintain effective riparian buffers (Chellaiah & Yule, 2018; Douglas 1999; Tulloch et al., 2016). Distally, the establishment of plantations at the loss of tropical forests significantly destabilises riparian bank structures, further increasing the scale of soil erosion from agricultural landscapes and inputs into the hydrological regime (Dislich et al., 2017; Horton et al., 2017). Oil palm plantations, particularly in Malaysia, contain irrigation and drainage ditches to aid in water level control and nutrient retention (Corley & Tinker, 2003); in other crops, the establishment of irrigation networks inflated local available concentrations of toxic metals by dissolving metals out of the soil and into the water (Hanson & Trout, 2001; Hou et al., 2014). If the extent of the irrigation network is sufficient, the water can draw these elements down the soil profile and, eventually, into ground water through a process known as metallic leaching. Tropical soils are naturally prone to nutrient leaching without these excess pressures from irrigation ditches and crop cultivation (Johnson et al., 1975); oil palm plantation management practices serve to further degrade soil fertility (Ah Tung et al., 2009; Kurniawan, 2016; Guillaume et al., 2016). Oil palm plantation drainage ditches can also accumulate excess metals (indeed, any agrochemical) from surface run off (Kee & Chew, 1996; Maena et al., 1979). These ditches drain directly into natural watercourses, and when flooding occurs, overflow, contaminating surrounding regions with a concentrated cocktail of chemicals (Chellaiah & Yule, 2018; Sulai et al., 2015).

The combined effects of soil loss and functional degradation in oil palm plantations require the application of fertilisers to sustain crop productivity (Bessou et al., 2017; Comte et al., 2012; Comte et al., 2013; Goh et al., 2003). Fertiliser usage in Asia has grown by a staggering 1900% in the last 40 years (Lu & Tian, 2017; Pretty, 2018; Zhao et al., 2006), and the palm oil industry is one of the largest consumers of mineral fertilisers in the region (Fairhurst & Härdter, 2003; Sheil et al., 2009). Application rates vary by plantation management scheme and crop age, and reportedly range from 500 to 1,000 kg of mineral fertiliser per hectare, with leaching commonly reported in heavily fertilised plantations (Caliman et al., 2002; Comte et al., 2013; Comte et al., 2012; Kurniawan et al., 2018). Fertilisers, particularly inorganic fertilisers, often contain significant concentrations of metals (Atafar et al. 2010; Carvalho, 2006; Combs et al., 1982; Gimeno-García et al., 1996; Molina et al., 2009; Nicholson et al., 2003; Zoffoli et al., 2013). According to rough calculations by Mattsson et al. (2000), the large-scale application of phosphorous fertilisers to Malaysian oil palm equated to an annual addition of 3,900 mg of toxic cadmium per crop hectare. Sakai et al. (2017) demonstrated elevated soil concentrations of nickel, zinc, arsenic, cadmium, and lead in Malaysian oil palm plantations compared to other land use types, and credited these findings to the excessive application of fertilisers. Dubos et al. (2017) also documented oil palm fertiliser application can increase soil concentrations of aluminum and manganese in Ecuador, as did Kurniawan (2016) in Indonesia. Furthermore, fertiliser application can significantly acidify crop soils (Dubos et al., 2017; Guo et al., 2010; Kurniawan et al., 2018), which strongly affects soil metal mobility and bioavailability (Walker et al., 2012). Increased heavy metal concentrations in waterways flowing through oil palm plantations have been documented and similarly attributed to fertiliser application (Sarmani et al., 1992).

Oil palm plantations also use a wide array of agrochemicals to control pests such as insects, rodents, fungi, and herbaceous weeds (Nurdiansyah, 2016; Wood, 2002). Mercury, arsenic, copper, and lead were once widely used active ingredients in agricultural pesticides and fungicides (Combs et al., 1982; Embrick et al., 2005), yet many of these compounds were banned or economically phased out in developed countries. Reports of Malaysian agrochemical mishandling, including a continued application of banned compounds due to low economic costs, are however worryingly prevalent (Ali & Shaari, 2015; Ali et al., 2018; Hossain et al., 2010). Sarmani et al. (1992) attributed elevated arsenic concentrations in a Malaysian watershed to usage of arsenical herbicides in oil palm plantations. Additionally, regulated agrochemicals with organic active ingredients can contain metallic impurities, often classified as ‘inert’ ingredients (Cox & Surgan, 2006; EPA, 1987). Defarge et al. (2018) explored the toxicity of the formulants in widely used organic pesticides, and identified significantly elevated concentrations of arsenic, chromium, cobalt, lead, and nickel in samples.

Lastly, the extraction process for oil palm production presents a threat to native aquatic ecosystems, as large volumes of palm oil mill effluent (hereafter POME) are produced after the fruit is harvested and processed (Comte et al., 2012). POME is a mixture of solid palm kernel waste, fat residues, and water generated at palm oil extraction mills, and can contain significant concentrations of both inorganic and organic pollutants (Donald, 2004; Ohimain et al., 2012). Indeed, estimates by Pamin et al. (1999) reported the daily production of 1,200 m^3 of POME creates a biological oxygen demand in aquatic ecosystems equivalent to that from sewage produced by 75,000 people. There are regulations in place regarding the cleansing and treatment of POME prior to release back into natural watercourses (Igwe & Onyegbado, 2007; Kushairi et al., 2018); however, many reports suggest the adherence to and enforcement of these regulations are lacking across the industry (Comte et al., 2013; McCarthy & Zen, 2010; Sheil et al., 2009). Notably for this study, work by Shavandi et al. (2012a,b) detected high concentrations of iron, zinc, and manganese in POME residues. High concentrations of heavy metals have been detected in fish in Malaysia, and the unregulated discharge of POME is the suggested cause (Sheil et al., 2009).

A paucity of data exists on the environmental effects of oil palm plantation establishment and maintenance within an ecotoxicological framework, and as such, studies are greatly required. A common investigative technique to evaluate environmental pollution is the usage of a focal organism as an indicator or sentinel species (Ruiz-Suárez et al., 2016; Stankovic et al., 2014). Carnivores are often such foci of toxicology studies; the combination of long lifespans, high trophic positions, and large spatial ranges elevate the probability of exposure to and accumulation of pollutants (e.g. artic foxes, *Vulpes lagopus,* Bocharova et al., 2013; domestic dogs *Canis lupus familiaris,* Harley et al., 2016; Iberian wolves *Canis lupus signatus,* Hernández-Moreno et al., 2013; golden jackals *Canis aureus,* Malvandi et al., 2010; grizzly bears *Ursus arctos horribilis,* Noël et al., 2015; review by Rodríguez-Jorquera et al., 2017). The Malay civet (*Viverra tangalunga*) and the common palm civet (*Paradoxurus hermaphroditus*) represent two potential landscape sentinels for the biomonitoring of metals in tropical rainforests and oil palm agriculture. Both species are, at least as of now, relatively abundant and accessible to trained researchers (Chapter 2; Evans et al. 2016a; Nakabayashi et al., 2016; Ross et al., 2016; Seymour et al., 2017). Civets are dietary generalists, although common palm civets are considered more frugivorous than Malay civets (Jothish, 2011; Nakashima et al., 2010a). The species have been recorded consuming insects, arachnids, worms, crustaceans, molluscs, amphibians, reptiles, birds, small mammals, herbaceous material, and various fruits, including oil palm fruits (Colón & Sugau, 2012; Joscelyne et al., unpublished data; Macdonald & Wise, 1979; Nakashima et al., 2013). Perhaps most significantly, both species demonstrate spatiotemporal utilisation of, and a degree of tolerance to, heavily degraded forests and oil palm landscapes (Chapter 4). The combination of these ecological and behavioural characteristics increases civet probability of exposure to anthropogenic pollutants, and thus, these animals represent ideal metal biomonitoring sentinel species.

Traditional ecotoxicology research utilises either direct organ biopsies or specific biomarkers, such as serum enzymes, to evaluate exposure to metallic pollutants (Alleva et al., 2006; Payne et al., 1996). An increasing number of studies have however begun using hair as an alternative and nonlethal bioindicator (e.g. Barbosa et al., 2005; Bencko, 1995; D'Havé et al., 2006; Legrand et al., 2004; Pozebon et al., 2017; Rodushkin & Axelsson, 2000; Sobanska, 2005; Steely et al., 2007). The structure of hair tissue creates a unique and non-specific matrix within which metals can be accumulated; elevated hair metal concentrations have been documented in a range of mammals persisting in contaminated environments (humans, Drobyshev et al., 2017; Hammer et al., 1971; Yokel, 1982; wood mice *Apodemus sylvaticus,* Marcheselli et al., 2010; brown antechinus *Antechinus stuartii,* and other Australian mammals, McLean et al., 2009; rodent spp., Pereira et al., 2004). At the follicle, hair is in continuous contact with the bloodstream, and the sulfurous keratin proteins readily bind circulating metals, resulting in the endogenous incorporation of metals into the growing hair (Beernaert et al., 2007; Rendón-Lugo et al., 2017; Sela et al., 2007). Hair metal concentrations positively correlate with more traditional organ biomarker concentrations across a range of species (hedgehogs *Erinaceus europaeus,* D'Havé et al., 2006; wood mice, Beernaert et al., 2007; bats *Pipistrellus* spp., Hernout et al., 2017). Indeed, hair can be a valuable detoxification tissue for the excretion, long-term storage, and eventual bioaccumulation of metals in mammals (Erry et al., 2005; Mohmand et al., 2015); hair mercury measurements can be over 200 times the levels measured in blood (Mergler et al., 2007; Syaripuddin et al., 2014; Wada et al., 2010). Hair has several logistical advantages over other biomarkers, as it minimally invasive to collect, does not necessitate specific safety training to handle, and does not require special storage conditions, an aspect particularly relevant for remote field work (Hernández-Moreno et al., 2013; Wang et al., 2009). Due to the low metabolic activity of hair, it serves as a stable and long-term matrix record of the body's metabolic processes, including the excretion of metallic compounds (D'Havé et al., 2006; Foo et al., 1993). In contrast, more traditional nonlethal metal biomarkers, such as blood or urine, provide only short-term, 'snapshot' insights to an individual's metal contamination (Gil et al., 2011). Furthermore, by analyzing segmental variations in elemental concentrations along the longitude of a hair shaft, the temporal nature of an element's excretion, and thus exposure, history can be evaluated (e.g. Bartkus et al., 2011; Kumtabtim et al., 2011; Noël et al., 2015; Pozebon et al., 2008; Stadlbauer et al., 2005).

This study therefore aimed to use two model small carnivore species with known ecological and spatial behavioural flexibility to explore the biological presence of metals in the agriculturally fragmented and degraded Lower Kinabatangan Wildlife Sanctuary landscape. This study specifically sought to i) develop a sound, repeatable, and nonlethal methodology to evaluate the presence and concentrations of 13 essential and nonessential metals in hair; ii) compare the resultant metal profiles in the two species and contextualize the results within the current extent of research on hair metal concentration; iii) explore factors influencing total hair metal content, including individual biological characteristics and landscape-level spatial parameters.

5.2 Methods

5.2.1 Study site

The study was located in the Lower Kinabatangan Wildlife Sanctuary (LKWS) within the Kinabatangan floodplain, in Sabah, Malaysian Borneo. For detailed descriptions of the site, please refer to previous chapters. The geology of the Kinabatangan floodplain is largely comprised of sedimentary rocks and relatively young alluvium deposits along the river's course (Fitch, 1958; Haile & Wong, 1965). The floodplain's basal sedimentary geology comprises the Labang Formation of Lower Miocene (Aquitanian) epoch containing grey and red shale, grey calcareous sandstone lenses, and occasional beds of limestone outcroppings. At the northernmost sampling extent of this study site, the Gomantong Limestone Formation of the Upper Miocene epoch contains foraminiferal, algal, and coral limestone (Haile & Wong, 1965). The alluvium contains sand, silt, clay and peat dating from the Quaternary period (Fitch, 1958; Haile & Wong, 1965). According to the 1976 Land Resource Study, there are no economically viable mineral deposits in the Kinabatangan region (Thomas et al. 1976); indeed, Sabah has only one documented mine, the Mamut Copper Mine active from 1975–1999, located approximately 165 km (Euclidean) away and on a different river catchment from the study site (Ali et al., 2004). The dominant soil types in the Kinabatangan floodplain are gleysols near the river channel and acrisols beyond the immediate banks (FAO, 1976; Acres & Folland, 1975); additionally, Wetlands International (2010) reported a large area of peat soil on the north bank of the study site. There have been no known detailed soil metal analyses conducted in the region.

Given the large-scale presence of palm oil plantations within the Kinabatangan floodplain (over 250,000 hectares; Chapter 1), concerns about metal pollution exist (Dayang Norwana, et al., 2011; Hai et al., 2001). One readily apparent issue is the high loading of suspended solids and sedimentation rates in the river; in 2000, an estimated 7.8 million tons of soil were lost from the landscape into the river (Horton et al., 2017; Juin et al., 2000). Oil palm plantations within the catchment are often bordered by very small, if any, native riparian vegetation, despite laws requiring the presence of buffers. Given the extent of plantation coverage in the floodplain, an estimated 372,000 tons of fertiliser have been applied within the region annually, although this is a now dated estimate (Balamurugan, 1999). Unfortunately, current crop management strategies, including agro-chemical treatment regimes, were unable to be obtained for the region due, at least in part, to political and racial wariness. At least 29 palm oil mills exist within the Kinabatangan watershed, and many have historically failed to meet water quality discharge standards (DOE, 2009). Only a handful of published traditional water quality parameters exist for the watershed, and high total suspended solids, dissolved organic matter, and conditions facilitating eutrophication have all been reported, all of which could at least be partially explained by large-scale land use changes (Harun et al., 2015a; Harun et al., 2015b; Harun et al., 2016; Jawan & Sumin, 2012). Several reports and/or presentations regarding non-specific pollution in the region have been made, which include observational statements from local communities (e.g. Dayang Norwana et al., 2011; Wilson, 2016), but most contain little to no scientific data, and none have been since published in peer-reviewed sources (e.g. Dhanasegaran, 2001; DOE, 2009; Hai et al., 2001).

5.2.2 Sample collection

Trapping periods for wild small carnivores spanned from March 2013 to January 2018. In-depth protocols of trapping, animal handling, and blood sample collection can be found in Chapters 2 and 3, with specific capture sites presented in Figure 2.2. In addition to recording the individual's sex, weight, and estimated age, a small patch of hair (approximately 2 x 2 cm) was shaved from the dorsal scapular junction of each anaesthetised animal using a commercial razor. This collection method was selected as the withers are the body region least likely to be contaminated by exogenous metal deposition (Hubbart et al., 2012); additionally, the close shaving facilitated the rapid identification of individuals previously sampled up to two months prior, thus avoiding unnecessary anaesthetic procedures. This shaved region also facilitated the sterile insertion of a subdermal identifying microchip during sampling. In some cases, additional shaved samples were opportunistically collected from the animal's forelimbs to facilitate venipuncture, per methods described in Chapter 2. Clippers were thoroughly washed with ethanol between sampling efforts. If an animal was not anaesthetised, attempts were made to collect hair samples through the trap prior to the animal's release. Samples were stored in clean polypropylene tubes, with metal-free desiccating silica beads (Sigma-Aldrich) in the bottom separated from direct contact with hair by sterile cotton gauze. Tubes were sealed with parafilm and stored at room temperature until analysis.

5.2.3 Hair preparation

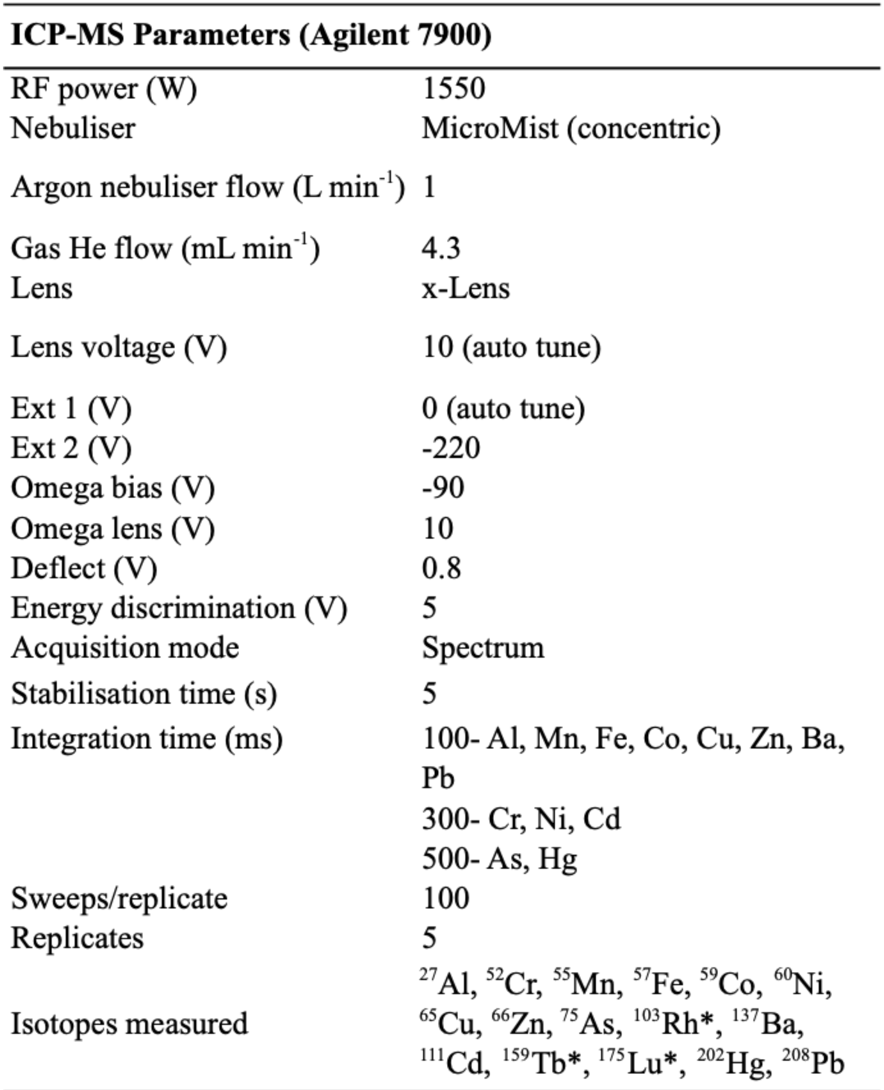
All hair samples were washed prior to analysis to remove exogenous lipids and any external metallic contamination. Hair was rinsed on filter paper (Whatman Grade 1, GE Healthcare, Little Chalfont, UK) using vacuum with 5 mL reagent-grade acetone (99.9% HPLC grade Chromasolv, Merk, Darmstadt, Germany), followed by two 5 mL rinses of Milli-Q ultrapure water (Type 1 [18.2 MΩ], Merck, Darmstadt, Germany) and a final 5 mL rinse of acetone, following methods outlined by the International Atomic Energy Agency (IAEA; Noël et al., 2015; Pereira et al., 2006; Ryabukin, 1978). Washed hair was left to dry at room temperature for at least 24 hours before further handling.

The metal content of hair was analyzed by inductively coupled plasma mass spectrometry (ICP-MS) after acid digestion. Shaved hair samples underwent complete acid digestion for 'bulk' analysis, a standard method in metallic ecotoxicology studies (see Hammer et al., 1971, Puchyr et al. 1998). All reagents used were analytical grade and trace metal certified, including washing reagents. All glassware was thoroughly washed with ultrapure water, soaked in ≥ 5 % HNO_3, and rinsed with ultrapure water prior to use. Washed and dried hair samples (100 ± 1 mg) were weighed accurately in acid-washed Teflon digestion vessels. The vessels were transferred to a fume hood and 10 mL concentrated HNO_3 (67–70% w/w TraceMetal Grade, Fisher Scientific, Hampton, USA) were added. For each digestion batch (n = 15 vessels), an acid blank underwent the complete digestion methodology to identify any methodological contamination. The closed vessels were placed in a microwave digestion system (ETHOS UP, Milestone Srl, Sorisole, Italy) and underwent a two-phase digestion program (1800 W ramp to 70°C over 5 min; hold at 70°C for 15 min; ramp to 115°C over 5 min; hold at 115°C for 15 min; cool for 60 min). An internal probe monitored the temperature and pressure of a reference vessel, allowing for the adjustment of microwave power during program execution while also minimising the risk of over-pressurisation. Following completion of the program, vessels were left to further cool and depressurise to avoid excessive loss of volatile compounds once containers were opened in the fume hood. The samples were quantitatively transferred to an acid-washed volumetric flask and made up to 50 mL with ultrapure water (PURELAB Flex 3, ELGA LabWater, High Wycombe, UK). Liquid samples were stored in pre-washed 60 mL LDPE plastic bottles (VWR, Lutterworth, UK) until analysis by ICP-MS. Following each digestion batch, vessels underwent an acid washing cycle whereby 5 mL ultrapure water and 5 mL HNO_3 were boiled at 200°C for 20 min. Following every three digestion and washing cycles, digestion vessels were gently heated to ensure they were thoroughly dry and remove NO_x gases.

5.2.4 Instrumentation and operating parameters

The metal content of hair samples was analyzed by an inductively coupled plasma mass spectrometer in He analysis mode (ICP-MS Agilent 7900, Agilent Technologies, Santa Clara, USA; Tables 5.1–5.2). Prior to analysis, nickel skimmer and sampler cones were cleaned in 5% Citranox solution (Alconox Inc., White Plains, USA), system tubing replaced, and the machine tuned to high system performance levels. In addition to standard washes and blanks, a 0.5 ppm Au-containing solution (Multi-element Calibration Standard #4, PerkinElmer, Waltham, USA) was run to clear any Hg persisting in the system prior to sample introduction. Batch blanks (every 15 samples) were run to identify any possible metal carryover from the digestion vessels. Metal content was reported using MassHunter software (Agilent Technologies), where each reading was comprised of five ICP-MS measurements per element. Digested civet samples were run twice, thus reported values per civet individuals are an arithmetic mean expressed as mg kg^{-1} dry weight of small carnivore hair.

Table 5.1: Instrumentation specifications and operating parameters for the analysis of metal content in small carnivore hair by ICP-MS.



ICP-MS Parameters (Agilent 7900)	
RF power (W)	1550
Nebuliser	MicroMist (concentric)
Argon nebuliser flow (L min^{-1})	1
Gas He flow (mL min^{-1})	4.3
Lens	x-Lens
Lens voltage (V)	10 (auto tune)
Ext 1 (V)	0 (auto tune)
Ext 2 (V)	-220
Omega bias (V)	-90
Omega lens (V)	10
Deflect (V)	0.8
Energy discrimination (V)	5
Acquisition mode	Spectrum
Stabilisation time (s)	5
Integration time (ms)	100- Al, Mn, Fe, Co, Cu, Zn, Ba, Pb 300- Cr, Ni, Cd 500- As, Hg
Sweeps/replicate	100
Replicates	5
Isotopes measured	^{27}Al, ^{52}Cr, ^{55}Mn, ^{57}Fe, ^{59}Co, ^{60}Ni, ^{65}Cu, ^{66}Zn, ^{75}As, ^{103}Rh*, ^{137}Ba, ^{111}Cd, ^{159}Tb*, ^{175}Lu*, ^{202}Hg, ^{208}Pb

**denotes internal standard (IS)*

Table 5.2. Sample uptake and rinse times of ICP-MS nebuliser

	Time (s)	**Peristaltic pump speed (rps)**
Sample uptake	30	0.5
Stabilise	20	0.3
Probe rinse (sample)	5	0.5
Probe rinse (Std)	5	0.5
Rinse 1	15	0.3

5.2.5 Calibration and quantitative analysis

Precision and accuracy of the analyses were controlled by external calibration with an internal standard for each target analyte. A 100 ppm multi-element internal standard diluted to 100 ppb (5188-6525, Agilent Technologies) was used to improve analysis accuracy, control for instrumental drift and matrix interferences; rhodium, terbium, and lutetium were selected as optimal internal standards for target analytes (Table 5.3). Two series of multi-elemental external calibration standards were created for quantitative analysis. For all target metals excluding Hg, a five-point calibration curve from 0–1 μg/mL was established by dilution of a 10 μg/mL standard (Multi-Element Calibration Standard #3, PerkinElmer) with 20% HNO_3; a five-point Hg calibration curve from 0–0.2 μg/mL was created by the same process (Multi-Element Calibration Standard #2A-HG, Agilent Technologies). Calibrations were performed every 45 samples and accepted curves had R-values of 0.992 or better (Figures A4.1–A4.13). To evaluate the methodology and examine any analytical interference, UK dog hair was acid-digested and spiked with 0.1 μg/mL of each target element; recovery rates fell between the accepted ranges of 90–120% (Table 5.3; Creed et al., 1994). If small carnivore samples contained metal concentrations above the calibration range (Fe and occasionally Al), samples were diluted with 2% HNO_3 and re-analysed.

Table 5.3: Description of target analyte specifications during ICP-MS analysis of civet hair. Detection limits displayed are the minimum and the maximum batch detection limits of the four calibration curves utilised to quantify the metal content of acid-digested hair samples throughout the analysis.

Target Analyte	**IS**	**Range of Detection Limits (mg/l)**	**Spiked Recovery Rates (%)**
^{27}Al	^{103}Rh	$3.656 \times 10^{-4} – 1.060 \times 10^{-3}$	96.50
^{52}Cr	^{103}Rh	$4.539 \times 10^{-5} – 7.530 \times 10^{-4}$	97.20
^{55}Mn	^{103}Rh	$2.568 \times 10^{-5} – 6.417 \times 10^{-5}$	96.30
^{57}Fe	^{103}Rh	$6.913 \times 10^{-4} – 5.800 \times 10^{-3}$	93.40
^{59}Co	^{103}Rh	$5.401 \times 10^{-6} – 1.705 \times 10^{-5}$	95.01
^{60}Ni	^{103}Rh	$4.431 \times 10^{-5} – 3.812 \times 10^{-4}$	106.7
^{65}Cu	^{103}Rh	$1.932 \times 10^{-5} – 6.515 \times 10^{-5}$	102.2
^{66}Zn	^{103}Rh	$1.276 \times 10^{-4} – 4.644 \times 10^{-4}$	92.18
^{75}As	^{103}Rh	$1.466 \times 10^{-5} – 2.560 \times 10^{-5}$	106.0
^{137}Ba	^{159}Tb	$1.776 \times 10^{-5} – 4.219 \times 10^{-5}$	97.07
^{111}Cd	^{159}Tb	$7.335 \times 10^{-7} – 1.612 \times 10^{-6}$	99.16
^{208}Pb	^{175}Lu	$3.355 \times 10^{-6} – 1.068 \times 10^{-5}$	100.2
^{202}Hg	^{175}Lu	$8.471 \times 10^{-6} – 4.390 \times 10^{-5}$	98.70

5.2.6 Data analysis

Analyses were performed using R 3.5.0 (R Core Team, 2018). Metal concentration values falling below the calibration batch limit of detection were set at half the batch limit of detection (Drobyshev et al., 2017; Flache et al., 2015; Gil et al., 2011; Hernández-Moreno et al., 2013). Metal concentration data were tested for normality with the Shapiro-Wilks test. Fisher exact tests determined equality of variances between datasets. Extreme outliers were identified as those values exceeding the group mean by 3 standard deviations, which is more data conservative than Tukey's outlier determination (Drobyshev et al., 2017; Heitland & Köster, 2006). However, these extreme outliers were not automatically removed from the dataset, as the discarding of laboratory-derived values based solely on parametric mathematical identification fails to acknowledge the possibility of natural hair metal variations in the wild system (Pollett & van der Meij, 2017).

