
Niche partitioning of 5 sympatric Bornean ungulates in response to spatiotemporal variation in fruit availability and resulting implications for predator-prey interactions

BY

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Author's watercolour depiction of a Sunda clouded leopard.

ABSTRACT

Borneo's rainforests are experiencing some of the fastest deforestation rates worldwide and are home to increasingly vulnerable species, most of which remain poorly understood. Bornean rainforests exhibit dramatic fluctuations in fruit and seed availability during mast-fruited events which can exert considerable influence on frugivore ecology. Comprehensive spatiotemporal assessments of habitat use, resource partitioning, and responses to fruit availability in mast-fruited rainforests are lacking for most species, including ungulates. The distribution and habitat use of an apex predator, the Sunda clouded leopard (*Neofelis diardi*), may be largely shaped by the availability of these ungulates. Yet, factors driving the spatial ecology of this elusive felid remain uncertain. I aimed to quantify spatiotemporal habitat use dynamics of these species and consequently inform effective conservation planning. Specifically, I quantified the effects of human activity, forest type, elevation, and mast-induced fluctuations in resources on the habitat use of lesser mousedeer (*Tragulus kanchil*), greater mousedeer (*T. napu*), Bornean yellow muntjacs (*Muntiacus atherodes*), red muntjacs (*M. muntjak*), and bearded pigs (*Sus barbatus*) in Gunung Palung National Park, West Kalimantan, Indonesian Borneo. I applied data from an extensive camera trapping study ($n = 42,610$ trap nights) to a modified single-season occupancy model to evaluate habitat use over space and time. I then applied estimates of occurrence (Ψ) of the five ungulate species to quantify if habitat use of the Sunda clouded leopard was influenced by prey occurrence and thus if this apex predator responded to bottom-up effects of resource variability. The results from the ungulate modelling revealed that forest type was an important predictor of habitat use of all ungulate species, each preferring different forest habitats. Habitat use estimates were highest in peat swamp forests for lesser mousedeer ($\hat{\Psi} = 0.92 \pm 0.05$), alluvial bench forests for greater mousedeer ($\hat{\Psi} = 0.52 \pm 0.08$), lowland granite forests for yellow ($\hat{\Psi} = 0.95 \pm 0.07$) and red muntjacs ($\hat{\Psi} = 0.98 \pm 0.09$), and freshwater swamp forests for bearded pigs ($\hat{\Psi} = 0.84 \pm 0.07$). Bearded pigs exhibited a link between variation in fruit availability and habitat use, indicating an ability to respond to resource variability. Occupancy modelling for Sunda clouded leopards revealed forest type, fruit availability, and bearded pig occurrence as the best predictors of habitat use. The highest estimates were associated with lowland granite forests ($\hat{\Psi} = 0.87 \pm 0.09$). My results reveal a novel pattern of niche partitioning through both food and habitat resources among five sympatric ungulate species and demonstrate that Sunda clouded leopards may use fruited events as a cue for abundant prey. My research sheds light on important factors influencing habitat use of understudied ungulates and an apex predator and can be

used to refine estimates of habitat suitability across a greater landscape to inform conservation practice amidst continually shrinking remnant forests in Indonesian Borneo.

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ACRONYMS

AB	Alluvial bench
AIC	Akaike Information Criterion
BP	Bearded pig (<i>Sus barbatus</i>)
CL	Sunda clouded leopard (<i>Neofelis diardi</i>)
CPRS	Cabang Panti Research Station
Dbh	Diameter at breast height
GMD	Greater mousedeer (<i>Tragulus napu</i>)
GNPN	Gunung Palung National Park
FS	Freshwater swamp
LG	Lowland granite
LMD	Lesser mousedeer (<i>Tragulus kanchil</i>)
LS	Lowland sandstone
PS	Peat swamp
RM	Red muntjac (<i>Muntiacus muntjak</i>)
RVI	Relative Variable Importance
UGM	Upland granite/montane
YM	Bornean yellow muntjac (<i>Muntiacus atherodes</i>)

Chapter 1. GENERAL INTRODUCTION

“We must not let a forest full of trees fool us into believing all is well.”

— *Kent H. Redford*

1.1 Introduction

The extraordinary biodiversity and ecological complexity of the tropics has been of interest to ecologists for over the two centuries. The latitudinal biodiversity gradient—the dramatic rise in species richness around the equator—was described as early as the 19th century by Alexander von Humboldt (Hawkins 2001). The majority of the world’s species, including 91% of the world’s terrestrial bird species and 77% of mammals (Barlow *et al.* 2018), are found in the tropics, many clinging to strongholds and refugia not yet destroyed by anthropogenic forces. The high degree of species richness is sustained by intricate patterns of resource partitioning and adaptations. However, these beautiful and diverse ecosystems are inseparable from human influence, with the tropics home to more than 40% of the global population (Edelman *et al.* 2014).

Although these ecosystems have indisputable global importance, tropical forests are disappearing at rates faster than forests anywhere else in the world (Austin *et al.* 2017). Increasing rates of habitat loss and disturbance are resulting in disproportionate defaunation in the tropics (Dirzo *et al.* 2014) and increasing extinction risks threaten to degrade biodiversity (Kerr & Burkey 2002, Vamosi & Vamosi 2008).

The dangers these tropical ecosystems face are exacerbated by the fact they remain severely understudied (Rodriguez 2003). The majority of ecological research is conducted by wealthy countries in temperate regions, leaving a paucity of research conducted in developing countries, most of which are situated around the equator (Tydecks *et al.* 2018). Research deficits in tropical ecosystems leave species further vulnerable to anthropogenic disturbances, exacerbating the current biodiversity crisis.

Borneo

Straddling the equator at the centre of the Malay Archipelago, the island of Borneo is an evolutionary hotspot of flora and fauna. The island is governed by three separate countries: Malaysia and Brunei in the north and Indonesia in the south. The majority of the island falls under Indonesian jurisdiction; however, the split governance creates challenges in conducting cohesive conservation efforts.

The 3rd largest island globally, Borneo supports a wealth of endemic species and rich biodiversity with the highest levels of species richness in South-East Asia (de Bruyn *et al.* 2014). Representing less than 0.2% of the global landmass, it is home to 5% of the world's vertebrate species (MacKinnon *et al.* 1996).

Although the diversity of this rainforest ecosystem has attracted researchers and naturalists since the 19th century (Beccari 1904, Shelford 1917), most notably A.R. Wallace (Wallace 1856), there remain many facets of its ecology that are not only not well understood but difficult to study. Researchers have been working in Bornean rainforests for decades, contributing towards a functional understanding of this valuable ecosystem. Although much progress has been made, there remain many knowledge gaps. This is due, in part, to the elusive nature of many key species that occur at low densities, making them challenging to study (Mathai *et al.* 2013). Additionally, the terrain in Borneo can make research efforts almost impossible as forests rise steeply up into central highlands that are difficult to access. Until recently, this inaccessibility had succeeded in protecting central highland forests which remained relatively untouched until the early 1990s (Bodmer *et al.* 1991). Today, these previously untouched areas of Borneo are now under threat from a number of anthropogenic forces.

Anthropogenic threats

Prior to the 1970s, three quarters of Borneo was covered in tropical forests and had largely escaped the exploitation of natural resources occurring around the globe (McAlpine *et al.* 2018). Unfortunately, although industrial-scale resource extraction arrived late to Borneo, it arrived with force. Indonesia, which governs the largest portion of Borneo, experienced a political coup in 1998, resulting in the decentralization of the government, giving regional autonomy to districts (Hill & Shiraishi 2007).

Given fresh authority over local resources, the Kalimantan province of Borneo (governed by Indonesia) experienced a boom in logging, land-use changes, and resource extraction as underdeveloped areas were put under financial strain (Resosudarmo 2005). The coincidence of this political change (Resosudarmo 2005), along with the Asian Financial Crisis (Hill & Shiraishi 2007), and growing demand for plantation products (Gaveau *et al.* 2016) led to large-scale deforestation, reducing remaining forests to less than 50% of the coverage that existed in 1973 (Ocampo-Penuela *et al.* 2020). Now exhibiting among the fastest rates of decline worldwide (Hansen *et al.* 2013), Borneo's forests are at risk of disappearing altogether, along with the unique ecosystems they hold.

Industrial logging of Borneo's rainforests, ongoing since the 1970s, is reducing remaining forest stands at an alarming rate (Gaveau *et al.* 2014). Between 1970 and the 1990s, more than half of the

tropical hardwood exports globally were from Borneo (Brookfield & Byron 1990). In addition to industrial operations, illegal logging is a prevalent and complex issue often targeting protected areas that contain some of the only remaining stands of valuable hardwoods (Curran *et al.* 2004, Hiller *et al.* 2004). Over two thirds of deforestation recorded in the Kalimantan province of Indonesian Borneo occurred within protected or proposed protected areas between 1997 and 2002 (Fuller *et al.* 2004). Limited resources and widespread involvement make it difficult to police/regulate illegal logging: with operations frequently involving entire communities and villages (Hiller *et al.* 2004). A 2008 survey of villages surrounding Gunung Palung National Park (West Kalimantan, Indonesian Borneo) found 47% of households were dependant on illegal logging as their primary source of income (Hiller *et al.* 2004). Although logging is a considerable threat to forests in Borneo, the primary driver of deforestation is plantation industries (Gaveau *et al.* 2016). Converting forests into plantations has shown to have a significantly worse influence on biodiversity long-term than forest loss due to logging (Wilcove & Koh 2010). Burivalova *et al.* (2020) have shown that after the initial deforestation from logging, logged areas recover biodiversity levels relatively quickly, with secondary forests showing higher floral species richness and rates of carbon storage than primary forests (Berry *et al.* 2010). As the global demand for products like palm oil and pulpwood has increased, Indonesia has sought to meet demand, resulting in an estimated 7.9 million ha of industrial palm-oil plantations in Borneo in 2015 (Gaveau *et al.* 2016). The demand for palm oil is predicted to continue to rise encouraging further land conversion (Corley 2009, Malins 2017).

As ongoing deforestation draws more attention towards conservation in Borneo, the extent of intact forest is frequently estimated to evaluate the threat facing forest-dwelling species (Proctor *et al.* 2011, Hearn *et al.* 2016, Miettinen *et al.* 2016, Cushman *et al.* 2017, Ocampo-Penuela *et al.* 2020). Focusing on the presence of trees does not guarantee a healthy forest and overlooks the extent of defaunation occurring within tropical forests (Redford 1992). Therefore, evaluating threats permeating forests is necessary to prevent the defaunation of these ecosystems.

One such threat in Borneo comes from poaching, which imposes considerable danger to target species. Increased access into forests from logging and new roads has been linked to increased poaching activity (Laurance *et al.* 2006, Mohd-Azlan & Lading 2006, Alamgir *et al.* 2019). Many species, such as orangutans (*Pongo pygmaeus*), bearded pigs (*Sus barbatus*), various ungulates, and small carnivores are hunted for bushmeat (Bernard *et al.* 2013, Marshall *et al.* 2006, Cheyne *et al.* 2010). Additionally, other species such as pangolins (*Manis javanica*), sun bears (*Helarctos malayanus*), freshwater turtles and Sunda clouded leopards (*Neofelis diardi*) are live-trapped and sold for the wildlife trade (Pantel & Chin

2009, D’Cruze & Macdonald 2015, Jensen & Das 2008) or medicinal purposes (Wong & Servheen 2010). Species targeted by poachers in Borneo are frequently driven to very low population numbers or even local extinction as poaching pressure remains consistent in chronically over-hunted areas (Brodie *et al.* 2014). Brodie *et al.* (2014) studied mammal occurrences across Malaysian Borneo and found that poaching pressure poses a more serious threat to species richness than logging, with poaching linked to a 31% decline in species richness compared to an 11% decline in freshly logged sites. Poaching also leads to indirect effects on many species by depleting the prey-bases of carnivore species (Burton *et al.* 2012, Hearn *et al.* 2017) and contributing to a ‘landscape of fear’ altering species behaviours (Oriol-Cotterill *et al.* 2015).

To effectively study the effect of anthropogenic threats on rainforest ecosystems, a basic understanding of individual species’ ecology is needed along with an understanding of how species interact within functional rainforest communities.

Importance of spatiotemporal studies

Understanding the impact of anthropogenic disturbances within forest ecosystems becomes an impossible task when there is a paucity of data about the species of interest (Morais *et al.* 2013, Pimm *et al.* 2014, Brodie 2009). Determining where a species is present is necessary to understand their basic habitat needs. Assessing the environmental and physical factors influencing species occurrence in an intact ecosystem can be used to develop Species Distribution Models (SDMs). This form of modelling can extrapolate known local distributions across large landscapes that could not be feasibly surveyed, determine potentially suitable habitats, and can be used to model changes to distributions in response to influential factors (e.g. climate change, human disturbance, habitat loss) (Rodriguez *et al.* 2007, Sinclair *et al.* 2010). While other research is necessary to gain a full understanding of a species’ needs, the study of distribution is at the heart of ecology and creates a foundation of knowledge that can be further built upon (Krebs 1972).

Comparing patterns of distributions amongst multiple species can provide further ecological insight by identifying possible species interactions and patterns of niche partitioning. Possible interspecific interactions can be inferred by analysing patterns of either overlapping or avoidant habitat use between species (Toft *et al.* 1982, Heithaus 2001, Razgour *et al.* 2011, Steinmetz *et al.* 2013). Identifying competitive interactions between species can then be applied to help describe patterns of niche partitioning—considered to be an attempt to reduce interspecific competition for a shared resource (i.e. habitat or food) (Hutchinson 1957, Holt 1987).

Studying patterns of habitat use, or distribution, solely on a spatial perspective can fail to identify temporal patterns of niche partitioning, and changes in response to natural or anthropogenic factors. Species competing for a shared resource may reduce competition by differentiating along several dimensions: either differentiating by habitat, specializing to a different food resource, or shifting activity patterns to use the same resource at a different time (Hutchinson 1959). Similarly, species may attempt to avoid predation by altering the habitats they use or time of day they use them (Sih 1980, Werner *et al.* 1983). A growing number of studies have focused on temporal patterns of habitat use, identifying species interactions and niche partitioning (Albrecht & Gotelli 2001, Gosselink *et al.* 2003, Hampton 2004, Valeix *et al.* 2007). Additionally, changes in habitat use occurring in response to variables may only be identified if observed over long periods. Fluctuations in resources, predator populations, disease, climate, and anthropogenic threats can alter patterns of habitat use leading to an incomplete depiction of overall patterns if observed as an instantaneous snapshot.

Examining patterns of habitat use, over both space and time, in communities is vital to inform individual species' ecology, identify interspecific interactions, and ultimately obtain a well-developed picture of an intact ecosystem to determine how it may respond to anthropogenic influences.

Camera traps

In recent years, the use of camera traps has become increasingly popular to collect data on understudied tropical ecosystems (Ahumada *et al.* 2011, 2013, Rovero *et al.* 2014). Although camera traps have been used in ecological studies in various forms over the past several decades, technological advances and lower prices have resulted in growing deployment. The development of infrared motion sensors and compact digital cameras with long battery lives have made camera traps a more cost-effective means to conduct ecological surveys. This technology has begun to replace traditional labour-intensive sampling methods like distance sampling (Burton *et al.* 2015).

In recent years, many studies using motion-triggered cameras have shifted focus from identifying individuals of a species to community biodiversity studies (Steenweg *et al.* 2017). This reflects the flexibility of this sampling method: which once set up can consistently collect data that can be used for a variety of analyses, including animal behaviour, species richness, abundance, and occupancy on multiple species simultaneously (Steenweg *et al.* 2017).

The use of camera traps was quickly adopted by ecologists studying large elusive carnivores that typically occur in low densities and have low detectability with traditional transect sampling approaches (Fragoso *et al.* 2016). There is a breadth of research using camera traps to study elusive cat species in

Borneo alone (Cheyne & Macdonald 2011, Brodie & Giordano 2013, Wilting *et al.* 2012, Wearn *et al.* 2013, Hearn *et al.* 2018b). However, without the use of consistent and standardized camera trap protocols or long study periods, differing detection probabilities or low number of detections can make it difficult to draw robust conclusions about density, distribution or activity patterns from findings (Cheyne *et al.* 2010, Wearn *et al.* 2013). A growing number of researchers have been calling for the use of standardized protocol and data sharing, allowing for global conservation collaborations (Ahumada *et al.* 2011, Meek *et al.* 2014, Schmeller *et al.* 2015). Camera trapping provides an opportunity for consistent, efficient, and cost-effective sampling that can be used to unite local projects into massive global initiatives like TEAM (Tropical Ecology Assessment and Monitoring) to effectively assess and monitor ecological communities (Rovero & Ahumada 2017, Galvez *et al.* 2016).

Occupancy modelling

A further advantage of using a camera trap framework for ecological research is its ability to provide large amounts of presence-absence data required for a robust form of analysis called occupancy modelling. Occupancy (Ψ) refers to the proportion of sites or patches occupied by a species (Mackenzie *et al.* 2002) and can be used as a surrogate for abundance, to infer distribution, evaluate species co-occurrence, and many other applications (Mackenzie & Nichols 2004).

Occupancy modelling was developed to account for imperfect detection, a prevalent weakness in abundance and distribution analysis (Mackenzie *et al.* 2002, Pollock *et al.* 2002, Royle *et al.* 2005). In a review of ecological papers in 2014, 77% neglected to account for imperfect detection despite available methods (Kellner & Swihart 2014). Occupancy modelling addresses this issue by explicitly modelling detection probabilities as a function of various environmental and sampling parameters and then adjusting estimates of occupancy accordingly. Accounting for imperfect detection directly in the modelling allows final occupancy estimates to reflect situations when an individual may have been present but failed to be detected.

Occupancy modelling works well in combination with camera trapping as this form of analysis requires a large amount of simple data (Rich *et al.* 2016). Instead of count data required for abundance estimates, occupancy modelling requires basic presence-absence data for a range of sampling sites within the study area. For robust estimates repeated sampling at each site is necessary, however, this is a labour-intensive and often unfeasible request for more traditional sampling techniques (Mackenzie *et al.* 2002). With camera trap studies, following the initial setup the continuous data acquired can be split into consecutive surveys to easily address this need.

The combination of camera trap data and occupancy modelling analysis is increasingly the method of choice for studies of species with little knowledge about their ecology (Galvez *et al.* 2016, Rich *et al.* 2016, Rovero *et al.* 2014, Tobler *et al.* 2015). Covariate analysis in an occupancy modelling framework enables researchers to use the simple presence-absence data in combination with various covariates to create estimates of habitat use and evaluate the factors affecting the occupancy of a species (Mackenzie *et al.* 2006). Conducting occupancy modelling in combination with a model selection approach, such as Information Theoretic Approaches and Akaike Information Criterion (AIC)(Burnham & Anderson 2002), allows a set of *a priori* candidate models to be designed and tested alongside each other (Mackenzie *et al.* 2006). Occupancy modelling has been valuable to researchers studying species where a wealth of abundance data is difficult to obtain and therefore relying on traditional approaches would provide weak inferences with a large margin of error (Rovero *et al.* 2014, Mackenzie *et al.* 2006, Galvez *et al.* 2016).

Knowledge gaps in Bornean rainforest ecosystems

Elusive species, occurring at low densities throughout large expanses of inaccessible terrain have provided significant hurdles to researchers in Borneo leading to numerous species remaining understudied (Struebig *et al.* 2008, Mathai *et al.* 2016, Mathai *et al.* 2010). As a result, the majority of ecological research conducted in Borneo has focused on a select few species and mostly comprises of descriptive studies overlooking assessments of population changes, cause-effect analysis, threats, and species interactions (Meijaard & Sheil 2007). Despite 16 Bornean mammal species listed as either critically endangered or endangered on the IUCN Red List of Threatened Species, of these only orangutans and other primates are well represented in the research literature (Meijaard & Sheil 2007, IUCN 2020). Many other species responsible for key ecological roles are often overlooked and remain poorly understood.

Ungulates play key roles in ecosystems as seed dispersers (Blate *et al.* 1998), assist forest regeneration (Webb and Peart 2008), and typically comprise a large portion of biomass in ecological communities; making up a prey base for many endangered carnivore species (Albert *et al.* 2015, Fritz *et al.* 2002). Despite decades of research on ungulates around the world, a paucity of research focuses on Artiodactyla within the tropical ecosystems. Historically, studying ungulates in Bornean rainforests has been challenging partially due to difficulties accurately identifying species during transect sampling and behaviours that reduce their detectability (Fragoso *et al.* 2016).

Borneo also supports a diverse guild of endemic carnivores, a large proportion of which are classified as threatened. However, there is a disproportionate lack of ecological knowledge of many of these species. A growing number of studies have focused on felid species in Borneo (Hearn *et al.* 2018b), although small sample sizes and study limitations combined with the elusive nature of carnivores have limited the extent of our knowledge base. Carnivores can exert crucial top-down regulation on ecological communities, maintaining food web stability and diversity, and their conservation must be prioritized accordingly (Allen *et al.* 2017).

In addition to several taxa remaining understudied in Bornean rainforests, the ecological response to dramatic spatiotemporal fluctuations in fruit resources remains understudied for many species. Tropical rainforest systems in South East Asia are frequently characterized by mast-fruiting, resulting in considerable fluctuations in fruit and seed resources (Ashton *et al.* 1988). The wide-spread synchronous fruiting of predominantly dipterocarp species during these events is followed by several years of little or no fruit production. The supra-annual basis of mast events is thought to be linked to the El Niño-Southern Oscillation (ENSO) cycles, however, the cause and reason for this phenomenon is still debated (Wich & Schaik 2000, Williamson & Ickes 2002). Fluctuations in fruit availability have been theorized to exert a bottom-up influence on frugivore species, however, this influence remains understudied in tropical systems with most research focusing on primate species (Marshall & Leighton 2006). Understanding the effect of dramatic variation in resource availability on consumer species, and potentially other trophic levels, should be a priority for research hoping to aid in the preservation of tropical rainforests.

To effectively conserve Borneo's rainforest ecosystems, it is necessary to fill the gaps in our ecological knowledge with further research, particularly with a focus on understudied species and dynamics that play key ecological roles. The application of a standardized camera trap methodology in Bornean forest ecosystems can help collect valuable information on ungulate and carnivore populations. Long-term studies of habitat use and distribution following an analytical framework that accounts for imperfect detection could result in robust estimates of habitat use that are critical for informed conservation and management actions.

1.2 Aims

Using data from a long-term camera trapping study, the objectives of my research are to 1) use occupancy modelling to develop an understanding of the spatial ecology of members of two taxonomic groups that remain poorly understood in an intact tropical rainforest, 2) evaluate the influence of

spatiotemporal fluctuations in fruiting resources on the habitat use of a top carnivore and 5 sympatric ungulate species, 3) investigate species co-occurrence patterns to inform an understanding of species interactions and niche partitioning within the rainforest community, and 4) generate baseline data for the distribution of some key species across an intact rainforest system site to inform future research, monitoring and conservation.

1.3 Study site

The data for this study were collected at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, in West Kalimantan, Borneo. The national park is 100,000 ha, covering a mosaic of diverse rainforest habitats (Paoli *et al.* 2001). Located on the southwest coast of Borneo, Gunung Palung is 130 km south of the provincial capital, Pontianak. Gunung Palung is one of the largest remaining primary lowland forests on Borneo, which despite having been protected since 1937 still experiences some illegal logging (Fawzi *et al.* 2018, Hiller *et al.* 2008).

The CPRS (Figure 1.1) is a 34 km² long-term research site within the National Park. Despite increasing population pressure in areas surrounding the park the limited access into the research area by foot or river has kept human disturbance at CPRS relatively low compared to other unprotected areas in Borneo. Gunung Palung National Park still experiences some poaching (A.J. Marshall, *personal communication* 2020), and illegal logging (Hiller *et al.* 2008, Felton *et al.* 2003) which remain a source of sustenance and primary income for local villagers (Hiller *et al.* 2008). The climate is considered tropical and aseasonal with little variation in temperature and rainfall across the year (Figure 1.2). CPRS encompasses mangrove forests and low-lying swamps around sea-level rising into a lowland forest that change abruptly into the next forest type as they follow the river upstream. The Air Putih river valley then rises on either side into two ridges leading to the upland montane habitat on the western slope of Mt. Palung (1080 m) and Mt. Panti (1100 m) (Curran and Leighton 2000).

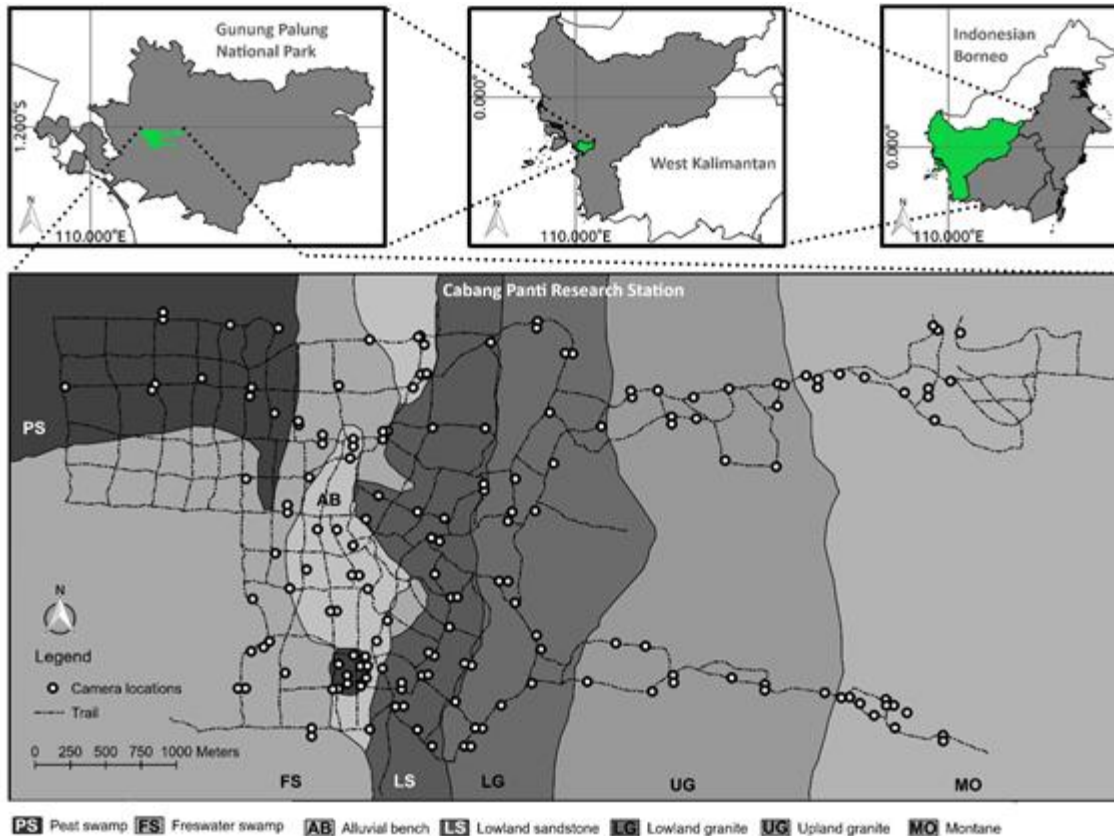


Figure 1.1: Map illustrating the location of Gunung Palung National Park within the west Kalimantan province of Indonesian Borneo. The primary image shows the habitat types, camera locations, and trail system throughout the study site at Cabang Panti Research Station. Forest types are indicated by two-letter abbreviations described in the legend beneath the image.

Forest types

The presence of 7 distinct forest habitat types across an elevational gradient makes CPRS an ideal site to study the variation in species distribution over space and time. The forest types differ in structure, levels of productivity, and species composition due to differences in soil composition and climate variation among the habitat types (Marshall 2009, Marshall *et al.* 2014).

The mosaic of forest types within the compact study area provides an opportunity to investigate relationships between species distributions and forest productivity, mast synchronicity, forest structure, and community composition. Much of the research that has been conducted at CPRS has accordingly focused on frugivore species (Knott 1999, Johnson *et al.* 2005, Marshall *et al.* 2014, Marshall 2009, Curran and Leighton 2000, Clink *et al.* 2017, Dillis *et al.* 2015) seed dispersal (Webb and Peart 2008, Blate *et al.* 1998), masting and forest productivity (Curran and Leighton 2000, Marshall *et al.* 2014), and forest reproduction (Cannon *et al.* 2007a, Cannon and Leighton 2004).

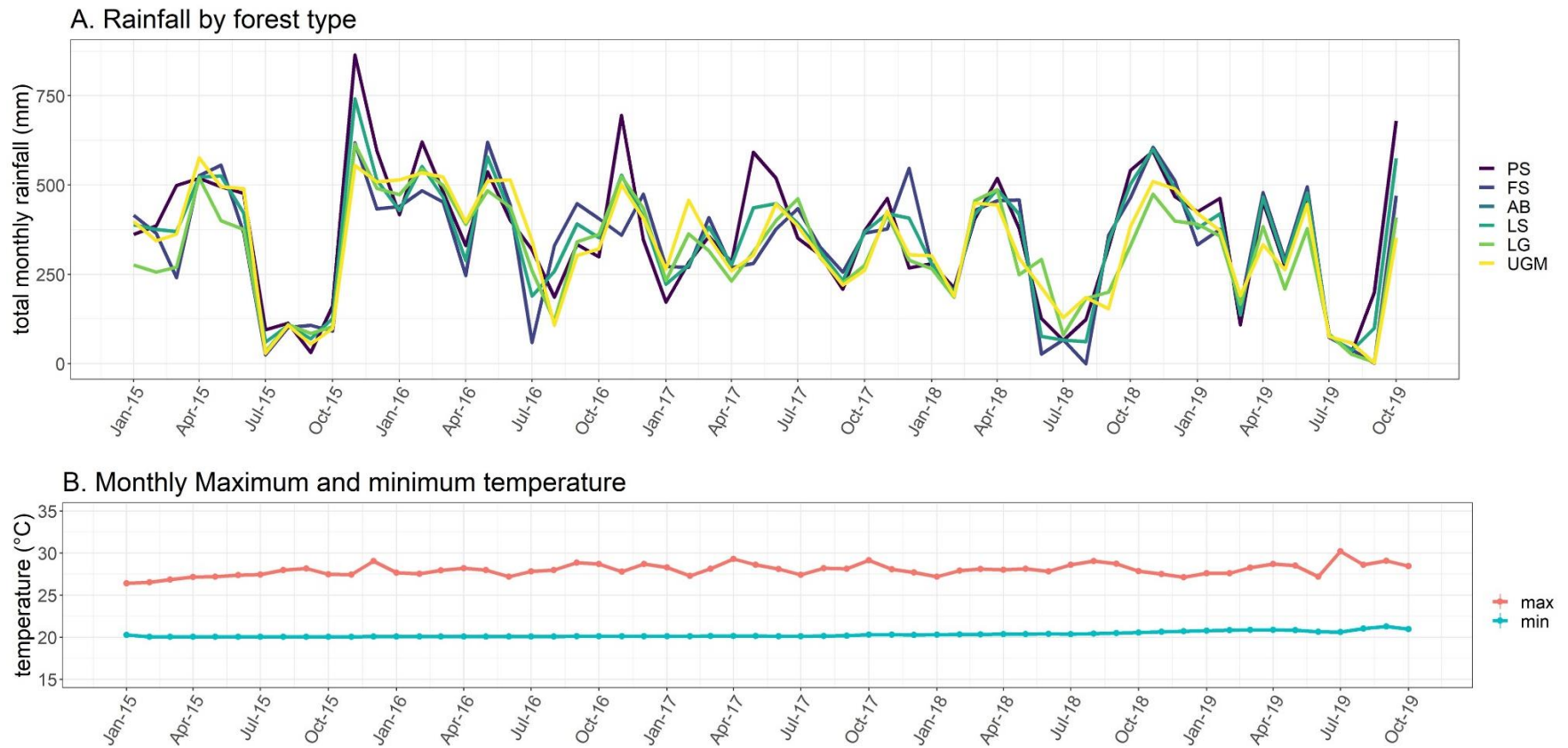


Figure 1.2: Climate at the Cabang Panti Research Station between July 2015 and October 2019. A) Total monthly rainfall by forest type (PS—peat swamp, FS—freshwater swamp, AB—alluvial bench, LS—lowland sandstone, LG—lowland granite, and UGM—upland granite/ montane), and B) maximum and minimum temperatures with error bars depicting the standard deviation (°C).

Mammal community

The study area at CPRS supports an intact rainforest community considered to remain largely unaffected by human disturbance (Laman *et al.* 1996, Blundell 1996, Marshall *et al.* 2009a). Under the protection of the park, the mammal community has remained diverse and is thought to remain at densities characteristic of undisturbed Bornean rainforest ecosystems (Marshall *et al.* 2009a). The mixture of forest types in the region and abundance of synchronous masting plants provide a rich food source sustaining a diverse guild of vertebrate frugivore species (Curran and Leighton 2000, Marshall *et al.* 2014). Five sympatric ungulates are frequently observed across the study site, feeding on a mixture of fruit and browse (Phillips 2016). Consisting of two chevrotain species (*Tragulus kanchil*, *T. napu*), a pair of muntjacs (*Muntiacus atherodes*, *M. muntjak*), and the bearded pig (*Sus barbatus*), little is known about how these species differentiate in resource or habitat use. The set of ungulates are thought to comprise a large portion of the prey base for Borneo's endangered carnivores (Hearn *et al.* 2018b, Ross *et al.* 2013). The Sunda clouded leopard (*Neofelis diardi*) is the top predator in Borneo, and the largest of the five sympatric felids. Alongside the Sunda clouded leopard is the leopard cat (*Prionailurus bengalensis*), Bornean bay cat (*Catopuma badia*), flat-headed cat (*Prionailurus planiceps*), and the marbled cat (*Pardofelis marmorata*). The co-occurrence of all five felid species is rarely recorded across Borneo as the Bornean bay cat and flat-headed cat are categorized as endangered by the IUCN (2020) (Cheyne *et al.* 2016, Hearn *et al.* 2018b, Mohamed *et al.* 2009). Over the past 20 years, all 5 species have been recorded at GPNP (Nowak 2012, Allen *et al.* 2016), indicating that it may remain an ecological stronghold, however, the contemporary occurrence within the study site is unclear.

Table 1.1: Characteristics of 7 distinct forest types present in Cabang Panti Research Station, Gunung Palung National Park, Indonesian Borneo (Whitmore 1984, Curran & Leighton 2000, Paoli *et al.* 2001, Cannon & Leighton 2004, Marshall *et al.* 2014).

Forest type	Elevation	Soil type	Dominant vegetation	Forest structure
Peat swamp (PS)	5-10 m asl	<ul style="list-style-type: none"> · Nutrient poor soil · Bleached-white soil topped with a layer of organic material 	<p><u>Dominant species:</u> <i>Palaquium leiocarpum</i> 10%</p> <p><u>Dominant family:</u> <i>Myrtaceae</i> 20%, <i>Sapotaceae</i> 13%, <i>Fabaceae</i> 6%</p>	<ul style="list-style-type: none"> · Predominantly small trees and woody climbers, · high density
Freshwater swamp (FS)	5-10 m asl	<ul style="list-style-type: none"> · Nutrient-rich soil · Poorly draining gleyic soil that is flooded seasonally 	<p><u>Dominant species:</u> <i>Pternandra coerulescens</i> 11%</p> <p><u>Dominant family:</u> <i>Melastomataceae</i> 12%, <i>Euphorbiaceae</i> 12%, <i>Annonaceae</i> 10%</p> <ul style="list-style-type: none"> · moderate proportion of figs · low species diversity 	<ul style="list-style-type: none"> · Mostly small trees and woody climbers · Low density of trees
Alluvial bench (AB)	5-50 m asl	<ul style="list-style-type: none"> · Nutrient-rich soil · Soils derived from alluvial deposits of upstream sandstone and granite parent material 	<p><u>Dominant species:</u> <i>Dipterocarpus sublamellatus</i> 9%</p> <p><u>Dominant family:</u> <i>Dipterocarpaceae</i> 20%, <i>Myristicaceae</i> 9%, <i>Euphorbiaceae</i> 8%</p> <ul style="list-style-type: none"> · Large proportion of figs 	<ul style="list-style-type: none"> · Slightly lower tree densities (small and large)
Lowland sandstone (LS)	20-200 m asl	<ul style="list-style-type: none"> · Nutrient-rich soil · Sandy well-drained soil derived from sandstone and quartzite sedimentary rock · High clay content 	<p><u>Dominant species:</u> <i>Strombosia ceylanica</i> 5%, <i>Dipterocarpus sublamellatus</i> 5%</p> <p><u>Dominant family:</u> <i>Euphorbiaceae</i> 10%, <i>Annonaceae</i> 7%</p> <ul style="list-style-type: none"> · Moderate proportion of figs · High fruit productivity · High species diversity 	<ul style="list-style-type: none"> · High density of large trees

Forest type	Elevation	Soil type	Dominant vegetation	Forest structure
Lowland granite (LG)	200-400 m asl	· Well-drained granite-derived podzolic soil	<u>Dominant species:</u> <i>Shorea crassa</i> 5% <u>Dominant family:</u> <i>Dipterocarpaceae</i> 20%, <i>Sapotaceae</i> 11% · High species diversity	· High density of small and large trees
Upland granite (UG)	350-800 m asl	· Well-drained granite-derived soil	<u>Dominant species:</u> <i>Shorea crassa</i> 5% <u>Dominant family:</u> <i>Dipterocarpaceae</i> 20%, <i>Sapotaceae</i> 11%	· High density of small and large trees · High density of small trees
Montane (MO)	750-1100 m asl	· Granite-derived soil	· Low species diversity · Low level of fruit production	· No large trees · Transitioning to predominantly small trees with stunted growth at higher elevations with Massenerhebung effect

1.4 Data collection

Motion-triggered camera traps (Bushnell TrophyCam, Overland Park, KS) were set up at 192 locations throughout Cabang Panti Research Station between June 2015 and October 2019 (n = 42,610 trap nights) to monitor terrestrial wildlife. Camera locations were randomly selected along trails (n = 134) and paired with off-trail cameras (n = 58) to evaluate differences in detection probability due to camera placement. Cameras were set up in each of the 7 habitat types with a minimum of 4 cameras active per habitat at any time (PS n = 28, FS n = 30, AB n = 38, LS n = 28, LG n = 22, UGM n = 48). Of the 7 distinct forest types identified (Table 1.1), I pooled the upland granite and montane forests (UGM) as phenological data was unavailable for the montane forest within the study period. The adjacent upland forests are considered to have substantial interdigitation and similar floral composition.

Sites were sampled on a rolling basis with an average of 31.8 sites actively surveyed during a 30-day survey period and each site was effectively resampled an average of 4.87 times. Camera traps were regularly serviced every 3-4 weeks to ensure the batteries remained active and the cameras had not been damaged or stolen. Cameras were programmed to record 20 s videos when triggered, with a refractory period of 10 s before becoming active again. All footage was reviewed by local wildlife experts and animals were identified to a species level. In some cases, closely related species that could not be clearly identified were recorded at the genus level and were omitted from analysis. To reduce autocorrelation, I treated multiple recordings of the same species at a site during a 24 h period (starting at 00:00) as one sighting.

Monthly data on fruit availability was compiled from phenology data collected by Dillis *et al.* (2015) using 10 randomly selected phenology plots, summing to 1.5 ha sampled in each forest type. Within plots, fruit availability was assessed for all trees with stems larger than 14.5 cm dbh, lianas larger than 3.5 cm dbh, and all hemi-epiphytic figs with roots touching the ground. Fruit availability was measured as the density of stems bearing ripe fruit and plot-specific values were averaged to obtain one monthly value for each forest type.

Chapter 2.

Habitat use and niche partitioning of ungulates in response to spatiotemporal variation in fruit availability at Gunung Palung National Park

2.1 Abstract

A paucity of data on the diets, distribution, and basic ecology of tropical ungulates contributes towards the vulnerability of tropical rainforest ecosystems to anthropogenic threats. Ungulates likely play key ecosystem roles through seed dispersal, forest regeneration, and in that they comprise a large portion of the prey biomass supporting carnivore populations. A detailed understanding of the spatial ecology and niche partitioning is lacking for ungulates in Borneo. I used remote camera traps and a modified single-season occupancy modelling approach, using time as a covariate, to study spatiotemporal habitat use patterns of 5 ungulate species in Gunung Palung National Park, West Kalimantan, Borneo, over a 4 ½ year period (n = 42,610 trap nights). Specifically, I estimated habitat use of lesser mousedeer (*Tragulus kanchil*), greater mousedeer (*T. napu*), Bornean yellow muntjac (*Muntiacus atherodes*), red muntjac (*M. muntjak*) and bearded pig (*Sus barbatus*) across 6 distinct forest types along an elevational gradient and a temporal gradient of fruit availability. Forest type was an important variable explaining habitat use and distribution of each species. Habitat use estimates peaked in peat swamp forests for lesser mousedeer ($\hat{\Psi} = 0.92 \pm 0.05$), alluvial bench forests for greater mousedeer ($\hat{\Psi} = 0.52 \pm 0.08$), lowland granite forests for yellow ($\hat{\Psi} = 0.95 \pm 0.07$) and red muntjacs ($\hat{\Psi} = 0.98 \pm 0.09$) and freshwater swamp forests for bearded pigs ($\hat{\Psi} = 0.84 \pm 0.07$). Bearded pigs were strongly linked to temporal variation in fruit availability, providing evidence of their ability to track changes in fruit availability. My results demonstrate a novel pattern of niche partitioning through distinct habitat and food resources among 5 sympatric ungulate species in a mast-fruiting tropical rainforest system. Given the increasingly negative impact of anthropogenic disturbances on these ecosystems, my results will aid in developing effective conservation strategies of threatened tropical ungulate communities.

2.2 Introduction

The interplay between resource availability, competition, and their effects on niche partitioning has been well studied and can be used to provide key information on species' distributions and the integral roles they play within their ecosystem. Niche partitioning can be described as occurring

when species who compete over a shared resource differentiate along an additional dimension (i.e. habitat, food resources, or time) to reduce interspecific competition (Hutchinson 1957, Holt 1987). Examining habitat and resource use among competing species is a simple way to identify patterns of niche partitioning (Schoener 1974).

A variety of factors, including species interactions, human activity, and physical/environmental factors can be at play, shaping the realized niche of species. The fundamental niche is shaped by environmental and physical characteristics influencing habitat suitability (i.e. climate, resource availability, elevation, etc.). Interactions between species—either as competition, mutualism, commensalism, or predation—differentiates a realized niche from the fundamental niche (Hutchinson 1957). The influence of humans either through direct negative interactions analogous to predation (i.e. poaching), or through passive human activity (i.e. researchers) can form a *landscape of fear* based on perceived predation risk and has the potential to similarly influence the distribution of a species (Lima *et al.* 1990, Laundre *et al.* 2001). Accordingly, to effectively describe the realized niche of a species, the influence of numerous factors must be evaluated collectively.

Mast-induced variation in fruit availability may be a key factor shaping niche partitioning within tropical rainforest ecosystems. In contrast to temperate forests that have predictable seasonal fruiting (Smith-Ramirez & Armesto 1994, Lechowicz 1995), a high degree of variation in resource availability, over both space and time, is characteristic of many tropical rainforest ecosystems (Wich & Van Schaik 2000). Mast events show extreme peaks in flowering and fruit production, occurring on a variable supra-annual basis and are thought to be linked to ENSO and triggered by specific climate conditions (Williamson & Ickes 2002, Ashton *et al.* 1988). Resource pulses can have pronounced responses rippling through ecological communities influencing individual fitness, habitat use, and species interactions (Yang *et al.* 2008, Bogdziewicz *et al.* 2016). The synchronized brief surge of fruit availability has been theorized to assist seedling recruitment through satiating seed predators (Janzen 1971) and more recently has been hypothesized to help escape seed predation through delays in nomadic seed predators arriving at regional masts (Curran & Leighton 2000). In Borneo, populations of bearded pig (*Sus barbatus*) have been reported to have a close link to mast cycles. They demonstrate mast-dependent reproduction with rutting behaviors timed with flowering, resulting in dramatic population booms during mast events (Caldecott & Caldecott 1985, Pfeffer & Caldecott 1986, Curran 1995). Additionally, the peak and subsequent lull in resources have been observed to result in emaciated bearded pig and sun bear (*Helarctos malayanus*) populations during long inter-mast periods (Curran & Leighton 2000, Fredriksson *et al.* 2006). Mast-fruiting events attract an influx of nomadic frugivores able to track asynchronous

fruiting across large landscapes (Levey 1988, Dove 1993, MacKinnon *et al.* 1996, Curran & Leighton 2000, Kimura *et al.* 2001, Kimura 2003, Granados *et al.* 2019). Curran and Leighton (2000) differentiated between the resource use of resident and nomadic frugivore species: proposing that resource switching occurs during mast events by resident species to reduce competition with the arrival of nomadic species that efficiently deplete mast-produced fruit supplies. While the influence of resource pulses on niche partitioning remains unknown, the fluctuating fruit availability undoubtedly affects the ecology of rainforest frugivores.

Within Borneo's rainforest ecosystems, the influence of mast-induced fluctuations in resources has been well studied, however, the ground-dwelling ungulate species have been largely overlooked (Blate *et al.* 1998, Knott 1999, Curran & Leighton 2000, Webb & Peart 2001, Felton *et al.* 2003, Cannon *et al.* 2007b, Marshall *et al.* 2009a, Marshall *et al.* 2014, Clink *et al.* 2017). Thus the basic ecology of Borneo's guild of ungulate species remains poorly understood despite facing encroaching threats from deforestation, poaching, and climate change. Studies of tropical ungulates are few and far between in contrast to the breadth of research on their temperate forest and grassland cousins (Ahrestani & Sankaran 2016). This is of particular concern as tropical forest ecosystems are facing the brunt of the global extinction crisis (Wilson 1985).

Gunung Palung National Park (GPNP) in West Kalimantan, Indonesian Borneo, is a mast-fruiting forest that supports 5 sympatric ungulate species across a dramatic range in body size (Table 2.1). The lesser mousedeer (*Tragulus kanchil*) and greater mousedeer (*T. napu*) are the world's smallest ungulate species with adults reaching 1.5 - 2.5 kg and 4 - 5.5 kg, respectively (Nowak 1999, Matsubayashi *et al.* 2003). The Bornean yellow muntjac (*Muntiacus atherodes*) and red muntjac (*M. muntjak*) are mid-sized cervids reaching 15 - 20 kg and 20 - 28kg at maturity (Heydon 1994, Phillips 2016). The bearded pig (*Sus barbatus*) reaches weights of between 60 - 200 kg when fully grown (Phillips 2016). Uncertainty remains surrounding the diets of GPNP's ungulate species as available knowledge is predominantly based on anecdotal evidence and observations. Studies of temperate ungulate ecology have found a strong relationship between ungulate body mass and diet quality—known as the Jarman-Bell Principle (Bell 1971, Jarman 1974, Geist 1974). While debate surrounds the mechanism responsible for this trend, the decline in diet quality with larger ungulate species has been well documented (Codron *et al.* 2007). This principle would predict resource partitioning between the ungulates in GPNP following the body mass relationship with mousedeer species diets consisting of higher quality fruit and seed resources; muntjacs consuming a mixture of lesser-quality browse and fruit; and bearded pigs relying on varied omnivorous diet.