Two-tailed, paired t-tests were used to examine the difference between mean metal concentrations of unwashed and washed hair samples. The differences in the mean metal concentrations between treatments were tested for normality using the Shapiro-Wilks test. The role of hair type—specifically dorsal scapular junction versus forelimb—in hair metal concentrations was similarly evaluated by two-tailed, paired t-tests or Wilcoxan signed-rank tests, based on normality of paired differences. Concentrations of Malay and common palm civet hair were compared using Mann-Whitney U (MWU) tests.

Multivariate analyses in the form of principal component analyses (PCA) were conducted on Malay civet hair concentrations to evaluate any evident shared exposure sources via heavy metal co-variance and co-linearity. Common palm civet hair metal relations were not assessed due to the small sample size. As these data were strongly skewed, metal concentrations were log-transformed prior to analysis, and all values were standardised using the scale.unit command. Using the packages *FactoMineR* (Le et al., 2008) and *factoextra* (Kassambara & Mundt, 2017), the total number of principal components (PC) was determined by evaluation of the scree plot, the relative variance explained by each PC, and an eigenvalue >1. Sequential comparisons of the PCA biplots (2-dimensional visual representations of the projected civet hair metal values paired with vectors describing the effects of each metal variable) were assessed to determine if metals correlated and co-varied within the multivariate space. Thus, metals with overlapping or closely related vector arrows in all possible biplot combinations suggest a shared source (Huong & Holmes, 2019).

To evaluate the potential role of landscape characteristics in Malay civet hair metal concentrations, each individual's sampling site was assigned a suite of descriptive values in ArcGIS 10.1 (ESRI, 2011). Shapefiles delineating oil palm plantations, oxbow lakes, and semi-permanent tributaries (defined as those structurally present when river levels were low) were created from the digitization of Google Earth Pro satellite images. The proximity of each animal's capture site to the nearest accessible oil palm plantation and semi-permanent tributary was measured as a Euclidean distance. Accessible was defined as a feature on the same riverbank as the civet capture site and within 4 km, corresponding to the average maximum nightly distance determined in Chapter 4. Access to an oxbow lake was further simplified into a binomial factor (denoting accessible or not accessible) for each given capture location.

To identify factors that may influence the concentrations of target metals in Malay civet hair, the effects of both biological and environmental features were evaluated by generalised linear modeling (GLM). For the biological models, civet sex, weight, and age category were included as fixed effects. Environmental models included the terms distance to oil palm plantation, distance to semi-permanent tributary, and accessible presence of an oxbow lake as fixed effects. Final model error distributions were set as gamma with log, identity, or square root link functions; link functions were optimized for each metal by evaluation of the global model's standardised residuals and minimisation of Akaike's Information Criteria (AIC; see Burnham & Anderson, 2002). Multimodal inference was performed by the information theoretic approach of model averaging using the corrected AIC determined by the dredge function in the *MuMIn* package (Bartón, 2018). All model parameters were standardised prior to model averaging (Gelman, 2008; Grueber et al., 2011). Top models, and thus the most efficient, were identified as those with a ΔAICc < 2, and those model parameters averaged using the natural average method to more wholly account for uncertainty in the model selection process (Burnham & Anderson, 2002).

5.3 Results

5.3.1 Sample collection

Hair from 71 Malay and 19 common palm civet individuals was collected within the LKWS and surrounding landscapes (Figure 2.2). An additional 25 samplings were conducted on previously captured individuals; all analyses presented hereon consist of first capture hair metal concentrations for those recaptured individuals. The majority of hair samples contained metal concentrations above instrumentation detection limits; however, 13 samples were below the limit of detection for Cr measurements; 2 for Ni; 18 for As; 1 for Cd, and 4 for Hg.

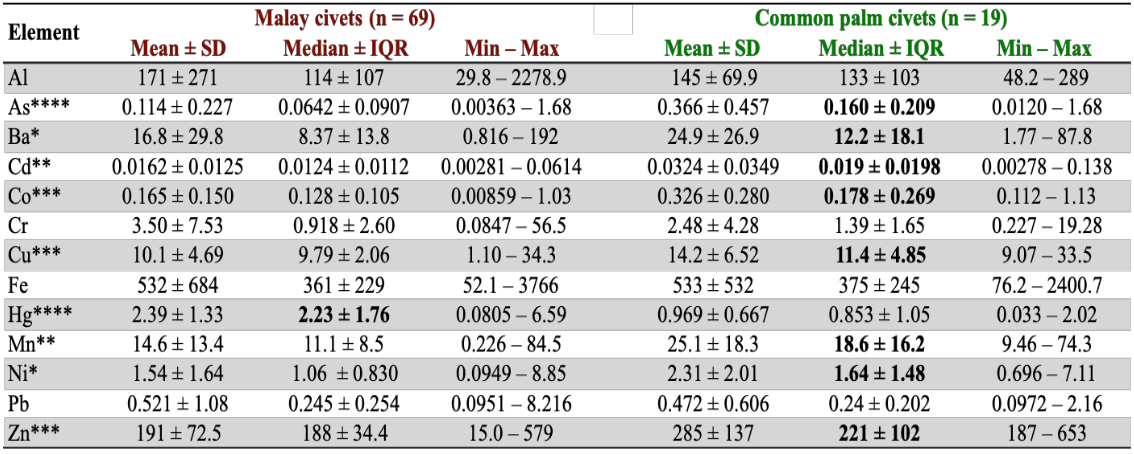
5.3.2 Civet hair metal profiles

Two Malay civets (MC F14 and MC M25) possessed hair metal concentrations classified as extreme outliers (> 3 times the SD from the study's elemental mean) for over half the target analytes and as such, these individuals were completely removed from the dataset (Drobyshov et al., 2017). These individuals were sampled under irregular conditions; neither could be anaesthetised, and hair samples were instead collected from the traps. As these values were already largely outside the recorded distribution of civet hair metal concentrations, these individuals were removed from the dataset to avoid including values that reflected a collection contamination error rather than excessive individual exposure.

In terms of method development, washing the hair prior to acid digestion only significantly altered the concentration of Hg in civet hair (Table A4.1). The mean Hg concentration in hair washed with ultrapure and acetone rinses (1.27 mg kg^{-1}) was significantly lower than in unwashed samples (2.06 mg kg^{-1}), with paired sample measurements decreasing a mean of 0.792 mg kg^{-1} following treatment ($t = 5.664$, $df = 3$, $p < 0.02$). Furthermore, most metal concentrations did not significantly differ by the type of hair collected from an individual, be it from the forelimb or the scapular junction (Table A4.2). Hg content did statistically differ by hair type, with forelimb hair containing a mean 1.08 mg kg^{-1} less Hg than hair from the scapular junction in the same individual (forelimb mean: 1.91 mg kg^{-1}; scapular mean: 2.99 mg kg^{-1}; $t = -7.366$, $df = 3$, $p < 0.01$).

Hair metal content varied between the two civet species (Table 5.4); not all metal concentrations were normally distributed, so both means and medians are presented for comparison with the literature. In terms of relative metal concentration within a sample, the highest concentrations were, in decreasing order, Fe, Zn, and Al in all hair samples, regardless of species. The lowest measured metal concentration in both species was Cd. Common palm civet hair contained statistically higher levels of Cd, Ba, Mn, Co, Ni, Cu, Zn, and As than hair from Malay civets (Table 5.4). Conversely, Malay civet hair contained significantly more Hg than common palm civet samples.

Table 5.4: Hair metal concentrations from two civet species trapped within the LKWS from 2012–2017, values expressed as mg kg^{-1}; bold text indicates the directionality of significance, such that bolded values represent the species with the statistically greater hair concentration of a given metal.



Element	Malay civets (n = 69)			Common palm civets (n = 19)		
	Mean ± SD	Median ± IQR	Min – Max	Mean ± SD	Median ± IQR	Min – Max
Al	171 ± 271	114 ± 107	29.8 – 2278.9	145 ± 69.9	133 ± 103	48.2 – 289
As****	0.114 ± 0.227	0.0642 ± 0.0907	0.00363 – 1.68	0.366 ± 0.457	**0.160 ± 0.209**	0.0120 – 1.68
Ba*	16.8 ± 29.8	8.37 ± 13.8	0.816 – 192	24.9 ± 26.9	**12.2 ± 18.1**	1.77 – 87.8
Cd**	0.0162 ± 0.0125	0.0124 ± 0.0112	0.00281 – 0.0614	0.0324 ± 0.0349	**0.019 ± 0.0198**	0.00278 – 0.138
Co***	0.165 ± 0.150	0.128 ± 0.105	0.00859 – 1.03	0.326 ± 0.280	**0.178 ± 0.269**	0.112 – 1.13
Cr	3.50 ± 7.53	0.918 ± 2.60	0.0847 – 56.5	2.48 ± 4.28	1.39 ± 1.65	0.227 – 19.28
Cu***	10.1 ± 4.69	9.79 ± 2.06	1.10 – 34.3	14.2 ± 6.52	**11.4 ± 4.85**	9.07 – 33.5
Fe	532 ± 684	361 ± 229	52.1 – 3766	533 ± 532	375 ± 245	76.2 – 2400.7
Hg****	2.39 ± 1.33	**2.23 ± 1.76**	0.0805 – 6.59	0.969 ± 0.667	0.853 ± 1.05	0.033 – 2.02
Mn**	14.6 ± 13.4	11.1 ± 8.5	0.226 – 84.5	25.1 ± 18.3	**18.6 ± 16.2**	9.46 – 74.3
Ni*	1.54 ± 1.64	1.06 ± 0.830	0.0949 – 8.85	2.31 ± 2.01	**1.64 ± 1.48**	0.696 – 7.11
Pb	0.521 ± 1.08	0.245 ± 0.254	0.0951 – 8.216	0.472 ± 0.606	0.24 ± 0.202	0.0972 – 2.16
Zn***	191 ± 72.5	188 ± 34.4	15.0 – 579	285 ± 137	**221 ± 102**	187 – 653

** denotes statistical significance related to $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ****$p < 0.0001$*

Multivariate analysis reported a reduction of data dimensionality following principal component analysis on log-transformed Malay civet hair metal concentrations. Four principal components (PC) accounted for 73.27% of the total data variance (Table A4.3). Based on the observations of the PC biplots (Figure A4.27), two consistently co-linear and co-varying metal associations were identified across all dimensions: 1) Co and Mn, and 2) Cu and Zn.

5.3.3 *Malay civet hair metal factors*

The role of civet sex, age category, and weight on hair metal concentrations was evaluated for Malay civets by averaged generalised linear modeling (Tables 5.5; A5.4–A5.5). Statistically significant associations between hair Hg, Ni, and Pb concentrations and these biological parameters were determined; the remaining metals did not statistically vary with these host parameters (Table A4.6). Hair Hg statistically increased with civet age category (z = 2.204, $p < 0.05$) and weight (z = 2.589, $p < 0.02$). Similarly, Pb increased with civet weight (z = 2.428, $p < 0.02$). In contrast, hair Ni decreased with civet weight (z = 3.056, $p < 0.01$).

Table 5.5: Model-averaged standardised estimates of biological fixed effects for statistically significant top-models of Malay civet hair metal concentrations. NS denotes statistically non-significant ($p > 0.05$) term. Bold terms indicate statistically significant parameters. SexM = male; AgecatM = mature civets. Intercept = standardised reference level for factorised predictor variables (ex: female, immature).

Element	Parameter	Estimate	Std. Error	z value	*p value*
Hg#	(Intercept)	1.509	0.0448	33.65	<0.0001
	AgecatM	0.3252	0.1476	2.204	<0.05
	Weight	0.3136	0.1212	2.589	<0.02
Ni	(Intercept)	1.179	0.0591	19.58	<0.0001
	Weight	-0.4406	0.1418	3.056	<0.01
	AgecatM	0.0622	0.1554	0.396	*NS*
	SexM	-0.0240	0.0702	0.337	*NS*
Pb	(Intercept)	-0.7782	0.1620	4.715	<0.0001
	AgecatM	-0.9588	0.6271	1.500	*NS*
	Weight	1.240	0.5015	2.428	<0.02
	SexM	0.1022	0.2384	0.423	*NS*

#denotes parameter with singular and final model structure (no models within 2 AICc of top model)

In terms of incorporating landscape-level parameters, statistically significant associations were determined between hair As, Ba, Cd, Cr, Fe, and Hg concentrations and capture site parameters; the remaining metal concentrations were not significantly explained by model structures containing landscape information (Table 5.6; Tables A4.7–A4.8). Hair As and Hg concentrations statistically decreased with proximity to a tributary (z = 2.512, $p < 0.02$; z = 2.343, $p < 0.02$, respectively). In contrast, hair Cd and Cr concentrations increased with proximity to a tributary (z = 3.328, $p < 0.001$; z = 4.195, $p < 0.0001$, respectively). Ba concentrations statistically increased with the presence of an oxbow lake near the capture site (z = 2.044, $p < 0.05$) and with proximity to a tributary (z = 3.088, $p < 0.01$). Lastly, hair Fe concentrations statistically increased with the presence of an oxbow lake near the capture site (t = 3.256, $p < 0.002$), with proximity to a tributary (t = -3.021, $p < 0.005$), and with proximity to oil palm plantations (t = -2.407, $p < 0.02$).

Table 5.6: Model-averaged standardised estimates of landscape fixed effects on Malay civet hair metal concentrations for metals with statistically significant results. NS denotes statistically non-significant ($p < 0.05$) term. Trib = proximity to accessible tributary; Plant = proximity to accessible oil palm plantation; Lake = factor term denoting access to oxbow lake. Interecept = standardised reference level for factorized predictor variable (ex: no accessible oxbow lake).

Element	**Parameter**	**Estimate**	**Std. Error**	**z value**	***p value***
As	(Intercept)	0.3246	0.0241	13.23	<0.0001
	Trib	0.1547	0.0605	2.512	<0.02
	Plant	-0.009512	0.0266	0.353	*NS*
Ba	(Intercept)	2.667	0.1680	15.58	<0.0001
	Lake	0.8456	0.4062	2.044	<0.05
	Plant	-0.2924	0.3754	0.771	*NS*
	Trib	-1.100	0.3499	3.088	<0.01
Cd	(Intercept)	0.01643	0.0014	11.27	<0.0001
	Lake	-0.005046	0.0043	1.153	NS
	Trib	-0.005642	0.0017	3.328	<0.001
	Plant	-0.001781	0.0027	0.645	NS
Cr	(Intercept)	1.806	0.2092	8.469	<0.0001
	Lake	0.3779	0.4399	0.848	NS
	Plant	0.3921	0.4311	0.897	NS
	Trib	-0.8247	0.1932	4.195	<0.0001
Fe#	(Intercept)	6.187	0.1031	59.99	<0.0001
	Plant	-0.5478	0.2276	-2.407	<0.02
	Trib	-0.6312	0.2090	-3.021	<0.005
	Lake	0.8380	0.2573	3.256	<0.002
Hg	(Intercept)	0.8285	0.0628	12.95	<0.0001
	Trib	0.3026	0.1268	2.343	<0.02
	Plant	0.05970	0.1125	0.526	NS
	Lake	0.03853	0.0980	0.389	NS

#*denotes parameter with singular and final model structure (no models within 2 AICc of top model)*

5.4 Discussion

This study was rigorously able to quantify metal exposure in two sentinel species persisting within oil palm-modified landscapes. These results represent the first documented metallic hair reference values for wild viverrids, and demonstrate metal concentrations significantly vary between Malay and common palm civet samples. Methodological design considerations were addressed through recommended standardisation of hair sampling and pre-analysis sample washing procedures. Detectable and varied concentrations of non-essential elements were detected. Variation in the detected concentrations of essential elements within the population suggest either differing internal processes or exposure events. Biological modeling of the Malay civet samples suggests Pb and Hg exposure varies with life history traits, while spatial modeling provides evidence of water-facilitated pollution of non-essential metals that is detectable in small carnivores.

5.4.1 Civet hair metal profiles

The hair metal profiles of these two generalist species are the first known of their kind, and provide insights into the biochemical and ecological baselines for the region's species. All the sampled individuals were at least visibly healthy (i.e. not actively suffering from apparent acute poisoning), and as such, these hair concentrations serve as preliminary references for civets persisting within agriculturally fragmented lowland ecosystems.

The detection of non-essential metals in civet hair from both species indicates there is an exposure to these metals within the population; exposure to these elements, even at sub-lethal concentrations, will at minimum exert physiological stress. On the cellular scale, upon exposure to sub-lethal concentrations of nonessential metals, organisms must either 'hide' the metal with the aid of a protein (such as metallothionein) or move to excrete the element (via insoluble intracellular granules, faeces, urine, or hair; Walker et al., 2012); all these processes result in a net energetic loss for the organism in addition to any concurrent physiological damage inflicted by the non-essential metal. Furthermore, individual civets contained non-essential metal concentrations statistically elevated relative to the LKWS population, suggesting differing magnitudes of exposure events occur at the individual civet scale. Overall, civet hair As concentrations were below the reported threshold value related to adverse affects in humans (1 mg kg^{-1}; Byrne et al., 2010; Hindmarsh, 2002;), but four individuals exceeded these concentrations, and two additional individuals contained concentrations nearing that limit. Similarly, civet hair Hg data were reported below the threshold related to neurochemical alterations in polar bears (*Ursus maritimus,* 5.4 mg kg^{-1}; Basu et al., 2009; Pilsner et al., 2010), yet samples from three Malay civets exceed this limit. Indeed, the EPA guideline of 1mg kg^{-1} hair Hg for normal humans (FAO/WHO, 2003) was exceeded by 73% of all civet samples. The determination of any possible physiological impacts (i.e. using parameters of Chapter 2) relative to these elevated hair metal concentrations within the sampled populations is strongly warranted.

In the case of essential metal hair concentrations, individual stochastic variations pose a more complicated narrative. This variation may reflect biokinetic feedback pathways related to viverrid-specific essential element baselines (particularly applicable to Fe, Ni, Zn, and Mn) or a natural variation in the dietary intake of these elements. Alternatively, this diversity could suggest exposure or deficiencies of these elements may occur on the individual civet scale. It is important to note that excessive exposure to these metals beyond a species' essential requirement can cause significant physiological damage (ATSDR, 2005a; 2005b; 2007; 2008; 2012a; 2012b); thus, from a precautionary position, further evaluations of the sources and impacts of these elements within the LKWS are recommended. These factors could begin to be teased apart by evaluation of hair metal concentrations of captive civets or those sampled from less anthropogenically-modified regions such as DVCA.

Major limitations to the interpretation of measured hair metal concentrations are the difficulties translating measurements back to quantifiably elevated exposure events and forward to physiological detriment to a given species (Kempson & Lombi, 2011; Mikulewicz et al., 2013). Despite its benefits as a biomonitoring tool, hair is still a nontraditional analytical medium, and the interpretative link connecting metal exposure to hair metal excretion is complicated by mode of exposure (i.e. ingestion vs. inhalation) and the toxicokinetics of metal incorporation into hair from blood (Peakall & Burger, 2003). Kinabatangan civets expressed elevated Al, Ba, Cr, Fe, Ni, Zn, and Mn hair concentrations relative to previous research (Figures A4.14–A4.20). but fell approximately within reported concentrations of Co, Cu, Hg, As, Cd, and Pb (Figures A4.21–A4.26). (For those metals where civet concentrations were largely below those reported in the literature (particularly Cd, Pb, As, and Hg), it is worth highlighting that these are some of the most widely researched elements across pollution studies, and this qualitative result should not mask the implications discussed above of these detectable concentrations within the LKWS civets). To date, there are no universally agreed upon hair metal concentration values beyond which marked physiological damage occurs. Even in human studies, the reported reference interval ranges for unexposed and healthy individuals appears to depend on sampling methodologies and study population factors (e.g. Figures A4.14–A4.26; Mikulewicz et al., 2013; Tamburo et al., 2015). Metal threshold concentration values do exist for more traditionally sampled tissues, such as liver, brain, or kidney, and are derived from extensive *in situ* toxicodynamic and toxicokinetic laboratory testing on target laboratory species (ex: No observed adverse effect levels [NOAEL]; lethal dose-50 [LD-50] values; dietary intake thresholds; Barbosa et al., 2005). The interpretation of elevated versus normal hair metal concentrations is further complicated by the species' effect in hair mineral content; some species display naturally greater physiological toxicity thresholds for particular metals (Morgan et al., 2007). Further experimental testing and analysis would be required to fully translate these hair metal concentrations beyond a summary exposure assessment and into a civet-specific risk assessment (See Brooks (2018)'s approach to pharmacology impacts and Depledge & Galloway (2005)'s discussion on informative biomarkers).

Common palm civet hair contained significantly greater concentrations of As, Ba, Cd, Co, Cu, Mn, Ni, and Zn compared to that of Malay civets. In contrast, Malay civet hair contained significantly elevated Hg concentrations relative to that of common palm civets. These differences could be due to the varied sample sizes paired with the stochastic variations in individual civet hair metal concentrations. However, the documentation of species' differences in metallic profiles is not altogether unexpected, as this is commonly reported in multi-species assessments (e.g. silver foxes *Vulpes vulpes* and arctic foxes, Filistowicz et al., 2012; Australian small mammals, McLean et al., 2009). As previously discussed, hair metal concentration is a function of both internal physiological processes and external exposure. In the case of essential elements (Co, Cu, Mn, Ni, and Zn), common palm civets may have differing physiological homeostatic baselines or excretory regulatory processes for these elements compared to Malay civets (Kempson & Lombi, 2011; McMeans et al., 2007). Further physiological research would be required to determine species-differences in the internal regulatory processes of hair metal concentrations. Such differences could be further modulated by species-specific ecological traits and behaviours, such as diet or habitat preferences, which would facilitate varied metal exposure histories (e.g. Brazilian canids, Curi et al., 2012; bat *spp*. Flache et al., 2015). Although both species are dietary generalists, common palm civets are considered more frugivorous than Malay civets (Jothish, 2011), and this dietary niche segregation could explain differing hair metal concentrations for both essential and nonessential elements (Chojnacka et al., 2010; Gall et al., 2015). Indeed, ingested vegetation can be substantial sources of heavy metals (moose *Alces alces,* Brekken & Steinnes, 2004; cattle *Bos taurus,* Miranda et al., 2009; invertebrate *spp*., Peterson et al., 2003), while more carnivorous diets are linked to increased Hg accumulation (fish *spp*., Kasper et al., 2012). Of particular regional relevancy is the documentation of Ni hyperaccumulator botanic species in successional and disturbed habitats within Sabah (van der Ent et al., 2015). Several of these listed species have been documented within the LKWS, such as *Walsura pinnata* and *Glochidion rubrum*, with varying prevalence (Stark, pers. comm.). High concentrations of Ni have been recorded within the fruiting structures of these plants (van der Ent & Mulligan, 2015), which could pose a risk to seed predators such as civets. Indeed, Colón and Sugau (2012) reported civet faeces collected in Danum Valley Conservation Area, Sabah, contained *Glochidion* seeds.

Alternatively, the differing spatial behaviours of these species may contribute to these differences in hair metal concentrations. GPS-collared male common palm civets held markedly smaller home ranges than Malay civets, and displayed differing rates of oil palm access (Chapter 4); these varied spatial behaviours could impact an individual's probability of contacting a given pollutant. If metal sources in the LKWS were localised (i.e. related to a specific natural [e.g. fruit] or anthropogenic [e.g. fertiliser] point-source) contained within an individual's home range, the smaller home ranges held by common palm civets could translate to elevated exposure rates. Complementarily, the larger ranges of Malay civets could offset these individuals' exposure likelihoods to point source pollution by decreasing their contact probabilities to a specific source. Research by Brown et al. (2014) reported tissues from ringed seals (*Pusa hispida*) with smaller and more intensely utilised home ranges located near a military station contained elevated polychlorinated biphenyl concentrations compared to those seals with larger home ranges. Similar findings were reported by Ragland et al. (2011) in the measured tissue concentrations of persistent organic pollutants in transient versus resident loggerhead sea turtles (*Caretta caretta*). More specific evaluations of how hair metal concentrations of the GPS-collared males differ based on habitat utilisation, with particular focus on the degree of oil palm access, could provide further context to these observations.

In contrast, hair concentrations of Al, Cr, Fe, and Pb did not differ between civet species. This could indicate a shared exposure to landscape-wide metal sources, be they natural or anthropogenic, particularly when considering these elements are non-essential. Natural sources of heavy metals could be explained by the soil and water profiles of the Kinabatangan floodplain. Unfortunately, little can be said at this time regarding the geological parent materials as potential sources of metallic baselines in the region (see Section 5.2.1), and further collaborative research is warranted to distinguish between geogenic and anthropogenic origins of these particular metals (e.g. Krami et al., 2013). Given the relatively high Al and Fe concentrations in civet hair, specific research evaluating the presence of acid sulphate soils within the LKWS is recommended (Shamshuddin et al., 2014). Further, both civet species have been documented feeding on invertebrates, including millipedes, scorpions, and earthworms (Colón & Sugau, 2010; Nakashima et al., 2013); there is substantial evidence that invertebrates naturally accumulate metals such as Cd, Pb, and Zn (Heikens et al., 2001; Hobbelen et al., 2006; Morgan et al., 2007; Nica et al., 2012). Alternatively, these elevated metal concentrations could be due to exposure to the same anthropogenic pollution sources, be they agricultural, industrial, or urban, across the LKWS. Al and Pb have both been traced to the application of mineral fertilisers to oil palm plantations (Dubos et al., 2017; Sakai et al., 2017), while Cr and Pb can occur in high concentrations in pesticides (Defarge et al., 2018). This finding does not necessarily indicate exposure to these metals occurs via a singular, joint source.

5.4.2 PCA results

Based on the results of the multivariate analysis of Malay civet hair, most assessed metals did not consistently relate or co-vary within the samples, the exception being Co and Mn, and Cu and Zn. These relationships could either be explained by internal, biochemical processes such as equivalent enzymatic pathways for these elements, or by a shared source of exposure to the elements (Chojnacka et al., 2010). As civet-specific biochemistry processes are not explicitly known nor the focus of this work, the latter suggestion will be discussed in further depth. Similar correlations between these metals were detected in the hair of Russian children (Drobyshev et al., 2017), maned wolves

Chrysocyon brachyurus, and crab-eating foxes *Cerdocyon thous* in Brazil (Curi et al., 2012); however, these authors made no postulations regarding possible joint-exposure sources. Barrio-Parra et al. (2018) reported an association between Co and Mn in environmental samples collected near industrial activities in the Mediterranean; similar associations were found in South African groundwater polluted by industrial activities (Elumalai et al., 2017). Anthropogenically-polluted environmental samples contain positive Cu and Zn relationships, particularly samples associated with urban runoff (Facchinelli et al., 2001; Nirel & Pasquini, 2010; Robert-Sainte et al., 2009).