The presence of 7 distinct forest types within a compact area at GPNP, existing across a range of elevations and with different inherent levels of productivity provides a rare opportunity to

simultaneously study the influence of multiple factors on patterns of habitat use. Evaluating the spatiotemporal patterns of habitat use in relation to varying levels of fruit availability, human activity, forest type, and elevation can provide insight on the spatial ecology of understudied species and partitioning among the 5 ungulates.

2.3 Aims

The purpose of my study was to investigate the patterns of habitat use over space and time of 5 sympatric ungulate species across a body mass continuum to inform an understanding of niche partitioning in a tropical rainforest system. Understanding the relationship between fruit availability and habitat use for each species will help inform an understanding of species-specific diets, dependence on mast resources, and will help determine if there is evidence of diet quality scaling with body mass in tropical rainforest ungulates in accordance with the Jarman-Bell Principle (Bell 1971, Jarman 1974, Geist 1974). To do so I used occupancy modelling based on camera trap data to investigate the influence of a) spatiotemporal fluctuations in fruit availability, b) human activity, c) forest type, d) elevation, and e) time on the habitat use of lesser mousedeer (*T. kanchil*), greater mousedeer (*T. napu*), the Bornean yellow muntjac (*M. atherodes*; yellow muntjac hereafter), red muntjac (*M. muntjak*), and the bearded pig (*Sus barbatus*). Additionally, I sought to evaluate the detection probability of each species at on and off trail camera traps to identify potential biases and inform methodology of future research.

Table 2.1: The comparative body mass, taxonomy, and conservation status of the ungulate species observed at CPRS.

Species	Family	Adult body mass (kg)	Diet	IUCN status		References
Lesser mousedeer Tragulus kanchil	Tragulidae	1-5-2.5	Primarily fruit, some browse	Least concern, population status unknown (last assessed Nov. 2014).		Heydon 1994, Matsubayashi <i>et al.</i> 2003, Meijaard & Sheil 2008, IUCN 2020
Greater mousedeer Tragulus napu	Tragulidae	4.5-5	Primarily fruit, some browse	Least concern, population decreasing (last assessed Nov. 2014).		Heydon 1994, Matsubayashi <i>et al.</i> 2003, Meijaard & Sheil 2008, IUCN 2020
Bornean yellow muntjac Muntiacus atherodes	Cervidae	15-20	Primarily browse, some fruit	Near threatened, population decreasing (last assessed Feb. 2015).		Heydon 1994, Meijaard & Sheil 2008, Phillips 2016, IUCN 2020
Red muntjac Muntiacus muntjak	Cervidae	20-28	Primarily browse, some fruit	Least concern, population decreasing (last assessed Nov. 2015).		Barrette 1977, Heydon 1994, Meijaard & Sheil 2008, Phillips 2016, IUCN 2020
Bearded pig Sus barbatus	Suidae	60-200	Fruit, seeds, roots, invertebrates, eggs, carrion, funghi, and leaves	Vulnerable, population decreasing (last assessed Feb. 2016).		Curran & Leighton 2000, Curran & Webb 2000, Hanock <i>et al.</i> 2005, Luskin & Ke 2017, IUCN 2020

2.4 Methods

2.4.1 Study Site

The study was conducted at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park (GPNP), West Kalimantan, Indonesian Borneo, as outlined in section 1.3.

2.4.2 Data Collection

Species detections and site-specific data were collected between July 2015 and October 2019 as outlined in section 1.4.

Camera traps

I used a network of motion-sensor activated cameras at 192 locations across a gradient of productivity, forest types, and elevation in CPRS—these were set up following a standardized camera trap protocol. Bushnell TrophyCam HD cameras were programmed to record 20 s video when triggered by motion, with a 10 s refractory period before becoming active again. All videos were analysed by a local expert in species identification. Sightings that had not been identified to a species level with confidence were omitted from the analysis.

Cameras were set up in each of the 7 distinct forest types within CPRS (Cannon *et al.* 2007a). However, for the purpose of this study I pool the upland granite and montane forest types into a single ‘upland granite/montane’ category. Pooling was necessary due to a lack of productivity data from the montane forest category for the duration of this study and justified based on and informed by past research suggesting interdigitation exists between these adjacent forest habitats (Curran & Leighton 2000). It is possible that pooling upland granite and montane forest types may lead to an underestimation of the effect of resource availability as montane forests may have a lower level of fruit available due to stunted growth patterns from the Massenerhebung effect (Whitmore 1984). Henceforth 6 forest types will be discussed: peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), and upland granite/montane (UGM).

Site-specific variables

Elevation and GPS coordinates at each camera site were recorded in the field and verified using ArcGIS software post-hoc. Climate and productivity data were sampled at multiple locations within each forest type monthly throughout CPRS. Fruit availability was measured at 10 randomly selected plots covering 1.5 ha in each forest type. All trees, lianas, and hemi-epiphytic figs meeting minimum size criteria were monitored and the density of stems bearing ripe fruit was recorded (see Marshall & Leighton 2006, Marshall *et al.* 2010, Dillis *et al.* 2015 for details). Plot specific values were then combined into monthly averages for each forest type. All continuous variables were standardized using a z-score normalization.

I separated all data into 13 sampling periods of equal duration spanning from July 2015 to October 2019. Each sampling period was 120 days and covered 4 vegetation surveys. Traditionally the term *season* is used in occupancy modelling, however, I chose the alternate term *sampling period* to avoid confusion as the timeframe in question did not reflect or align with a biological concept of a season. The study site at GPNP does not exhibit clear seasonality, therefore I chose sampling periods to reflect fluctuations in forest productivity (Figure 2.1). Henceforth I will describe the modelling *seasons* for this study as *sampling periods*.

I formatted data from camera traps and site-specific covariates into 30-day surveys. I chose a 30-day period based on the low detection rate of some species in the dataset. For effective modelling, the temporal scale of data should be chosen to optimize the balance of detections and non-detections (Mackenzie *et al.* 2006). If the dataset were formatted over longer surveys the data would skew towards consistent detections and if it were over shorter surveys detections would be too scarce to model.

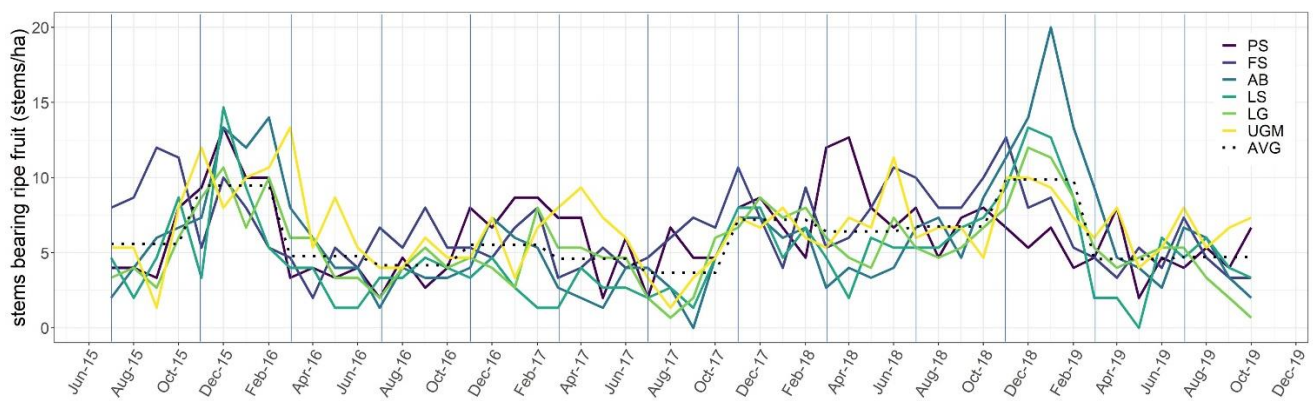


Figure 2.1: Trends in fruit availability at CPRS across 6 forest types between July 2015 and October 2019. Vertical blue lines delineate the sampling periods chosen to reflect trends in forest productivity. The dashed black line represents the density of ripe fruit per hectare averaged across habitat types and sampling periods to obtain the covariate used to represent fruit availability in my modelling.

2.4.3 Occupancy modelling

To assess the spatial and temporal patterns of ungulate habitat use throughout CPRS I conducted repeated single-species occupancy modelling using a variation on a single season framework. I performed all analysis in R (R Core Team 2013) and created detection histories for each of the focal species using the *camtrapR* package (Niedballa *et al.* 2016). I conducted occupancy modelling using the *RPresence* package developed by Mackenzie & Hines (2018).

Occupancy modelling is a form of analysis that uses detection/ non-detection data to obtain estimates of a species occurrence across an area by accounting for imperfect detection. The occupancy probability of a species (Ψ), or the probability of a randomly selected site being occupied by the species, is estimated as a function of detection probability (p). Both occupancy and detection probability can be modelled using site-specific variables, allowing the influence of these covariates to be determined.

I used a variation on a standard simple season occupancy analysis (Mackenzie *et al.* 2006) to estimate habitat use and detection probabilities across the 13 sampling periods. Multi-season occupancy modelling approaches are available (Mackenzie *et al.* 2003); however, they require consistent resampling of each location over sampling periods. This requirement was not met as camera trapping was carried out in a rolling method across the sample site and therefore the majority of sites were not resampled across more than 2 sampling periods (see section 1.4). Multi-season approaches also involve the estimation of parameters for colonization and extinction to explain underlying relationships resulting in changes to occupancy at a site. This was not of interest to my study as the focus was on patterns of habitat use and not underlying site emigration or immigration.

Alternatively, I used a simple single-season occupancy modelling framework, with time as a covariate, to concurrently analyse habitat use and detection across multiple sampling periods without estimating extinction or colonization parameters (Fuller *et al.* 2016, Burnett & Roberts 2015, Linden & Roloff 2013). This “stacked” approach combines survey sites with all sampling periods and treats each site-period combination as a separate sampling location (Ahlering & Merkord 2016). This approach has the advantage of extending the effective sample size and supports the assumption of open populations at each study site as the occupancy in subsequent sampling periods are independent. Additionally, this data structure can improve issues of poor model fit, although the error for parameter estimates can be subsequently underestimated (Burnett & Roberts 2015).

Occupancy modelling functions on the assumption of closure, meaning that sites are ‘closed’ preventing an individual from being recorded at multiple sites during a survey. As species were able to travel between sampling sites, different terminology must be used for this study. Instead of considering the occurrence of a species at a study site as an indication of its *occupancy*, for this study, this can be considered as an indication of the species’ *use* of the site (Mackenzie *et al.* 2006, Tan *et al.* 2017, Gould *et al.* 2019). This is a necessary distinction as the free movement of individuals violates the assumption of closure. As individuals are not prevented from leaving a site, the occupancy of the site could change throughout the sampling period. Therefore, if an individual is present, the site is instead defined as being *used* not *occupied*.

Another assumption of occupancy modelling is that an individual is never falsely detected at a site when it was absent. This assumption was addressed by using local experts to identify species present on high-quality camera footage. Any individuals that were not identified with confidence due to poor images or uncertainty were excluded from modelling.

Table 2.2: A description of the covariates used in habitat use and detection models. All data was collected between July 2015-October 2019 at CPRS. All continuous variables are standardized using z-score normalization.

Covariate	Measure	Range of values
<i>fruit</i>	Density of stems bearing ripe fruit / ha averaged over 120-day periods for each forest type. Standardized using z-score normalization.	2.5-14.67 stems/ha
<i>forest type</i>	Categorical covariate identifying between 6 distinct forest types	Peat Swamp (PS), Freshwater Swamp (FS), Alluvial Bench (AB), Lowland Sandstone (LS), Lowland Granite (LG), Upland granite/montane (UGM)
<i>elevation</i>	Elevation measured as distance from sea-level to describe a linear relationship along an elevational gradient. Standardized using z-score normalization.	6-1050 m above sea level (asl)
<i>elev²</i>	A quadratic relationship of elev + elev ² to describe a non-linear response to elevation. Standardized using z-score normalization.	
<i>time</i>	120-day sampling periods as a continuous covariate, aligning with periodical fluctuations in forest productivity (figure 2.1).	1-13
<i>humans</i>	Index of human activity of researchers and poachers at each site. Calculated as total number of sightings of researchers and poachers at a site during a sampling period/ sampling effort.	0-6.93 sightings/trap night
<i>off-trail</i>	Indicator variable describing the camera placement either on or off trail.	Binary value indicated ON (0) or OFF (1) trail
<i>effort</i>	The proportion of days a camera at a sampling site was active during a 120-day sampling period	0-1

2.4.4 Hypothesized predictors of habitat use and detection

The influence of several spatial and temporal factors on the habitat use and detection of ungulate species within CPRS are assessed in this study (Table 2.2).

Habitat use

I predict the occurrence of ungulate species in CPRS to be differentially influenced by variation in resource availability and human activity across the study site.

A) Resource availability

The bottom-up influence of resource availability on the habitat use of ungulates across a body-size gradient was modelled using the covariates *fruit*, *forest*, *elev*, and *elev*². Temporal variation in fruit availability, constant within forest types, was modelled using the *fruit* covariate and was predicted to have a strong influence the probability of bearded pigs using a site. Bearded pigs are thought to be ‘mobile specialists’ able to track fruit availability across landscapes and their arrival into areas often coincides with mast events (Curran & Leighton 2000, Yang *et al.* 2008, Granados *et al.* 2019). A mast event was recorded at GPNP in May-July 2014 prior to our study commencing, with minor fruiting events in December 2015 and January 2019, leading up to another major mast just following this study in early 2020. Distinct characteristics varying by forest type—including distinct spatial variation in productivity between forest types—was modelled using the *forest* covariate. According to the Jarman-Bell Principle, increasing body size in mammalian herbivores scales inversely with minimum diet quality (Bell 1970, Jarman 1974). Accordingly, I predict that reliance on high-quality fruit and browse resources available in highly productive forest types will scale inversely with body size. The probability of the smallest ungulate species using habitats (lesser mousedeer and greater mousedeer) is predicted to be strongly influenced by forest type. This would result in a positive association with highly productive habitats but no relationship with the *fruit* covariate as mousedeer likely stay in small ranges and do not track pulses in resources across landscapes (Nowak 1999, Yang *et al.* 2008, Kusuda *et al.* 2013). I predict that the mid-sized ungulates—yellow and red muntjacs—will not show strong associations with either spatial (*forest*) or temporal (*fruit*) variation in resource availability as their diet likely consists primarily of browse (Heydon 1994, Meijaard & Sheil 2008, Phillips 2016). Selective habitat use independent of productivity and fruit availability is represented by *elev* and *elev*² models, describing a linear and a quadratic relationship, respectively.

B) Human activity

I modelled the potential influence of human activity on the habitat use of target species using the covariate *humans*. This variable was calculated as an index of combined researcher and poacher sightings throughout CPRS to reflect potential negative effects associated with both lethal and non-lethal activities. Poachers were recorded on camera traps throughout the duration of the study: identified as individuals carrying guns or carcasses, and not belonging to the research teams working

at CPRS. Sparse detections (n =126) prevented separate analysis of the effect of poachers throughout the study site. Instead I pooled detections of researchers and poachers and calculated an index based on the total sightings of humans at a site standardized by the sampling effort (active trap nights/sampling period). Real and perceived threats of predation from natural predators may depend on the body size of herbivores (Sinclair *et al.* 2003, Hopcraft *et al.* 2012, Riginos 2014). Species with lower body mass may be more affected by a 'landscape of fear' (Lima *et al.* 1990, Laundre *et al.* 2001) and exhibit human avoidance. Based on this theory, I predict that human activity will have a negative influence on the occurrence of smaller ungulate species in CPRS and less of an effect on the larger species.

C) Population trends

Additionally, the presence of any temporal population-level trends amongst the species was assessed by modelling the covariate *time* which identified the sampling period, functioning as a series of time steps over the duration of the study. I used this model to determine if temporal variation in habitat use was described by a consistent linear trend over time.

Detection models

For this study, I assumed probabilities of detection to be equal among surveys, and therefore limited covariates to those describing site-specific factors influencing detectability.

I modelled changes to the detection probability of individuals due to differences in sampling effort among sites using the *effort* covariate. I calculated this covariate as an index of sampling effort from the number of days a camera was active in a sampling period over the length of a sampling period (120 days). I predict increased sampling effort will result in higher probabilities of detection.

I evaluated the influence of camera placement either on or off trails using the *off-trail* covariate. Camera trapping studies frequently place their cameras on trails to maximize the detection rate of species. Some species including large carnivores have been shown to use trail systems for easy movement throughout a territory, however, prey species may actively avoid these high-use areas to reduce the risk of predation (Harmsen *et al.* 2010). I predict that camera placement on vs. off-trail influences the detection probability of species, with different preferences between species.

2.4.5 Modelling the effects of covariates on occupancy and detection probabilities

I estimated habitat use and detection probabilities using covariates through use of a logit link function. The probability of site i being used (Ψ_i) is expressed using a logit link as a function of U covariates at site i ($x_{i1}, x_{i2}, \dots, x_{iU}$):

$$\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 x_{i1} + \alpha_2 x_{i2} + \dots + \alpha_U x_{iU},$$

with α_0 and $\alpha_1, \alpha_2 \dots \alpha_U$ representing the intercept or constant term, and regression coefficients for each covariate, respectively. The α terms are the parameters being estimated. For example, a model estimating the influence of site-specific elevation and fruit availability on site-use Ψ (*elevation + fruit*) would be described as

$$\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 \text{elev}_i + \alpha_2 \text{fruit}_i.$$

Detection probability can be similarly modelled using site-specific covariates, however, as detection is not assumed to stay constant throughout a sampling period, survey-specific covariates can be included as well. Typically, this can include covariates reflecting changes in survey conditions such as observer or weather. The use of camera traps in this study for collecting detection histories removed sampling biases due to variation in observer skill associated with traditional sampling techniques. A lack of climate variation at the study site further removed the need for survey-specific covariates to account for potential factors altering detection probabilities within sampling periods. For this study, I modelled detection probabilities similarly to site occupancy and assumed detection to be constant throughout a sampling period. Detection probability at site i is modelled as

$$\text{logit}(p_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_U x_{iU},$$

with β_0 and $\beta_1, \beta_2, \beta_U$ representing the intercept and regression coefficients to be estimated.

2.4.6 Candidate models

I created a set of *a priori* candidate models to test the predictions outlined in Section 2.4.4 (Ψ $n = 19$, p $n = 4$, Table S.1-S.2). I designed candidate models to evaluate ecological predictions with the use of covariates described in Table 2.2. I chose not to use an exhaustive all-possible-combinations approach as this has been found to increase support for spurious variables (Anderson & Burnham 2002). I developed the set of candidate models to assess the influence of a series of non-exclusive factors on habitat use and detection instead of mutually exclusive hypotheses. Therefore, I included models with permutations of two separate covariates to assess factors working in combination (Table S.1). I limited models to two covariates to avoid overparameterization. I only included covariates with a Spearman or Pearson correlation coefficient of ≤ 0.6 in the same model. I also included null models in the model set. I modelled detection and habitat use, holding a parameter in a general model while estimating the other.

I used Akaike Information Criterion (AIC) to rank candidate models, selecting for the most parsimonious fit to the data. I considered models with $\Delta\text{AIC} \leq 4$ to have a substantial amount of empirical support, $\Delta\text{AIC} \leq 7$ to have significantly less support, and models with $\Delta\text{AIC} > 7$ were deemed to have no support and were excluded from model averaging and post-hoc analysis (Burnham & Anderson 2002).

I calculated the relative variable importance (RVI) for each covariate by summing the model weights of all models that included the covariate (Giam & Olden 2016). RVI can be used in an information-theoretic framework to determine which covariates appear to be strong or weak predictors of occupancy or detection in relation to each other (Mackenzie *et al.* 2006, Giam & Olden 2016). I tested the fit of the most parsimonious model for each species, according to AIC, using a parametric bootstrap test ($n = 1,000$). I further assessed model fit by comparing the observed and expected data using a Pearson chi-square statistic (χ^2) and calculating the overdispersion parameter (\hat{c}) (Mackenzie & Bailey 2004).

2.4.7 Spatial overlap analysis

I tested the model-averaged estimates of habitat use from each species, derived from models with a $\Delta\text{AIC} \leq 7$, against each other using a Pearson correlation test. I interpreted the degree of correlation of habitat use estimates between species as the degree of spatial overlap with positive r values greater than 0.6 indicating a significant positive association and negative r values less than -0.6 indicating significant evidence of spatial avoidance. I then graphically represented the results using *corrplot* package in R (Wei & Simko 2017).

2.5 Results

All 5 ungulate species were detected during the camera trap survey (Table S.3). Bearded pigs were detected at the most sites ($n = 150$), followed by red muntjacs ($n = 106$), yellow muntjacs ($n = 96$), and lesser mousedeer ($n = 74$). Greater mousedeer were the least detected species, detected at less than a quarter of the camera sites ($n = 43$). Bearded pigs, yellow muntjacs, and red muntjacs were detected at all six forest types (Figure 2.2). Neither lesser mousedeer or greater mousedeer were detected in the lowland granite forest type and lesser mousedeer were additionally absent from the upland granite/montane. Note that raw detection data shown in Table S.3-4 and Figure 2.2-2.3 do not account for the imperfect detection of individuals.

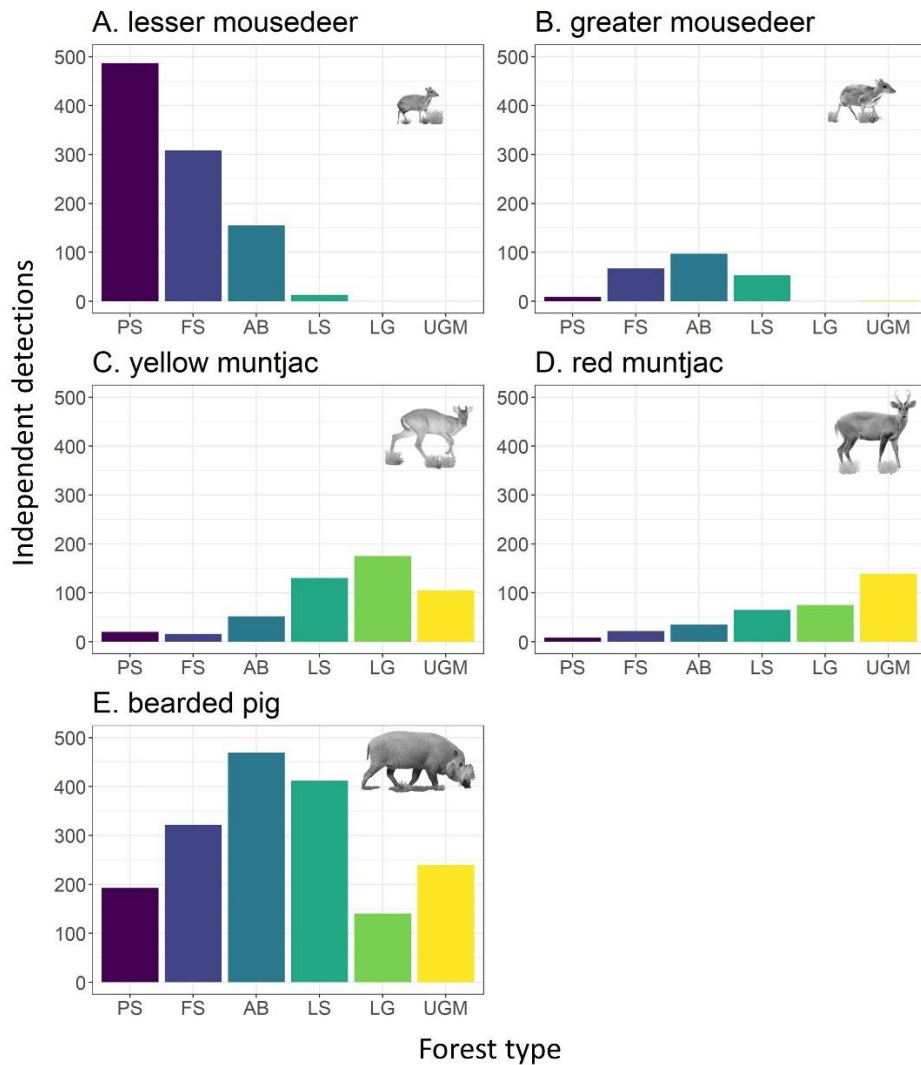


Figure 2.2: The independent detections of 5 ungulate species across forest types in CPRS recorded by motion triggered cameras between July 2015 and October 2019. Forest types in order of increasing elevational gradient are identified by the following abbreviations: Peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), upland granite/montane (UGM).

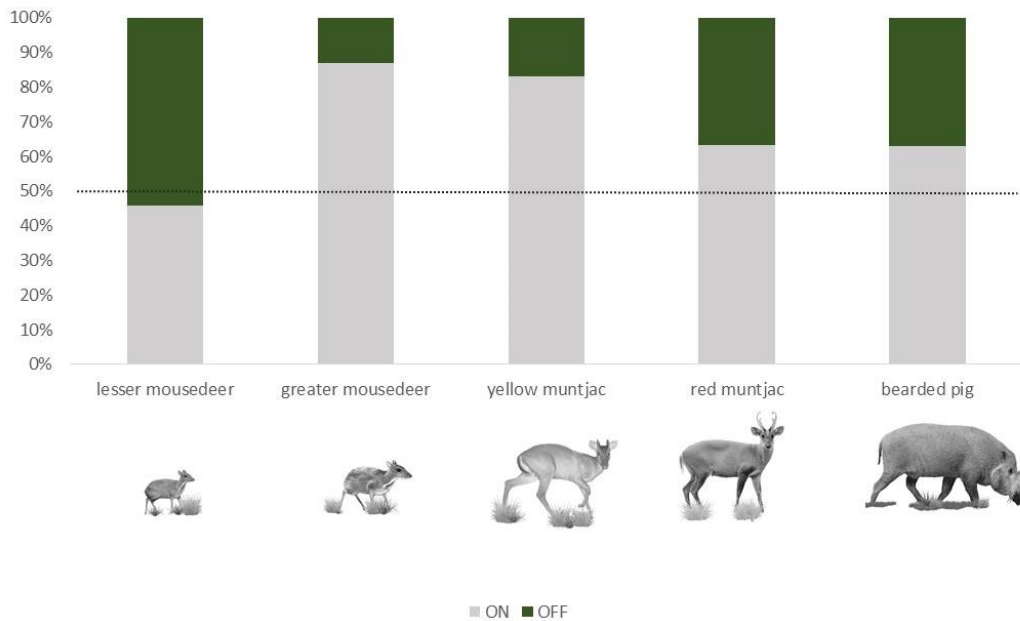


Figure 2.3: The proportion of ungulate detections at on and off trail camera locations at CPRS between July 2015 and October 2019. The number of detections was corrected for different sampling effort on ($n = 134$) and off trail ($n = 58$). Ungulate species are ordered from left to right in order of increasing body mass.

2.5.1 Lesser mousedeer

Forest type, human activity, and fruit availability best explained habitat use of lesser mousedeer ($\Delta AIC < 4$, Table 2.3). The most important variable was forest type (RVI: 0.99), followed by human activity (RVI: 0.63), and fruit availability (RVI: 0.22). Forest type was present in all top-ranked models. Habitat use of lesser mousedeer was highest in peat swamp forests ($\hat{\Psi}_{PS} = 0.92 \pm 0.05$), followed by freshwater swamp forests ($\hat{\Psi}_{FS} = 0.75 \pm 0.08$), alluvial bench forests ($\hat{\Psi}_{AB} = 0.44 \pm 0.08$) and lowland sandstone forests ($\hat{\Psi}_{LS} = 0.11 \pm 0.04$) (Figure 2.4). Lesser mousedeer were not detected in either lowland granite or upland granite/montane forests preventing the calculation of associated standard error and confidence intervals (Table 2.3). The relationship between habitat use of lesser mousedeer and human activity was positive (Figure 2.6). Fruit availability had a negative relationship with lesser mousedeer habitat use; however, this variable was associated with only 21.5% of the model weight in the top models.

Sampling effort and camera placement on or off trails were the explanatory variables present in the best performing detection probability models for lesser mousedeer (Table 2.4). Sampling effort was the most important variable (RVI: 0.97), followed by camera placement (RVI: 0.51). Sampling effort had a positive relationship with detection probability, and camera placement off trails was negatively associated with detection of lesser mousedeer ($p_{on-trail} = 0.40 \pm 0.07$,

$p_{off-trail} = 0.35 \pm 0.08$, Figure 2.5), contrary to the predicted relationship evident in the raw sightings (Figure 2.3).

Table 2.3: AIC comparisons of top ranked habitat use models ($\Delta AIC > 7$) for ungulates at CPRS. ΔAIC is the relative difference in AIC values compared to the top ranked model, K is the number of parameters in a model, w is the AIC model weight, α is the estimated intercept or constant term, β are they estimated regression coefficients for each parameter. Forest types are represented by the following abbreviations: freshwater swamp (FS), peat swamp (PS), lowland swamp (LS), lowland granite (LG), upland granite/montane (UGM). For all models the detection model $p(\text{effort} + \text{off-trail})$ was used. The null model is represented as $\Psi(\cdot)$.

Model	K	ΔAIC	w	α	β_{fruit}	β_{humans}	β_{time}	β_{elev}	β_{elev^2}	β_{forest}	
Lesser Mousedeer											
<i>forest + humans</i>	10	0	0.63	-0.35 ± 0.29		1.22 ± 0.54				PS	2.66 ± 0.66
										FS	1.31 ± 0.44
										LS	-1.97 ± 0.44
										LG	-27.35 ± 106131.7
										UGM	-34.43 ± 648651.6
<i>forest + fruit</i>	10	2.14	0.22	-0.12 ± 0.26	-0.29 ± 0.17					PS	2.97 ± 0.77
										FS	1.50 ± 0.45
										LS	-1.84 ± 0.42
										LG	-27.73 ± 134228.4
										UGM	-26.28 ± 46904.1
<i>forest</i>	9	3.47	0.11	-0.04 ± 0.26						PS	2.79 ± 0.70
										FS	1.37 ± 0.45
										LS	-1.77 ± 0.41
										LG	-27.20 ± 103824.9
										UGM	-26.16 ± 41512.4
<i>forest + time</i>	10	5.23	0.05	0.13 ± 0.44			-0.03 ± 0.05			PS	2.79 ± 0.70
										FS	1.33 ± 0.45
										LS	-1.77 ± 0.41
										LG	-25.78 ± 51929.9
										UGM	-29.97 ± 200892.6
$\Psi(\cdot)$	4	331.72	0	-0.66 ± 0.11							
<i>RVI</i>					0.22	0.63	0.05			0.99	
Greater mousedeer											
<i>forest + time</i>	10	0	0.88	1.05 ± 0.51			-0.14 ± 0.05			PS	-2.4 ± 0.54
										FS	-0.52 ± 0.43
										LS	-1.10 ± 0.43
										LG	-26.76 ± 76970.17

Model	<i>K</i>	ΔAIC	<i>w</i>	α	β_{fruit}	β_{humans}	β_{time}	β_{elev}	β_{elev^2}	UGM	β_{forest}
<i>forest</i>	9	5.47	0.057	0.15 ± 0.34						PS	-4.28 ± 0.79
										FS	-2.37 ± 0.53
										LS	-0.40 ± 0.43
										LG	-1.05 ± 0.42
										UGM	-26.48 ± 73612.03
<i>forest + fruit</i>	10	6.58	0.033	0.13 ± 0.34	-0.14 ± 0.15					UGM	-4.18 ± 0.78
										PS	-2.35 ± 0.53
										FS	-0.35 ± 0.43
										LS	-1.09 ± 0.43
										LG	-26.44 ± 71023.96
<i>forest + humans</i>	10	6.69	0.031	0.08 ± 0.35		0.43 ± 0.48				UGM	-4.13 ± 0.78
										PS	-2.42 ± 0.54
										FS	-0.42 ± 0.43
										LS	-1.14 ± 0.44
										LG	-26.84 ± 86407.31
$\Psi(.)$	4	102.81	0	-1.40 ± 0.16							
<i>RVI</i>					0.03	0.03	0.88				0.99
Yellow muntjac											
<i>forest + time</i>	10	0	0.94	0.42 ± 0.41			-0.15 ± 0.04			PS	-0.67 ± 0.44
										FS	-0.97 ± 0.47
										LS	1.87 ± 0.52
										LG	3.48 ± 1.35
										UGM	0.06 ± 0.36
<i>forest + humans</i>	10	5.68	0.06	-1.02 ± 0.36		2.37 ± 0.86				PS	-0.90 ± 0.46
										FS	-1.00 ± 0.49
										LS	1.67 ± 0.52
										LG	4.72 ± 5.09
										UGM	0.09 ± 0.38
$\Psi(.)$	4	90.95	0	-0.03 ± 0.14							
<i>RVI</i>						0.06	0.94				0.99
Red muntjac											
<i>forest + time</i>	10	0	0.72	-1.25 ± 0.63			0.18 ± 0.08			PS	-0.06 ± 0.57
										FS	-2.08 ± 0.64
										LS	1.38 ± 0.67
										LG	4.456 ± 6.57
										UGM	2.16 ± 0.90

Model	<i>K</i>	ΔAIC	<i>w</i>	α	β_{fruit}	β_{humans}	β_{time}	β_{elev}	β_{elev^2}		β_{forest}
<i>forest + fruit</i>	10	3.36	0.13	-0.08 ± 0.38	0.32 ± 0.20					PS	-0.31 ± 0.52
										FS	-1.83 ± 0.58
										LS	1.54 ± 0.68
										LG	3.50 ± 3.36
										UGM	1.64 ± 0.71
<i>forest</i>	9	4.24	0.09	-0.06 ± 0.38						PS	-0.23 ± 0.51
										FS	-1.82 ± 0.58
										LS	1.35 ± 0.65
										LG	3.27 ± 3.15
										UGM	1.64 ± 0.70
<i>forest + humans</i>	10	4.87	0.06	0.08 ± 0.41		-0.65 ± 0.56				PS	-1.81 ± 0.58
										FS	-0.23 ± 0.51
										LS	1.48 ± 0.70
										LG	2.82 ± 1.86
										UGM	1.61 ± 0.68
$\Psi(.)$	4	57.13	0	0.52 ± 0.24							
<i>RVI</i>					0.13	0.06	0.72				1.0
Bearded pig											
<i>fruit + forest</i>	10	0	0.46	1.83 ± 0.45	0.49 ± 0.17					PS	-1.14 ± 0.52
										FS	0.36 ± 0.76
										LS	-0.04 ± 0.56
										LG	-1.21 ± 0.53
										UGM	-1.70 ± 0.50
<i>fruit + elev</i>	6	0.67	0.33	1.03 ± 0.16	0.46 ± 0.16				-0.62 ± 0.12		
<i>fruit + elev²</i>	7	2.61	0.12	1.03 ± 0.16	0.47 ± 0.16				-0.72 ± 0.48		
<i>forest + humans</i>	10	6.30	0.02	1.75 ± 0.42		-0.82 ± 0.38				PS	-0.91 ± 0.49
										FS	0.55 ± 0.66
										LS	0.09 ± 0.56
										LG	-1.03 ± 0.50
										UGM	-1.31 ± 0.44
<i>elev + humans</i>	6	6.78	0.02	1.16 ± 0.18		-0.80 ± 0.36			-0.52 ± 0.11		
<i>elev + time</i>	6	6.95	0.02	1.44 ± 0.28			-0.07 ± 0.03		-0.53 ± 0.11		
$\Psi(.)$	4	27.30	0	0.93 ± 0.14					0.10 ± 0.45		
<i>RVI</i>					0.92		0.02	0.36	0.12		0.48

Table 2.4: AIC comparison of the top ranked detection models ($\Delta AIC > 7$) for ungulates at CPRS. ΔAIC is the relative difference in AIC values compared to the top ranked model, K is the number of parameters in a model, w is the AIC model weight, α is the estimated intercept or constant term, β are they estimated regression coefficients for each parameter. For all models the occupancy model $\Psi(\text{elev} + \text{time} + \text{humans} + \text{fruit})$ was used. The null detection model is represented as $p(\cdot)$.

Model	K	ΔAIC	w	α	β_{off}	β_{effort}
Lesser mousedeer						
<i>effort + off-trail</i>	8	0	0.51	-0.40 ± 0.27	-0.39 ± 0.26	1.06 ± 0.34
<i>effort</i>	7	0.21	0.46	-0.49 ± 0.27		1.11 ± 0.34
<i>p(\cdot)</i>	6	7.70	0.01	0.38 ± 0.10		
<i>RVI</i>					0.51	0.97
Greater mousedeer						
<i>p(\cdot)</i>	6	0	0.38	700.69		
<i>off-trail</i>	7	0.60	0.28	699.30	-0.71 ± 0.55	
<i>effort + off-trail</i>	8	1.44	0.18	698.13	-0.96 ± 0.57	-0.63 ± 0.60
<i>effort</i>	7	1.77	0.16	700.46		-0.25 ± 0.53
<i>RVI</i>					0.46	0.34
Yellow muntjac						
<i>effort</i>	7	0	0.56	-1.37 ± 0.27		1.09 ± 0.31
<i>effort + off-trail</i>	8	0.53	0.43	-1.29 ± 0.28	-0.35 ± 0.29	1.04 ± 0.31
<i>p(\cdot)</i>	6	10.13	0	-0.48 ± 0.11		
<i>RVI</i>					0.43	0.99
Red muntjac						
<i>effort + off-trail</i>	8	0	0.75	-1.92 ± 0.23	0.53 ± 0.20	0.62 ± 0.27
<i>off-trail</i>	7	3.36	0.14	-1.45 ± 0.09	0.43 ± 0.20	
<i>p(\cdot)</i>	6	6.00	0.04	-1.38 ± 0.08		
<i>RVI</i>					0.89	0.75
Bearded pig						
<i>effort</i>	7	0	0.40	-0.28 ± 0.20		0.39 ± 0.23
<i>p(\cdot)</i>	6	0.68	0.29	0.027 ± 0.07		
<i>effort + off-trail</i>	8	1.80	0.17	-0.25 ± 0.21	-0.08 ± 0.17	0.37 ± 0.24
<i>off-trail</i>	7	2.08	0.14	0.05 ± 0.08	-0.13 ± 0.17	
<i>RVI</i>					0.31	0.57

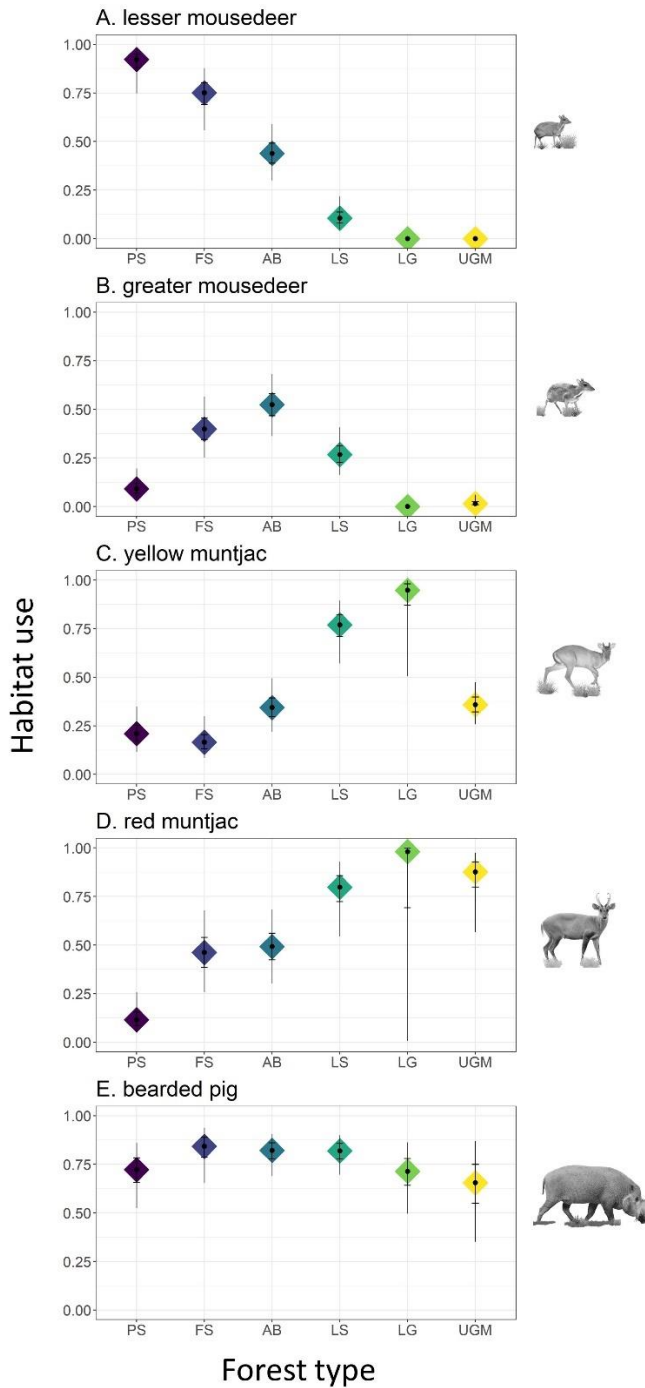


Figure 2.4: Model-averaged estimates of ungulate habitat use ($\hat{\Psi}$) across 6 forest types at CPRS. Vertical bars illustrated the model averaged 95% confidence interval and whiskers define the 50% confidence intervals. Forest types are represented in order of increasing elevation, identified by the following abbreviations; peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), and upland granite/montane (UGM).

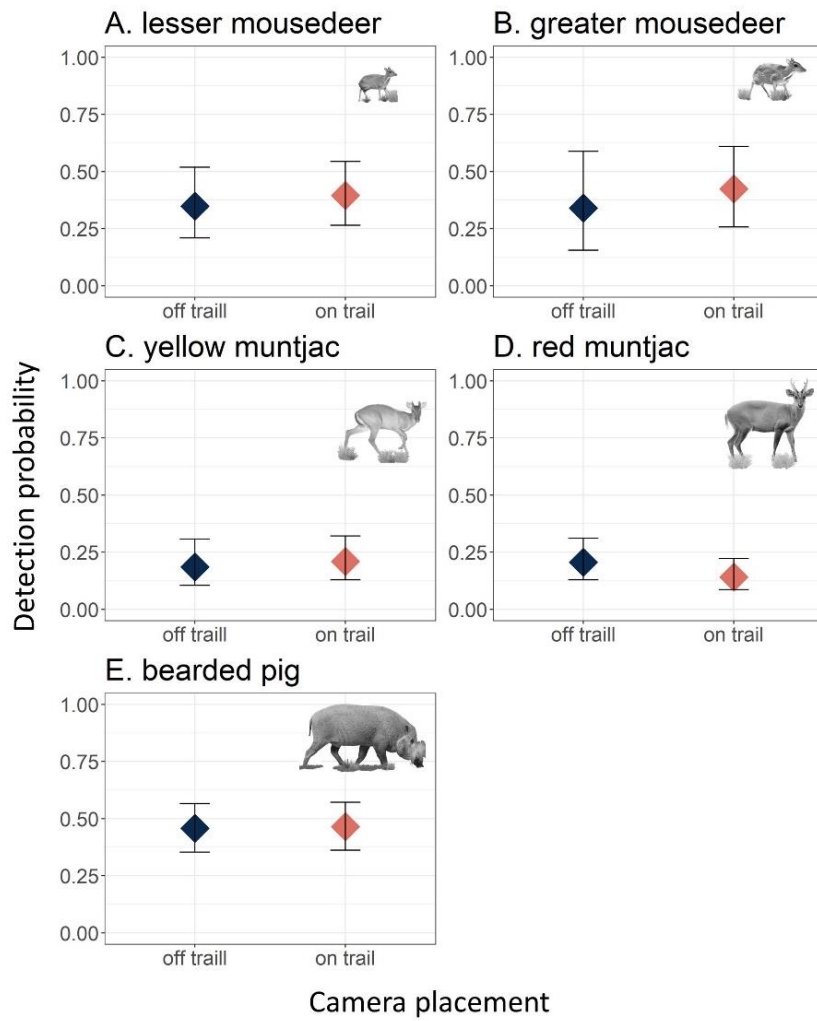


Figure 2.5: The model-averaged ($\Delta AIC > 7$) probability of detecting ungulates at on and off trail camera stations at CPRS. Error bars illustrate the 95% confidence intervals.

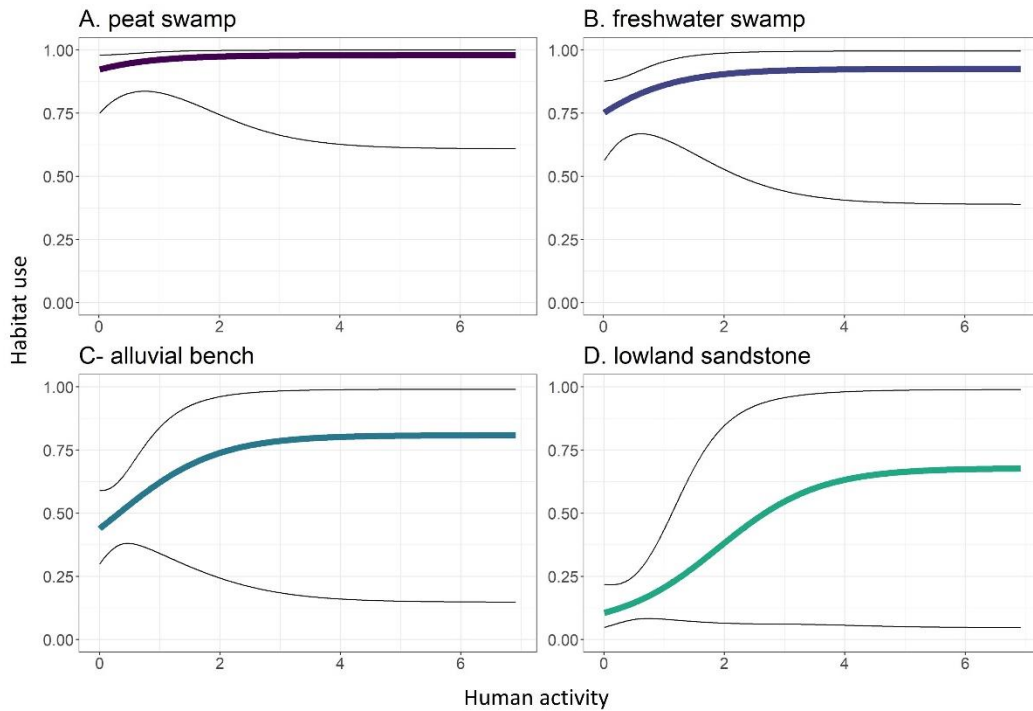


Figure 2.6: The relationship between human activity and habitat use of lesser mousedeer using model-averaged estimates of habitat use ($\hat{\Psi}$) ($\Delta\text{AIC} > 7$). The relationship is shown for each forest type (A-D) with lowland granite and upland granite/montane omitted due to non-detection in those forest types. The black lines illustrate the model averaged 95% confidence intervals.