5.4.3 Malay civet hair metal factors

In evaluating the role of age category, weight, and sex on Malay civet hair concentrations, only Hg, Pb, and Ni varied statistically. The higher concentrations of Hg in mature compared to immature civets agrees with trends documented across a wide array of species, and when paired with the positive effect of an individual's weight, suggests Hg exposure varies with life history stages in Malay civets (as documented in pine snakes *Pituophis melanoleucus,* Burger et al., 2017; brown bears *Ursus arctos* Lazarus et al., 2018, Noël et al., 2016; dogs, Park et al., 2005; review by Peakall & Burger, 2003). Similarly, the positive relationship between civet weight and measured hair Pb agrees with the findings of Hernández-Moreno et al. (2013), who documented increased hair Pb concentrations in larger adult wolves contrasted against smaller and younger wolves. These patterns could be interpreted two ways: specific exposure pathways to these metals may vary by a civet's life history (e.g. dietary selection, and thus exposure, varies by civet age); or may suggest a lifetime cumulative exposure to these elements. There is no immediately apparent biochemical explanation for the negative relationship between civet hair Ni and weight (Cempel & Nikel, 2006; Eisler, 1998); however, laboratory experiments using domestic dogs fed high concentrations of nickel sulfate over two years resulted in an observed 40% decrease in body weight (ATSDR, 2005a). The relationship between hair metal and civet body weight was not directly assessed by this specific chapter, yet given this preliminary relationship, further investigation in the deleterious impacts of high Ni is warranted.

Malay civet hair concentrations of As, Ba, Cd, Cr, Fe, and Hg were related to accessible proximity to various landscape-level structures such as semi-permanent tributaries, oxbow lakes, and/or oil palm plantations. Malay civets captured closer to tributaries contained significant and predictably greater hair Ba, Cd, Cr, and Fe concentrations, suggesting tributaries may be exposure sources of these metals. Specific exposure modes could be either from civets directly using the tributaries as drinking water, or ingesting food items from these riparian regions. One possible explanation is that the Kinabatangan tributaries are polluted with palm oil extraction by-product, POME, which can contain excessive concentrations of these metals prior to treatment (Ohimain et al., 2012). Research by Jamal et al. (2007) determined raw Malaysian POME contained Cr and Cd levels 120 and 170 times greater, respectively, than the US EPA's maximum contaminant levels for drinking water (EPA, 2019). Similarly, POME collected from Thailand contained over 40 ppm of Fe prior to treatment (Agustin et al., 2008). Alternatively, or perhaps concurrently, these metals may be applied to the oil palm yet are distally transported into the LKWS system via surface runoff into the tributaries; Cd, Cr, and Fe are documented contaminants in mineral fertilisers (Atafar et al., 2010; Molina et al., 2009), while barium carbonate is the active agent in some rodenticides (Kravchenko et al, 2014). Given the size of the Malay civet dataset, these models were unable to distinguish between specific tributaries; some of the semi-permanent LKWS tributaries are little more than drainage ditches directly flowing from plantations, while others pass through upwards of 100 km of watershed. To explicitly determine the sources of these contaminants within the limnological system, long-term assessments of the metal concentrations of water and sediment samples from these major tributaries would begin to disentangle these results.

Both Ba and Fe concentrations were further elevated by the presence of accessible oxbow lakes relative to civet sampling location; as all the assessed oxbow lakes were located within the forests of the LKWS, this may indicate civet exposure to Ba and Fe is facilitated by drinking water contaminated from a geogenic source. Indeed, assessments by the DOE reported significantly high Fe concentrations were detected in all sampled wells across Sabah (DOE, 2015), although this was attributed to agricultural processes.

The interpretation of the significantly positive relationships between hair As and Hg concentrations and the distance between a civet's capture location and accessible tributary is not readily apparent, but suggests exposure to these metals is unlikely to be via contaminated water. As previously stated, further research into the possible sources of these elements is recommended, particularly considering the organismal toxicity of these metals (Dietz et al., 2013; Eisler et al., 1988).

Interestingly, only hair Fe varied with the distance from a civet's capture site to an accessible oil palm plantation; civets captured closer to the agriculture expressed elevated hair Fe. This relationship suggests exposure to Fe may be occurring within the agriculture in addition to via the waterways as discussed above. However, given the essentiality of Fe to biological processes and thus the homeostatic mechanisms regulating the total body Fe burden, these results should be further explored within the context of civet clinical health parameters (Chapter 2).

As very little is known regarding the crop management schemes of the region's plantations, these models may not appropriately account for site-specific variations in agricultural practices (see Kurniawan et al., 2018), which in turn, would alter civet metal exposure probabilities across the landscape. Geostatistical analyses that take into consideration the position of civet captures across the landscape, such as kriging, are recommended to tease apart if specific oil palm plantations or tributaries act as metal sources (e.g. Ha et al., 2014). Further, the proximity of a capture site to the nearest oil palm plantation may not directly equate to the probability of a civet utilising the agriculture (and thus directly exposed to any plantation-specific pollutants). Other factors not accounted for in hair metal models, such as plantation understory structure, large drainage ditches, or the presence of dogs (see discussion of Chapter 4) could be more influential in determining the probability of oil palm plantation usage by a Malay civet than proximity of capture site; this could in turn cloud the determination of possible plantation-linked pollution sources. Specific evaluations of hair metal concentrations of the GPS-collared males with known spatial behaviours would provide further indications of oil palm plantation pollution sources.

5.4.4 Future research

Future studies aiming to explore metallic pollution within the LKWS landscape must focus on several technical and theoretical aspects this study was unable to answer. Firstly, and most apparently, environmental monitoring must be conducted. Metal contents of soil, water, and vegetative samples should be determined, following rigorous methodologies such as those conducted by Islam et al. (2015). These data would more clearly paint a background picture for what is considered geogenically 'normal' within the LKWS region, while simultaneously uncovering source and sink dynamics of localised metal pollution. More targeted efforts to uncover the region's POME treatment processes and oil palm plantation crop management schemes should be undertaken to develop and test specific hypotheses regarding potential sources of anthropogenic metal pollution.

Complementarily, more explicit studies of small carnivore dietary composition should be undertaken within an ecotoxicological framework to begin to determine specific exposure pathways. Although several descriptive studies exist reporting the diversity of civet diets, the metallic contents of these items have not been assessed, and such findings would begin to establish dietary metal sources for small carnivores. Research linking carnivore hair metal excretion to dietary sources has been conducted in natural systems, particularly Hg (foxes, Bocharova et al., 2013; grey wolves, McGrew et al., 2014; grizzly bears, Noël et al., 2014). Generalist species, including civets, often adopt flexible dietary strategies in order to better adapt to disturbed habitats (Dunlop et al., 2017; Habtamu et al., 2017; Nakashima et al., 2013); it is therefore crucial to include these considerations when evaluating pollution risks to apparently adaptable wildlife in agricultural landscapes. Indeed, the results of Chapter 2 suggest Malay civets captured closer to oil palm may have a different diet than those in the larger forest lots of the Sanctuary. Although the usage of a sentinel species is a valuable investigative tool, to more deeply evaluate the risks posed by metals within the LKWS and associated biodiversity as a whole, a trophically-dynamic sampling regime should be undertaken through the diversification of biotic sampling units. Such a study would further evaluate if the Kinabatangan community is experiencing detectable heavy metal transference and biomagnification, such as research conducted by Luo et al. (2015) or reviewed by Gall et al. (2015).

In addition to the difficulties translating civet hair metal concentrations into explicitly risky exposure events, the usage of hair as a biomonitoring tissue has several additional limitations. In terms of mammalian physiology, the lifecycle, and thus metal excretion rates, of hair is dynamic. In humans, Tobin et al. (2005) reported 90% of hair follicles actively synthesise hair (deemed the anagen phase), while the remainder is dormant in the telogen phase. Animals can have more distinct hair growth cycles, such as those species that undergo seasonal moulting events (Hernout et al., 2016); no such cycle is known to exist for civet species. The review conducted by Kempson and Lombi (2011) suggested differing hair growth cycles could thus add to intra- and inter-individual variations in hair metal measurements. In this study, our preliminary method development analyses contrasting the metal concentrations of scapular versus forelimb hair reported little variation between the two except for Hg. As such, it is recommended that further hair studies follow a standardised scapular junction collection method to avoid toxicokinetic bias from sampling differing hair types. Further research into the roles of hair growth rates and hair types on metal excretion rates would aid in the development of civet hair as a biomonitoring tissue.

At the species-level, additional research evaluating civet-specific biokinetics of these metals is warranted to more clearly evaluate the risks posed by metallic pollutants at a given hair concentration measurement. First, an exploration of the relationship between metal concentrations in civet hair and in more traditional samples (i.e. blood or urine) and excretory organs (i.e. liver, brain, kidneys) would enhance the weight of these results. Whole-body metal burden and tissue correlation research such as that by Dainowski et al. (2015), Hernández-Moreno et al. (2013), and Hernout et al. (2016) would be relatively straightforward to replicate given adequate resources; with the growing intensity of road development in Borneo (Alamgir et al., 2019; Laurance, 2016), the prevalence of roadkilled carnivore specimens will increase (e.g. Laton et al., 2017; Nájera et al., 2013). The opportunistic collection of carcasses could expand both the biokinetic scope and the spatial scale of ecotoxicology evaluations across Sabah. Secondly, hair metal concentrations reported here, particularly those of non-essential metals, should attempt to be related to physiologically detectible clinical health repercussions to more fully evaluate the physiological effects of elevated civet hair metal concentrations.

A metal's bioavailability and toxicity can depend on the chemical speciation of the target element (Yokel et al., 2006; Peakall & Burger, 2003). This could refer to the specific form of the element as a part of an organometallic compound; for example, methyl mercury (MeHg) is significantly more toxic for mammals than inorganic mercury (Basu et al., 2005; Clarkson, 2002). Alternatively, the oxidation states of metallic ions can influence its biotoxicity; trivalent chromium (Cr[III]) is an essential element for some species, while hexavalent chromium (Cr[VI]) is environmentally toxic at small concentrations (Rakhunde et al., 2012). Some research exists on the chemical form of metals stored in hair tissue; Kehrig et al. (1998) reported 90% of measurable hair mercury was methylmercury, but similar analyses are lacking for the other metals analysed here. The techniques employed in this study return total concentrations of each metal element, not explicit chemical speciation information; more targeted analyses would be required to evaluate the forms, and thus biotoxicity, of these metals within civets and the Kinabatangan (see Caruso et al., 2003; Feldmann et al., 2018).

It is important to emphasize that no civet is a figurative metal-accumulating island within the Kinabatangan ecosystem, and other pollutants often synergistically act on wildlife, which may eventually undermine any foothold these adaptable species have managed to carve out in the landscape. Inorganic pollution occurs in the larger context of plantation contaminants as a whole, which includes a suite of organic agrochemicals such as rodenticides, herbicides (Carvalho, 2006), and oxide pollution (Hewitt et al., 2009). In the even larger context, other Southeast Asian pollution stressors such as traffic-related pollution

(Praveena, 2018), macro- and micro-plastics (Praveena et al., 2018), sewage (Zhao et al., 2006), pharmaceutical pollutants, and long-range globally persistent pollutants (Leong et al., 2007) will invariably additively impact the region's biodiversity. Large regional fires associated with intensifying El Niño-Southern Oscillation events and (illegal) agricultural practices (Chapter 4) will release more metals, carbon, and other harmful pollutants into the floodplain (Dislich et al., 2017; Fuller & Murphy, 2006). Studies aimed at uncovering the conservation status of LKWS wildlife should acknowledge the potential additive effects of these varied anthropogenic pressures.

Although exact sources cannot be immediately determined solely from these hair metal profiles, the usage of civets as landscape sentinels provide justification for more extensive studies into pollution risk assessments across this fragmented landscape. These results will require future studies to elucidate the exact routes and implications of metal exposure, and more importantly, design appropriate mitigation actions for the benefit of the ecosystem.

Appendix IV. Supplementary information for ecotoxicology analyses

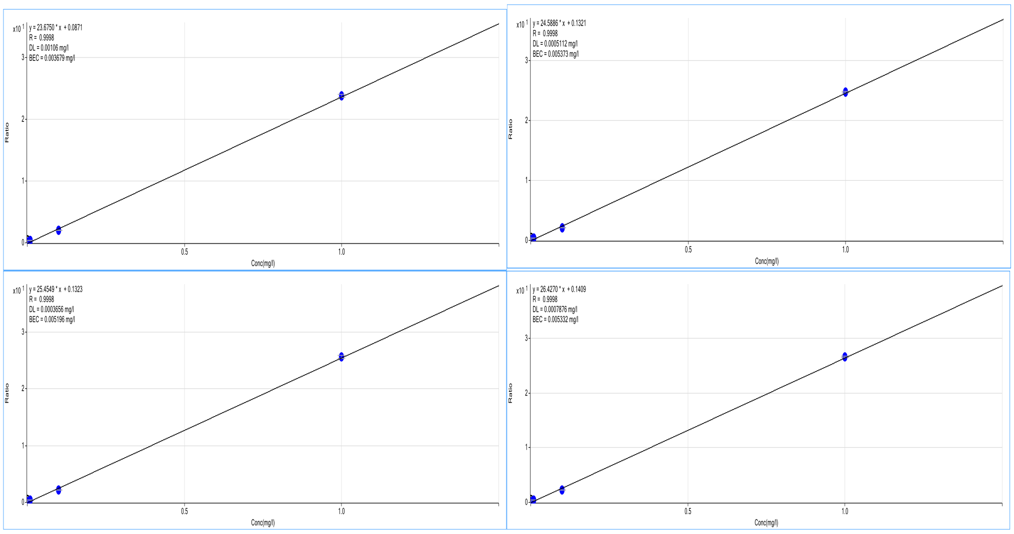


Figure A4.1. Calibration curves and detection limits for aluminum analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

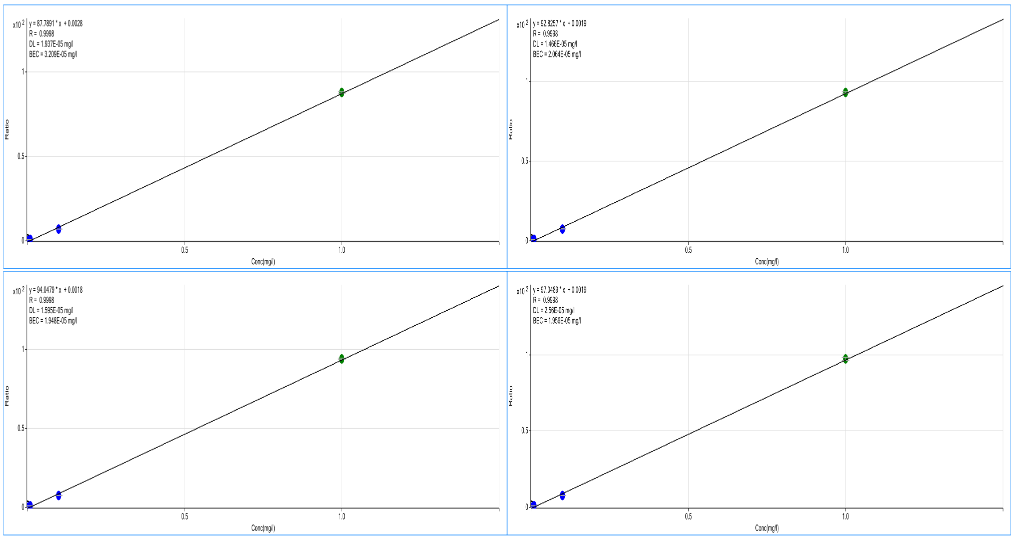


Figure A4.2. Calibration curves and detection limits for arsenic analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

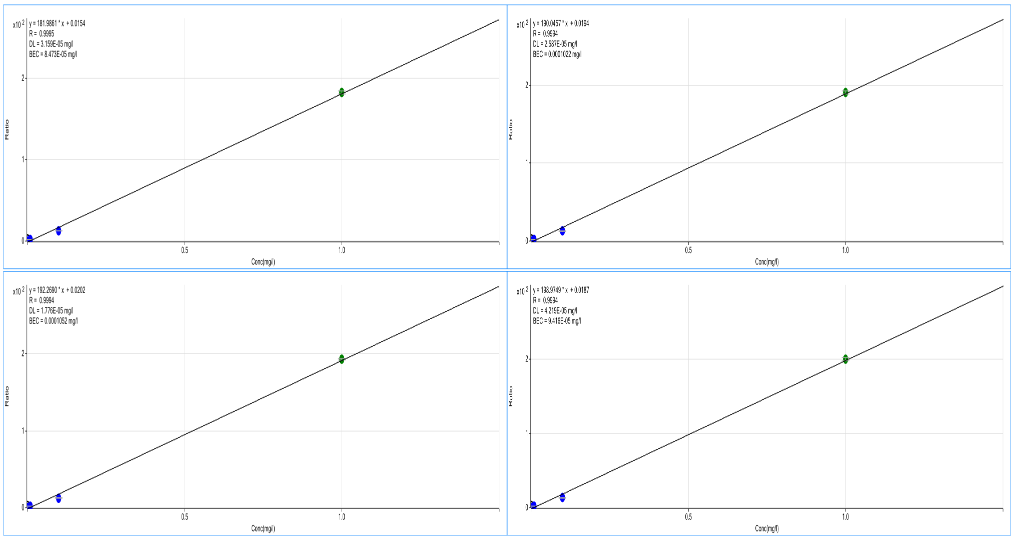


Figure A4.3. Calibration curves and detection limits for barium analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

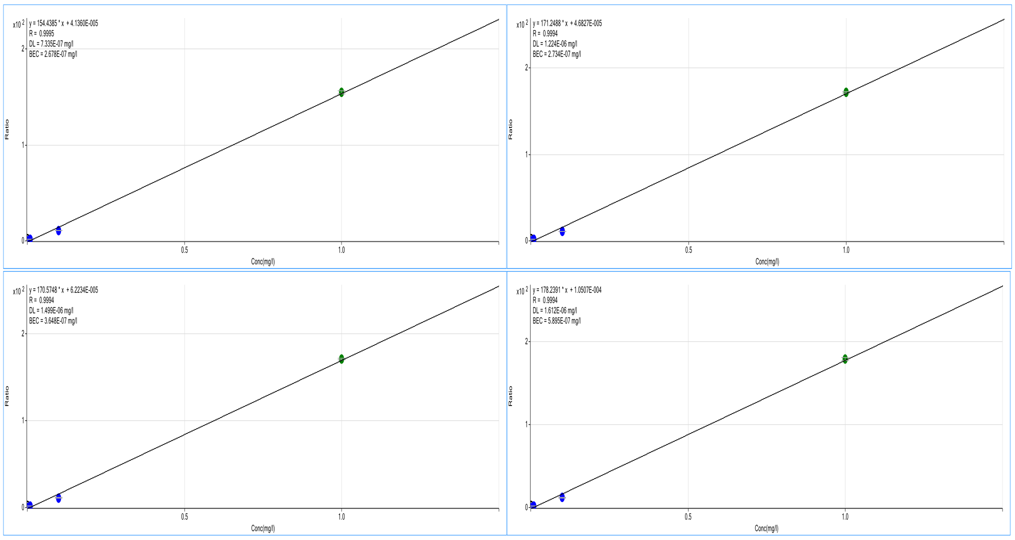


Figure A4.4. Calibration curves and detection limits for cadmium analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

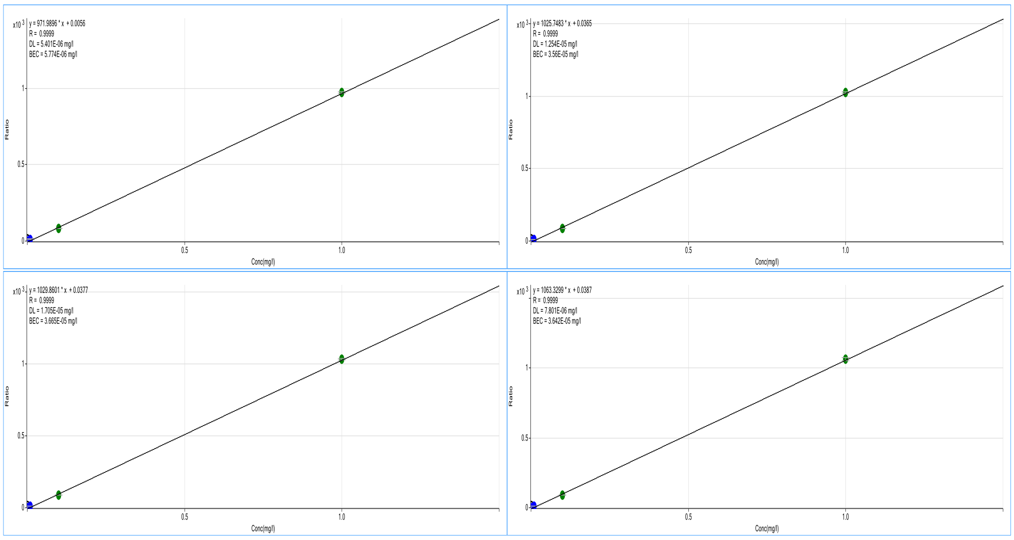


Figure A4.5. Calibration curves and detection limits for cobalt analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

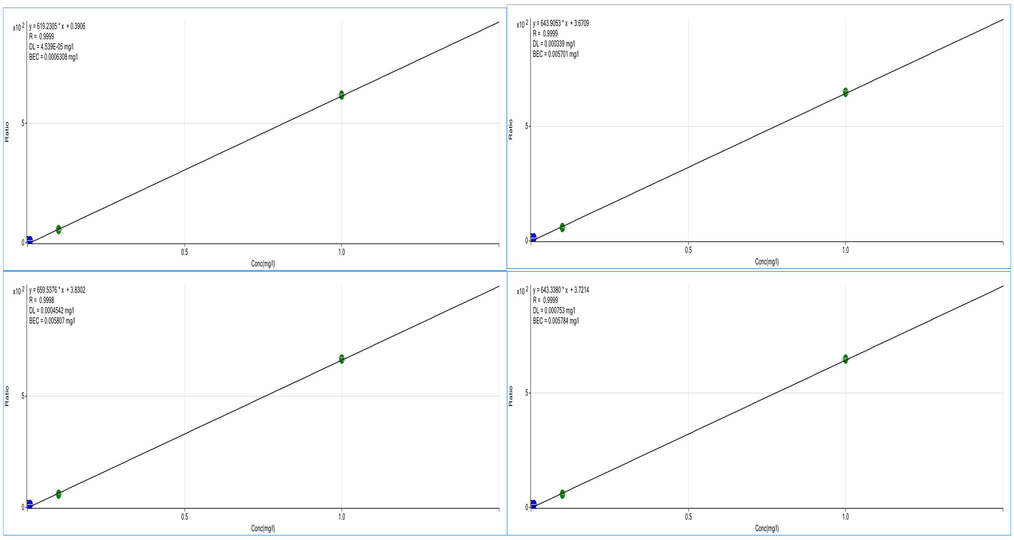


Figure A4.6. Calibration curves and detection limits for chromium analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

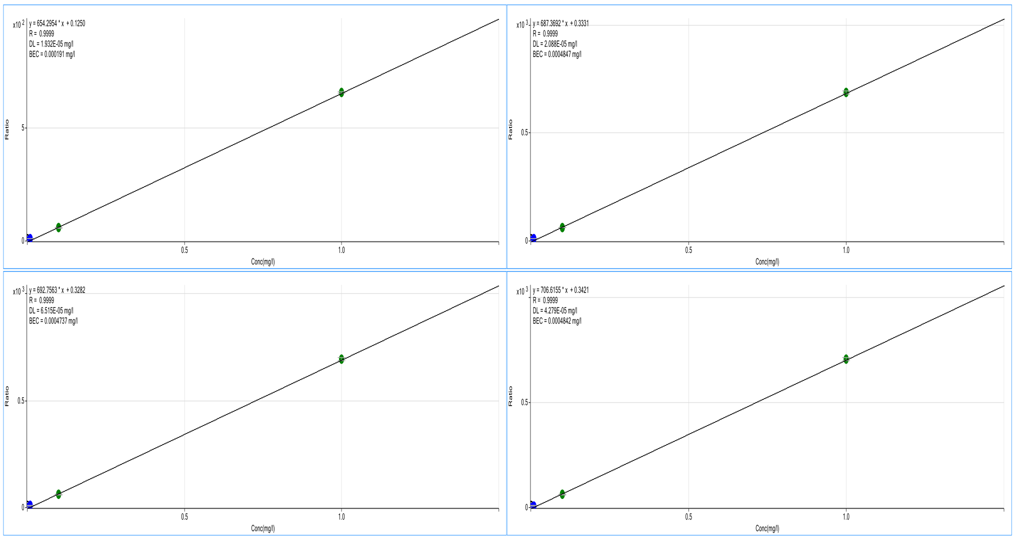


Figure A4.7. Calibration curves and detection limits for copper analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

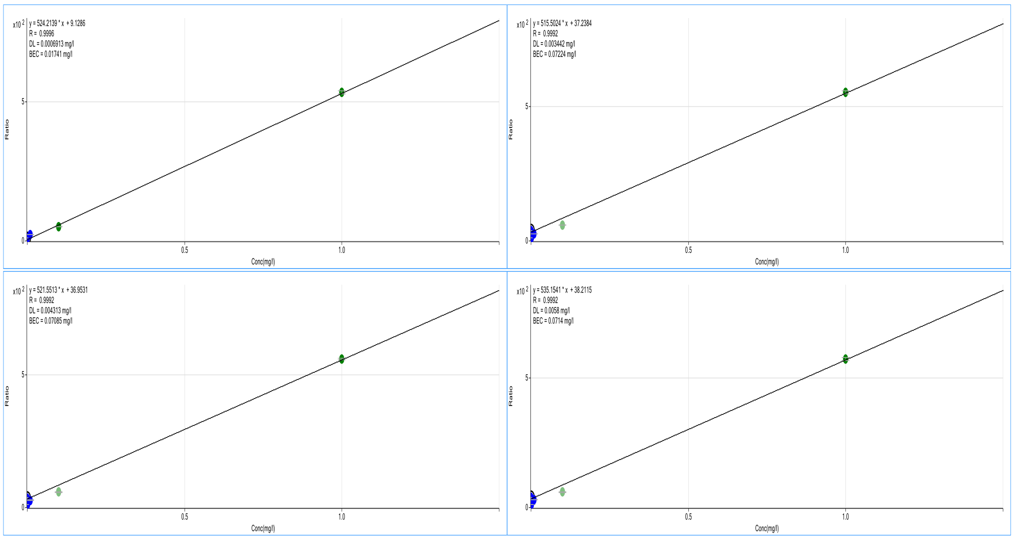


Figure A4.8. Calibration curves and detection limits for iron analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

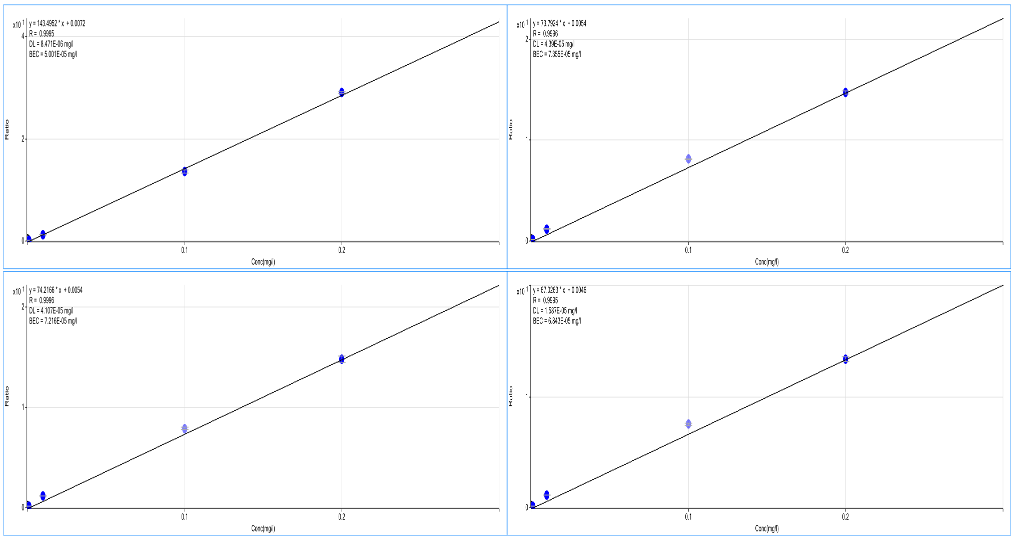


Figure A4.9. Calibration curves and detection limits for mercury analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

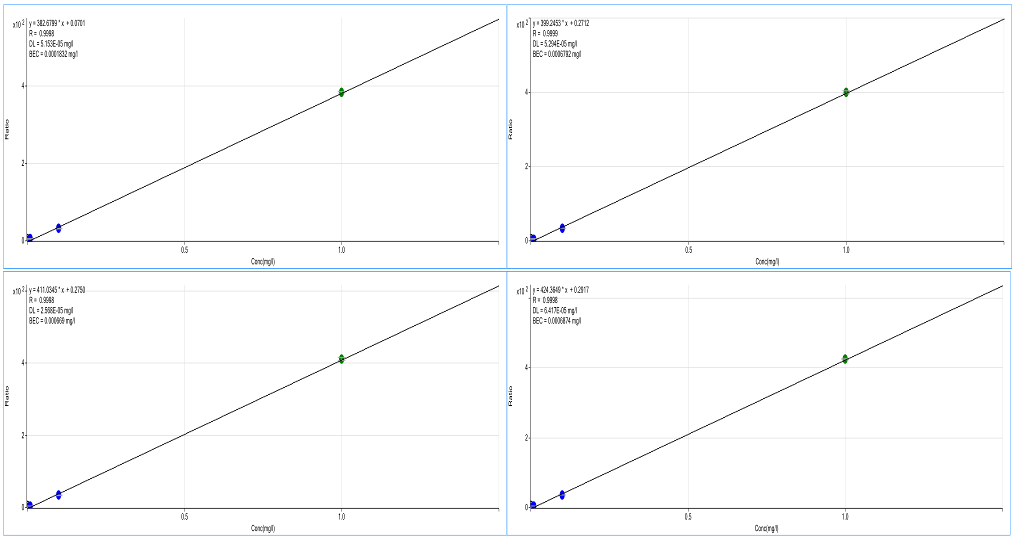


Figure A4.10. Calibration curves and detection limits for manganese analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

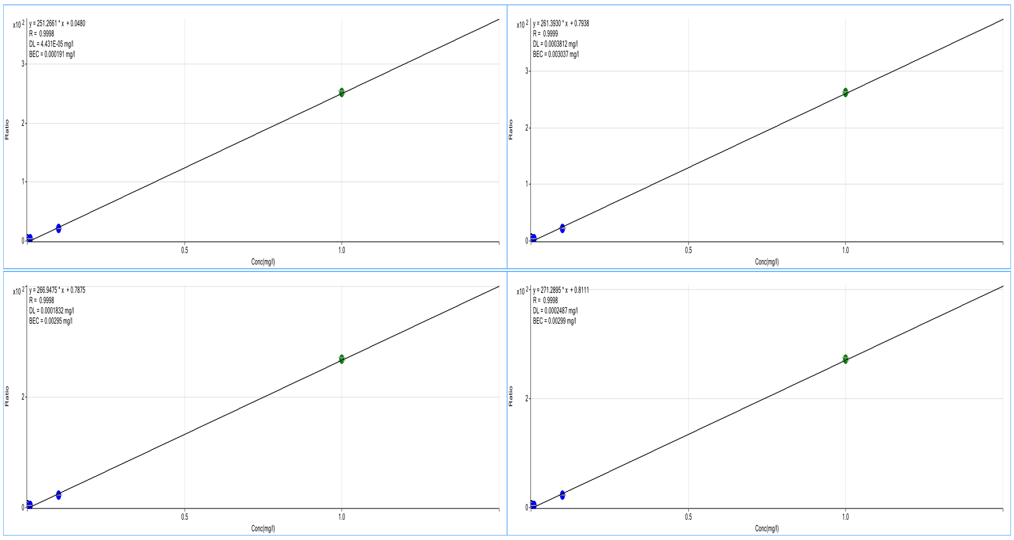


Figure A4.11. Calibration curves and detection limits for nickel analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

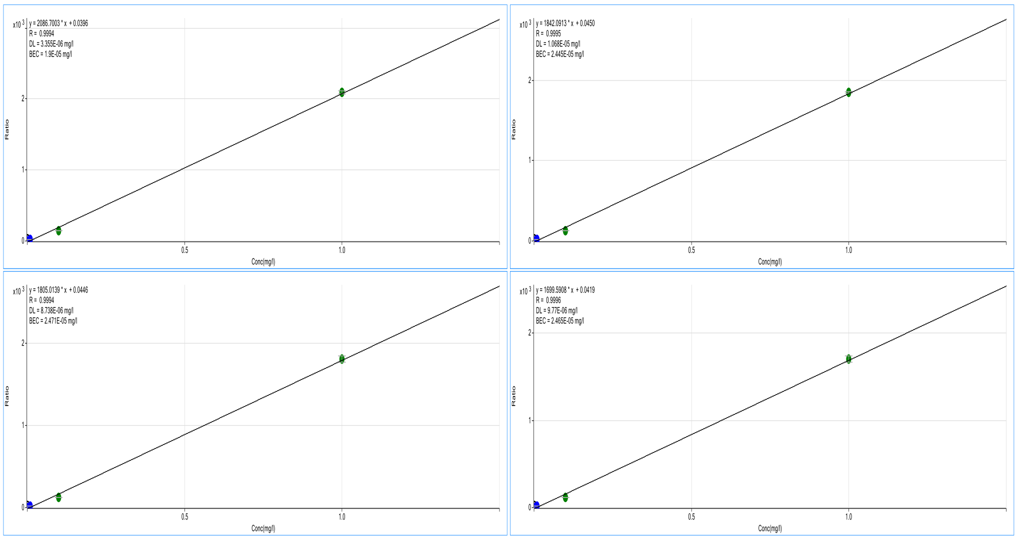


Figure A4.12. Calibration curves and detection limits for lead analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

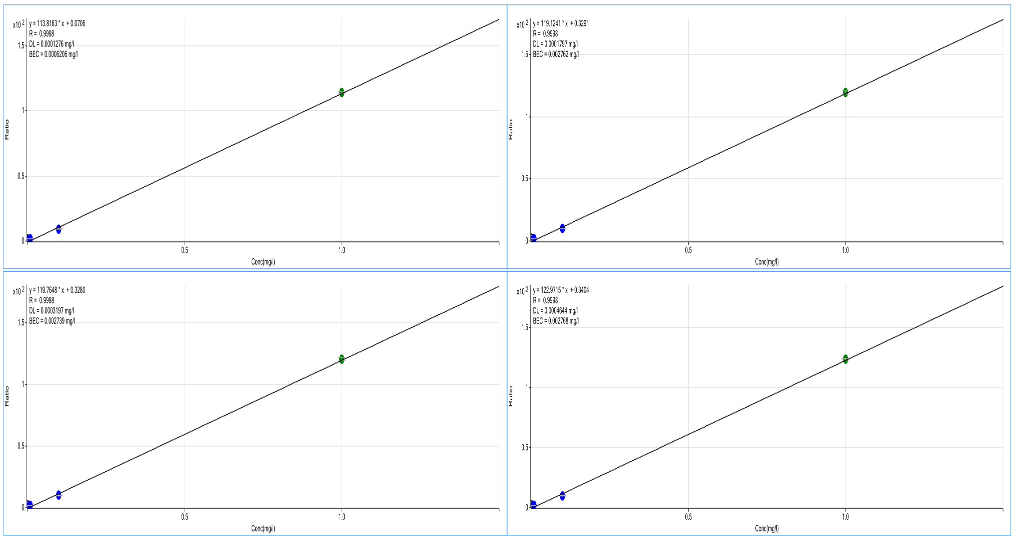


Figure A4.13. Calibration curves and detection limits for zinc analysed by bulk acid-digestion ICP-MS; presented in quadruplets. DL denotes batch detection limit, in mg/l; R is the linear correlation value; BEC denotes background equivalent concentration.

Table A4.1: Paired t-test results evaluating the role of pre-analysis washing on Malay civet hair metal concentrations (n = 4); treatment values expressed as mean ± SE, mg kg^{-1}

Element	Unwashed	Washed	Mean metal concentration difference following treatment	t value
Al	110 ± 20.2	86.3 ± 20.1	-23.9	1.969
As	0.014 ± 0.0201	0.0444 ± 0.0375	0.0321	-1.225
Ba	11.7 ± 5.03	10.9 ± 5.49	-0.826	0.351
Cd	0.0124 ± 0.00793	0.0112 ± 0.00582	-0.00126	0.981
Co	0.125 ± 0.0688	0.278 ± 0.179	0.154	-1.524
Cr	5.16 ± 3.86	3.00 ± 1.67	-2.16	1.820
Cu	6.71 ± 1.7	8.34 ± 3.33	1.63	-1.247
Fe	440 ± 126	353 ± 197	-87.8	1.360
Hg*	2.06 ± 0.694	1.27 ± 0.427	-0.792	5.664
Mn	17.6 ± 16.3	25.7 ± 20.9	8.07	-1.282
Ni	0.745 ± 0.375	1.32 ± 0.863	0.575	-0.959
Pb	0.203 ± 0.186	0.197 ± 0.132	-0.00617	0.176
Zn	140 ± 30.3	164 ± 72.2	24.6	-0.839

**denotes statistically significant differences between treatments, such that $p < 0.05$*

Table A4.2: Comparative hair metal concentration results between paired scapular junction and forelimb Malay civet samples (n = 4). Values expressed as mean ± SE ($^\wedge$or median ± IQR), mg kg^{-1}

Element	Forelimb	Scapular Junction	Mean metal concentration difference by type	Test statistic
Al	234 ± 146	123 ± 74	-111.2	1.672
As	0.0939 ± 0.105	0.0939 ± 0.1	0.0000931	-0.015
Ba$^\wedge$	23.2 ± 52.5	16.9 ± 14.1	-6.3	8.000
Cd	0.0188 ± 0.00485	0.0087 ±0.0061	-0.0101	2.242
Co	0.169 ± 0.133	0.0974 ± 0.0517	-0.0721	1.015
Cr	1.37 ± 0.691	0.932 ± 0.398	-0.442	1.409
Cu	10.1 ± 2.69	8.5 ± 3.44	-1.59	0.746
Fe$^\wedge$	536 ± 515	398 ± 69.5	-138	9.000
Hg**	1.91 ± 0.133	2.99 ± 0.386	1.082	-7.366
Mn	12.2 ± 3.26	8.62 ± 3.42	-3.56	1.106
Ni$^\wedge$	0.578 ± 0.403	0.526 ± 0.758	-0.052	3.000
Pb	0.446 ± 0.241	0.175 ± 0.0877	-0.271	1.952
Zn	186 ± 64.5	176 ± 60.3	-9.86	0.217

$^\wedge$*denotes differences were non-normally distributed, so elements were analysed by Wilcoxan paired tests and summary statistics presented are median ± IQR; test statistic is V*

***denotes statistically significant differences between hair types, such that p < 0.01*

A4.1 Literature meta-analysis of other hair metal studies

To contextualise the observed hair metal concentrations in this study, a literature meta-analysis was undertaken; hair metal concentration studies in peer-reviewed literature were compiled and contrasted with civet values. If hair metal concentrations did not differ by civet species (Table 5.4), these datasets were combined. Literature included values collected from a range of species, including humans. For further visualisation purposes, studies were subdivided into those evaluating ‘normal’ or ‘exposed’ hair metal concentrations; studies reporting hair metal concentrations of subjects from explicitly stated and identified pollution sources (i.e. mine, industrial operations, etc.) were deemed ‘exposed’.

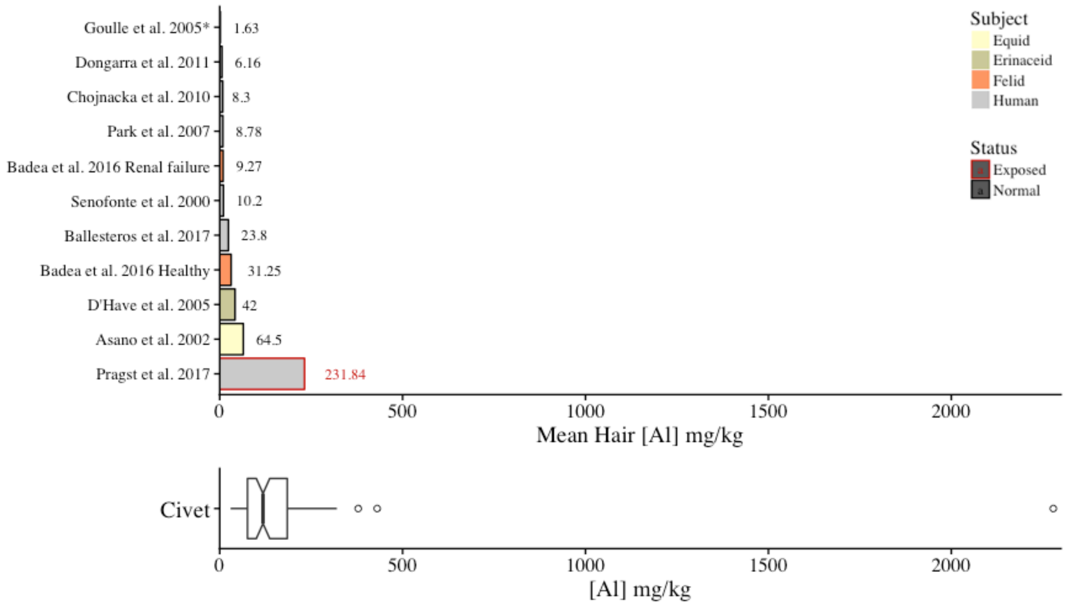


Figure A4.14. Graphic overview of mean reported hair aluminum (Al) concentrations contrasted with the boxplot representation of the current study's datasets.

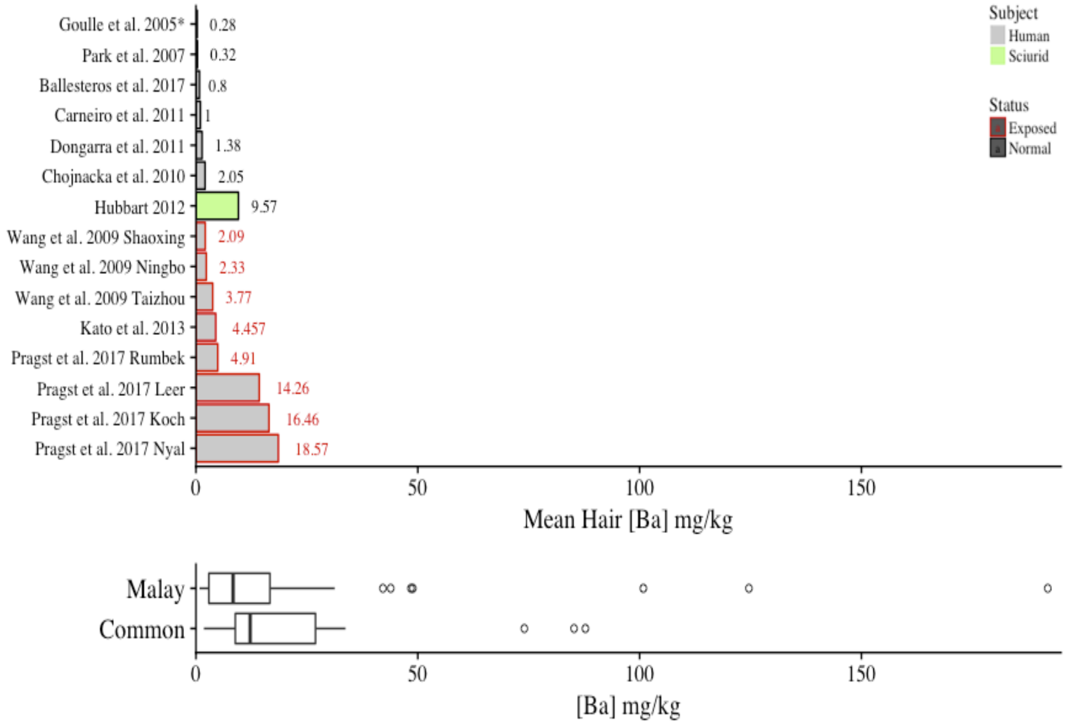


Figure A4.15. Graphic overview of mean reported hair barium (Ba) concentrations contrasted with the boxplot representation of the current study's datasets.

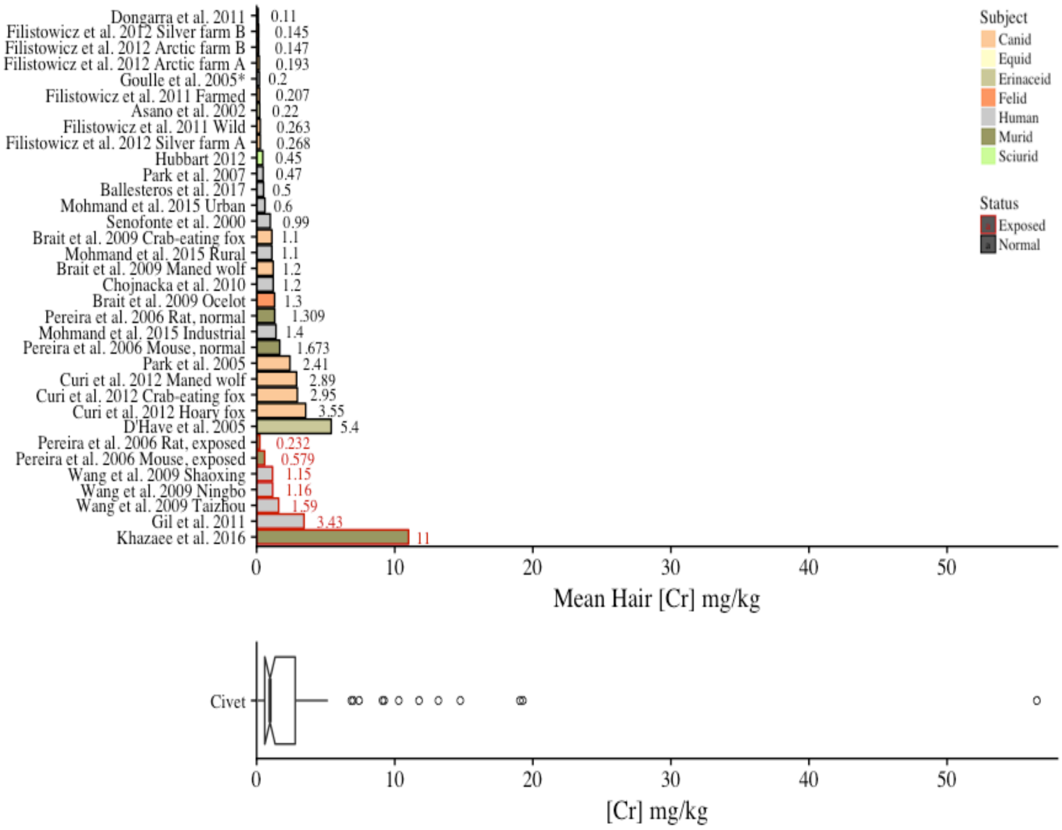


Figure A4.16. Graphic overview of mean reported hair chromium (Cr) concentrations contrasted with the boxplot representation of the current study's datasets.

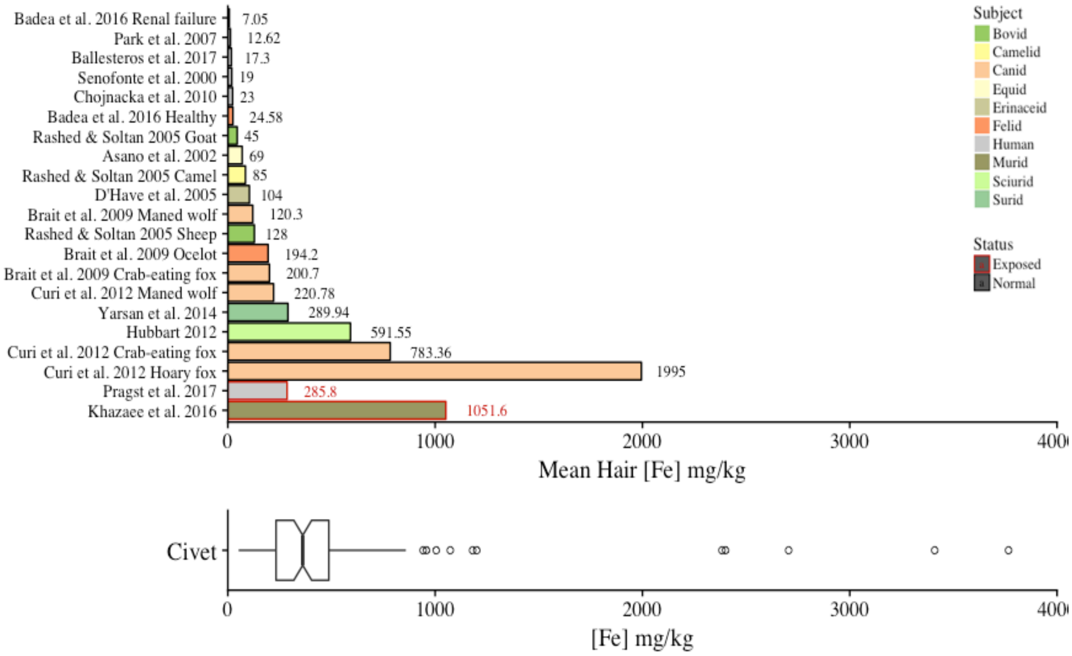


Figure A4.17. Graphic overview of mean reported hair iron (Fe) concentrations contrasted with the boxplot representation of the current study's datasets.

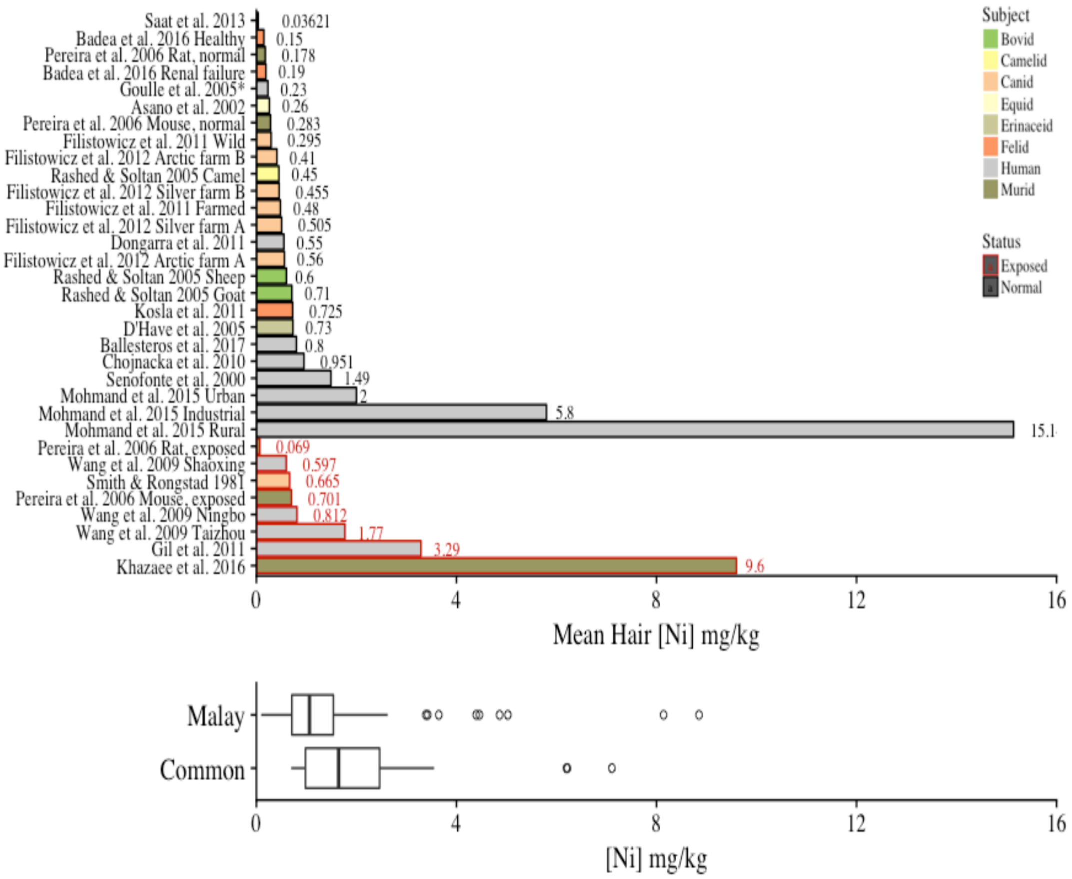


Figure A4.18. Graphic overview of mean reported hair nickel (Ni) concentrations contrasted with the boxplot representation of the current study’s datasets.

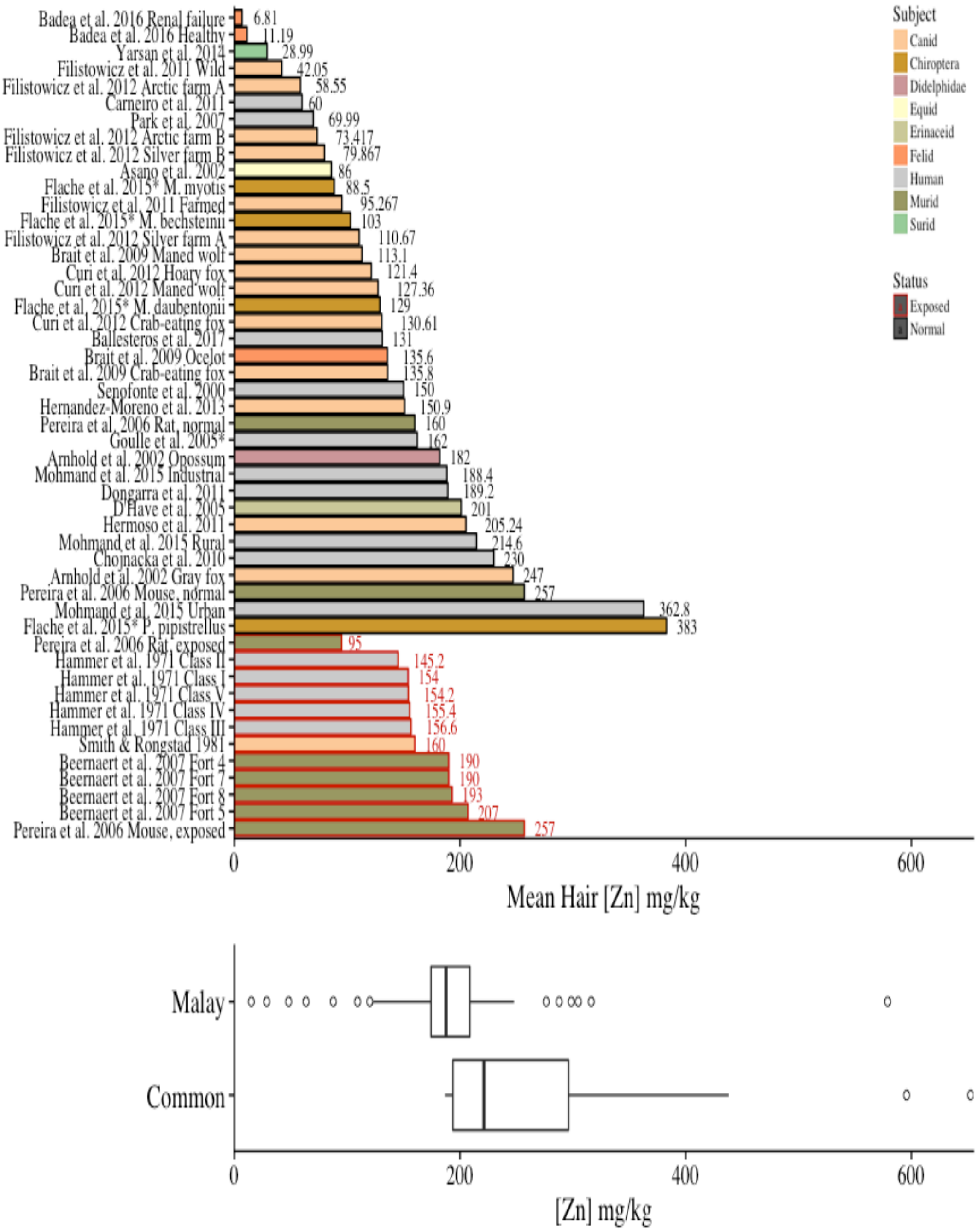


Figure A4.19. Graphic overview of mean reported hair zinc (Zn) concentrations contrasted with the boxplot representation of the current study's datasets.