2.5.2 Greater mousedeer

Forest type and time best explained habitat use of greater mousedeer ($\Delta\text{AIC} < 4$, Table 2.3). Only one model, $\Psi(\text{forest} + \text{time})$, was considered to have substantial support. Forest type was the most important covariate, present in all the models with $\Delta\text{AIC} < 7$ (RVI: 0.99). Habitat use of greater mousedeer was highest in alluvial bench forests ($\hat{\Psi}_{AB} = 0.52 \pm 0.08$), followed by freshwater swamp forests ($\hat{\Psi}_{FS} = 0.40 \pm 0.08$), lowland sandstone forests ($\hat{\Psi}_{LS} = 0.27 \pm 0.06$), peat swamp forests ($\hat{\Psi}_{PS} = 0.09 \pm 0.04$), and upland granite/montane forests ($\hat{\Psi}_{UGM} = 0.02 \pm 0.01$, Figure 2.4). Greater mousedeer were not detected in lowland granite forests. An extremely small amount of detections in upland granite/montane forests ($n = 1$) prevented successful calculation of associated standard errors. Variation in habitat use of greater mousedeer was also explained by time was (RVI: 0.88) with a negative trend of habitat use over time (Figure 2.7). Fruit availability and human activity were explanatory variables alongside forest type in models with little support ($\Delta\text{AIC} < 7$) with a combined model weight of only 0.06 (Table 2.3). Both models performed worse than the $\Psi(\text{forest})$ model, meaning these covariates did not

significantly explain further variation in habitat use. Elevation had no support as an explanatory variable for greater mousedeer habitat use.

All candidate models for detection probability of greater mousedeer, including the null model, had a delta AIC < 2, indicating that they cannot be differentiated in importance. Camera positioning on or off trails explained some variability (RVI: 0.46) with detection probability at off-trail sites estimated to be slightly lower than on-trail sites ($\hat{p}_{ON} = 0.4 \pm 0.09$, $\hat{p}_{OFF} = 0.34 \pm 0.12$, Table 2.4, Figure 2.5). Sampling effort (RVI: 0.34) appeared to have a negative influence on detection, however, the standard error overlaps zero indicating that the direction of the relationship cannot be determined with confidence.

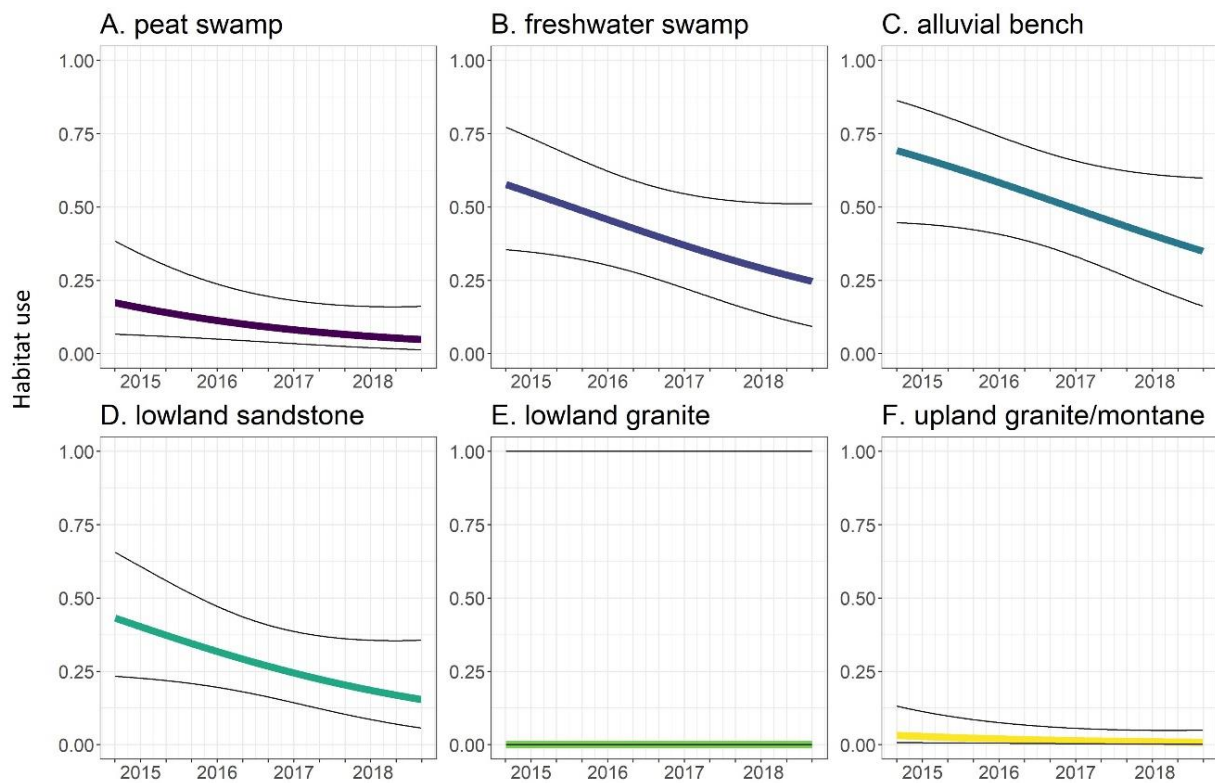


Figure 2.7: The relationship of habitat use of greater mousedeer over time using model-averaged estimates of habitat use ($\hat{\Psi}$) ($\Delta AIC > 7$). The relationship is shown for each forest type (A-F). The black lines illustrate the model averaged 95% confidence intervals.

2.5.3 Yellow muntjac

Forest type (RVI: 0.99) and time (RVI: 0.94) best explained habitat use of yellow muntjacs. Δ AIC values of all other candidate models were > 4 , and therefore had considerably less support. Habitat use of yellow muntjacs was highest in lowland granite forests ($\hat{\Psi}_{LG} = 0.95 \pm 0.07$), followed by upland granite/montane forests ($\hat{\Psi}_{UGM} = 0.36 \pm 0.06$), lowland sandstone forests ($\hat{\Psi}_{LS} = 0.77 \pm 0.08$), alluvial bench forests ($\hat{\Psi}_{AB} = 0.34 \pm 0.07$), peat swamp forests ($\hat{\Psi}_{PS} = 0.21 \pm 0.06$), and freshwater swamp forests ($\hat{\Psi}_{FS} = 0.17 \pm 0.05$) (Table 2.3, Figure 2.4). Time negatively influenced the probability of use across all forest types over the study period (Figure 2.8). Human activity, fruit availability, and elevation were absent from the top-ranked models.

Both sampling effort (RVI: 0.99) and camera positioning (RVI: 0.43) explained the detection probability of yellow muntjacs (Table 2.4). Sampling effort had a positive effect on detection probabilities, while camera positioning off-trail had a negative effect on detection probabilities ($p_{ON} = 0.21 \pm 0.05$, $p_{OFF} = 0.19 \pm 0.05$) (Figure 2.5).

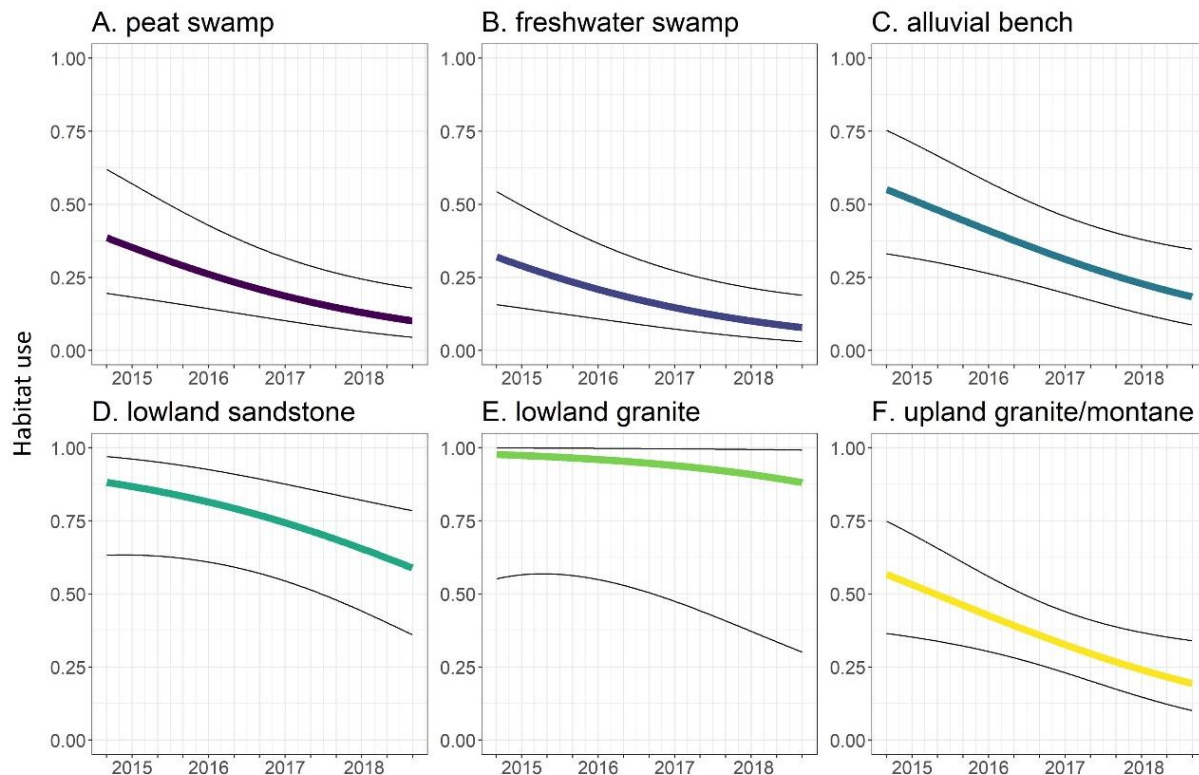


Figure 2.8: The relationship between time and the probability of yellow muntjac using sites, using model-averaged estimates of habitat use ($\hat{\Psi}$) (Δ AIC > 7). The relationship is shown for each forest type (A-F). The black lines illustrate the model averaged 95% confidence intervals.

2.5.4 Red muntjac

Forest type (RVI: 1) and time (RVI: 0.72) best explained habitat use of red muntjacs. The forest type covariate was present in all 4 top models, which performed significantly better than all other models including the null model (Table 2.3). Habitat use of red muntjacs was highest in lowland granite forests ($\hat{\Psi}_{LG} = 0.98 \pm 0.09$), followed by upland granite/montane forests ($\hat{\Psi}_{UGM} = 0.88 \pm 0.09$), lowland sandstone forests ($\hat{\Psi}_{LS} = 0.80 \pm 0.09$), alluvial bench forests ($\hat{\Psi}_{AB} = 0.90 \pm 0.10$), freshwater swamp forests ($\hat{\Psi}_{FS} = 0.46 \pm 0.11$), and finally peat swamp forests ($\hat{\Psi}_{PS} = 0.12 \pm 0.05$, Figure 2.4). The next most important explanatory variable was time which had a positive effect on habitat use (Figure 2.9). Fruit availability was a covariate in the set of top-performing models (RVI: 0.06) with a positive effect on habitat use. Human activity was not present in the best performing models ($\Delta AIC < 4$), however, there was some support (RVI: 0.06) that it negatively influenced habitat use of red muntjacs. Models containing elevation as a covariate did not reach acceptable convergence and were omitted from findings.

Both camera placement (RVI: 0.89) and sampling effort (RVI: 0.75) explained the detection probability of RM (Table 2.4). Red muntjacs had higher detection probabilities off-trail ($\hat{p}_{ON} = 0.14 \pm 0.03$, $\hat{p}_{OFF} = 0.21 \pm 0.05$) and at cameras operated for longer periods of time (Figure 2.5). The increased detection probability off-trails is in contrast to the predicted relationship evident in the raw sightings (Figure 2.3).

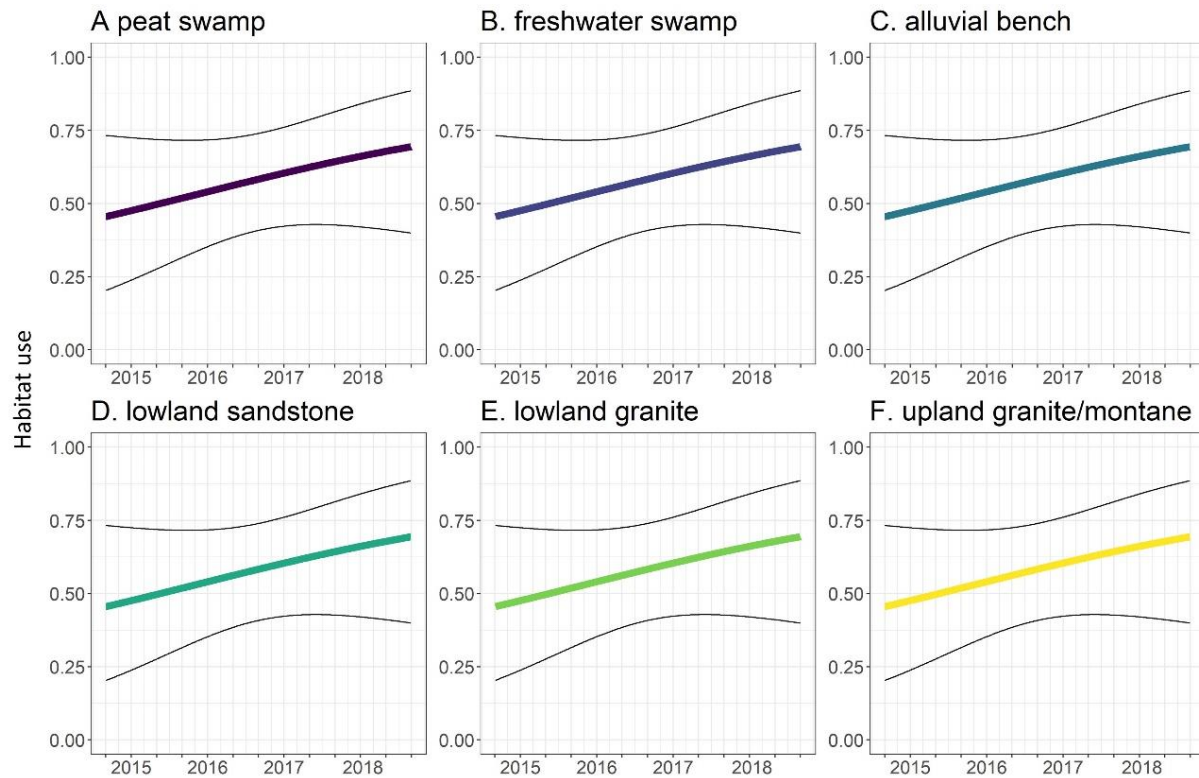


Figure 2.9: The relationship of habitat use of red muntjacs over time using model-averaged estimates of habitat use ($\hat{\Psi}$) ($\Delta\text{AIC} > 7$). The relationship is shown for each forest type (A-F). The black lines illustrate the model averaged 95% confidence intervals.

2.5.5 Bearded pig

Fruit availability best explained habitat use of bearded pigs (RVI: 0.92). The *fruit* covariate was present in all top models (Table 2.3) and had a positive influence on habitat use (Figure 2.10). Forest type (RVI: 0.48) and elevation (RVI_{elev1}: 0.36, RVI_{elev2}: 0.12) further explained habitat use of bearded pigs. Habitat use of bearded pigs was highest in freshwater swamp forests ($\hat{\Psi}_{FS} = 0.84 \pm 0.07$), followed by alluvial bench and lowland sandstone forests ($\hat{\Psi}_{AB,LS} = 0.82 \pm 0.05$), peat swamp forests ($\hat{\Psi}_{PS} = 0.72 \pm 0.09$), lowland granite forests ($\hat{\Psi}_{LG} = 0.71 \pm 0.10$), and upland granite/montane forest forests ($\hat{\Psi}_{UGM} = 0.65 \pm 0.14$, Figure 2.4). Elevation had a negative linear relationship with habitat use in the second-best model indicating greater use of low elevations. Human activity and time were absent from the best models suggesting a comparatively insignificant relationship with habitat use of bearded pigs.

All candidate models for detection probability of bearded pigs, including the null model, had a delta AIC < 2, indicating that they cannot be differentiated in importance (Table 2.4). Sampling effort

(RVI: 0.57) appeared to have a slight positive effect on detection. No clear relationship was evident with camera placement ($\hat{p}_{ON} = 0.47 \pm 0.05$, $\hat{p}_{OFF} = 0.46 \pm 0.05$, Figure 2.5).

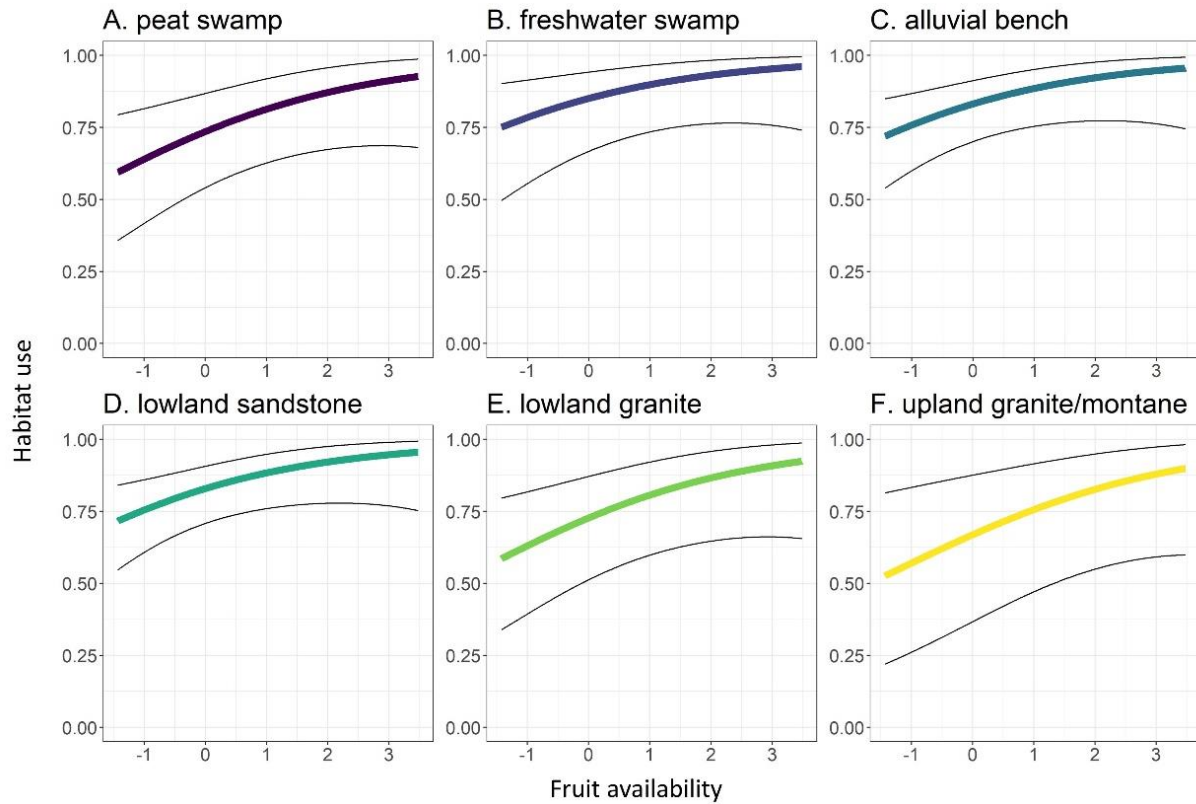


Figure 2.10: The relationship of fruit availability and habitat use of bearded pig at CPRS using model-averaged estimates of habitat use ($\hat{\Psi}$) ($\Delta AIC > 7$). Fruit availability was measured as the density of ripe fruit per ha in each forest type on a monthly basis. The relationship is shown for each forest type (A-F). The black lines illustrate the model averaged 95% confidence intervals.

Table 2.5: Estimates from null models of habitat use and detection assuming constant estimates among sites.

Species	Ψ (.) estimate of habitat use probability	p (.) estimate of detection probability
<i>Lesser mousedeer</i>	0.34 ± 0.02	0.59 ± 0.02
<i>Greater mousedeer</i>	0.20 ± 0.03	0.39 ± 0.04
<i>Yellow muntjac</i>	0.49 ± 0.04	0.38 ± 0.03
<i>Red muntjac</i>	0.63 ± 0.06	0.20 ± 0.03
<i>Bearded pig</i>	0.72 ± 0.03	0.51 ± 0.02

2.5.6 Model fit

Model fit for both habitat use and detection probabilities was further assessed for the top performing general model for each species based on overdispersion (\hat{c} , Table 2.6). All \hat{c} values were greater than 1, indicating overdispersion, however, values were below commonly accepted thresholds of $\hat{c} < 3$ (Lebreton *et al.* 1992).

Table 2.6: The dispersion parameter (\hat{c}) for the best performing general habitat use and detection models for each species. The goodness of fit was calculated using a parametric bootstrap (n=1,000). $\hat{c} > 1$ indicates overdispersion, and $\hat{c} < 1$ indicates under dispersion. $\hat{c} < 3$ are considered acceptable (Lebreton *et al.* 1992).

Species	Top model	\hat{c}
<i>Lesser mousedeer</i>	$\Psi(\text{forest} + \text{humans})$	2.24
	$p(\text{effort} + \text{off-trail})$	2.13
<i>Greater mousedeer</i>	$\Psi(\text{forest} + \text{time})$	1.40
	$p(\text{effort} + \text{off-trail})$	1.45
<i>Yellow muntjac</i>	$\Psi(\text{forest} + \text{time})$	1.51
	$p(\text{effort} + \text{off trail})$	1.58
<i>Red muntjac</i>	$\Psi(\text{forest} + \text{time})$	1.09
	$p(\text{effort} + \text{off-trail})$	1.79
<i>Bearded pig</i>	$\Psi(\text{forest} + \text{fruit})$	1.89
	$p(\text{effort})$	2.06

2.5.7 Spatial overlap analysis

Patterns of spatial avoidance and overlapping habitat use were evident from spatial overlap analysis. The greatest spatial overlap in model-averaged habitat use was between bearded pigs and greater mousedeer ($r = 0.68$, $p < 0.05$, Figure 2.11). The strongest evidence of spatial avoidance was between lesser mousedeer and red muntjacs ($r = -0.85$, $p < 0.05$) and lesser mousedeer and yellow muntjacs ($r = -0.62$, $p < 0.05$). All Pearson correlation coefficients had p values below 0.05. Correlation coefficients below a threshold of 0.6 were not considered to have biologically significant effect sizes.

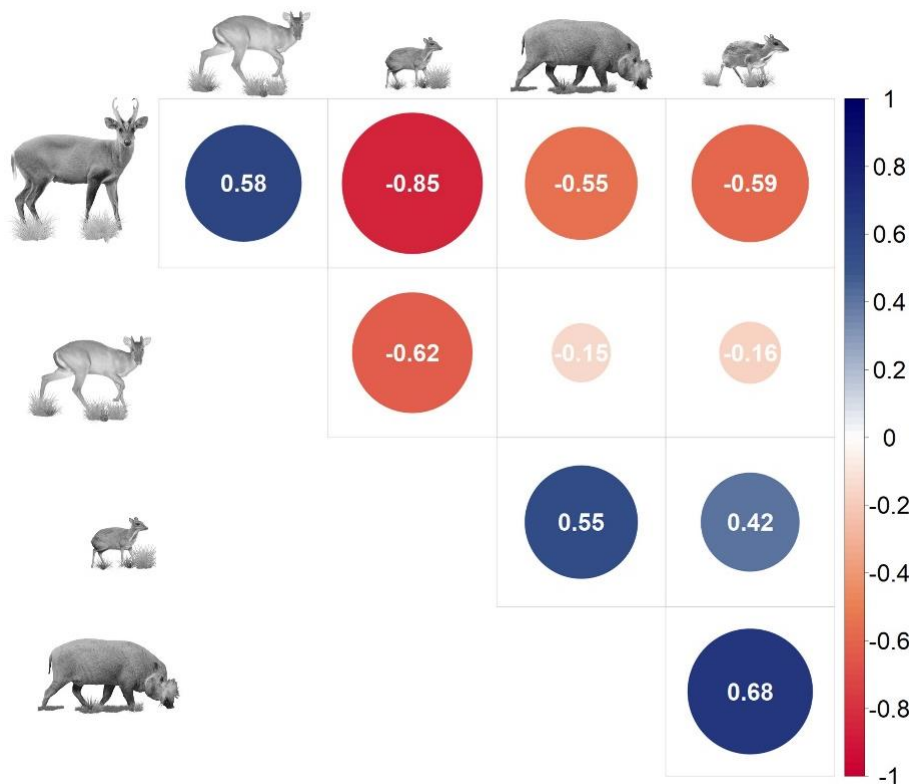


Figure 2.11: The correlation (Pearson) between the model-averaged habitat use estimates of ungulates species at CPRS. Positive correlations indicate spatial overlap between species (blue, $r > 0.6$). Significant negative correlations indicate spatial avoidance between species in the Cabang Panti Research Station (red, $r < -0.6$).