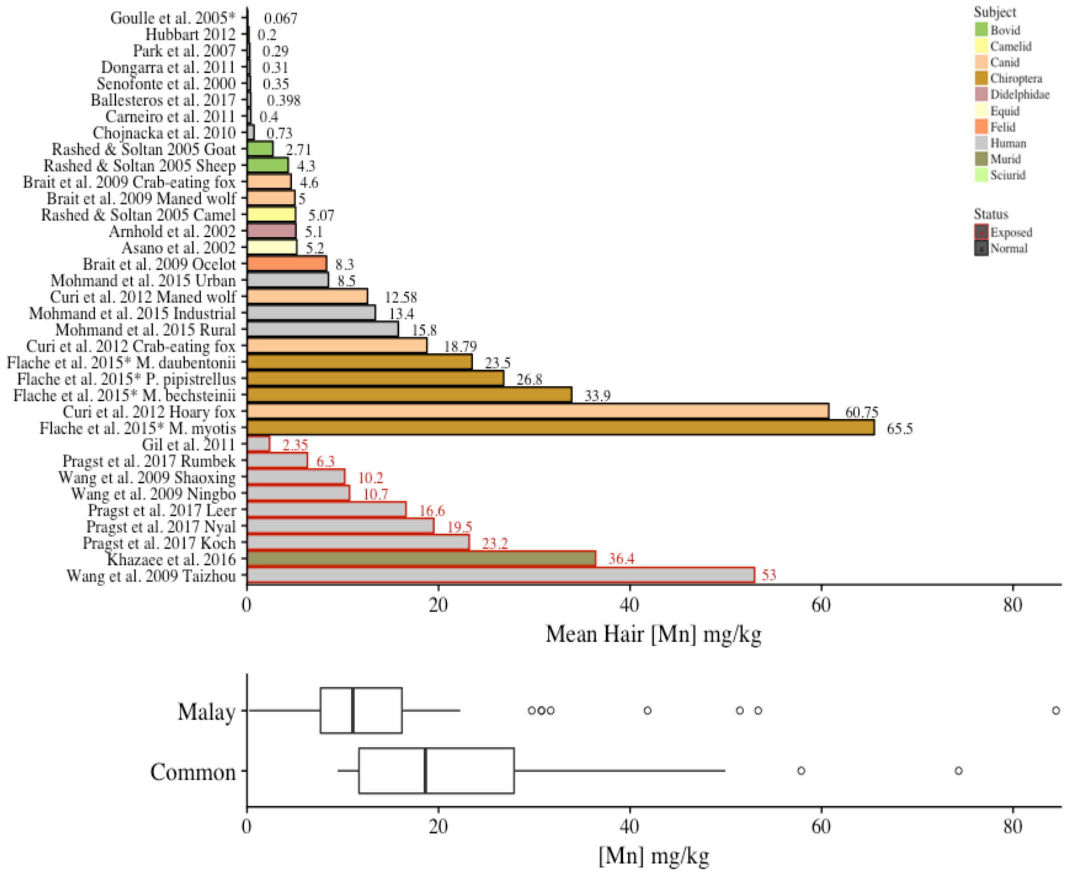


Figure A4.20. Graphic overview of mean reported hair manganese (Mn) concentrations contrasted with the boxplot representation of the current study's datasets.

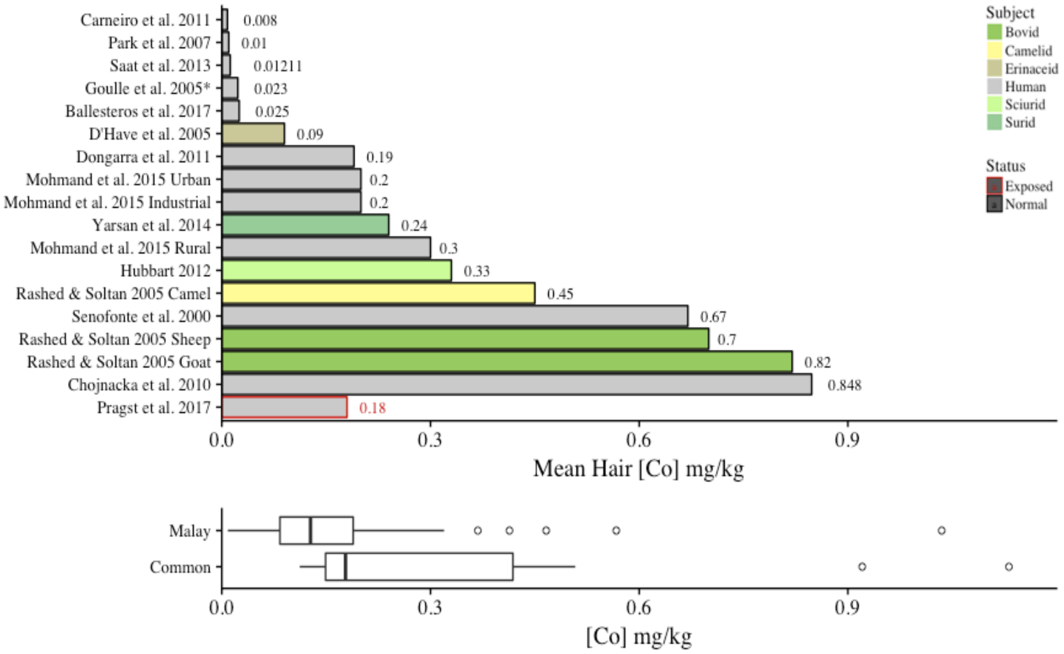


Figure A4.21. Graphic overview of mean reported hair cobalt (Co) concentrations contrasted with the boxplot representation of the current study's datasets.

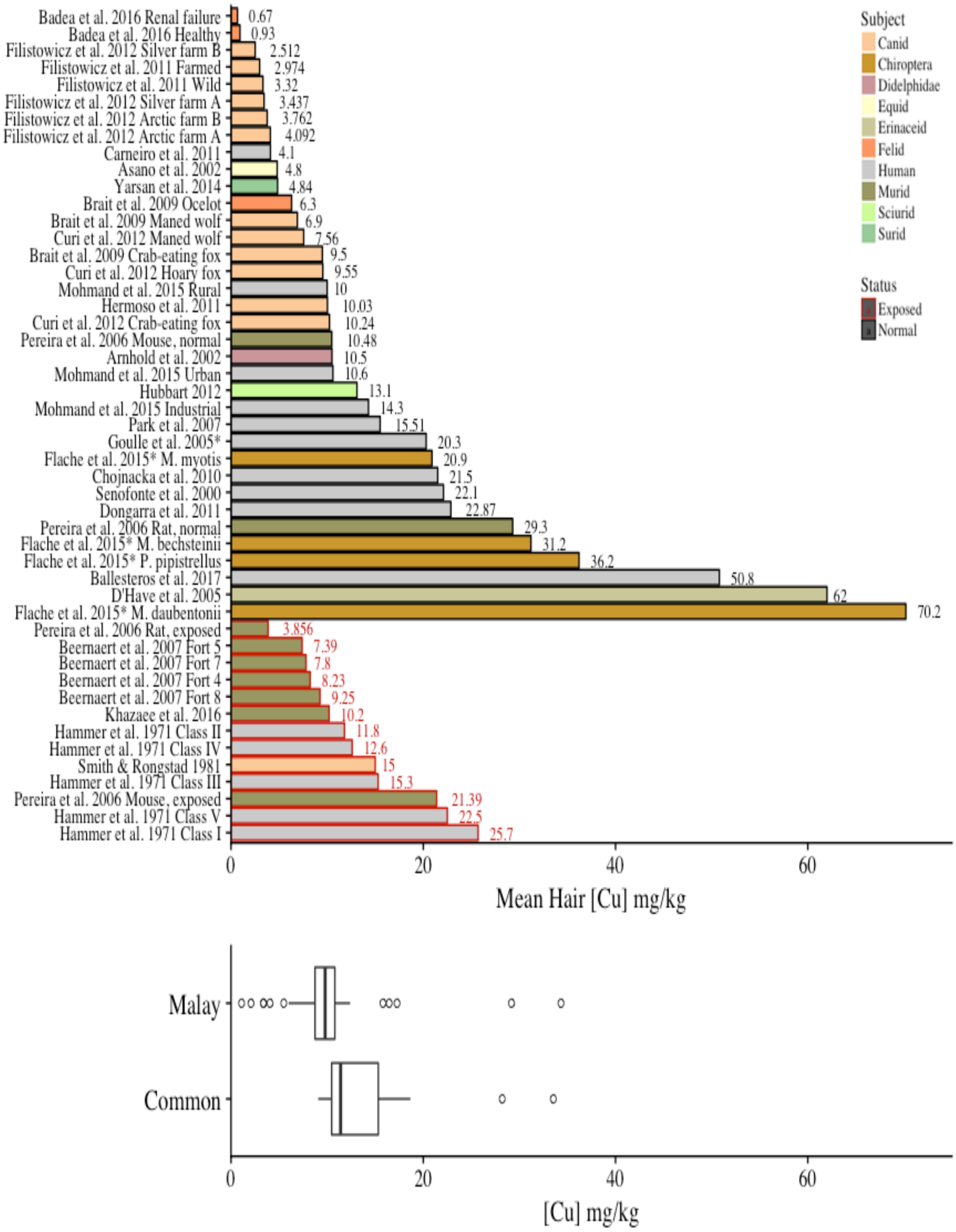


Figure A4.22. Graphic overview of mean reported hair copper (Cu) concentrations contrasted with the boxplot representation of the current study's datasets.

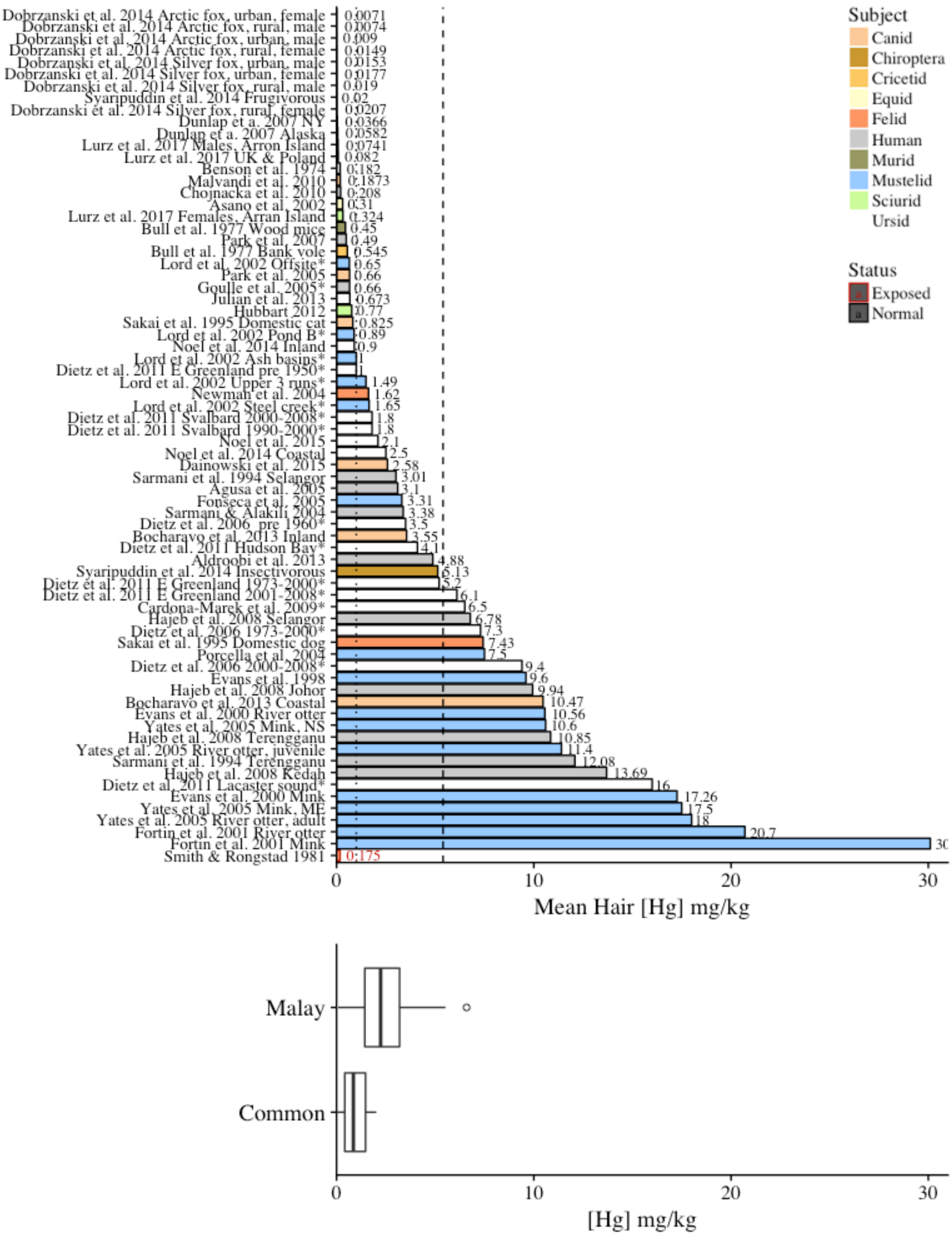


Figure A4.23. Overview of mean reported hair mercury (Hg) concentrations contrasted with the boxplot representation of the current study's datasets. The U.S. EPA maximum guideline Hg concentration for human hair (1mg/kg, cited in FAO/WHO, 2003) is indicated by the vertical dotted line. The vertical dashed line (5.4 mg/kg) represents the polar bear hair concentration threshold beyond which neurochemical alterations have been documented (Basu et al., 2009; Pilsner et al., 2010).

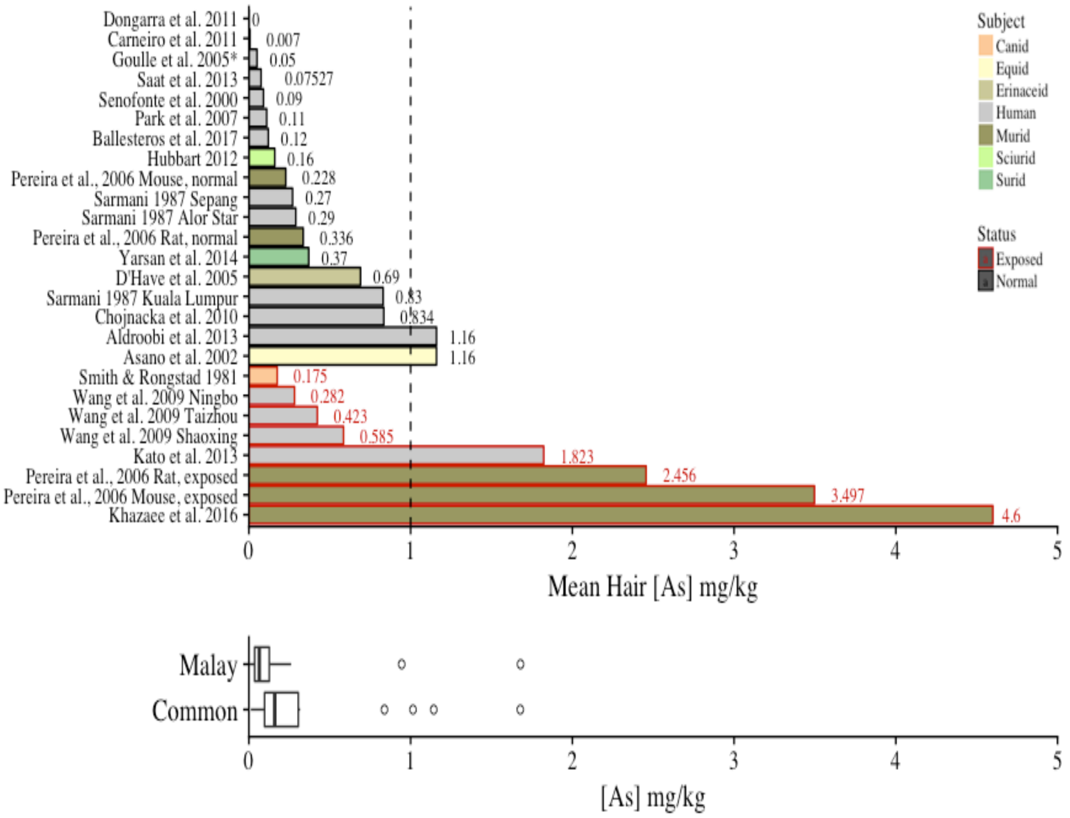


Figure A4.24. Graphic overview of mean reported hair arsenic (As) concentrations contrasted with the boxplot representation of the current study's datasets. The observed effect threshold level for human hair (1mg/kg, Hindmarsh, 2002; Byrne et al., 2010) is indicated by the vertical dashed line.

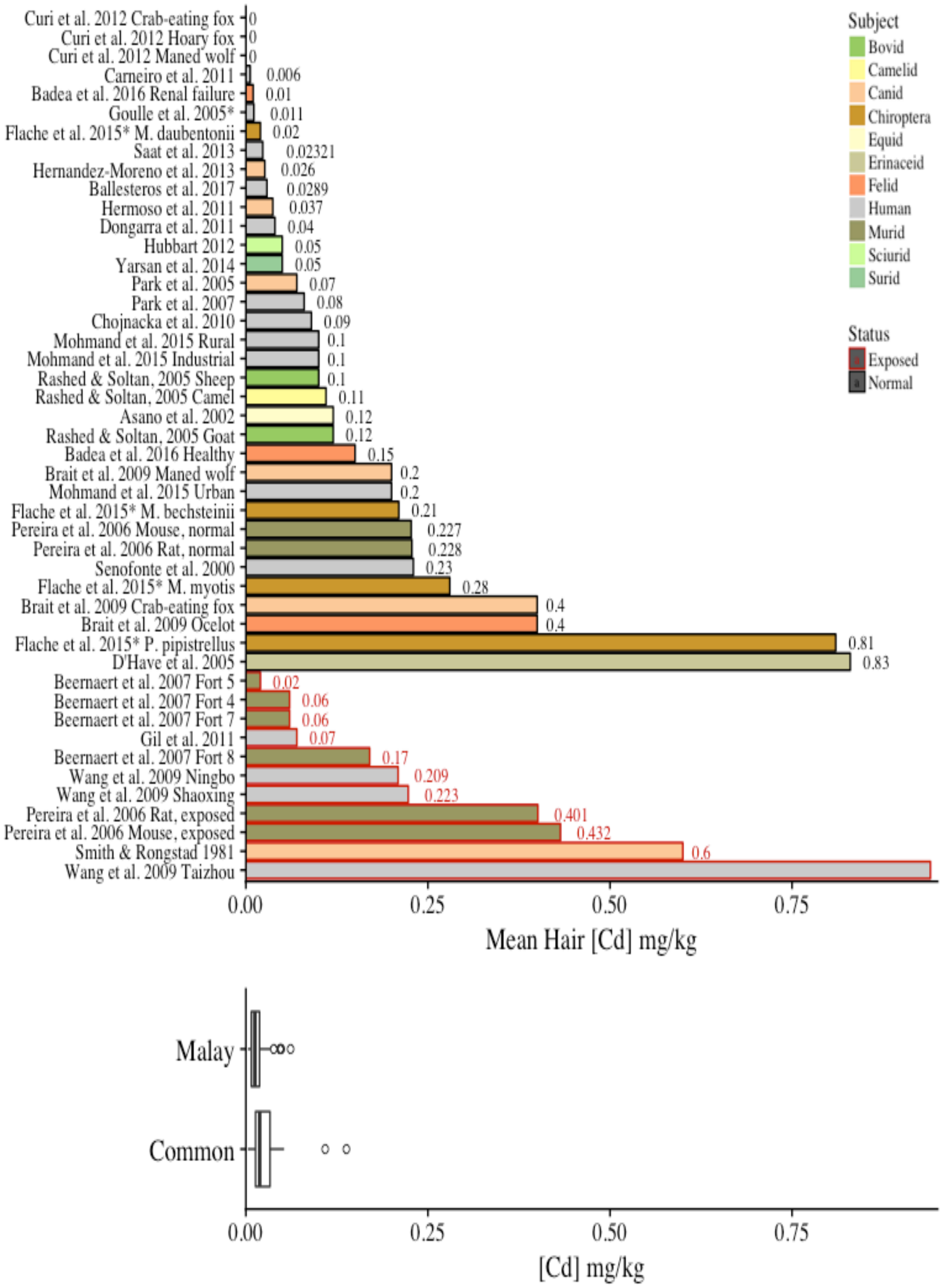


Figure A4.25. Graphic overview of mean reported hair cadmium (Cd) concentrations contrasted with the boxplot representation of the current study's datasets.

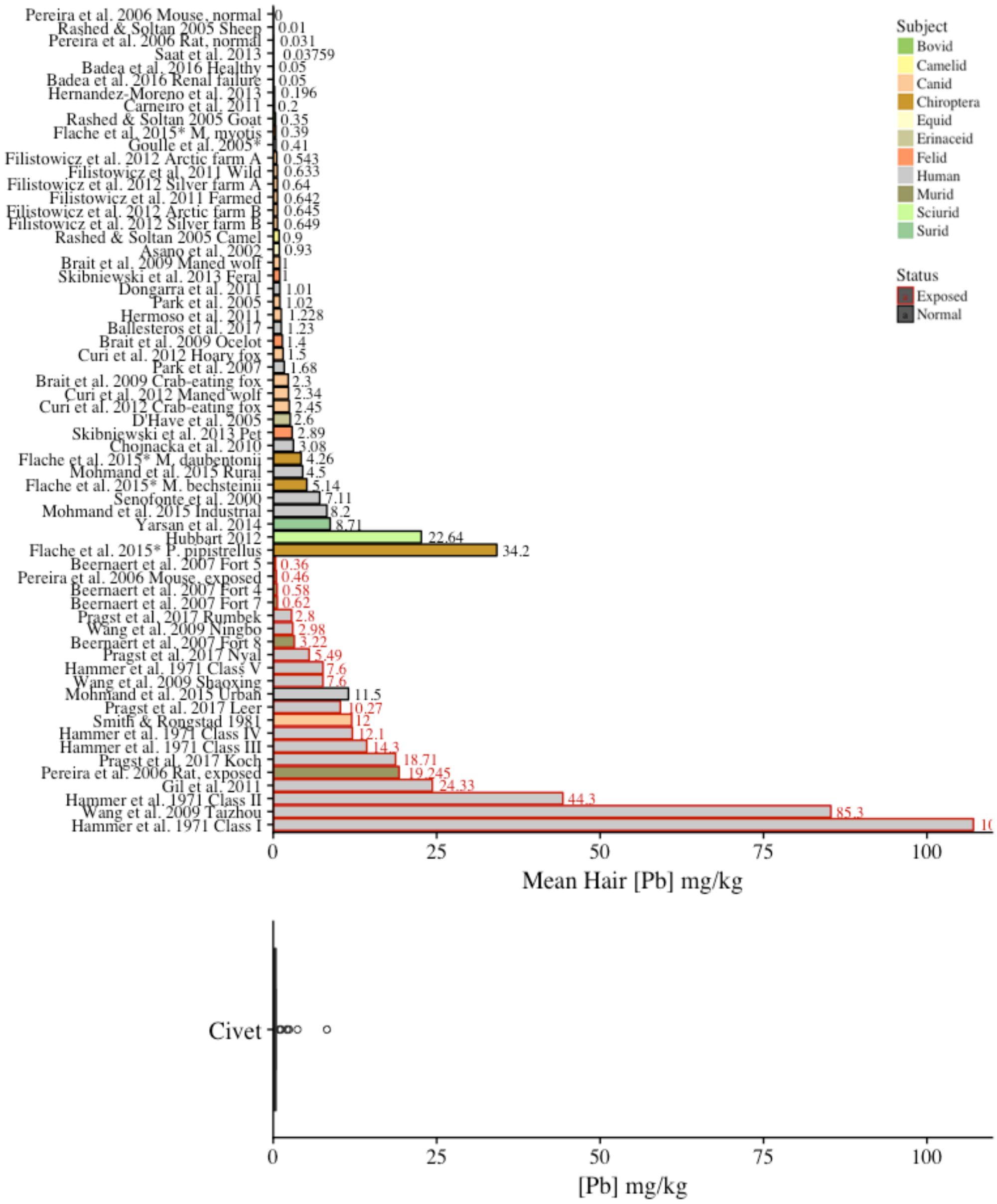
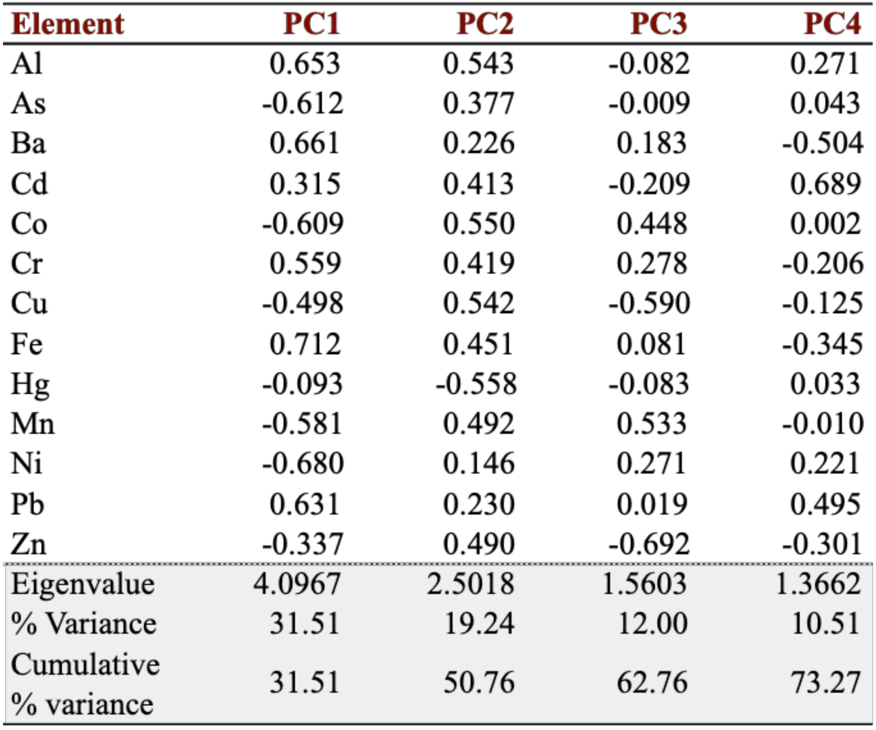


Figure A4.26. Graphic overview of mean reported hair lead (Pb) concentrations contrasted with the boxplot representation of the current study's datasets.