2.6 Discussion

My results provide insight into the influence of spatial and temporal factors on habitat use and niche partitioning of an understudied tropical ungulate guild. My findings suggest that habitat use of ungulates in a Bornean lowland rainforest ecosystem are influenced by forest type, temporal variation in fruit availability, and human activity. As predicted, habitat partitioning was evident within the ungulate guild with habitat use for each species peaking in different forest types.

Forest type and spatial niche partitioning

Forest type was a strong predictor for the habitat use of all 5 ungulate species with clear evidence of species-specific habitat preference.

Habitat partitioning was evident between the sympatric mousedeer species as peak habitat use estimates were observed in distinct forest types, with estimates dropping off in adjacent habitats. The pattern of overlapping habitat use with spatially separate peaks suggest habitat partitioning has occurred. The spatial separation of high-use areas suggests that each species may have specialized in

resources specific to different forest types to reduce competition. This pattern of habitat partitioning may be a product of the distinct floral species assemblages, and thus a distinct array of fruit and seeds, present in each forest type (Table 1.1).

According to the study of forest composition at CPRS conducted by Cannon & Leighton (2004), the peat swamp forest, for which I estimated the highest habitat use of lesser mousedeer, is predominantly composed of plant species that produce fleshy fruits and legumes (20% *Myrtaceae*, 13% *Sapotaceae*, 6% *Fabaceae*). The alluvial bench forest, where greater mousedeer habitat use estimates peaked, is predominately composed of masting dipterocarp species (20%), as well as plants producing dry starching fruits and seeds (9% *Myristicaceae*, 8% *Euphorbiaceae*). The consistently high level of fruit resources in the peat swamp forest (Table S.5) supports the prediction that the smallest ungulate in this study system, the lesser mousedeer, would be associated with a forest type providing consistent high-quality diet resources. As an ungulate with a very small body mass, the lesser mousedeer would have a limited ability to buffer the effects of low resources during periods of low fruit-availability. In contrast, the slightly larger greater mousedeer (Table 2.1), was associated with habitat where many plants only produce fruit during masts, leaving a potentially lower proportion of fruit consistently available. A less dependable level of fruit and seed resources supports the prediction that greater mousedeer would similarly have high-quality fruit and seed-based diets with the possible addition of some browse or other resources in times of low fruit availability.

A clear pattern of habitat partitioning was less evident between yellow and red muntjacs. Habitat use of both species appears to peak in lowland granite forests. However, the large uncertainty of this estimate for red muntjacs along with the trend evident from the raw detection data suggests that red muntjacs may actually peak in upland granite/montane forests (Figures 2.2 and 2.3). Overlapping habitat use of yellow and red muntjacs could arise if the sympatric species have specialized to share habitat by consuming separate food resources. Both lowland and upland granite/montane forests are composed predominantly of masting dipterocarp species (20% for lowland granite and upland granite, respectively). While non-mast fruit and seed resources remain available in these forest types, the drop in availability during inter-mast periods indicates yellow and red muntjacs may have fallback foods they rely on during low seed and fruit availability. Fallback foods have become increasingly recognized in tropical mast-systems where the dramatic fluctuations in resources require species to switch to different diets when their preferred food is unavailable (Hanya & Bernard 2012, Marshall *et al.* 2009b).

Bearded pigs used all forest types at CPRS and exhibited relatively low variation in habitat use estimates in each forest type. The relative homogeneity of bearded pig habitat use, overlapping all other

ungulates at CPRS, suggests a lack of niche differentiation on a spatial dimension. As bearded pigs are thought to primarily consume fruit resources, similarly to the other ungulates in this study, niche differentiation to reduce competition is most likely evident along another dimension.

Temporal variation in fruit availability

As predicted, temporal variation in fruit availability was an important explanatory variable for bearded pigs which showed a positive relationship with fruit availability. This suggests that their habitat use is more strongly influenced by temporal patterns in resources than spatial patterns. This finding supports previous research that has described the ability of bearded pigs to track spatially and temporally variable fruit resources (Curran & Leighton 2000, Dove 1993, MacKinnon *et al.* 1996). Previously tracking of resources has been recorded during long-distance migrations during mast events, however, little is known about their resource use during inter-mast periods. The timing of this study immediately followed a significant mast event, encompassed one small mast event, and ended at the onset of another large mast. The link between bearded pig habitat use during the inter-mast period at CPRS and fruit availability indicates that resource tracking may additionally occur on a smaller spatial scale between mast events. Ideally, the habitat use of bearded pigs should be studied over a longer timeframe that encapsulates both mast and inter-mast periods to better understand this relationship.

In contrast, lesser mousedeer had a negative relationship with fruit availability. Lesser mousedeer habitat use was best predicted by forest type, with the highest estimates of use in the peat and freshwater swamp forest types which had high fruit productivity over the study period (Figure 2.1, S.5). This suggests that habitat use for this species is primarily dictated by spatial distributions of fruit resources and additionally influenced by temporal trends of fruiting. The negative relationship with temporal fruiting patterns indicates that lesser mouse deer actively avoid masting areas that attract bearded pigs when fruit availability is high. Spatial avoidance during periods of high fruit availability supports the theory by Curran & Leighton (2000) that resident frugivore species switch to other fruit resources during masts and avoid mast-produced resources that attract nomadic frugivores.

The results of this study provide further evidence that bearded pigs are dependent on temporal fluctuations in fruit resources associated with mast events in tropical dipterocarp forests. Other species that track available fruit resources have been found to have negative energetics during inter-mast periods and rely on the abundant fruit during mast events for reproduction (Knott 1998, Fredriksson *et al.* 2006). Past observations of widely emaciated pigs during long inter-mast periods suggest that bearded pig populations are similarly not sufficiently supported by non-mast resources alone (Curran &

Leighton 2000) highlighting conservation concerns for bearded pigs trapped in small, isolated forest fragments. Increasing forest fires, deforestation, and climate change threatening dipterocarp forests has already had serious consequences for other species reliant on mast resources in Bornean rainforests. For example, Fredriksson *et al.* (2006) recorded an ~80% reduction in sun bear (*Helarctos malayanus*) densities following 1997-1998 forest fires that wiped out a large proportion of the mast produced fruit the bears were dependent on.

Human activity

Human activity was an important explanatory variable for lesser mousedeer habitat use, accounting for 63% of model weight. For the remaining species, models including human activity were only marginally supported (3-6% of model weight). In contrast to my prediction, human activity had a positive influence on lesser mousedeer habitat use. Although comparatively insignificant, the influence on yellow muntjacs was also positive, while bearded pig and red muntjac habitat use showed a negative relationship with human activity. The positive association of human activity across CPRS and lesser mousedeer habitat use may be a result of a 'human-shield effect' (Nowak *et al.* 2014). Researchers have had a consistent presence at CPRS for the past few decades and regularly visited and maintained the camera grid throughout the study area. The natural predators of mousedeer are likely primarily the members of the local felid guild composed of 5 obligate carnivore species (Brodie & Giordano 2013). Additionally, mousedeer are a prey of preference for local poachers (Bernard *et al.* 2013). The presence of researchers may deter both poachers, wanting to avoid detection, and inherently avoidant natural predators. To further test this possibility and quantify any shielding effect of researchers, future studies could compare densities of both ungulates and predators within CPRS and elsewhere in the national park.

Diet

Patterns of niche partitioning evident among the 5 ungulate species provide some information about their likely diet preferences. The smallest bodied ungulate, lesser mousedeer, was associated with a high-fruit forest habitat. Additionally, the larger-bodied ungulates (greater mousedeer, yellow muntjacs, red muntjacs) were linked to masting forest habitats where fruit and seed availability varies substantially, indicating these species' diets consist to a larger degree of other more reliable food sources, such as browse. Ungulates associated with masting forest types may be a result of the wealth of seedlings produced following mast events and not a direct link to fruit availability. For example,

habitat use of bearded pigs was not focused in a distinct habitat and may indicate a lack of habitat preference, travelling to benefit from resources across all forest types. These findings support the prediction that diet quality scales negatively with body mass in ungulates at CPRS, in keeping with the Jarman-Bell Principle (Bell 1970, Jarman 1974).

Time

An overall temporal trend in habitat use was evident in greater mousedeer, yellow muntjacs and red muntjacs. The probability of greater mousedeer and yellow muntjacs using sites declined over the study, suggesting a possible decline in the local population. The probability of red muntjacs using sites increased and may similarly be explained by a change in the local density of red muntjacs. These temporal trends are reported here with caution for a couple reasons. The first being that inferences about abundance should be drawn with caution due to the failure of the assumption of closure. Secondly, the 4.5-year duration of this study may be sufficient to indicate population trends. However, a longer study period is necessary to exclude possible fluctuations in density occurring naturally from either regular population cycles (i.e. due to movements) or changes in life-history parameters (i.e. birth and deaths).

Detection probability

Lesser mousedeer had the highest estimates of detection probability despite being the smallest-bodied ungulate—a potential disadvantage for detection by camera traps (Anile & Devillard 2016). This was followed by bearded pigs, then yellow muntjacs, greater mousedeer, and red muntjacs with the lowest detection probabilities (Table 2.12).

For greater mousedeer and bearded pigs, the variation provided by detection covariates did not supply sufficient explanation for the data compared to the null model. This suggests that the detection probability of greater mousedeer and bearded pigs remained constant across sites and sampling periods ($p_{GMD} = 0.39 \pm 0.04$, $p_{BP} = 0.51 \pm 0.018$). Sampling effort was an important covariate that positively influenced the detection probability of lesser mousedeer, red muntjacs, and yellow muntjacs. Camera position on or off trails was a strong predictor for the detection probabilities of lesser mousedeer, yellow muntjacs, and red muntjacs. lesser mousedeer and yellow muntjacs' detection were higher on trails while red muntjacs' detection was higher at off-trail sites.

The inclusion of covariates to explain heterogeneity in detection probability across the study improves estimates of detection and habitat use, however, large error values associated with detection

covariates in this study indicate that other variables that were not measured may better explain heterogeneity in detection probabilities.

Study limitations

Limitations of this study that may reduce the strength of inferences should be considered. Logistical constraints prevented a more thorough sampling of sites throughout CPRS. Improved coverage of sites, combining to sample a greater proportion of the total study area, as well as more consistent resampling, would improve the confidence of model estimates. Furthermore, the patterns of habitat partitioning among distinct forest types observed in this study may be the result of additional characteristics unique to each forest type (other than fruit availability) that were not measured in this study (i.e. forest structure). Future research should account for other forest specific variables that could provide alternative explanations for the patterns I observed.

Occupancy modelling was used to account for imperfect detection by estimating detection probabilities, however, logistical constraints limited the inclusion of more variables potentially influencing detection. Unexplained heterogeneity in detection probability remained despite using sampling effort and camera placement to improve estimates.

The detection probabilities may differ between species as the motion-triggered cameras have a detection bias towards larger body mass. Accordingly, the habitat use of smaller-bodied ungulates may be underestimated. Additionally, a regularly serviced camera trap framework has the potential for detection bias against human-avoidant species if scent traces are left from regular servicing visits. Occupancy modelling on a fine temporal scale could test for this bias by estimating different detection probabilities over additional surveys following the servicing of cameras.

Conclusion & future directions

The results from my study demonstrate a pattern of habitat and resource partitioning of an understudied guild of 5 sympatric ungulates in a tropical rainforest system. Furthermore, my findings indicate differential use of resources among five ungulate species with the smaller mousedeer species relying on forest habitats with consistent fruit resources to provide high-quality nutrition; muntjac species using higher elevation forest habitats that provide opportunistic availability of mast resources; and bearded pigs following temporal patterns of fruiting across CPRS. This study provides support for extending the Jarman-Bell Principle (Bell 1970, Jarman 1974) to ungulates in tropical ecosystems. The partitioning of resources between consistent non-mast and variable pulses in mast resources provide an additional

dimension for niche partitioning, reducing intraguild competition. Human activity in the research station did not appear to negatively impact ungulate species and in contrast, a human-shield effect may benefit smaller species. The inferences from these findings could be further tested through long-term studies of bearded pig abundance paired with GPS collaring to understand movement patterns of this fruit-tracking species.

Chapter 3.

Spatiotemporal habitat use patterns of Sunda clouded leopard (*Neofelis diardi*) in a mast-fruiting rainforest: influence of forest type, prey occurrence, humans, and fluctuations in fruit resources.

3.1 Abstract

The spatial ecology of Borneo's top predator—the Sunda clouded leopard (*Neofelis diardi*)—remains poorly understood despite accelerating deforestation reducing available rainforest habitats. I sought to contribute insight into factors that influence the habitat use of clouded leopards, to better inform range predictions, habitat suitability, and conservation planning. I used camera trap data from 4 ½ years and a single-season occupancy modelling approach, with time as a covariate, to estimate the influence of site-specific covariates on the habitat use of clouded leopards over space and time, while accounting for imperfect detection. Habitat use was quantified across 6 distinct forest types and along gradients of human activity, prey occurrence, elevation, and temporal fluctuations in fruit resources in Gunung Palung National Park, West Kalimantan, Indonesian Borneo. I found the habitat use of clouded leopards was strongly influenced by forest type, negatively associated with areas of high human activity, and positively associated with temporal fluctuations in fruit availability and bearded pig occurrence. Habitat use differed significantly between forest types and was highest in the lowland granite forest ($\hat{\Psi}_{LG} = 0.87 \pm 0.09$), moderate in the upland granite/montane forests ($\hat{\Psi}_{UG} = 0.41 \pm 0.07$), low in both lowland sandstone and peat swamp forests ($\hat{\Psi}_{PS} = 0.14 \pm 0.05$, $\hat{\Psi}_{LS} = 0.11 \pm 0.05$) and remained undetected in the freshwater swamp and alluvial bench forests. High estimates of habitat use associated with bearded pig occurrence and fruiting events suggest that bearded pigs are an important prey of clouded leopards and fruiting may act as a cue, signaling available prey for the top carnivore. Areas of high researcher and poacher activity were associated with lower estimates of habitat use, indicating a possible 'landscape of fear'. My findings contribute new information on the spatial ecology of clouded leopards and factors influencing habitat use that can be applied to improve the efficacy of conservation efforts.

3.2 Introduction

Exhibiting the fastest rates of deforestation and land-conversion worldwide, the natural landscape of Indonesian Borneo (Kalimantan) has undergone an alarming transformation since the 1970's with potentially catastrophic consequences for native wildlife (Curran *et al.* 2004, Hansen *et al.* 2013,

Ocampo-Penuela *et al.* 2020). The increasingly fragmented landscape and reduction in the size of forested areas puts carnivores under further pressure (Noss *et al.* 1996, Woodroffe & Ginsberg 1998, Macdonald *et al.* 2018). The Sunda clouded leopard (*Neofelis diardi*; subsequently referred to as the clouded leopard) is the apex predator in Borneo's rainforest ecosystems and among the world's most vulnerable, elusive, and poorly understood felid species (IUCN 2020). The medium sized felid, 15-25 kg, is considered a semi-arboreal species and is largely restricted to forested areas with dense canopy cover (Hearn *et al.* 2016, 2018a). A 50% loss of forested areas on the island of Borneo between 1973 and 2015 (Ocampo-Penuela *et al.* 2020), and increasingly degraded 'protected' areas (Curran *et al.* 2004), have restricted clouded leopards into remnant forest fragments resulting in populations 26% over carrying capacity (Kaszta *et al.* 2019).

Effective conservation planning to protect the Sunda clouded leopard is reliant on a thorough understanding of factors influencing their habitat use and distribution. Determining environmental and physical factors (i.e. elevation, climate, forest type) associated with habitat use is fundamental in identifying suitable habitats for protection and achieving functional connectivity across wider landscapes. The rainforest ecosystems in Borneo experience mast-fruiting and consequently dramatic fluctuations of fruit resources. The resource pulses are thought to have considerable 'bottom-up' influence on frugivore populations (Ostfeld & Keesing 2000, Wong *et al.* 2005, Kanamori *et al.* 2017, Chapter 2). This elicits considerable ecological response from consumer populations, the response of clouded leopards to fluctuations in fruit resources through changes in prey populations remains unknown and merits investigation. Furthermore, the influence of anthropogenic disturbance on the spatial ecology of clouded leopards is increasingly important to consider as few areas remain unaffected by encroaching settlements and infrastructure development. Human activities may influence clouded leopard distribution and habitat use through direct effects of poaching or through developing a 'landscape of fear' (Lima *et al.* 1990, Laundre *et al.* 2001, Oriol-Cotterill *et al.* 2005) further restricting effective ranges. Additionally, the occurrence of prey species is a useful predictor for habitat use of carnivore species and may help identify important species interactions shaping patterns of clouded leopard spatial ecology (Burton *et al.* 2012, Ross *et al.* 2013, Wisz *et al.* 2013).

A growing body of research has sought to shed light on clouded leopard ecology in Borneo, but insight has been limited due to challenges studying an elusive low-density carnivore species across difficult terrain (Hearn *et al.* 2013, 2019). A low number of detections frequently inhibit solid inferences despite extensive sampling efforts (Bernard *et al.* 2013, Cheyne *et al.* 2016). Hearn *et al.* (2016) used questionnaires to link researchers' observations of clouded leopards to habitat types, finding the highest

apparent suitability in lowland and upland forests, while montane and mangrove habitats were associated with the least detections. Additionally, the influence of landscape-scale factors was investigated by Macdonald *et al.* (2018) on clouded leopards in both Sumatra and Borneo, finding negative influences from nearby human population, forest loss, and plantations. Positive correlations were found between clouded leopard sightings and canopy cover, forest connectivity, and degree of lowland forests present (Macdonald *et al.* 2018). Poaching and live-trade of clouded leopards in Borneo (D’Cruze & Macdonald 2015, Nijam *et al.* 2019), as well as evidence of clouded leopards avoiding deforested and human-altered areas suggests a negative impact from human disturbance (Macdonald *et al.* 2018, Hearn *et al.* 2019), however, clouded leopards’ response to human activity within a forest landscape has not yet been studied. Additionally, the influence of prey occurrence on clouded leopard habitat use and distribution is not yet understood as the diet and prey preference of clouded leopards are undetermined. Anecdotal observations and co-occurrence patterns indicate Sambar deer (*Rusa unicolor*), muntjacs (*Muntiacus spp.*), mousedeer (*Tragulus spp.*), and bearded pigs (*Sus barbatus*) may be important prey species but further research is needed to substantiate this possibility (Rabinowitz *et al.* 1987, Ross *et al.* 2013, Hearn *et al.* 2018b).

In recent years camera traps have become a popular research tool that amass enough data to evaluate densities (Wilting *et al.* 2012), activity patterns (Cheyne & Macdonald 2011, Hearn *et al.* 2013), abundance (Wearn *et al.* 2013), and behavioral observations (Allen *et al.* 2016) in an efficient, cost-effective, and easily replicated manner. Large amounts of presence/absence data from camera traps provide an effective foundation for modelling the occurrence of elusive species while accounting for imperfect detection (Rolland *et al.* 2011, Galvez *et al.* 2016, Li *et al.* 2018). The combination of occupancy modelling and motion-triggered cameras have been effectively used to study factors influencing the habitat use of other large felid species including lynx (*Lynx lynx*) (Rolland *et al.* 2011), leopards (*Panthera pardus*) (Burton *et al.* 2012, Edwards *et al.* 2018), bobcats (*L. rufus*), and pumas (*Puma concolor*) (Lewis *et al.* 2015).

3.3 Aims

The goal of my study was to examine the influence of site-specific characteristics, human activity, and prey occurrence on spatiotemporal patterns of clouded leopard habitat use in an ecologically intact mast-fruiting rainforest system. Habitat use estimates from occupancy modelling of five ungulate species across a body size gradient (1.5-200 kg; Chapter 2)—identified as potential prey for clouded leopards—were directly incorporated to model habitat use of clouded leopards. Additionally, I used

phenological data describing temporal variation in fruit availability among 6 forest types to determine the influence of mast-induced resource variation. Analyses were based on a long-term extensive camera trapping effort from July 2015-October 2019 and single-species occupancy modelling to evaluate the influence of site-specific covariates. Gaining a more comprehensive understanding of the spatial ecology of Borneo's top predator is vital to inform effective conservation planning and reverse the decline of this charismatic species.

3.4 Methods

3.4.1 Study site

This study was based within the Cabang Panti Research Station (CPRS) located in Gunung Palung National Park (GPNP), West Kalimantan, Indonesian Borneo (Section 1.3). CPRS is an approximately 34 km² site covering 7 distinct forest types along an altitudinal gradient from sea level to ~ 1,100 m (Figure 1.1). GPNP exhibits strong pulses in resource availability during mast-events and the occurrence of 7 distinct forest types, within a compact area, make it a prime location to study responses to fluctuating fruit resources. The study site remains relatively undisturbed by humans although there is an extensive trail system frequently used by researchers.

3.4.2 Data collection

Data were collected between July 2015 and October 2019 at 192 camera sites throughout CPRS. Sites were chosen randomly along trail and off trails in all 7 forest types covering the available elevational gradient. The presence or absence of species were assessed at each site using motion-triggered cameras. To maintain independence among detections, multiple subsequent detections at a site were pooled on a daily basis. Camera traps (Bushnell TrophyCam) were used in preference to more invasive methods such as capturing and fitting individual clouded leopards with GPS collars and to maximize the detection of a wide range of species. Cameras were programmed to record 20 s videos when triggered, followed by a 10 s refractory period. Due to resource limitation, cameras were rotated between sites to sample as large of a portion of the study site as possible. On average, 31.8 sites were sampled during a survey with a minimum of 4 active camera locations maintained in each forest type. Cameras were regularly serviced to ensure batteries were charged and cameras remained active. Cameras were placed along trails (n = 134) as well as off-trail (n = 58) to test for differences in detection rates from camera placement.

Species

To understand the effect of prey on habitat use of clouded leopards, I used data from 5 possible ungulate prey species across a body size gradient (Table 2.1) as covariates—lesser mousedeer (*Tragulus kanchil*, LMD), greater mousedeer (*T. napu*, GMD), Bornean yellow muntjac (*Muntiacus atherodes*, YM), red muntjac (*M. muntjak*, RM), and bearded pig (*Sus barbatus*, BP) (Chapter 2).

Site-specific covariates

Several site-specific covariates were measured at each camera-location for inclusion in occupancy and detection modelling. Elevation was measured as meters above sea level and was standardized using a z-score normalization.

Forest type was classified for each site and was included in analysis as a categorical covariate. Seven distinct forest types are present in CPRS (Table 1.1). I pooled the upland granite and montane forest types together in this study as there was a lack of phenological data available for the montane forest type during the study period. The upland granite and montane forests exhibit considerable interdigitation and share similar floral composition and productivity, therefore I believe pooling these forest types to be reasonable if inferences are treated with caution. The forest types I include in this study are peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG) and upland granite/montane (UGM).

I used phenology data, collected by Dillis *et al.* (2015), to determine temporal variation in fruit availability in each forest type over the sampling period. The density of stems bearing ripe fruit was measured from all trees with stems larger than 14.5 cm dbh, lianas larger than 3.5 cm dbh, and all hemi-epiphytic figs with roots touching the ground. Measurements were taken on a monthly basis from 10 randomly selected sampling plots, covering 1.5 ha of each forest type. Values were averaged to obtain one monthly estimate per forest type. I standardized values using a z-score normalization before analysis.

I used site-specific estimates of habitat use for each of the 5 potential prey species from single-species occupancy models (Section 2.5) to describe prey occurrence. To avoid confounding influence of covariates, I took data from the conditional estimates from the null occupancy model to describe the occurrence of each species while only accounting for imperfect detection. No covariates are used to model habitat use in the null model, resulting in conditional habitat use estimates with values of either '1' when a species was detected, or a probability value reflecting the chance of presence when there was no detection.

I calculated human activity as an index of all human detections at each site standardized by the sampling effort (trap nights/sampling period). Human activity was a combination of researcher and poacher sightings. Although poachers were detected consistently throughout the study period, the sparse frequency of detections prevented the influence of poachers to be determined separately. I used the index approach instead of occurrence estimates from occupancy models as researchers were detected at a high frequency, reducing the level of variation between sites.

3.4.2 Occupancy modelling

A simple single-species occupancy modelling approach (Mackenzie *et al.* 2006) was used to model habitat use of clouded leopards across CPRS and evaluate the influence of site-specific covariates on habitat use and detection. All analyses were conducted in R (R Core Team 2013) using the RPresence package (Mackenzie & Hines 2018).

Traditionally, occupancy modelling is based on the assumption of closure, meaning species cannot move between sampling sites during a survey. In relation to the spatial scale of this study, I believe this assumption is not met as clouded leopards may have home ranges as large as 16 km² for females and > 50 km² for males (Hearn *et al.* 2013, Mohamed *et al.* 2019). Occupancy at a site can thus not be determined as an individual detected at one site may be able to travel and be detected a separate site within a survey. Alternatively, the *use* of a site can be estimated using the same approach. Accordingly, in this study I estimate the habitat *use* (Ψ) and detection probability (p).

I created detection histories for each sampling site using the camtrapR package (Niedballa *et al.* 2016). I broke continuous histories into 30-day survey periods starting July 1st, 2015. I grouped four consecutive surveys, totaling to a period of 120 days, into *sampling periods*. In this study, I will be using the term *sampling period* instead of the traditional *sampling season* as there are no climatic seasons at CPRS. Instead of aligning with the occurrence of climatic seasons I designed the sampling periods to align with fluctuations in fruit availability (Figure 2.1).

I formatted all data into distinct camera location x sampling period combinations and subsequently treated these as distinct sites ($n = 2,496$). This data structure permitted me to estimate clouded leopard habitat use across CPRS with limited temporal replication, and without estimating site emigration and immigration. This approach also allowed me to estimate the influence of fluctuations in fruit availability without using a multi-season approach typically used with temporal covariates. Using this approach, sometimes referred to as a *stacked* single-season approach, the occupancy at a site is estimated independently of previous or consecutive sampling periods (Fuller *et al.* 2016). I believe this

to be acceptable for the purpose of this study as the interest is in estimating habitat use and not site-occupancy.

I modelled the detection of clouded leopards at $i = 1, \dots, 2496$ site-periods during $j = 1, \dots, 4$ surveys as $y_{ij} \sim \text{Bernoulli}(z_i \times p_{ij})$. z_i is the latent variable indicating if site i is used or not by a species (1 or 0) and p_{ij} is the site and survey-specific probability of detection given an individual is present. The site-specific probability of use by clouded leopards is described by (Ψ_i) and latent states of use as $z_i \sim \text{Bernoulli}(\Psi_i)$.

I modelled the effects of covariates on habitat use and detection using logit-link functions. The probability of a site being used by clouded leopards was modelled as $\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 x_{ij}$, and the probability of detection was modelled as $\text{logit}(p_{ij}) = \beta_0 + \beta_1 x_{ij}$, where the covariate at site i and survey j is represented by x_{ij} , and β_1 and α_1 are the associated regression coefficients. The intercept or constant term (for categorical variables) is represented by β_0 or α_0 .

I modelled occupancy as a function of forest type (with lowland sandstone as the constant), temporal variation in fruit availability as a site x sampling period specific variable, elevation (both as a linear and quadratic terms), human activity represented as an index of human detections per trap night, sampling period, and as a function of occurrence of each of the 5 ungulate species using conditional habitat use estimates from the standard model. I modelled detection as a function of sampling effort (the proportion of days a camera was active at the site during a sampling period), and as a function of camera placement—a categorical covariate identifying placement either on or off trails.

Using the site-specific covariates, I designed a set of *a priori* candidate models for modelling habitat use and detection probability (Ψ $n = 204$, p $n = 4$). I tested all possible combinations of covariates that described biologically relevant hypotheses, with a maximum of three covariates in a model to prevent over parameterization and avoid non-convergence issues. I assessed any correlation between variables and omitted correlated covariates ($r > 0.6$) from the same model.

I used a two-step approach for model fitting, focussing on modelling habitat use first as it is the primary parameter of interest for this study. Modelling habitat use first with a general model for detection enabled me to assess inferences about habitat use without a confounding influence from the constraints applied to detection probability (MacKenzie *et al.* 2006). Following this first step, I then modelled detection probability using the best performing model for habitat use. I checked models following the first two steps by fitting all top habitat use models with all detection models to confirm the selection process. Using a parametric bootstrap ($n = 1,000$) to compare the observed and expected data

(χ^2) for the most general model, I assessed model fit and calculated the overdispersion parameter (\hat{c}) (Mackenzie & Bailey 2004).

I used Aikake’s Information Criterion (AIC) to rank models and determine the most parsimonious model with the best fit to the data. I included models with significant support ($\Delta AIC < 7$) in model selection tables and model-averaging (Burnham & Anderson 2002). I graphically represented all results using the *ggplot2* package (Wickham 2016) in R and using the *viridis* colour scale designed for colour-blindness (Garnier 2018).

3.5 Results

Between July 2015 and October 2019, a total of 42,610 trap nights across 192 sites at CPRS resulted in 276 independent detections of clouded leopards. Clouded leopards were detected at 22% of the sites, with the highest amount of detections in the lowland granite forests (Table 3.1). There were no detections of clouded leopards in the freshwater swamp or alluvial bench forests during the study period despite a combined 12,020 trap nights. Without the influence of covariates clouded leopards had a naïve detection probability of 0.21 ± 0.02 .

Table 3.1: Detections of clouded leopards across CPRS by forest type between July 2015-October 2019.

Forest type	Detections	Trap nights	Detections per trap night
<i>Peat swamp (PS)</i>	8	6575	0.001
<i>Freshwater swamp (FS)</i>	0	5747	0
<i>Alluvial bench (AB)</i>	0	6273	0
<i>Lowland sandstone (LS)</i>	15	7084	0.002
<i>Lowland granite (LG)</i>	156	5514	0.028
<i>Upland granite/montane (UGM)</i>	97	11417	0.009
TOTAL	276	42610	0.007

3.5.1 Habitat use

Habitat use of clouded leopards was best described by forest type and bearded pig occurrence, which were consistently present in all top performing models ($\Delta AIC < 7$; Table 3.2). Fruit availability was present in two of the top nine models. The inclusion of the *fruit* covariate in the top model allowed for more variation in the data to be explained despite the penalty associated with increased parameterization.

The highest estimates of habitat use were associated with the lowland granite forest ($\hat{\Psi}_{LG} = 0.87 \pm 0.09$, Figure 3.1), followed by the upland granite/montane forest ($\hat{\Psi}_{UGM} = 0.41 \pm 0.07$). Clouded leopards used peat swamp ($\hat{\Psi}_{PS} = 0.14 \pm 0.05$) and lowland sandstone forests ($\hat{\Psi}_{LS} = 0.11 \pm 0.05$) less frequently. Alluvial bench and freshwater swamp forests were associated with a strong negative relationship on clouded leopard habitat use as there were no detections in these habitats during the study period. The complete lack of detections prevented accurate estimation of standard errors and habitat use estimates approached zero.

Bearded pig occurrence had a strong positive association with clouded leopard habitat use (Figure 3.2). The β values associated with the *BP* covariate remained ~ 1.5 across all models, indicating that clouded leopards were between 4.3-4.8 times more likely to use sites where bearded pigs were detected.

The availability of ripe fruit had a positive relationship with clouded leopard habitat use. The probability of clouded leopards using a site increased 1.46 times for every 1-unit increase in density of ripe fruit available at the site.

Human activity had a negative effect on the probability of clouded leopards using sites. The *human* covariate was present in one of the top models ($\Delta AIC < 2$) which should be considered to have support insignificantly different from the 1st and 2nd ranked models (Burnham & Anderson 2002). The associated $\hat{\beta}$ values (Table 3.1) indicate that clouded leopards are 1.27 times less likely to use a site for every 1-unit increase in human activity. The lesser mousedeer (*LMD*), greater mousedeer (*GMD*), yellow muntjac (*YM*) and red muntjac (*RM*) covariates appeared in the set of best performing models, however, the standard error associated with the beta values overlapped zero. Accordingly, the influence of mousedeer and muntjac occurrence cannot be reported with any confidence.

The *time* covariate was present in two of the best performing models and described a slight negative trend in the probability of clouded leopards using habitats over the duration of the study. Habitat use was estimated to decline by 1.07 - 1.08 times with each sampling period.

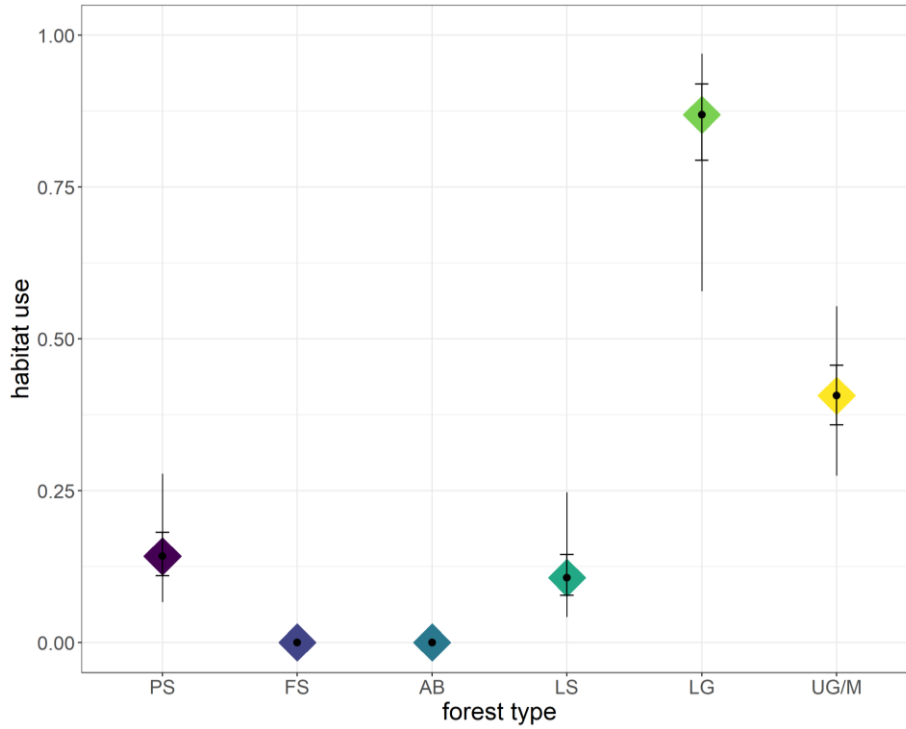


Figure 3.1: Clouded leopard habitat use by forest type at CPRS. Habitat use estimates are model-averaged ($\Delta AIC < 7$). Forest types are ordered along an increasing elevational gradient and identified by the following abbreviations: Peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG) and upland granite/montane (UGM). Vertical lines represent the 95% confidence interval and whiskers demonstrate the 50% confidence interval.

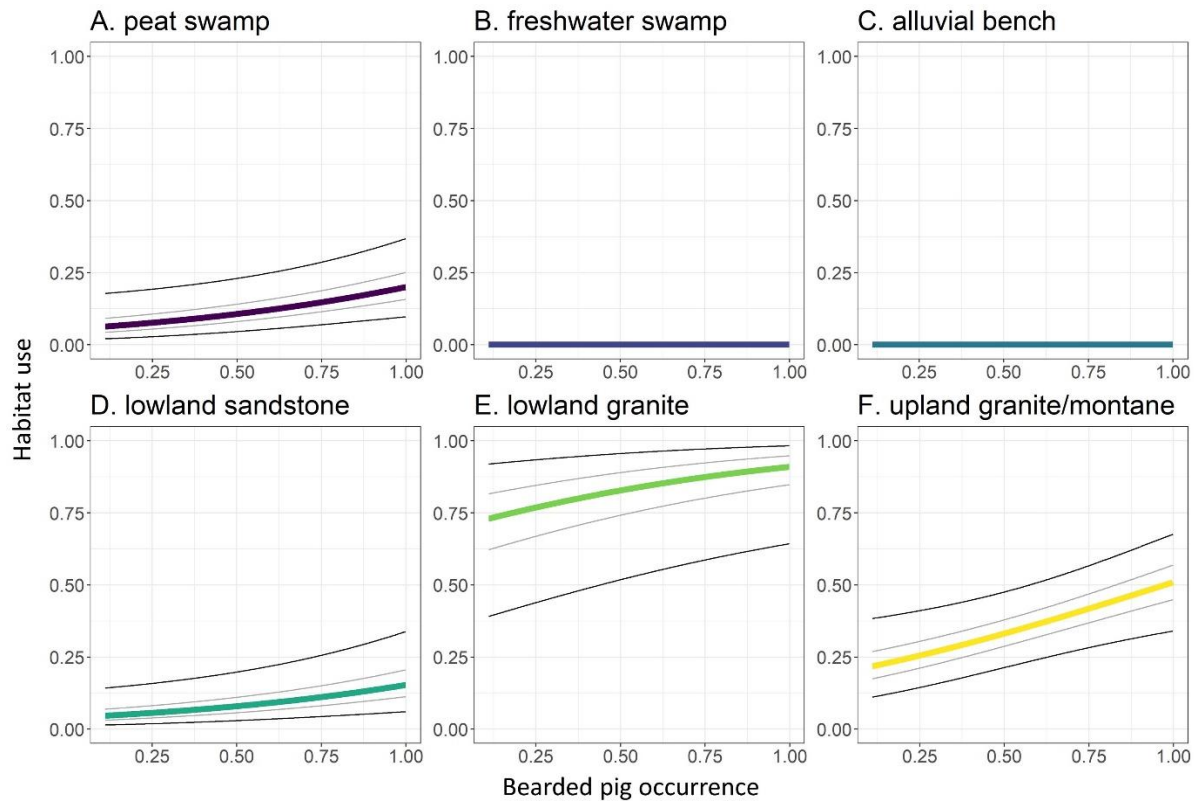


Figure 3.2: The relationship between bearded pig occurrence and clouded leopard habitat use across forest types in CPRS. Clouded leopard habitat use estimates are model averaged ($\Delta AIC < 7$). Black boundaries represent the model-averaged 95% confidence interval and grey boundary lines represent the model-averaged 50% confidence interval.

3.5.2 Detection

The detection probability of clouded leopards was best described by both *effort* and *off-trail* covariates (Table 3.3). Sampling effort had a positive relationship with detection probability, while camera placement off-trail had a strong negative relationship (Figure 3.3). The odds of detecting a clouded leopard were 13-15 times higher at on-trail sites than off-trail. The *off-trail* covariate best described the heterogeneity in detection probability between sites, evident from the strong $\hat{\beta}$ value as well as the performance of the $p(\text{off-trail})$ model $\Delta AIC = 1.34$, indicating that its performance was comparable with the top model (Burnham & Anderson 2002).

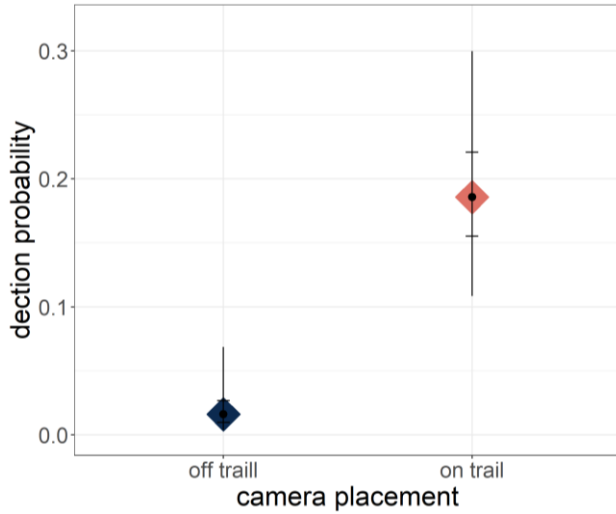


Figure 3.3: The probability of detecting Sunda clouded leopards at camera stations on and off trails given presence at the camera site. Estimates of detection probability are model-averaged ($\Delta AIC > 7$). Vertical bars illustrate the 95% confidence interval and whiskers identify the 50% confidence interval.

3.5.3 Model fit

Model fit was assessed using a parametric bootstrap for the most general model Ψ (*fruit + forest + BP*), $p(\text{effort} + \text{off-trail})$. The dispersion parameter (\hat{c}) was calculated to be 1.93, indicating slight overdispersion and suggesting that some variation in the data remains unexplained. A dispersion parameter value below 3 is considered acceptable (Lebreton *et al.* 1992), and further influence from additional factors is probable as I limited models to include a maximum of 3 covariates.

Table 3.2: AIC comparison of top ranked habitat use (Ψ) models ($\Delta AIC < 7$) for the Sunda clouded leopard. Habitat use was modelled with general detection model p (effort + off-trail). The null model is represented as $\Psi(.)$. ΔAIC is the relative difference in AIC values compared to the top ranked model, K is the number of parameters in a model, w is the AIC model weight, α is the estimated intercept or constant term, β are the estimated regression coefficients for each covariate on the logit scale. Forest types are represented by the following abbreviations: freshwater swamp (FS), peat swamp (PS), lowland swamp (LS), lowland granite (LG), upland granite/montane (UGM). The values reported in grey represent models that did not reach convergence.

Model	ΔAIC	w	β_{fruit}	β_{forest}	β_{BP}	β_{GMD}	β_{LMD}	β_{RM}	β_{YM}	β_{time}	β_{humans}
<i>fruit + forest + BP</i>	0	0.28	0.38 ± 0.22	PS	-0.50 \pm 0.60						
				FS	-27.75 \pm 265789						
				AB	-24.75 \pm 62876	1.45					
				LS	-2.76 \pm 0.60	± 0.52					
				LG	3.75 \pm 0.86						
				UGM	1.31 \pm 0.47						
<i>forest + BP</i>	1.29	0.15		PS	-0.30 \pm 0.58						
			FS	-25.43 \pm 107741							
			AB	-25.45 \pm 105541	1.51						
			LS	-2.95 \pm 0.58	± 0.51						
			LG	3.72 \pm 0.87							
			UGM	1.52 \pm 0.45							
<i>forest + humans + BP</i>	1.44	0.13		PS	-0.36 \pm 0.59						
			FS	-44.45 \pm 6603108							
			AB	-46.44 \pm 689319	1.53						
			LS	-2.71 \pm 0.60	± 0.51						
			LG	3.71 \pm 0.86							
			UGM	1.42 \pm 0.45							
<i>forest + time + BP</i>	1.56	0.13		PS	-0.26 \pm 0.58						
			FS	-22.68 \pm 27264							
			AB	-23.26 \pm 39439	1.47						
			LS	-2.52 \pm 0.66	± 0.52						
			LG	3.79 \pm 0.93							
			UGM	1.53 \pm 0.46							
<i>forest + GMD + BP</i>	2.46	0.08		PS	-0.40 \pm 0.59						
			FS	-23.31 \pm 38980							
			AB	-21.81 \pm 17512	1.57						
			LS	-2.81 \pm 0.6	± 0.52						
			LG	3.59 \pm 0.89							
			UGM	1.40 \pm 0.47							
	2.56	0.08		PS	0.21 \pm 0.84						

Model	ΔAIC	w	β_{fruit}	β_{forest}	β_{BP}	β_{GMD}	β_{LMD}	β_{RM}	β_{YM}	β_{time}	β_{humans}
<i>forest + LMD + BP</i>				FS	-25.47 ± 131767	1.52 ± 0.50	-0.75 ± 0.89				
				AB	-30.12 ± 706424						
				LS	-2.84 ± 0.59						
				LG	3.58 ± 0.85						
				UGM	1.43 ± 0.46						
<i>forest + YM + BP</i>	3.26	0.05		PS	-0.27 ± 0.6	1.51 ± 0.51			0.07 ± 0.45		
				FS	-32.95 ± 1743967						
				AB	-33.60 ± 1777397						
				LS	-2.99 ± 0.65						
				LG	3.71 ± 0.87						
UGM	1.54 ± 0.47										
<i>forest + RM + BP</i>	3.29	0.05		PS	-0.3 ± 0.61	1.51 ± 0.51		0.01 ± 0.6			
				FS	-31.87 ± NA						
				AB	-34.55 ± NA						
				LS	-2.95 ± 0.7						
				LG	3.72 ± 0.87						
UGM	1.52 ± 0.45										
<i>fruit + forest + time</i>	6.79	0.01	0.44 ± 0.21	PS	-0.65 ± 0.6					-0.08 ± 0.05	
				FS	26.63 ± 176210						
				AB	-27.83 ± 364534						
				LS	-1.04 ± 0.49						
				LG	3.19 ± 0.68						
UGM	1.02 ± 0.45										
$\Psi(.)$	877.97	0									

Table 3.3: AIC comparison of top ranked models of Sunda clouded leopard detection (p) ($\Delta AIC < 7$).

Habitat use was modelled with general model Ψ (elev + fruit + time). ΔAIC is the relative difference in AIC values compared to the top ranked model, K is the number of parameters in a model, w is the AIC model weight, α is the estimated intercept or constant term, β are the estimated regression coefficients for each covariate on the logit scale. e^β represents the back-transformed β estimate describing the odds associated with the covariate.

Model	ΔAIC	w	α	β_{effort}	$e^{\beta_{effort}}$	$\beta_{off-trail}$	$e^{\beta_{off-trail}}$
<i>effort + off-trail</i>	0	0.66	-1.66 ± 0.29	0.61 ± 0.34	1.84	-2.6 ± 0.73	-13.46
<i>off-trail</i>	1.34	0.34	-1.18 ± 0.1			-2.71 ± 0.72	-15.03

3.6 Discussion

My results demonstrate clear spatiotemporal patterns of habitat use of the Sunda clouded leopard in CPRS. Using an occupancy modelling framework enabled habitat use to be quantified among camera sites while accounting for imperfect detection. The habitat use of clouded leopards in the Bornean rainforest ecosystem was strongly influenced by forest type and bearded pig occurrence, and, to a lesser degree, human activities, and temporal fluctuations in fruit availability.

Forest type

Clouded leopard habitat use patterns showed clear preferences for distinct forest types at CPRS. The lowland granite forest (200-400 m asl) was the most frequently used habitat followed by the upland granite/montane (350-800 m asl) with moderate use. Containing a large portion of dipterocarp species, both the lowland and upland granite forests exhibit considerable pulses in fruit resources during mast-events (Cannon & Leighton 2004). These forests also have a high density of both large and small trees which may facilitate any arboreal behaviours of clouded leopards (Table 1.1). The presence of ridgelines in these forests, which have been linked with large-scale movement patterns of male clouded leopards (Macdonald *et al.* 2018), may further explain high estimates of habitat use.