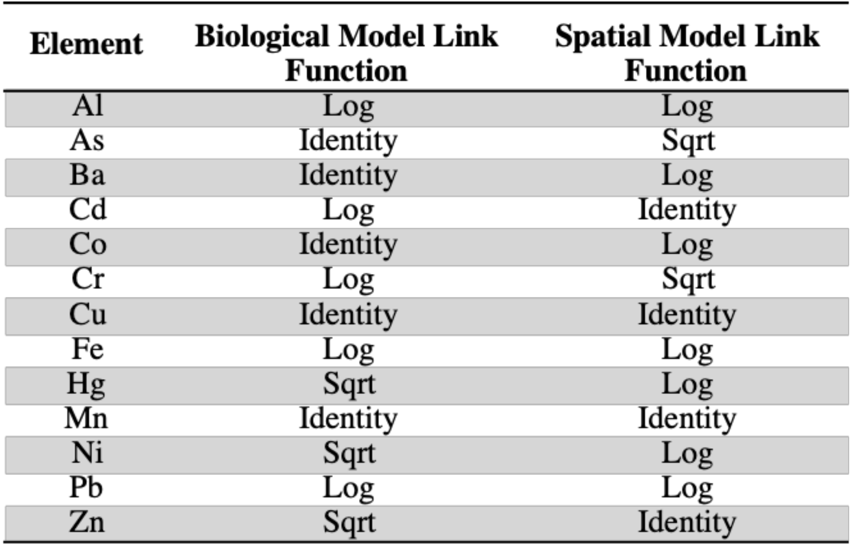
Table A4.3: PCA results of log-transformed Malay civet hair concentrations (n = 69). Values indicate the correlation between each variable (metal) and each principal component (e.g. PC1).



Element	PC1	PC2	PC3	PC4
Al	0.653	0.543	-0.082	0.271
As	-0.612	0.377	-0.009	0.043
Ba	0.661	0.226	0.183	-0.504
Cd	0.315	0.413	-0.209	0.689
Co	-0.609	0.550	0.448	0.002
Cr	0.559	0.419	0.278	-0.206
Cu	-0.498	0.542	-0.590	-0.125
Fe	0.712	0.451	0.081	-0.345
Hg	-0.093	-0.558	-0.083	0.033
Mn	-0.581	0.492	0.533	-0.010
Ni	-0.680	0.146	0.271	0.221
Pb	0.631	0.230	0.019	0.495
Zn	-0.337	0.490	-0.692	-0.301
Eigenvalue	4.0967	2.5018	1.5603	1.3662
% Variance	31.51	19.24	12.00	10.51
Cumulative % variance	31.51	50.76	62.76	73.27

Figure A4.27. PCA biplot diagrams of log-transformed Malay civet hair metal concentrations (n = 69). Points represent the study observations (individual civets), and dark red arrows indicate the study variables (metals). Axes denote the presented principal component, each also indicating the variance explained by each axis (Dim 1–4, as presented in Table A4.3). Element vectors consistently grouped across all plots indicate covariance in the original dataset. Civets within the same quadrant as a metal vector indicate a high corresponding metal value in that dimension.

Table A4.4: Summary of link functions utilised in the generalised linear mixed modeling of the influence of biological and landscape-level parameters on hair element concentrations. All models were fitted to a Gamma error distribution and link functions were determined by optimisation of model assumptions and fit (i.e. lowest AIC and most normal standardised residual plots)



Element	Biological Model Link Function	Spatial Model Link Function
Al	Log	Log
As	Identity	Sqrt
Ba	Identity	Log
Cd	Log	Identity
Co	Identity	Log
Cr	Log	Sqrt
Cu	Identity	Identity
Fe	Log	Log
Hg	Sqrt	Log
Mn	Identity	Identity
Ni	Sqrt	Log
Pb	Log	Log
Zn	Sqrt	Identity

Table A4.5: Top candidate (ΔAICc<2) model predictor variables, log-likelihood(Log*L*), Akaike's Information Criterion with the small sample bias adjustment(AICc), and Akaike weights (*wi*) for predicting association between standardised biological parameters and Malay civet hair metal concentrations. Sex = male or female; Agecate = immature or mature.

Element	Candidate Model	df	Log*L*	AICc	ΔAICc	*wi*
Al	Weight	3	-411.39	829.15	0	0.24
	Sex	3	-411.42	829.21	0.07	0.23
	Agecat + Weight	4	-410.34	829.31	0.16	0.22
	Sex + Weight	4	-410.46	829.56	0.42	0.19
	Agecat + Sex + Weight	5	-409.78	830.54	1.39	0.12
As	(Null)	2	80.45	-156.71	0	0.50
	Agecat	3	81.09	-155.81	0.90	0.32
	Weight	3	80.55	-154.72	1.99	0.18
Ba	(Null)	2	-259.39	522.96	0	0.29
	Agecat + Weight	4	-257.43	523.49	0.53	0.22
	Agecat	3	-258.84	524.05	1.09	0.17
	Sex	3	-258.85	524.08	1.12	0.17
	Agecat + Sex	4	-257.82	524.27	1.32	0.15
Cd	(Null)	2	221.70	-439.22	0	0.42
	Weight	3	222.20	-438.02	1.21	0.23
	Sex	3	221.93	-437.48	1.74	0.18
	Agecat + Weight	4	223.01	-437.39	1.83	0.17
Co	(Null)	2	59.03	-113.87	0	0.43
	Weight	3	59.45	-112.53	1.34	0.22
	Sex	3	59.30	-112.22	1.65	0.19
	Agecat + Weight	4	60.33	-112.02	1.85	0.17
Cr	Agecat	3	-147.02	300.42	0	0.43
	Agecat + Sex	4	-146.06	300.75	0.33	0.37
	Agecat + Weight	4	-146.68	301.99	1.57	0.20
Cu	(Null)	2	-191.51	387.21	0	0.54
	Agecat	3	-191.14	388.66	1.45	0.26
	Weight	3	-191.39	389.16	1.95	0.20
Fe	Agecat + Sex + Weight	5	-487.53	986.02	0	0.31
	Sex	3	-489.91	986.20	0.18	0.29
	Agecat + Sex	4	-489.13	986.89	0.87	0.20
	Agecat + Weight	4	-489.15	986.94	0.92	0.20
Hg#*	Agecat + Weight	4	-99.40	201.40	NA	1.00
Mn	(Null)	2	-246.58	497.35	0	0.43
	Agecat + Weight	4	-245.00	498.63	1.29	0.23
	Weight	3	-246.35	499.08	1.74	0.18
	Agecat	3	-246.46	499.29	1.95	0.16
Ni*	Weight	3	-82.25	170.88	0	0.48
	Agecat + Weight	4	-81.70	172.04	1.16	0.27
	Sex + Weight	4	-81.79	172.21	1.33	0.25
Pb*	Agecat + Weight	4	-13.94	36.52	0	0.62
	Agecat + Sex + Weight	5	-13.28	37.52	1.00	0.38
Zn	Agecat	3	-387.69	781.75	0	0.49
	(Null)	2	-389.20	782.59	0.84	0.32
	Weight	3	-388.68	783.74	1.99	0.18

**denotes metals with final averaged structures containing statistically significant terms ($p < 0.05$)*

[#] *denotes a singular and final model structure (no models within 2 AICc of top model)*

Table A4.6: Model-averaged estimates of biological fixed effects for statistically non-significant averaged top-models of Malay civet hair metal concentrations. NS denotes statistically non-significant ($p > 0.05$) term. SexM = male; AgecatM = mature civets. Intercept = standardised reference level for factorised predictor variables (ex: female, immature).

Element	Parameter	Estimate	Std. Error	z value	*p value*
Al	(Intercept)	5.132	0.1597	31.54	<0.0001
	Weight	0.308	0.4076	0.745	*NS*
	SexM	0.1612	0.2822	0.564	*NS*
	AgecatM	-0.1638	0.4164	0.388	*NS*
As	(Intercept)	0.1148	0.0272	4.143	<0.0001
	AgecatM	0.01325	0.03553	0.368	*NS*
	Weight	0.002835	0.02262	0.123	*NS*
Ba	(Intercept)	17.02	3.616	4.62	<0.0001
	AgecatM	-6.443	11.62	0.548	*NS*
	Weight	2.786	7.049	0.392	*NS*
	SexM	1.769	4.727	0.369	*NS*
Cd	(Intercept)	-4.12	0.09272	43.62	<0.0001
	Weight	0.08998	0.1939	0.459	*NS*
	SexM	-0.0193	0.08922	0.213	*NS*
	AgecatM	-0.06976	0.211	0.328	*NS*
Co	(Intercept)	0.166	0.01843	8.84	<0.0001
	Weight	-0.02484	0.04466	0.552	*NS*
	SexM	0.004183	0.01787	0.231	*NS*
	AgecatM	0.01353	0.04036	0.332	*NS*
Cr	(Intercept)	1.189	0.1814	6.436	<0.0001
	AgecatM	-0.92	0.5361	1.687	*NS*
	SexM	0.1467	0.2887	0.503	*NS*
	Weight	0.07797	0.2893	0.266	*NS*
Cu	(Intercept)	10.01	0.5719	17.19	<0.0001
	AgecatM	-0.303	0.9514	0.314	*NS*
	Weight	-0.1055	0.5723	0.181	*NS*
Fe	(Intercept)	6.251	0.1361	45.07	<0.0001
	AgecatM	-0.5263	0.5722	0.911	*NS*
	SexM	0.3607	0.3089	1.154	*NS*
	Weight	0.3455	0.4525	0.757	*NS*
Mn	(Intercept)	14.69	1.63	8.844	<0.0001
	AgecatM	2.362	4.817	0.487	*NS*
	Weight	-2.484	4.393	0.562	*NS*
Zn	(Intercept)	13.75	0.3178	42.49	<0.0001
	AgecatM	-0.756	0.9748	0.77	*NS*
	Weight	-0.1245	0.3885	0.317	*NS*

Table A4.7: Top candidate (ΔAICc<2) model predictor variables, log-likelihood(Log*L*), Akaike's Information Criterion with the small sample bias adjustment(AICc), and Akaike weights (*wi*) for predicting association between standardised landscape parameters and Malay civet hair metal concentrations. Lake = has access to an oxbow lake; Plant = distance from capture site to oil palm plantation; Trib = distance from capture site to nearest semi-permanent tributary.

Element	Candidate Model	df	Log*L*	AICc	ΔAICc	*wi*
Al	Lake + Plant + Trib	5	-405.96	822.88	0	0.70
	Lake + Plant	4	-407.99	824.62	1.74	0.30
As*	Trib	3	87.91	-169.45	0	0.69
	Plant + Trib	4	88.25	-167.86	1.59	0.31
Ba*	Lake + Plant + Trib	5	-249.09	509.15	0	0.55
	Lake + Trib	4	-250.48	509.59	0.44	0.45
Cd*	Lake + Trib	4	226.72	-444.80	0	0.49
	Lake + Plant + Trib	5	227.47	-443.98	0.82	0.32
	Plant + Trib	4	225.78	-442.93	1.87	0.19
Co	Trib	3	60.91	-115.44	0	0.55
	(Null)	2	59.03	-113.87	1.56	0.25
	Plant + Trib	4	61.05	-113.47	1.97	0.20
Cr*	Lake + Plant + Trib	5	-139.33	289.63	0	0.46
	Plant + Trib	4	-140.96	290.55	0.92	0.29
	Lake + Trib	4	-141.11	290.85	1.21	0.25
Cu	(Null)	2	-191.51	387.21	0	0.54
	Plant	3	-190.59	387.56	0.35	0.46
Fe#*	Lake + Plant + Trib	5	-480.91	972.80	0	1.00
Hg*	Trib	3	-107.28	220.93	0	0.43
	Plant + Trib	4	-106.43	221.49	0.56	0.33
	Lake + Trib	4	-106.76	222.15	1.22	0.24
Mn	(Null)	2	-246.58	497.35	0	0.33
	Trib	3	-245.84	498.05	0.70	0.23
	Plant	3	-246.06	498.50	1.16	0.18
	Plant + Trib	4	-245.25	499.13	1.78	0.13
	Lake	3	-246.45	499.28	1.93	0.12
Ni	(Null)	2	-89.14	182.47	0	0.65
	Trib	3	-88.68	183.73	1.25	0.35
Pb	Plant	3	-20.41	47.20	0	0.35
	Lake + Plant	4	-19.31	47.26	0.06	0.34
	Plant + Trib	4	-20.00	48.64	1.44	0.17
	Lake + Plant + Trib	5	-19.04	49.04	1.84	0.14
Zn	(Null)	2	-389.20	782.59	0	0.64
	Plant	3	-388.70	783.78	1.19	0.36

denotes metals with final averaged structures containing statistically significant terms ($p < 0.05$)

$^{\#}$*denotes a singular and final model structure (no models within 2 AICc of top model)*

Table A4.8: Model-averaged estimates of landscape-level fixed effects for statistically non-significant averaged top-models of Malay civet hair metal concentrations. NS denotes statistically non-significant ($p > 0.05$) term. Lake = has access to an oxbow lake; Plant = distance from capture site to oil palm plantation; Trib = distance from capture site to nearest semi-permanent tributary. Intercept = standardised reference level for factorised predictor variables (ex: does not have access to oxbow lake).

Element	**Parameter**	**Estimate**	**Std. Error**	**z value**	***p value***
Al	(Intercept)	5.0999	0.1435	34.87	<0.0001
	Lake	0.5962	0.3572	1.638	*NS*
	Plant	-0.4252	0.3164	1.319	*NS*
	Trib	-0.2760	0.2990	0.912	*NS*
Co	(Intercept)	-1.81016	0.1021	17.41	<0.0001
	Trib	-0.27841	0.2355	1.170	*NS*
	Plant	-0.02056	0.0990	0.204	*NS*
Cu	(Intercept)	10.0126	0.5661	17.37	<0.0001
	Plant	-0.6559	1.032	0.630	NS
Mn	(Intercept)	14.6596	1.584	9.084	<0.0001
	Trib	-1.2019	2.117	0.563	*NS*
	Plant	0.9496	2.271	0.413	*NS*
	Lake	0.1968	1.339	0.145	*NS*
Ni	(Intercept)	0.35938	0.1163	3.033	<0.01
	Trib	-0.06296	0.1614	0.385	NS
Pb	(Intercept)	-0.70727	0.1978	3.510	<0.0001
	Plant	-0.66066	0.4174	1.553	*NS*
	Lake	0.18327	0.3913	0.462	*NS*
	Trib	-0.06744	0.2417	0.275	*NS*
Zn	(Intercept)	189.384	8.626	21.56	<0.0001
	Plant	-6.5	13.29	0.484	*NS*

Chapter 6. Synthesis: Life on the edge

6.1 Introduction

Wildlife conservation research is a multi-facetted, dynamic, and occasionally contradictory process of recording observed patterns and striving to translate these patterns into elegant causative narratives embodying population-level implications. Globally, wildlife individuals, populations, and communities face multiple stressors at any given temporal and spatial scale; reviewing the subsequent patterns and processes of wildlife responses to such pressures remains a central focus of conservation ecology (Soulé, 1985). Such a task, however, presents complex theoretical and technical challenges (e.g. Lydy et al., 2004; Munns Jr., 2006); yet, when faced with the current global biodiversity crisis (Chapter 1), the impetus to enact informed and effective conservation actions remains paramount.

Integrated, multi-disciplinary research approaches such as conservation physiology (Cooke et al., 2013; Wikelski & Cooke, 2006), landscape movement ecology (Allen & Singh, 2016), and behavioural ecotoxicology (Peterson et al., 2017) have identified and, in some cases, mitigated, anthropogenic threats to species' survival. For example, research by Serieys et al. (2018) determined that bobcats (*Lynx rufus*) surviving along urbanised edges in California were more likely to be exposed to anticoagulant rodenticides, and that this further elevated an individual's susceptibility to mange. Differences in the home ranges and foraging behaviours of ringed seals (*Pusa hispida*) strongly determined an individual's probability of exposure to polychlorinated biphenyls (PCBs) in Canada (Brown et al., 2014). Ingestion of contaminated insects by flycatchers (*Ficedula* sp.) in Poland resulted in significantly diminished nest fledgling success, and Swiergosz et al. (1998) determined this was most likely due to heavy metal-induced anaemia. Despite the substantial lack of baseline data concerning the health, spatial ecology, or toxin exposure histories of wild species, bringing together such varied data streams can provide valuable indications of impacts of anthropogenic activities.

This final synthesis chapter thus seeks to bring together the findings presented in Chapters 2–5 to evaluate holistically and tease apart the ecological costs incurred by a landscape sentinel, the Malay civet, persisting within the LKWS and surrounding oil palm plantations. The first aim of this synthesis was to evaluate if the utilisation of oil palm plantations was indeed related to the capture locations of the GPS-collared Malay civet males. Secondly, differences between the blood profiles of the GPS-collared civets were assessed to determine the influence of an animal's spatial ecology on its health. The differences between hair metal concentrations of GPS-collared civets based on their utilisation of oil palm or forested habitats were also assessed to evaluate the possible risks of exposure from close association with agriculture. Lastly, this synthesis sought to evaluate if hair concentrations of selected heavy metals subsequently correlated with changes to the haematology and serum biochemistry profiles of Malay civets in the LKWS.

6.2 Methods

6.2.1 Spatial: Spatial

Using R 3.5 (R Core Team, 2018), a Bernoulli generalised linear model evaluated if the probability of a Malay civet entering oil palm was related to the proximity of the agriculture to the capture site. The model was fitted with a probit link family to minimise the model's overall AIC and optimise fit.

6.2.2 Health: Spatial

GPS-collared male Malay civets were grouped according to the habitat types accessed in their total home ranges throughout their collaring periods ('forest only' or 'mixed' habitat individuals). Blood parameters of these groups were compared by either t-tests or Mann-Whitney U (MWU) tests, as appropriate based on normality of each health parameter. No further analyses were conducted due to the small sample size.

6.2.3 Spatial: Ecotoxicology

Hair metal concentrations of GPS-collared male Malay civets using only forests and those using both forests and agriculture were compared using either t-tests or MWU tests, as appropriate based on normality of metal data. For those metals that significantly differed between these spatial groups, general additive models

(GAMs) evaluated the influence of a civet's intensity of oil palm plantation utilisation on the observed variation in hair metal concentrations. Specifically, Malay civet hair metal concentrations were contrasted with the proportion of each individual's core home range (50% BRB UD, Chapter 4) contained within oil palm using the package *mgcv* (Wood, 2006). Models were set to Gamma or Gaussian error families with log or square root link functions, as selected by observation of model residual plots and minimisation of model AIC and GCV values. The relationship between oil palm usage and metal concentrations was fitted with thin-plate regression splines, with the number of knots set to 3, per guidelines suggested by Wood (2011) for small sample sizes. If linear relationships were determined by GAM outputs (edf = 1), the model was refitted to include the effect of the variable with the smoothing removed. Model validation was conducted by the graphic evaluation of the normality of model residuals using the gam.check function.

6.2.4 Health: Ecotoxicology

To best evaluate the interplay between hair metal concentrations and detectable impacts on the health of Malay civets, selected metals were contrasted against blood indices (for selection process, see Table A5.1). This targeted approach aimed to minimise the detection of spurious relationships while being the most statistically stringent. The relationships between Malay civet hair metal concentrations and blood parameters were assessed by Spearman linear correlation plots using the packages *Hmisc* (Harrell Jr. et al., 2018) and *ggpubr* (Kassambara, 2017). Hair metal data were either log or square root transformed to meet the assumptions of normality for correlation analysis and minimise the effect of outliers.

6.3 Results

6.3.1 Spatial: Spatial

GPS-collared Malay civets with home ranges that contained oil palm plantations were captured closer to the agriculture (mean distance from capture site to oil palm for mix habitat males: 443 m) than those animals that solely utilised forest (mean distance: 1734 m; t = 3.194, df = 6.645, $p < 0.02$). When this relationship was assessed with a Bernoulli model, however, there was no significant relationship between agricultural proximity and the probability of an individual entering oil palm plantation ($F_{1,13} = 0.220$, $p = 0.65$). Therefore, the utilisation of the following case studies may better evaluate civet ecology within the patchwork LKWS landscape.

6.3.2 Health: Spatial

Overall, Malay civet males that did not access oil palm (n = 6) had significantly elevated mean corpuscular haemoglobin (MCHC), low density lipoprotein (LDL), and serum urea concentrations compared to those that used both forest and oil palm plantations (n = 6; Tables A5.2–A6.4). There were near significant differences in mean corpuscular volume (MCV) values and monocyte counts between these groups; given the small sample sizes, these results are presented for discussion.

Malay civets that resided solely in forests expressed significantly elevated MCHC compared to those individuals that entered the agriculture (t = 3.039, df = 9, $p < 0.02$; Figure 6.1A). Specifically, forest only males expressed a mean MCHC value 26 g/L greater than those that entered oil palm. Malay civet MCV nearly varied significantly between civet home range behaviours (Median ± IQR: Forest only animals = 51.0 ± 2.0 fL; mix habitat animals = 53.5 ± 2.5 fL; W = 4; $p = 0.054$; Figure 6.1B).

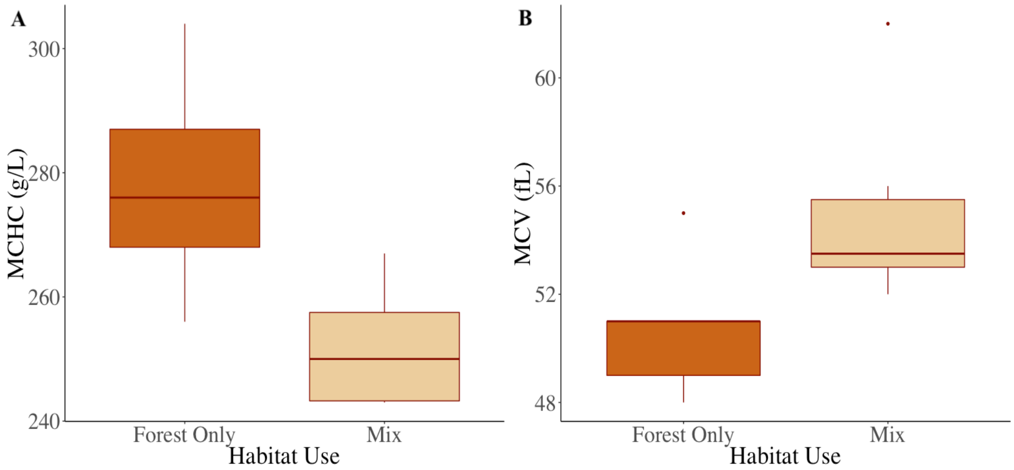


Figure 6.1. Comparison between measured A) MCHC (g/L) in GPS-collared Malay civets grouped by spatial behaviours; and B) near significant comparison between the measured MCV (fL) in GPS-collared civets grouped by spatial behaviours (n = 5 forest only, n = 6 mixed habitats).

Civet monocyte counts nearly differed significantly with Malay civet spatial behaviours (Median ± IQR: Forest only animals = 7.0 ± 8.0 x 10^8/L; mix habitat animals = 2.0 ± 2.0 x 10^8/L; W = 22; $p = 0.056$, Figure 6.2); no other leukocyte counts differed between the two groups.

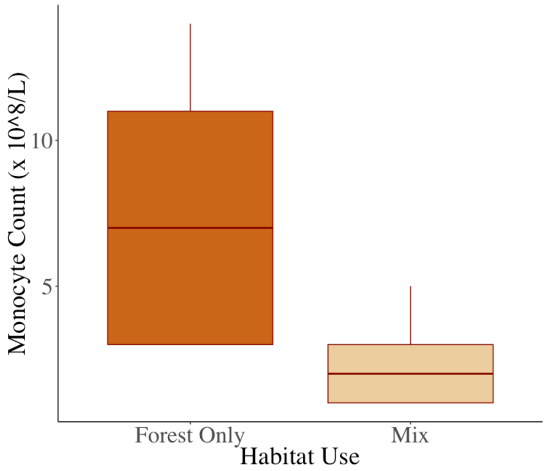


Figure 6.2. Near significant difference in monocyte counts (x 10^8 g/L) of GPS-collared Malay civets grouped by spatial behaviours (n = 5 forest only, n = 5 mixed habitats).

Civets that resided solely in the forests (n = 5) expressed significantly elevated LDL and urea concentrations compared to those individuals that entered the agriculture (n = 6; t = 2.439, df = 9, $p < 0.05$; t = 4.666, df = 9, $p < 0.002$, respectively, Figure 6.3). Specifically, forest only animals expressed a mean serum LDL value 0.53 mmol/L greater than those that entered oil palm, while animals that only utilised forests expressed a mean urea concentration 4.48 mmol/L greater than those that entered oil palm.

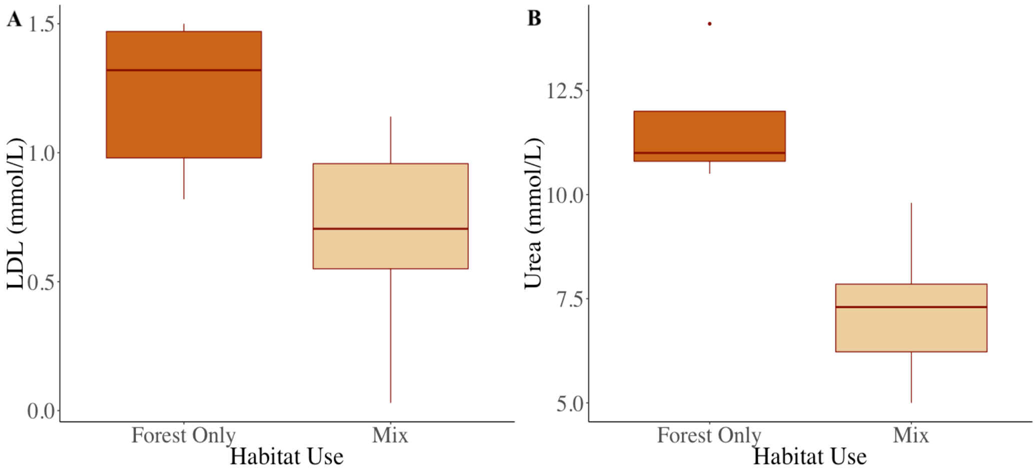


Figure 6.3. Comparison between measured serum A) LDL (mmol/L) and B) urea (mmol/L) of GPS-collared Malay civets grouped by spatial behaviours (n = 5 forest only, n = 6 mixed habitats).