Highest occurrences of clouded leopards in lowland and upland forests was similarly reported by Hearn *et al.* (2016) from a questionnaire of researchers that found habitat suitability peaked in lowland and upland forests and dropped off at higher elevation montane forests. By pooling the higher elevation montane forest with the upland granite forest in this study, any disparity between habitat use of clouded leopards in upland granite and montane forests is lost and may have resulted in underestimates

of habitat use in the upland granite forest. Of the 93 detections in the pooled 'upland granite/montane' forest (Table 3.1), 44 were detections of clouded leopards in the montane forest habitat and 53 were at sites in the upland granite forest. Habitat use was not estimated separately for montane forests due to a paucity of fruit availability data, however the number of detections suggest a slight decline of habitat use in upper montane forests.

Previous studies have reported increased occurrence of clouded leopards at higher elevations (Allen *et al.* 2016, Tan *et al.* 2017), however I found that elevation was not a good predictor for habitat use. Describing clouded leopard occurrence by elevation oversimplified patterns of habitat use, as clouded leopards used the low-lying peat swamp forests and habitat use may decline at higher elevations. Habitat use should be used to inform and prioritize protection efforts, however, habitats that demonstrate low levels of use should not be dismissed as unimportant. Fallback foods, a concept used to describe resources that are critical to a species during periods of food scarcity, may drive species to travel outside common habitats and alter their ranges (Marshall *et al.* 2009b). Although used comparably less than other forest types, the low elevation peat swamp and lowland sandstone forests may provide key resources vital to population persistence. Clouded leopards were not detected in either the freshwater swamp forest and lowland sandstone forest over 4 ½ years. The low-density of trees in the freshwater swamp or lowland sandstone forests may make these forest habitats unsuitable for clouded leopards. If unsuitable for hunting or other key behaviours, the low-density forests may still function to maintain connectivity to other key habitats.

Prey occurrence

The occurrence of bearded pigs was a strong predictor of habitat use of clouded leopards across CPRS, indicative of a predator-prey relationship between clouded leopards and bearded pigs. Bearded pigs have been recorded travelling in large groups during mast-events, arriving at mast-fruiting areas in the 100's (Curran & Leighton 2000, Dove 1993, MacKinnon *et al.* 1996). Pulses in occurrence, in combination with a hunting strategy distinct from most mid-sized felids may enable clouded leopards to predate on bearded pigs when available. Clouded leopards are adept at climbing trees and their unique canine morphology is indicative of a hunting strategy of dropping from above and delivering a nape bite to sever the spinal column (Christiansen 2007, 2008). Although some studies have suggested bearded pigs could be a potential prey species for clouded leopards (Ross *et al.* 2013), others have dismissed this possibility due to the disparity in body size of an adult bearded pig (up to 200 kg) and clouded leopards (15-25 kg) (Mohamed *et al.* 2015). Carbone *et al.* (1999) described the energetic constraints of

carnivores and predicted that carnivores with body mass < 21.5 kg would feed primarily on small prey (< 45% of carnivore mass). Sunda clouded leopards straddle the distinction between small and large prey based on energetic constraints. High availability of large prey could lead to favorable trade-off between energy expenditure from hunting and gains from successful kills.

A large degree of sexual dimorphism between females (~12 kg) and males (~24 kg) may differentially influence choice in prey species. Based on energetic constraints, smaller females may differ from males by preying primarily on small prey (Carbone *et al.* 1999). Hearn *et al.* (2018) used temporal overlap to inform predator-prey associations and found female clouded leopards were associated with mousedeer while male clouded leopards were associated with sambar deer (*Rusa unicolor*). My research did not identify clouded leopards by sex and most-likely disproportionately describes habitat use patterns of male clouded leopards, as females have extremely low detection rates possible due to a more arboreal hunting behaviour (Cheyne & Macdonald 2011, Sollmann *et al.* 2014).

Fluctuations in fruit resources

Pulses in fruit availability in GPNP may act as a cue for clouded leopards indicating high occurrence of prey. This novel finding links bottom-up effects of resource availability to an apex predator in a mast-fruiting rainforest system. High fruit availability attracts frugivore species (Moegenburg & Levey 2003) and I previously showed bearded pigs track available fruit across large areas (Chapter 2). Additionally, mast events create periods of high resources suitable for reproduction and can lead to population growth of frugivore species (Ostfeld & Keesing 200, Hessen *et al.* 2013). Reproduction of bearded pigs is thought to be timed to coincide with mast events as mating behavior is observed during the flowering period and piglets are observed only during fruiting events (Curran & Webb 2000). The appearance of large numbers of bearded pigs and their young as well as other species capable of tracking food resources, is marked by fruiting events that occur at slightly different times across large landscapes (Caldecott 1991). The coincidence of fruiting and a rise in available prey enables clouded leopards to use fruit availability as a cue for conditions ideal for hunting. The link between mast events and clouded leopard habitat use emphasizes the importance of preserving the dipterocarp forests in Borneo. Protecting these quickly disappearing forests is vital to maintaining suitable habitats for clouded leopards, as well as the innumerable species dependent on mast-fruiting resources.

Human activity

Human activity was associated with a reduction in clouded leopards habitat use, indicative of a potentially negative influence of passive human activity on this apex predator within the National Park. The index of human activity recorded at sampling sites throughout the park included both researchers and poachers. I was unable to assess the impact of poaching on clouded leopards due to sparse detections of poachers, however, direct impact on clouded leopards is considered to be low as poachers in Borneo are thought to primarily target ungulate species (Corlett 2007, Bernard *et al.* 2013). A negative influence on clouded leopards from passive human activity exists through the formation of a 'landscape of fear' (Lima *et al.* 1990, Laundre *et al.* 2001). The perceived threat from human activity can alter carnivore behavior, leading to increased vigilance, reduction in time hunting, and avoidance (Griffiths & Van Schaik 1993, Buij *et al.* 2007, Ciuti *et al.* 2012a, b). Ultimately the perceived threat from humans can result in extirpation from an area or reduced fitness of individuals (Ciuti *et al.* 2012a).

Although direct impacts from poachers is thought to be minimal, poaching may indirectly impact clouded leopards through competition for prey species and should be investigated. Detections of poachers declined with elevation (Figure S.1), most likely a result of increasingly difficult terrain and distance from entry points. Sambar deer may have been extirpated from the area from over-hunting as there were no sightings throughout CPRS between 2015-2019, and it is possible that other prey species are under similar threat. Poaching may also push affected species to higher elevations to seek refuge and result in clouded leopards following prey to low-disturbance areas.

Detection probability

The probability of detecting Sunda clouded leopards was substantially higher along trails in accordance with previous research on clouded leopards (Cheyne & Macdonald 2011, Cheyne *et al.* 2016). Camera trap studies for large mammals frequently deploy cameras along trails and ridgelines to increase the probability of detecting low-density species (Williams *et al.* 2002). Movement patterns associated with patrolling and scent-marking behaviors in clouded leopards may be facilitated by wildlife trails, human-made trails, and ridgelines (Wilting *et al.* 2006, Gordon & Stewart 2007, Allen *et al.* 2016). Although my finding of higher detections of clouded leopards on trails suggests camera trap methodology employed to increase detections of felids would be successful with clouded leopards, studies should avoid an entirely on-trail setup that may lead to biased detections between species or sexes (Wearn *et al.* 2013, Kolowski & Forrester 2017, O'Connor *et al.* 2017). Female clouded leopards, often sighted with young, were found to have different fine-scale habitat use, and possibly avoid encountering males that use

roads and ridgelines for long-distance movements (Hearn *et al.* 2018). Different fine-scale habitat use between sexes may explain consistently low detections of females in clouded leopard studies. Increased arboreality or avoidance of trails by females would result in underestimates of females from studies using only on-trail cameras.

Conclusion

My findings build on previous research to indicate bearded pigs are an important prey species for the Sunda clouded leopard, and demonstrates a novel link between fruiting events, bearded pig occurrence, and Sunda clouded leopard habitat use possibly suggesting that fruiting is used as a cue for prey occurrence. Additionally, my results show the importance of lowland and upland granite/montane forests, necessitating protection as key habitats for the Sunda clouded leopard. Lastly, I found human activity to be linked with lower levels of habitat use, indicating a possible 'landscape of fear'. Together, these findings provide novel insight into factors influencing the habitat use of the Sunda clouded leopard and can be applied to better inform range predictions, habitat suitability models, and conservation planning. The rate at which the forests of Borneo are disappearing and remaining paucity of information about its rainforest ecosystems necessitates a swift and effective move to conserve this charismatic felid. Conservation efforts targeting the Sunda clouded leopard will likely benefit innumerable other species that share dependencies on similar habitats and resources. More research is urgently needed to further refine our understanding of clouded leopard diet, threats, and sex-dependent differences in habitat and resource use.

The purpose of my research was to shed light on the spatial ecology of understudied ungulates and a top predator in a mast-fruiting Bornean rainforest. In Chapter 2, I provided evidence of niche partitioning among 5 sympatric ungulate species along a fruit resource gradient. Mousedeer (*Tragulus kanchil*, and *T. napu*) and muntjac (*Muntiacus atherodes* and *M. muntjak*) species differentially used distinct forest types, indicating different foraging strategies: with smaller bodied mousedeer using forests with high-quality resources and larger muntjacs differentiating by using forests with more variable resources. However, bearded pigs (*Sus barbatus*) did not select for any forest types but instead appeared to track pulses of abundant fruit across the landscape. These findings describe, for the first time, niche partitioning among the ungulates present at Cabang Panti Research Station (CPRS) and more generally improve our understanding of resource use of an ungulate guild varying in body size from 1.5 to 200 kg in a mast-fruiting rainforest. In chapter 3, I used data on forest type, ungulate prey occurrence, fluctuation fruit resources, and human activity throughout CPRS as predictors of habitat use of Sunda clouded leopard (*Neofelis diardi*; clouded leopard hereafter). Habitat use of clouded leopards was strongly influenced by forest type, indicating differences in suitability that should be accounted for when assessing potential habitat. Occurrence of bearded pigs and, to a lesser degree, fruit availability also explained spatial and temporal variability in habitat use of clouded leopards. In the absence of detailed data on diet composition and prey preference, I interpreted these findings as evidence that bearded pigs are likely an important prey species and clouded leopards may use fruiting events as a cue for their availability.

Hunting strategy

The hunting strategy of clouded leopards remains unobserved, however past research together with my findings illustrates a possible hunting strategy enabling clouded leopards to target large prey feeding in areas with high fruit availability. Clouded leopards, particularly females, have been well-documented to be skilled at climbing trees and moving through canopies, resulting in their description as a semi-arboreal species (Brodie & Giordano 2013, Sollmann *et al.* 2014, Macdonald *et al.* 2018). Additionally, multiple studies on felid tooth morphology have identified clouded leopards as an outlier with considerably long and narrow ‘blade-like’ canines (Freeman & Lemen 2007, Christiansen 2006, 2007, 2008). The canine morphology is inconsistent with typical allometric scaling and possibly indicative of a hunting strategy of dropping from above and delivering a nape bite to sever the spinal column

(Christiansen 2007, 2008). Furthermore, a paralyzing bite would enable large prey to be quickly incapacitated, allowing clouded leopards to target species that would be considered too large based on energetic constraints (Christiansen 2007, Carbone *et al.* 1999). The spatiotemporal association between clouded leopards, bearded pigs, and fruiting that I describe in Chapter 3 indicates that bearded pigs may be an important prey for clouded leopards and that clouded leopards track bearded pigs through their association with fruiting events. To my knowledge, there have been no direct observations of clouded leopards hunting ungulates, however, their skill climbing trees, tooth morphology, and spatial association with both bearded pigs and fruiting events indicates a possible strategy of waiting in fruiting trees and dropping down to predate on bearded pigs below.

Forest type

The influence of forest type on habitat use was evident for both mousedeer and muntjac species, as well as the clouded leopards. The distinct forest types present in CPRS exhibit clear differences in forest structure, floral composition, soil type, and productivity. The variation occurring among forest types inside Borneo's rainforests necessitates incorporating forest type into species conservation in Borneo. Predicting current ranges and suitable habitat are important steps in assessing populations and planning conservation efforts. Physical and environmental covariates known to influence the habitat use of a species can be applied to models that can predict use across a larger landscape—eliminating the need to directly survey large areas. Currently, range and habitat suitability models for ungulates and clouded leopards on Borneo have been limited to regional assessments or coarse models on a landscape-scale based on elevation, canopy cover and human-altered landscapes (Hearn *et al.* 2016, 2018b, 2019, Macdonald *et al.* 2018, Kaszta *et al.* 2019). My findings of forest type preference should be applied to refine current estimates of range and the remaining habitat across Borneo. Classifying forested areas in Borneo by forest type would increase the accuracy of these estimates. This would most likely lead to a reduction in range estimates and remaining suitable habitat. With little research informing current models in Borneo, estimates likely overestimate the extent of remaining suitable habitat which could have serious consequences for threatened populations. Further modelling is required to incorporate my findings into predictions of habitat suitability and range across Borneo.

Baseline for further research

My evaluation of the current habitat use of ungulates and the clouded leopards at CPRS provides a baseline and steppingstone to further research that is needed to inform effective conservation. Long-

term research is needed to identify any changes in habitat use paired with abundance estimates over time to better quantify species' response to threats. Climate change, land-use conversion, and poaching threaten to push ungulates and clouded leopards out of low-lying forests, shifting their ranges up an elevational gradient and further compressing distributions into less suitable habitats. Land-use conversion disproportionately affects lowland forests (Curran *et al.* 2004) and access into forests by poachers is facilitated by logging roads and proximity to forest edge (Laurance *et al.* 2006, Mohd-Azlan & Lading 2006). My research provides a snapshot of current habitat use of ungulates and clouded leopards in GPNP, however, the reported distributions function as a baseline to be compared over time and among populations. Additionally, my research has uncovered avenues that merit further investigation regarding the movement patterns of bearded pigs and clouded leopards across the landscape. The association of both bearded pigs and clouded leopards with fruiting across CPRS was evident in my research, however, radio-collaring could be used to solidify this finding and better understand this relationship. Furthermore, I was unable to evaluate differences in habitat use or detection between male and female clouded leopards but a rising levels of evidence indicates sex-dependant differences in habitat use and prey selection (Cheyne & Macdonald 2011, Wilting *et al.* 2012, Hearn *et al.* 2018b). Substantially higher detection rates of male clouded leopards are creating a research base that may disproportionately describe male-specific findings and overlook insight on females vital to effective conservation. Lastly, my research demonstrates patterns of habitat partitioning between sympatric ungulate species and linked clouded leopard habitat use to bearded pig occurrence—shedding light on the previously understudied diets of these species. However, further research focusing on feeding ecology of clouded leopards is needed to compile comprehensive dietary assessments.

Mast resources

My research provides evidence of the bottom-up effects of mast-induced fluctuations in fruit availability having a permeating influence across trophic levels in a Bornean rainforest. Habitat and resource partitioning found amongst the ungulate species indicated the presence of different resource strategies. The mousedeer and muntjac species appear to differentially use specific forest types and did not follow spatiotemporal patterns of fruiting. In contrast, bearded pigs did not appear to differentiate among forest types. Instead, habitat use was closely tied to patterns of fruit availability, suggesting an ability to track resources across a large area. Large groups of bearded pigs, often containing over 100 individuals, have been described following mast events and travelling long-distances to arrive in a masting area

(Curran & Leighton 2000, Dove 1993, MacKinnon *et al.* 1996). This strategy of utilizing the concentrated and short-lived resources from fruiting events has trade-offs as the timing of such events can be irregular. In the past, long inter-mast periods have resulted in populations of bearded pigs and sun bears (*Helarctos malayanus*), who are similarly associated with mast resources, becoming emaciated and numerous individuals were found to have died from apparent starvation (Wong *et al.* 2005). Dependence on a variable resource leaves species highly vulnerable to disruptions in fruiting patterns.

The bottom-up influence of fruit availability is not limited to consumers like bearded pigs or sun bear. The link between bearded pig occurrence and clouded leopard habitat use that I outline in Chapter 3 describes the mechanism by which the top carnivore is influenced by cycles of fruit availability. Furthermore, bearded pig reproduction has been linked to significant mast events that provide enough resources to support lactating females (Oliver 1993, Hancock 2005, Luskin & Ke 2017). The abundance of available prey as bearded pigs and their young coinciding with fruiting events creates an indirect association between clouded leopards and fruit availability.

The dependence on mast-fruiting resources, either directly (bearded pigs) or indirectly (clouded leopards), leaves species increasingly vulnerable as climate change and human disturbance (i.e. logging) impact the timing and availability of mast resources. Although the timing and triggering of mast-fruiting events are not fully understood, the El Nino Southern Oscillation (ENSO) cycles are thought to be a significant factor (Wich & Schaik 2000). A growing pool of evidence suggests that climate change is altering the nature of El Nino events (Yeh *et al.* 2009), their frequency (Trenberth & Hoar 1997), and subsequently affects fruiting (Chapman *et al.* 2005). Additionally, climate change and reduction in forest cover (McAlpine *et al.* 2018) are resulting in a drier hotter climate in Borneo that has led to an increase in forest fires decimating remaining habitats (Goldammer & Seibert 1990). A further nail in the coffin is the ongoing deforestation occurring in Borneo due to logging and conversion into plantations (Curran *et al.* 2004, Hansen *et al.* 2013, Ocampo-Penuela *et al.* 2020). In combination, these threats are reducing the extent of remaining dipterocarp forests in Borneo and altering the timing of fruiting events. Increasingly arrhythmic mast-events in diminishing forest fragments are eliminating key resources that could trigger cascading effects throughout rainforest ecosystems. Reduced and unpredictable fruiting resources could have dire consequences for both bearded pigs and the clouded leopards—as well as innumerable other species for whom the link to mast-fruiting has not yet been identified. The findings of my research underscore the need for more rigorous protection of the dipterocarp forests in Borneo, further research expanding our understanding of the vulnerable mast-fruiting forest communities, and

refinement of estimates of species' range and suitable habitats integrating information from ongoing research into efficacious conservation plans.

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SUPPLEMENTARY MATERIAL

Table S.1: Set of candidate models for modelling habitat use of lesser mousedeer (*Tragulus kanchil*), greater mousedeer (*T. napu*), Bornean yellow muntjac (*Muntiacus atherodes*), red muntjac (*M. muntjak*), and bearded pigs (*Sus barbatus*). Detection was kept as a general model defined as $p(\text{effort} + \text{off-trail})$.

Model	No. parameters (K)
Ψ (.)	4
Ψ (humans)	5
Ψ (fruit)	5
Ψ (elev)	5
Ψ (elev ²)	6
Ψ (habitat)	9
Ψ (time)	5
Ψ (humans + fruit)	6
Ψ (humans + elev)	6
Ψ (humans + elev ²)	7
Ψ (humans + habitat)	10
Ψ (humans + time)	6
Ψ (fruit + elev)	6
Ψ (fruit + elev ²)	7
Ψ (fruit + habitat)	10
Ψ (fruit + time)	6
Ψ (elev + time)	6
Ψ (elev ² + time)	7
Ψ (habitat + time)	10

Table S.2: Set of candidate models for detection probabilities of lesser mousedeer (*Tragulus kanchil*), greater mousedeer (*T. napu*), Bornean yellow muntjac (*Muntiacus atherodes*), red muntjac (*M. muntjak*), and bearded pigs (*Sus barbatus*). Habitat use was kept as a general model defined as Ψ (elevation + fruit + time + humans).

Model	No. parameters (<i>K</i>)
<i>p</i> (.)	6
<i>p</i> (effort)	7
<i>p</i> (off-trail)	7
<i>p</i> (effort + off-trail)	8

Table S.3: The independent detections of ungulate species across forest types in CPRS. To reduce the likelihood of recording the same individual twice, multiple sightings at a location within a day are pooled.

Forest type	<i>Lesser mousedeer</i>	<i>Greater mousedeer</i>	<i>Bornean yellow muntjac</i>	<i>Red muntjac</i>	<i>Bearded pig</i>
Peat swamp	487	9	20	8	193
Freshwater swamp	308	67	16	22	322
Alluvial bench	155	97	52	35	469
Lowland sandstone	13	53	130	65	412
Lowland granite	0	0	175	75	140
Upland granite/montane	0	1	105	139	239
total	963	227	498	344	1775

Table S.4: The detections of ungulates at on and off trail locations in CPRS standardized for number of cameras (n = 134 on trail, n = 58 off trail).

Camera placement	<i>Lesser mousedeer</i>	<i>Greater mousedeer</i>	<i>Bornean yellow muntjac</i>	<i>Red muntjac</i>	<i>Bearded pig</i>
ON trail	4.75	1.59	3.42	2.05	10.57
OFF trail	5.64	0.24	0.69	1.19	6.24

Table S.5: The average fruit availability and variability for each forest type between July 2015-October 2019 at CPRS. Fruit availability was calculated as the density of stems bearing ripe fruit per hectare, averaged across all sampling periods and associated standard deviation.

Forest type	Average fruit availability	Standard deviation
Upland granite/montane	6.68	2.50
Freshwater swamp	6.62	2.51
Peat swamp	6.15	2.71
Alluvial bench	5.95	3.90
Lowland granite	5.41	2.55
Lowland sandstone	4.88	3.12

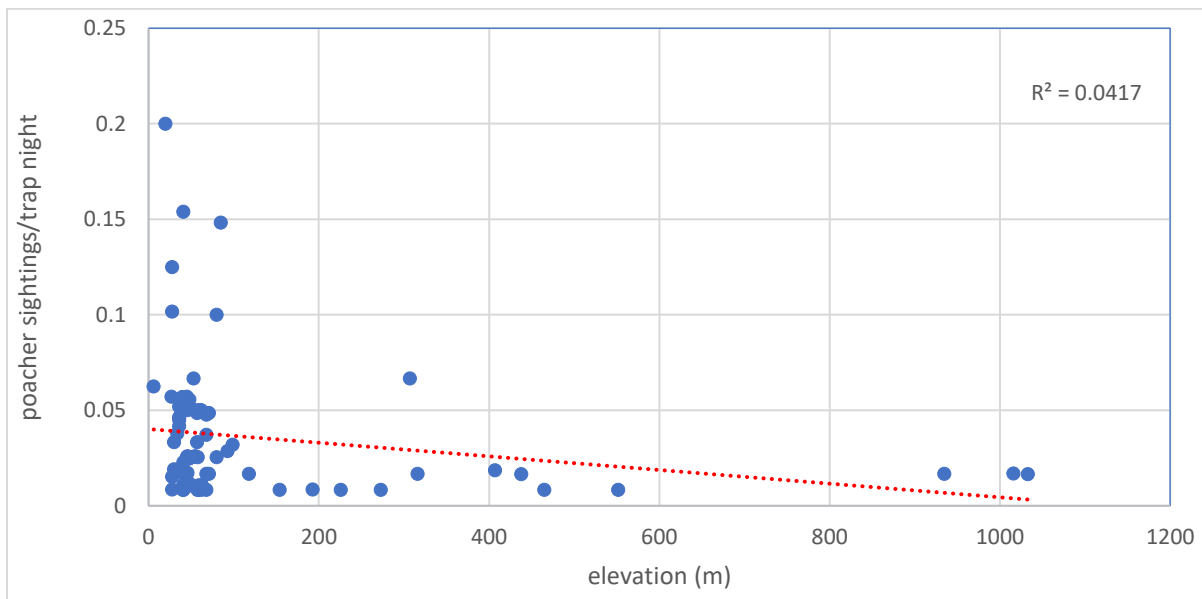


Figure S.1: Index of detections of poachers at camera sites in CPRS along an elevational gradient. Poaching index is calculated as the number of sightings at a location in a sampling period over the number of active trap nights for that camera during the same period.