6.3.3 Spatial: Ecotoxicology

Hair metal concentrations were determined for the 16 GPS-collared Malay civet males. Hair As, Ba, Co, Cr, Cu, Fe, Mn, Ni and Zn concentrations did not statistically differ between civets that utilized oil palm plantations and those that did not (Table A5.5). The hair of Malay civets that utilised the agriculture contained statistically significantly elevated concentrations of Cd, Pb, and Al compared to forest only males (W = 5, $p < 0.01$; W = 11, $p < 0.05$; W = 12, $p < 0.05$, respectively; Figure 6.4A–D, respectively). Hair from Malay civets that utilised solely forest contained a mean Hg concentration 1.72 mg kg^{-1} greater than those that used both habitat types (t = 3.782, df = 14, $p < 0.005$).

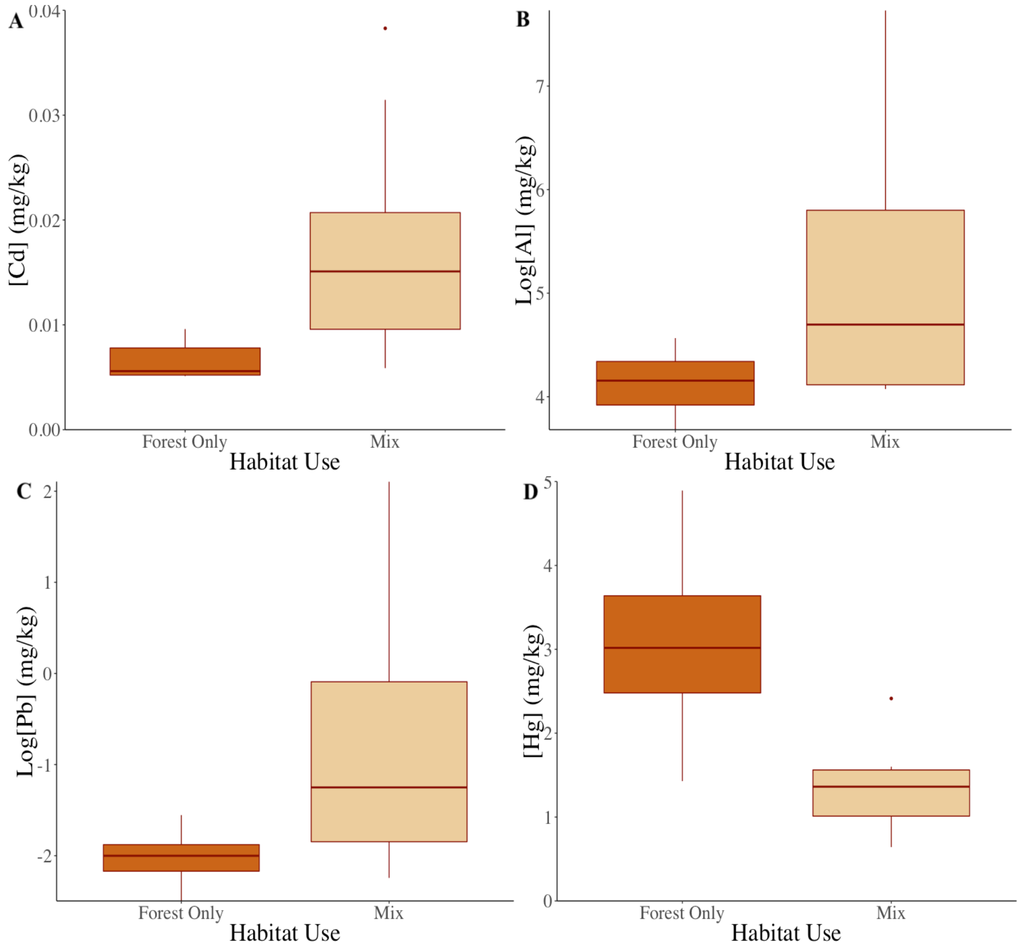


Figure 6.4. Statistically significant differences between the hair metal content (mg kg^{-1}); A) Cd; B) log(Al); C) log(Pb); and D) Hg of GPS-collared male Malay civets using solely forest (n = 8) compared to those that entered oil palm plantations (‘mix’, n = 8). Dots represent statistical outliers (> 3 SD from the group median). Log transformations were only conducted for visualisation purposes; due to the non-normal distribution of these datasets, MWU tests were conducted on the raw data.

The concentrations of these four metals also varied predictably with the intensity of each individual’s utilisation of oil palm, as represented by the proportion of agriculture contained within an animal’s core home range (50 % BRB UD; Figure 6.5, Table 6.1). Hair Cd, Al, and Pb increased with an increased intensity of oil palm utilisation by a civet, while Hg decreased with decreasing intensity of oil palm usage.

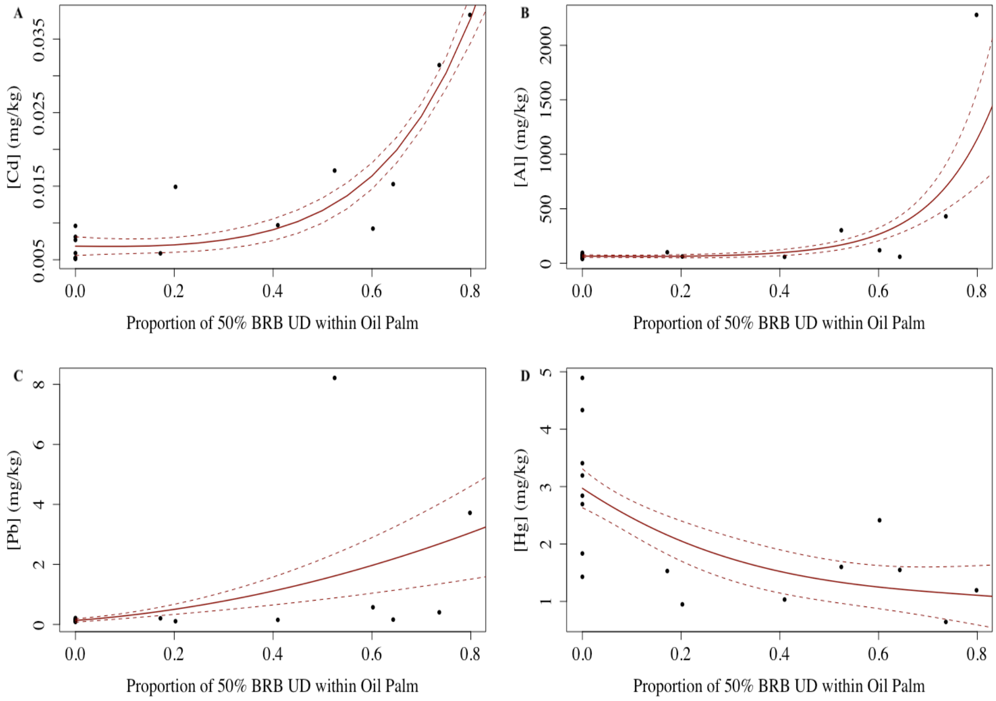


Figure 6.5. Modelled relationships between the proportion of male Malay civet core home ranges (50% BRB UD, n = 16) contained within oil palm plantations and hair metal concentrations (mg kg^{-1}): A) Cd; B) Al; C) Pb; D) Hg). Red lines indicate predictions from the general additive model, and dashed lines represent the model's standard error.

Table 6.1: General additive models (GAMs) evaluating associations between Malay civet hair metal concentrations and the proportion of an animal's core home range (50% BRB UD, n = 16) containing oil palm plantation. edf = effective degrees of freedom; Ref.df = reference degree of freedom.

Cd Adj. R^2= 0.853 Deviance explained= 87.1% GCV: 1.71E-5 AIC= -128.8				
Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Prop50OP)	1.90	1.99	46.97	<0.0001
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	-4.61	0.11	-40.71	<0.0001

Al Adj. R^2= 0.624 Deviance explained= 82.6% GCV: 0.44 AIC= 183.0				
Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Prop50OP)	1.83	1.97	21.86	<0.0001
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	4.79	0.14	35	<0.0001

Pb Adj. R^2= 0.119 Deviance explained= 59.7% GCV: 1.34 AIC= 10.9				
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	0.362	0.0774	4.68	<0.0005
Prop50OP	1.734	0.573	3.02	<0.01

Hg Adj. R^2= 0.381 Deviance explained= 43.4% GCV: 1.12 AIC= 48.9				
Smoothed terms				
	edf	*Ref.df*	*F statistic*	*p-value*
s(Prop50OP)	1.29	1.49	5.51	<0.05
Parametric coefficients				
	Estimate	*Std. Error*	*t value*	*p-value*
(Intercept)	0.72	0.14	5.14	<0.0002

6.3.4 Health: Ecotoxicology

A total of 41 Malay civets had both haematology and hair metal profiles successfully established, while 48 unique serum biochemistry and hair metal profiles were collected. There were several statistically significant correlations between hair metal concentrations and the erythrocyte profiles of Malay civets (Figure 6.6; Figures A5.1–A5.2). Hair Cr concentration positively correlated with mean corpuscular volume (MCV; Figure 6.6B) and negatively correlated with mean corpuscular haemoglobin concentration (MCHC; Figure 6.6A). Animals with higher hair Fe had a similar elevation in measured haemoglobin concentration (Figure 6.6C) and packed cell volume (PCV; Figure 6.6D). Lastly, increases in hair Pb correlated with increases in Malay civet platelet counts (Figure 6.6E). Variations in hair Al, As, Ba, Cd, or Hg did not significantly correlate with linear changes in haematology parameters (Figures 6.1–6.2).

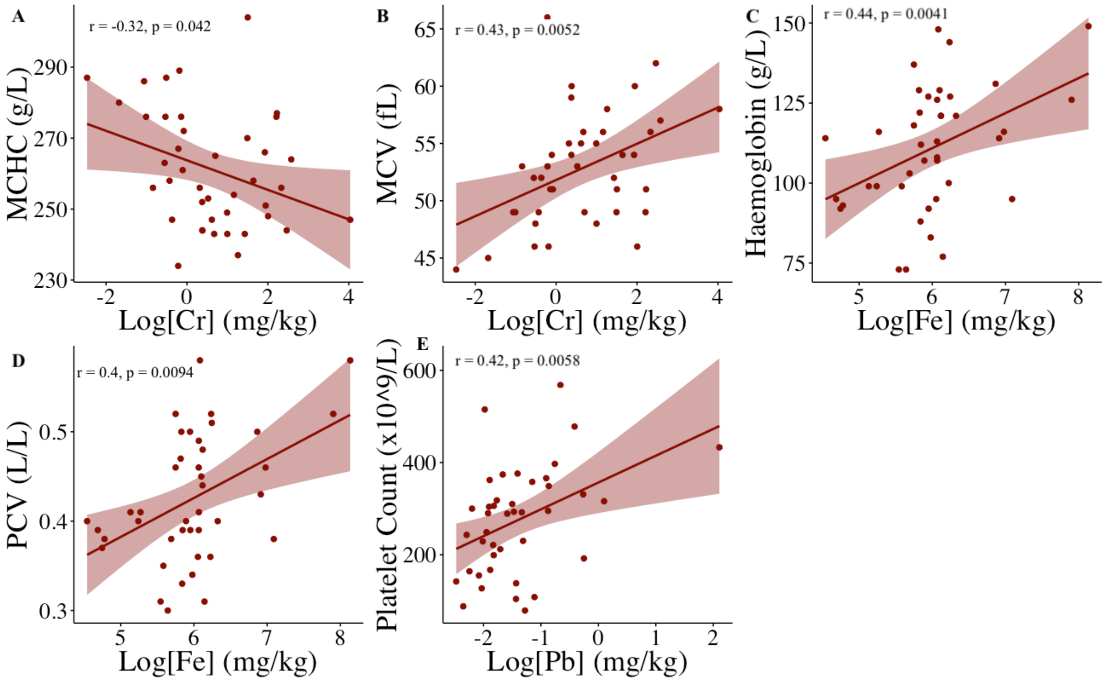


Figure 6.6. Statistically significant Spearman correlation relationships between transformed Malay civet hair metal concentrations and haematology parameters (n = 41). Shorthand for health parameters match those presented in Table A2.1. r values displayed on the plots denote the Spearman correlation coefficient (rho), while the *p* value denotes the statistical significance of the correlation. Shaded regions represent the confidence intervals of the linear correlation.

There were three statistically significant correlations between hair metal concentrations and civet serum biochemistry profiles (Figure 6.7; Figures A5.3–A5.4). Hair Cd concentration positively correlated with low-density lipoprotein concentration (LDL; Figure 6.7A). Increases in both hair Al and Cd correlated with increases in aspartate aminotransferase activity (AST; Figure 6.7B–C). Variations in As, Cr, Fe, Hg, or Pb did not significantly correlate with linear changes in assessed serum biochemistry parameters (Figures A5.3–A5.4).

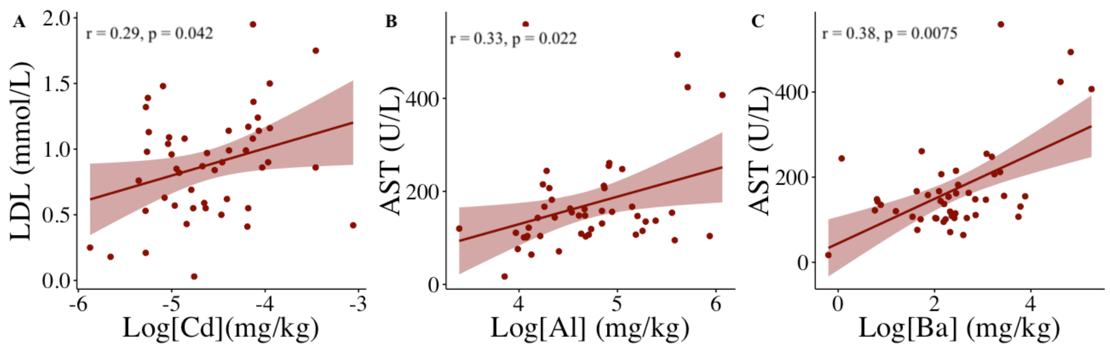


Figure 6.7. Statistically significant Spearman correlation relationships between transformed Malay civet hair metal concentrations and serum biochemistry blood parameters (n = 48). Shorthand for health parameters match those presented in Table A2.2. r values displayed on the plots denote the Spearman correlation coefficient (rho), while the *p* value denotes the statistical significance of the correlation. Shaded regions represent the confidence intervals of the linear correlation.

6.4 Discussion

6.4.1 Spatial: Spatial

The distance from a civet's capture site to oil palm plantation did not significantly predict if an individual entered the agriculture, suggesting the utilisation of Euclidean distance measures in the population-level evaluation of civet health parameters and metal exposure may be less accurate than hoped. As suggested in Chapter 4, a civet's utilisation of oil palm plantations may be a more nuanced process than a simple dichotomy of 'near' or 'far'; habitat preferences and selection processes are most likely involved. Further investigations into what drives preferences of civets for specific habitat types would expand our understanding of how the species interacts with the oil palm matrix, in turn allowing more detailed evaluations of topics such as civet metal exposure or health ramifications across the landscape. Information regarding civet habitat preferences could be used to build an agent-based model (ABM; see review by McLane et al., 2011) describing the predicted spatial behaviours of those sampled civets not explicitly GPS-collared. ABMs are computational simulation models that create a set of individual reactive agents (i.e. civets), and model the responses of these agents within a given system (i.e. the heterogeneous environment of the Kinabatangan). The successful building of such a model would provide a more informed prediction of each sampled civets' spatial ecology, ideally including an indication of the likelihood of an animal to utilise oil palm plantations. This would improve upon the current usage of simple Euclidean proximity measurements of capture sites to landscape characteristics in question, and may uncover more nuanced narratives of how civet health parameters and exposure to pollution vary across the fragmented landscape (e.g. AGM of wood mice [*Apodemus sylvaticus*] in agricultural habitats and pesticide applications, Liu et al., 2013; population model of kit fox [*Vulpes macrotis mutica*] exposure to rodenticides, Nogeire et al., 2015). For now, however, these findings support the consideration of the following case studies evaluating the metal exposure and health status of GPS-collared Malay civet males despite the reduced sample size and decrease of statistical power.

6.4.2 Health: Spatial

The blood parameters of the GPS-collared Malay civets compared well to the entire sample population and the modelled landscape patterns (Chapter 2). The significantly depressed MCHC in GPS-collared males utilising oil palm plantations, paired with the tendency towards macrocytic MCV profiles, agree with the previous hypothesis of regenerative anaemia occurring in civets associating with agriculture. As suggested in Chapter 2, examination of reticulocyte counts would provide further supporting evidence of such a condition. The clinical triggers of regenerative anaemia can include chronic stress, exposure to toxins, and blood loss via parasitic infections (Johnstone et al., 2011); more targeted evaluations determining the root of the condition would provide a broader context to discuss small carnivore health in oil palm landscapes.

In contrast, the leukocyte profiles of GPS-collared civets did not wholly agree with previously postulated neutropenia-mediated immunosuppression in individuals sampled nearer to oil palm plantations (Chapter 2); however, the collared individuals that accessed oil palm expressed a near significant reduction in circulating monocyte counts relative to forest only civets. This does not immediately negate the hypothesis that oil palm agriculture may be resulting in population-wide immunosuppression; these findings simply shift the mode of the condition from neutrophils to monocytes in this specific case. Monocytes function in both innate and adaptive immunity and are considered a good indication of overall immune system fitness (Roquiz et al., 2016). As with anaemia, further research into the specific biochemical processes that may result in these landscape-mediated patterns of immunosuppression is warranted; stress, toxins, and certain acute infections can all reduce immune functioning (Davis et al., 2008; Repetto & Baliga, 1997). Of note, there were no significant linear correlations between leukocyte counts and assessed hair metal concentrations (Figures A5.1–A5.2).

Lastly, LDL cholesterol and urea values were significantly decreased in civets utilising oil palm compared to those that remained in the forest. This is similarly consistent with the population-level findings of Chapter 2, suggesting there may be dietary or lipid metabolism differences between the spatial groups.

6.4.3 Spatial: Ecotoxicology

Hair metal concentrations of GPS-collared Malay civet males that utilised oil palm contained elevated Cd, Al, and Pb concentrations compared to males that remained within the forest. Generalised additive modelling demonstrated significant positive relationships between an individual's intensity of oil palm utilisation and hair metal concentrations. These findings suggest civets are experiencing elevated exposure to Cd, Al, and Pb due to spatial associations with oil palm plantations. All three metals have been identified as pollutants due to excessive fertiliser application in agricultural regions worldwide, including oil palm plantations (Atafar et al., 2010; Dubos et al., 2017; Kurniawan, 2016; Mattsson et al., 2000; Rai et al., 2019; Sakai et al., 2017). Civets may thus be exposed to these metals through direct contact with or consumption of fertiliser pellets, ingestion of contaminated soils or irrigation ditch water, or consumption of polluted palm oil kernels, invertebrates, or small mammals. Alternatively, research by Defarge et al. (2018) demonstrated common agro-chemicals, including glyphosate compounds known to be applied in oil palm plantations in Sabah, can contain high concentrations of heavy metals. Given the lack of explicit knowledge regarding the crop management protocols in the Kinabatangan, the specific metal sources and modes of civet exposure can only be postulated at this point. Explicit evaluations of the heavy metal content of oil palm plantation soils, irrigation ditch water, fruit kernels, and invertebrates contrasted against samples collected in forested areas would provide a more mechanistic narrative of heavy metal pollution and mammalian exposure in the agriculture (see approach proposed by Nacci et a., 2005; Shanley et al., 2012).

In contrast, hair Hg concentrations were greater in the forest animals than in those that accessed both oil palm and forest. As suggested by the blood results in Chapter 2 and further supported above, there is evidence that Malay civets living in close association with oil palm may have diets lower in protein than those animals that remain in the forest. As methyl-Hg is bioaccumulated and biomagnified across trophic levels, a more carnivorous diet will result in a higher intake and thus accumulation of Hg. Such dietary differences determining Hg concentrations have been documented in birds (American species, Cristol et al., 2008; eagle owl *Bubo bubo*, Lourenço et al., 2011; Bicknell's thrush *Catharus bicknelli*, Rimmer et al., 2010), grizzly bears (*Ursus arctos horribilis,* Felicetti et al., 2004; Noël et al., 2014), and artic foxes (*Vulpes lagopus*, Bocharova et al., 2013; Kalisińska et al., 2009). Little is known regarding the mercury biocycling processes of Southeast Asian rainforests (Wang et al., 2016). Research in the Neotropical (Almeida et al., 2005; Fostier et al., 2000; Teixeira et al., 2017) and boreal forests (St. Louis et al., 2001) report high atmospheric deposition of mercury in these biomes. Determining the explicit source-sink dynamics and the chemical speciation of Hg within the LKWS system will be crucial in understanding the threat to both wildlife and people in the region.

6.4.4 Health: Ecotoxicology

The relationship between elevated hair Cr and haematology parameters suggests the metal may be driving regenerative anaemia within the Malay civet population. Mechanistically, this type of anaemia occurs when erythrocytes are either lost or destroyed at an elevated rate, which triggers the compensatory release of immature red blood cells (reticulocytes) from the bone marrow (Johnstone et al., 2011). There is molecular evidence that exposure to hexavalent Cr can trigger eryptosis (premature red blood cell death; Lupescu et al., 2012; Ray, 2016; Zhang et al., 2014), which may stimulate regenerative anaemia in civets with elevated hair Cr concentrations. Similar haematological profiles have been reported in fish exposed to hexavalent Cr (Abedi et al., 2013; Bhatkar, 2011; Singh, 1995; Vutukuru, 2005). Given the positive relationship between

Malay civet hair Cr levels and proximity to semi-permanent tributaries (Chapter 5), we suggest civets are most likely being exposed to Cr (VI) due to its toxicity and prevalence as an aquatic pollutant (Gorny et al., 2016). In order to concretely assess the interplay between Cr exposure and civet health, the oxidative state of the metal should be determined within the LKWS, as Cr bio-toxicity strongly depends on the chemical speciation (Rakhunde et al., 2012). Further, laboratory experiments evaluating civet haematology following controlled exposure to the relevant Cr species would provide concrete evidence of predictable deleterious effects of the metal to Malay civets.

Hair Fe concentration positively correlated with Malay civet haemoglobin and packed cell volume. Iron is essential to the formation of haemoglobin through its incorporation into heme (Harvey, 2008). Positive correlations between hair and serum Fe concentrations have been established and haematology parameters have been documented to be similarly responsive to both measures (Kempson & Lombi, 2011; Sahin et al., 2015; Shah et al., 2011). Thus, the detection of this expected positive relationship between Malay civet hair and blood profiles reinforces the suitability of this preliminary analytical approach.

Hair Pb was positively correlated with civet platelet count, which clinically suggests secondary thrombocytosis may occur following exposure to Pb. The clinical research of Pb exposure contains case reports of both thrombocytosis (e.g. Al Momen, 2010; Mugahi et al., 2003) and thrombocytopenia (e.g. Adham et al., 2011; Barman et al., 2014). Mechanistically, lead exposure can result in Fe deficiency, as the elements compete for biochemical binding sites; secondary thrombocytosis can be a symptom of Fe deficiency, which may explain these results in Malay civets (Brace, 2016). In humans, lead poisoning commonly results in microcytic anaemia, as lead inhibits heme synthesis pathways (Patrick et al., 2006; Wani et al., 2015); however, Malay civet anaemia parameters did not correlate with changes in hair Pb concentration. These results may be early indications of the effects of sub-lethal Pb exposure on Malay civet physiology or may simply be an artefact of the data structures. More specific evaluations of lead exposure biomarkers, such as ALAD (delta-aminolevulinic acid dehydratase) activity, contrasted against serum iron and ferritin stocks would further determine if Pb exposure is triggering haematologically deleterious Fe deficiencies in civets (Depledge & Galloway, 2005; Hoffbrand et al., 2006).

In terms of serum biochemistry responses to civet hair metal concentrations, a positive relationship between Cd and LDL cholesterol was observed. This was unexpected, given the negative relationship between oil palm utilisation and civet LDL and the positive relationship between oil palm utilisation and hair Cd. Experimental assessments into the impacts of Cd on the lipid profiles of laboratory animals and human case studies suggest exposure can elevate an individual's risk of cardiovascular disease (Buhari et al., 2018; Samarghandian et al., 2015; Türkcan et al., 2015; Zhou et al., 2016); which agrees with the correlation documented here. Further research into the interplay between civet diet, lipid profiles, and Cd exposure sources are warranted to untangle the potentially confounding results within this dataset.

The positive correlations between hair Al and Ba concentrations and AST activity indicate exposure to these metals may result in liver damage (Kerr, 2002). Elevation of serum AST activity has been reported following exposure to As, Cd, Cr, Cu, Hg, Ni, Pb, and Zn (Adham et al., 2011; Bersényi et al., 2003; Firat & Kargin, 2010; Jayawardena et al., 2017; Li et al., 2016); experimental Al exposure has increased AST activity in rats (Geyikoglu et al., 2012; Moshtaghie et al, 2003; Tripathi et al., 2009). There is significantly less available research regarding the impacts of Ba on liver functionality (Kravchenko et al., 2014; however, see elevated AST in rats following administration of two forms of barium salts by Mohammed & Ishmail, 2017). Civet hair contained elevated concentrations of both of these metals compared to values reported in previous research (Chapter 5); thus, these preliminary deleterious results strongly warrant further research into the status of these metals in the LKWS system.

Lastly, linear correlations between hair metal concentrations and Malay civet health parameters are in no sense meant to infer causation; given the lack of reference intervals for what constitutes a normal 'healthy' value for both blood parameters and hair metal concentrations for this species, these analyses are meant to be exploratory and facilitate discussion. It is crucial to once again highlight these results have not been collected via carefully controlled, laboratory-based experiments; these data have come from a notably understudied species persisting within a complex, dynamic, and similarly understudied ecological system. Factors not accounted for in this study, such as viral infections, diet, microbiome diversity, or exposure to organic compounds such as rodenticides or pesticides almost certainly impact the overall health of individual civets. Further, even when considering the available data, the 1:1 correlations conducted in this chapter are simply the first steps towards evaluating the potential physiological risks posed by specific metals; each civet has been exposed to a suite of metals, which, in reality, can inflict additive or potentiating effects on an individual's health (e.g. Heys et al., 2016; Lydy et al., 2004; Rodea-Palomares et al., 2015). For example, rats experimentally exposed to the insecticide cypermethrin displayed dose-dependent immunotoxic responses; these responses, however, were modulated when the animals were additionally exposed to Cd and Pb (Institóris et al., 1999). Evaluating these potential interplays was outside the scope of the current study; indeed, until explicit anthropogenic source tracking and geogenic baselines can be established, more complex multivariate analyses risk uncovering spurious findings. More importantly, when paired within the delicacy of conservation politics, this could undermine mitigation applications of this work.

Appendix V. Supplementary information for synthesis analyses

Table A5.1. Table summarizing the selection process of target metals for assessing possible and detectable health impacts in civets.

	Element												
	Al #	**As #**	**Ba #**	**Cd #**	**Co**	**Cr #**	**Cu**	**Fe #**	**Hg #**	**Mn**	**Ni**	**Pb #**	**Zn**
Non-essential?	X	X*	X	X		X*			X			X	
Similar between civet species?	X					X		X				X	
Elevated relative to literature?	X		X			X		X		X[%]	X		X
Evidence of biological differences in hair concentration (i.e. sex, weight, age category; Chapter 5)?									X		X	X	
Evidence of spatially-mediated exposure potential (i.e. tributary, lake; Chapter 5)?		X	X	X		X		X	X				
Significant variation between habitat usage of GPS-collared civets?	X			X					X			X	

#denotes metals selected for further health impact assessment

**some debate in the literature regarding level of essentiality, and toxicity depends on chemical form*

[%]Common palm civet hair concentrations only

Table A5.2. Summary haematology parameters of GPS-collared male Malay civets with home ranges solely in the forest and those known to enter palm oil plantations; bold text denotes the directionality of significance, such that bolded values represent the dataset with the statistically elevated parameters. Parameter shorthand matches those presented in Table A2.1.

		Forest Only			Mix		
Parameter	**Unit**	**n**	**Mean**	**SD**	**n**	**Mean**	**SD**
Haem	g/L	5	124	7.84	6	117	20.6
RBC	x 10^{12}/L	5	8.83	0.91	6	8.46	1.36
PCV	L/L	5	0.45	0.049	6	0.47	0.078
MCV'^	fL	5	51.0	2.0	6	53.5	2.5
MCH^	pg	5	14.0	0.0	6	14.0	0.0
MCHC**	g/L	5	**278**	18.3	6	252	10.0
RDW	%	5	21.2	1.12	6	20.8	1.97
WBC	x 10^9/L	5	13.6	5.86	6	9.52	1.56
Neut^	x 10^9/L	5	8.60	6.10	5	6.40	4.40
Lymp^	x 10^9/L	5	1.70	1.20	5	1.00	1.00
Mono^'	x 10^9/L	5	0.70	0.80	5	0.20	0.17
N:L^	-	5	4.2	1.06	5	6.4	13.4
Plat	x 10^9/L	5	231	78.8	6	311	100
Gluc^	mmol/L	5	5.8	3.0	6	5.5	2.58

'denotes near statistical significance related to p value < 0.06

***denotes statistical significance related to p value < 0.02*

^denotes data were non-normally distributed and thus summary statistics presented are median and IQR

Table A5.3. Summary serum biochemistry parameters of GPS-collared male Malay civets with home ranges solely in the forest and those known to enter palm oil plantations; bold text denotes the directionality of significance, such that bolded values represent the dataset with the statistically elevated parameters. Parameter shorthand matches those presented in Table A2.2.

		Forest Only			Mix		
Parameter	**Unit**	**n**	Mean	SD	**n**	Mean	SD
Tchol	mmol/L	5	3.3	0.48	6	3.2	0.30
Tri	mmol/L	5	0.71	0.23	6	0.79	0.24
HDL	mmol/L	5	1.92	0.36	6	2.15	0.45
LDL*	mmol/L	5	**1.22**	0.30	6	0.687	0.40
Tot:HDL	-	5	1.7	0.21	6	1.5	0.27
Na	mmol/L	5	148	3.21	6	150	5.38
K^	mmol/L	5	4.1	0.30	4	4.2	0.13
Cl	mmol/L	5	118	3.97	6	114	8.08
Ur**	mmol/L	5	**11.7**	1.47	6	7.22	1.67
Creat^	umol/L	5	75	5.0	6	69	17
Co_Ca	mmol/L	5	2.37	0.11	4	2.53	0.19
P^	mmol/L	5	1.34	0.36	6	1.78	0.47
TotProt	g/L	5	82.6	8.35	6	79.0	7.29
Alb^	g/L	5	30.0	1.00	6	29.0	7.25
Glob	g/L	5	51.8	7.79	6	52.2	8.77
AlbGloRatio^	-	5	0.60	0.10	6	0.65	0.18
AlkPho	U/L	5	51.2	44.0	4	20.6	15.8
AST^	U/L	5	215	109	6	112	233
ALT	U/L	5	99.2	33.4	6	130.7	78.2

**denotes statistical significance related to p value <0.05*

***denotes statistical significance related to p value < 0.01*

^denotes data were non-normally distributed and thus summary statistics presented are median and IQR

Table A5.4. Summary description of non-significant binomial serum biochemistry parameters of GPS-collared male Malay civets with home ranges solely in the forest and those known to enter palm oil plantations; UA= uric acid; Bili= bilirubin; GGT=Gamma-glutamyl transpeptidase.

		Forest Only (n=5)			Mix (n=6)		
Parameter	**L.D.**	**<LD**	**Elevated**	**Min – Max (elevated)**	**<LD**	**Elevated**	**Min – Max (elevated)**
UA	0.01 mmol/L	4	1	0.05	5	1	0.01
Bili	2 umol/L	2	3	2 – 5	1	5	2 – 9
GGT	3 U/L	1	4	3 – 58	3	3	6 – 195

Table A5.5. Hair metal concentrations of GPS-collared male Malay civets with home ranges solely in the forest and those known to enter palm oil plantations; values expressed as mg kg^{-1}; bold text denotes the directionality of significance, such that bolded values represent the dataset with the statistically greater elemental concentrations.

	Forest Only (n=8)		**Mix (n=8)**	
Element	Median	IQR	Median	IQR
Al*	64.0	26.2	**110**	**273**
As	0.063	0.0495	0.0319	0.0644
Ba	9.95	10.6	11.3	26.9
Cd**	0.00558	0.00259	**0.0151**	0.011
Co	0.166	0.0882	0.0826	0.197
Cr	0.847	0.74	4.25	5.16
Cu	9.58	1.03	9.62	1.49
Fe	341	235	316	2686
Hg**^	**3.08**	1.16	1.36	0.541
Mn	14.5	8.68	9.59	6.33
Ni	0.885	0.563	0.681	0.957
Pb*	0.135	0.0384	**0.303**	1.20
Zn	189	37.1	182	50.1

**denotes statistical significance related to p value< 0.05*

***denotes statistical significance related to p value< 0.01*

^denotes parameter was normally distributed, thus summary statistics presented are mean and SD

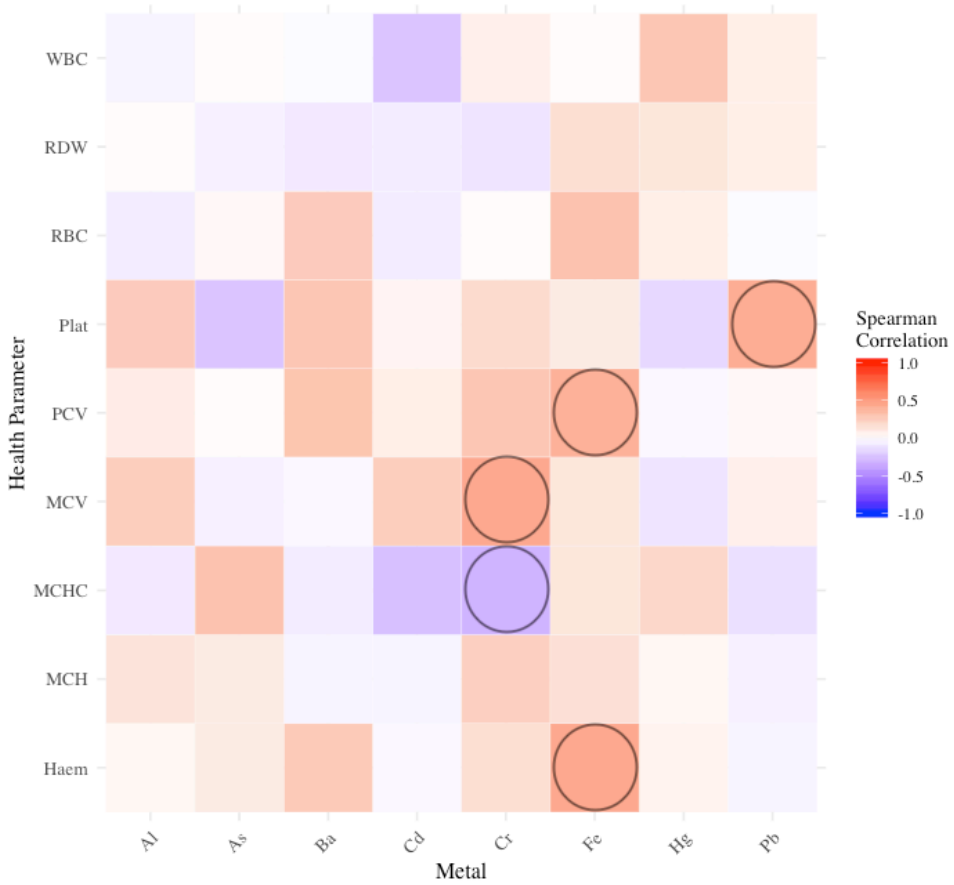


Figure A5.1. Malay civet (n= 41) haematology and transformed hair metal concentrations Spearman correlation plots, with tile colours denoting directionality of correlation (Spearman's correlation coefficient, rho; +1 is a highly positive linear correlation, while -1 is a highly negative relationship). Circled relates to statistically significant correlations ($p < 0.05$).

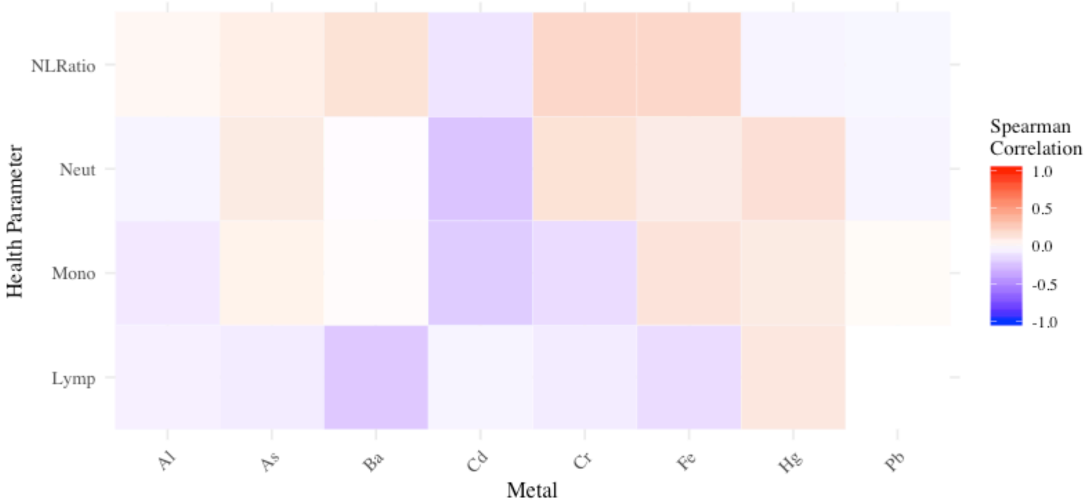


Figure A5.2. Malay civet (n=39) haematology and transformed hair metal concentration Spearman correlation plots, with tile colours denoting directionality of correlation (Spearman's correlation coefficient, rho; +1 is a highly positive linear correlation, while -1 is a highly negative relationship). None of these relationships were statistically significant (all $p > 0.05$).

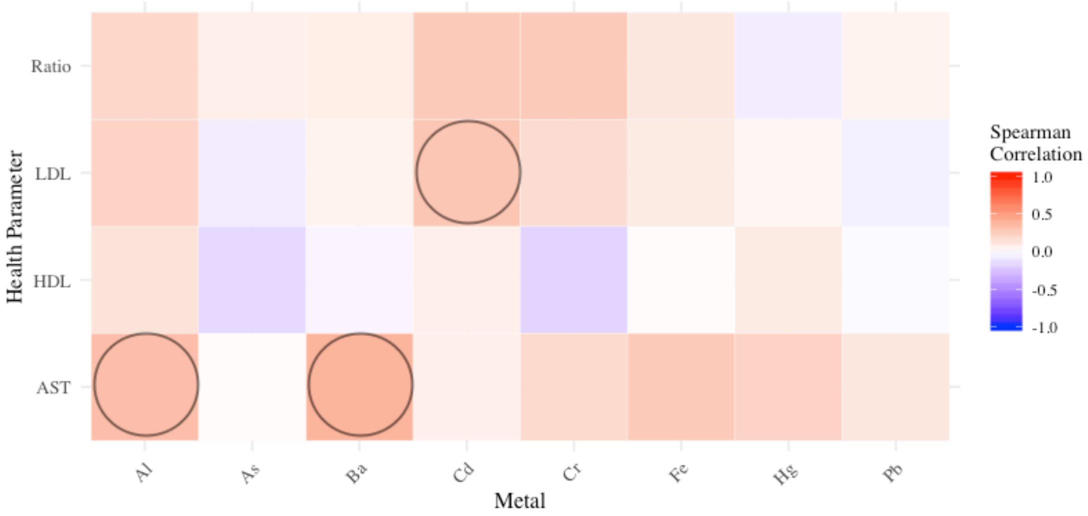


Figure A5.3. Malay civet (n=48) serum biochemistry and transformed hair metal concentration Spearman correlation plots, with tile colours denoting directionality of correlation (Spearman's correlation coefficient, rho; +1 is a highly positive linear correlation, while -1 is a highly negative relationship). Circled relates to statistically significant correlations ($p < 0.05$).

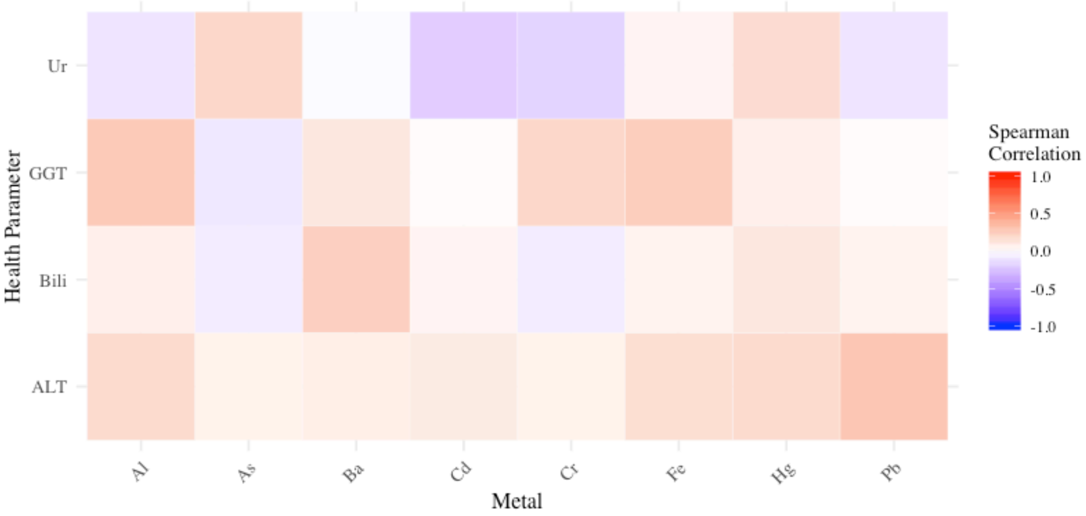


Figure A5.4. Malay civet (n=47) serum biochemistry and transformed hair metal concentration Spearman correlation plots, with tile colours denoting directionality of correlation (Spearman's correlation coefficient, rho; +1 is a highly positive linear correlation, while -1 is a highly negative relationship). None of these relationships were statistically significant (all $p > 0.05$).

Chapter 7. Conclusions

The loss, fragmentation, and degradation of natural landscapes by human activities pose clear and present dangers to global biodiversity, with carnivore species particularly threatened. The future of Southeast Asia's biodiversity is precariously balanced in the face of booming agricultural, industrial, and urban development; regions such as Sabah, Malaysia are poised to become poignant case studies of irreconcilable loss. It is now, more so than ever, crucial to utilise targeted and innovative research to understand how species are affected by anthropogenic land use changes. If conservation solutions can be effectively tailored and implemented via the addition of scientific research (Di Minin et al., 2016), there might yet be hope; Hoffmann et al. (2010) estimated global extinction rates would be 20% higher if the past four decades of conservation actions had not been executed.

Overall, the research presented across the previous six chapters significantly enriches the current scientific knowledge of civet natural history parameters, physiological status, and behavioural ecology. Beyond the intrinsic value of such data, the employment of a 'sentinel species' approach has provided a multi-facetted narrative regarding the behavioural plasticity and risks facing wildlife within human-modified landscapes. The broader implications of anthropogenic changes can be discussed with the explicit goals of developing effective conservation actions not just for civets, but also for the LKWS biodiversity as a whole.

The results of this research demonstrate the importance of natural canopy for these civet species; all GPS-collared animals accessed forested habitats, at least to some degree (the smallest being Malay civet Male 3's 45.9 ha home range completely encompassed within the ~ 450 m wide forest strip between the Kinabatangan River and Hilco oil palm plantation). The high conservation value of protected patches and riparian corridors like the LKWS has been similarly reported in other anthropogenically-altered ecosystems (Lindenmayer, 2019; Wintle et al., 2019; Saura et al., 2014). Unsurprisingly, the river acted as a hard barrier for civets—there is little natural history evidence to suggest these species would cross large bodies of water to re-colonise an isolated forest fragment—which means the maintenance of functional connectivity on both sides of the river is crucial for long-term persistence of the species in the region. The theoretical research of Villard & Metzger (2014) discusses how the impacts of large scale losses of native habitats can be balanced by the configuration of the remnant patches. Landscape configurations which facilitate the unimpeded dispersal of civets will be crucial for the species' long-term conservation, as this would stabilise the region's population source/sink dynamics despite agricultural pressures (e.g. grey wolf *Canis lupus* persistence in the USA; Mladenoff et al. 1995). The high degree of forest patch isolation in the upper Kinabatangan may constrict civet metapopulations, which could result in patch inbreeding or reduced diversity measures (e.g. ringtail possums *Pseudocheirus peregrinus,* Lancaster et al., 2016). It is thus important that the protected areas of the Kinabatangan are not only maintained, but that the establishment of more continuous natural corridors be attempted to ensure civet dispersal. Indeed, Malay civet Male 10 was consistently documented within a 50 m wide riparian reforestation area, and common palm civet Male 1 spent a large amount of time in a 20 m wide strip of natural riparian vegetation adjacent to an oil palm plantation. These observations demonstrate the species can utilise even relatively small increases in a forested area. Given their ecological roles as effective seed dispersers (Joscelyne et al., unpublished data; Nakashima et al., 2010a), it is possible civets may themselves positively contribute to the maintenance of effective landscape connectivity, as documented by frugivorous bats (*Dermanura watsoni*) in Costa Rica (Ripperger et al., 2015). The maintenance of riparian vegetation structures across the watershed would not only provide more habitat for civets and other species (Chapter 1; review by Luke et al., 2018), but would also improve riverbank stability (Horton et al., 2017), minimise agricultural soil degradation (Dislich et al., 2017; Guillaume et al., 2016), improve water quality (Chellaiah & Yule, 2018; Luke et al., 2017), and reduce flooding hazards (Abram et al., 2014). These findings thus highlight the importance of protected forests for these species, while dually suggesting the maintenance and reestablishment of native riparian forests will positively facilitate the long-term persistence of the population.

Concurrently, this research also demonstrates that oil palm plantations did not necessarily pose inhospitable habitats or hard barriers to the assessed civet species, as individuals both foraged and slept within the agricultural matrix. Thus, the maintenance of not just protected and connected forested areas (i.e. land-sparing), but also of plantation characteristics that facilitate successful civet utilisation of the agriculture (i.e. land-sharing) are warranted (Perfecto & Vandermeer, 2010). Camera-trapping research by Pardo et al. (2019) reported Colombian oil palm plantations with elevated understory density and intact riparian corridors had greater occurrences of mammalian species. Civet utilisation of the palm stands, riparian boundaries, and those unplanted fallow patches within the landscape suggest there are opportunities to develop oil palm agriculture that may be less detrimental to small carnivores. In other patchy landscapes across the globe, carnivore assemblages have been maintained through the conservation of native habitat fragments within agriculture matrices deemed permeable to carnivore movements (jaguar *Panthera onca,* Boron et al., 2016; reviewed by Ferreira et al., 2018; Brazilian carnivores, Lyra-Jorge et al., 2008; Chilean carnivores, Moreira-Arce et al., 2016; jaguar and puma *Puma concolor,* Paviolo et al., 2018; caracal *Caracal caracal,* Ramesh et al., 2017; puma, Smith et al., 2019; review by Verdade et al., 2011). These results suggest land-sharing practices may facilitate civet persistence within oil palm agricultural areas.

These recommendations, however, are not to be construed as a 'silver bullet' for ensuring carnivore survival in oil palm landscapes; this research also suggests oil palm agriculture may pose an ecological trap to behaviourally adaptive small carnivores. It is of utmost importance that those secondary stressors be minimised and mitigated prior to fostering long-term civet association with agriculture. This study highlights the disturbance effects of oil palm clearance practices through the opportunistically recorded spatial and behavioural changes of common palm civet Male 1 (Chapter 4). A widespread practice in oil palm cultivation, mature trees are either manually or chemically felled and replanted with young trees ever 15–20 years (Appendix III; Yaap et al., 2010). The documented changes in Male 1's spatial behaviour suggest this practice is detrimental to civet use of oil palm agriculture; luckily for this individual, the

LKWS Lot 6 was accessible during the clearance process. Careful design of oil palm landscapes, such as variable retention schemes (Luskin & Potts, 2011), alley-cropping or polycropping systems (Ashraf et al., 2018; Azhar et al., 2014), or small stands of trees of alternating ages (Koh et al., 2009), are recommended to minimise the disruptive impact of canopy clearance on small carnivores. The complementary maintenance of forested patches within developing oil palm plantations of minimum size to hold an adult civet's home range would further assist in the maintenance of small carnivore populations in the landscape.

Additionally, the detection of elevated civet heavy metal concentrations within the LKWS supports active mitigation of potential anthropogenic metal sources. The usage of mineral fertilisers within plantations could be replaced with organic alternatives derived directly from oil palm cultivation, such as fresh and empty fruit bunches or pruned fronds (Comte et al., 2013; Tohiruddin & Foster, 2013). Indeed, beyond the reduction of metal contamination (particularly Cd), the usage of organic fertilisers in oil palm plantations has been linked to economic, human health, and overall biodiversity benefits (Caliman et al., 2007; Kushairi et al., 2018; Tao et al., 2016). Further, the application of pesticides, which may contain excessive concentrations of deleterious metals (Defarge et al., 2018) while simultaneously posing direct risks to human and ecological health (Ali & Shaari, 2015; Fernandez et al., 2002; Jaacks & Staimez, 2015), should be replaced with alternative practices such as integrated pest management (IPM) schemes (Pretty & Bharucha, 2015; Wood, 2002). Several plantations in Peninsular Malaysia have greatly reduced their application rates of rodenticides by fostering barn owls (*Tyto alba*) and leopard cats (*Prionailurus bengalensis*) within the crop (Hansen, 2007; Jennings et al., 2015; Silmi et al., 2013). Indeed, given their dietary flexibility, both common palm and Malay civets could provide similar rodent-control benefits in oil palm plantations (Verwilghen, 2015); carnivore exclusion experiments and evaluation of resultant losses could provide monetary estimates of these species' value to palm oil yields.

Finally, this discussion of small carnivore conservation occurs within the context of additional threats facing these species (Chapter 1). Persistent local perceptions of civets as pest species due to chicken raiding result in the persecution of individual civets. As with most of the wildlife in Southeast Asia, civets are under increasing pressure from local and the burgeoning international bushmeat trade. In August 2019, Malaysian customs seized 90 live common palm civets off the coast of Kelantan (Abdullah, 2019); officials believed the animals were to be sold as exotic meat to Vietnam and Thailand. Reports of common palm civets kept as pets are increasing; work by Roberts (2019) highlights the extent of the situation both in Indonesia and abroad, with nearly one million civet owners interacting across multiple Facebook groups. The *kopi luwak* industry will continue to negatively impact civet populations, particularly given relatively high economic incentives and low enforcement efforts (Roberts, 2019). Urban development projects, such as the construction of the Pan-Borneo Highway, will increase the frequency of civet road kills and human encroachment into forested areas. The establishment of a gold mining project in Tawau is currently under environmental impact assessment (EIA), which could have serious implications for the biodiversity of the region (e.g. Alvarez-Berríos & Aide, 2015; Asner & Tupayachi, 2016; Goix et al., 2019). Lastly, both stochastic events (e.g. forest fires, floods, disease outbreaks) and global pressures (e.g. climate change, Bamber et al., 2019; McAlpine et al., 2018; persistent organic pollutants, McKinney et al., 2015; Yadav et al., 2015) will invariably influence the survival of civet individuals and populations.

Regardless of the numerical value a civet might represent in terms of reduced loss agriculture, the relative profit impact will unlikely be enough to motivate widespread and large-scale industry changes. The cultural acceptance of the intrinsic importance of biodiversity in terms beyond a profit margin is the only way to foster sustainable futures across the globe (for further ethical debates and musings of morality, see Maier, 2018; Martín-López et al., 2008; Pyron, 2017 and Pyron's own condemnation of the original piece). In the end, humans need biodiversity; biodiversity does not necessarily need us.

Conservation recommendations

In addition to the execution of further scientific research suggested throughout this thesis, recommended actions for the conservation of civets in the Kinabatangan are as follow:

- Continued and enforced maintenance of the protected habitats of the Kinabatangan (LKWS & Forest Reserves);
- Maintenance of riparian buffer zones composed of natural vegetation, ideally a minimum of 400 m in width;
- Maintenance of remnant non-agricultural patches within oil palm plantations, particularly those less than 1 km apart;
- Reclamation and restoration (active or passive) of underproductive oil palm stands both within and along the edges of the agriculture;
- Adjustment of oil palm plantation design and temporal planting schedules to avoid the large-scale and complete clearance of old trees from a given area;
- A complete halt of open burning practices of oil palm vegetation;
- Reduction of mineral fertiliser, glyphosate-based herbicide, and rodenticide applications; openly accessible and clear assessments of environmental impacts of other unknown agrochemicals;
- Regular and stringent POME regulatory assessments of the region's mills;
- Enforcement of illegal hunting and keeping of small carnivores;
- Control of domestic animals within protected areas and oil palm agriculture;
- Crafting of effective education and outreach initiatives to empower and economically benefit local communities while instilling conservation values into cultural norms;
- Continuation of high-quality scientific monitoring of the impacts of above recommendations.

The successful execution of these actions would not solely improve the conservation status of small carnivores, but also many of the other species persisting within the ecosystem. Conspecific research conducted within the region has consistently recommended similar actions to facilitate long-term biodiversity viability, including orang-utans (*Pongo pygmaeus,* Bruford et al., 2010), Sunda clouded leopards (*Neofelis diardi*, Hearn et al., 2018), Bornean elephants (*Elephas maximus borneensis*, Evans et al., 2018; Othman, 2017; Othman et al., 2019), saltwater crocodiles (*Crocodylus porosus*, Evans, 2016), proboscis monkeys (*Nasalis larvatus*, Stark, 2018), and Asian water monitor lizards (*Varanus salvator*, Guerrero-Sanchez, 2019). Execution of these recommendations may also improve oil palm yields and public relations (Abram et al., 2014; Horton et al., 2018), stabilise the high rates of riverbank erosion (Horton et al., 2017), begin to restore the river's impoverished fisheries (Dayang Norwana et al., 2011), improve human health (Ali & Shaari, 2015; Fornace et al., 2016), and facilitate the sustainable development of community-led wildlife tourism (e.g. Hamid et al., 2016). Although there are ample opportunities for additional scientific research to be conducted within the Kinabatangan, the future of the region rests solely on the timely execution and enforcement of conservation actions by local communities, authorities, and industry partners.

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