Assessing the influence of anthropogenic disturbance on sympatric felids on Borneo with special reference to the Sunda clouded leopard

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Abstract

For decades, Borneo's once extensive and pristine forests have been increasingly exposed to a suite of anthropogenic disturbance and deforestation processes as a result of selective and illegal logging, hunting, droughts, fires and the conversion to plantations, chiefly oil palm. Such disturbance is likely impacting the Sunda clouded leopard, *Neofelis diardi*, and other threatened, sympatric Bornean felids, yet few studies have attempted to address these issues. In this thesis, I used data from intensive camera trap surveys throughout Sabah, Malaysian Borneo and high-resolution GPS data from tagged Sunda clouded leopards to examine the influence of forest disturbance on the abundance, distribution, movements and population connectivity of Sunda clouded leopards and other sympatric felids on Borneo, and to provide some of the first data regarding the ecological interactions and patterns of coexistence among this felid assemblage. I showed that Sunda clouded leopard movement was facilitated by forest cover with high canopy closure, and highly resisted by oil palm plantations with low canopy closure. Models of population connectivity across Sabah identified a number of isolated populations of these felids, which may be particularly threatened with extinction. Analysis of camera trap detection data revealed that the Bornean felids exhibit evidence of resource segregation along the temporal, spatial and prey niche axes, and showed that Sunda clouded leopards, bay cats, *Catopuma badia*, and marbled cats, *Pardofelis marmorata* exhibited broad scale avoidance of disturbed habitats but varied in their selection of optimal foraging habitat at fine scales. Conversely, leopard cats, *Prionailurus bengalensis*, were associated with forest disturbance and likely benefit from such changes. I developed some of the first estimates of population density for Sunda clouded leopards and the first such data for marbled cats. The results are discussed in the context of the conservation of these felids on Borneo.

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I remember thinking to myself that that would never happen; as it turns out, I was wrong.

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Statement of contribution

As Principle Investigator, I, Andrew James Hearn, contributed the primary intellectual input to design, data collection, data analysis and writing of the contents of this thesis. A number of the chapters in this thesis have been developed and written in collaboration with the following coauthors, and their respective affiliations and contributions are highlighted below.

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Chapter 3:

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Conceived and designed the experiments: AJH, JR, DWM. Data collection: AJH, JR. Analysed the data: AJH, JR. Wrote the paper: AJH. Improvements to manuscript: HB, SAB, LTBH, DWM, JR.

Chapter 6:

Conceived and designed the experiments: AJH, JR, DWM. Data collection: AJH, JR. Analysed the data: AJH. Wrote the paper: AJH. Improvements to manuscript: DWM, JR, LTBH.

Contents

Chapter 1. General introduction

Summary

The island of Borneo is a centre of biodiversity and endemism, and until recently supported one of the world's largest, relatively undisturbed contiguous blocks of tropical rainforest. In recent decades, forest degradation, deforestation and conversion to agriculture, and a growing pressure from hunting and trade have had an increasing impact on Bornean wildlife and many species are now threatened with extinction (Meijaard et al., 2005a; Wilcove et al., 2013). The Sunda clouded leopard is the largest member of a guild of five felids found in Borneo's forests. Other members are the bay cat *Catopuma badia*, marbled cat *Pardofelis marmorata*, flat-headed cat *Prionailurus planiceps*, and leopard cat *Prionailurus bengalensis*. Two of these felids are considered by the IUCN as Endangered, one Vulnerable, and their presumed primary habitat is rapidly being lost, fragmented and/or altered in the region (Wilting et al., 2015; Ross et al., 2015, 2016; Hearn et al., 2016a, b). The ecology of these species is not well-known and the impact of anthropogenic habitat modification on each is unclear. It is becoming increasingly clear that maximal gains to conservation could be achieved if management of production forests was enhanced to minimise negative impacts on biodiversity (Meijaard and Scheil 2008). However, such optimisation approaches, based on science and an understanding of how these felids respond to forest management practices and other anthropogenic disturbances, are currently lacking, and addressing this knowledge gap is a conservation priority.

The overall aim of this DPhil thesis is to enhance knowledge of the influence of forest disturbance on the abundance, distribution, movements and population connectivity of Sunda clouded leopards and other sympatric felids on Borneo, and to offer new and much needed insights into the ecological interactions and patterns of coexistence

among this felid assemblage, with the goal of contributing to the development of appropriate conservation action.

In this introductory chapter, I provide a brief review of the relatively recent anthropogenic changes that continue to threaten Borneo's forests, and explore the literature to gain insight into the way in which wildlife is influenced by these changes. Lastly, I introduce the Bornean felid assemblage, and provide a concise overview of our current understanding and gaps in our knowledge regarding these felids' ecology, framed within the context of providing insight into their possible responses to anthropogenic change.

Anthropogenic disturbance of Borneo's forest landscape

Nestled within the heart of Southeast Asia, the island of Borneo, the world's third largest island, is an evolutionary hotspot and centre of biodiversity and endemism (Woodruff, 2010; De Bruyn et al., 2014). Akin with much of Southeast Asia, however, Borneo's rich biological diversity is now threatened by disturbance from selective logging and deforestation (e.g., Sodhi et al., 2004; 2010; Meijaard et al., 2005a; Sheil et al., 2009; Wilcove et al., 2013), coupled with increased pressures from hunting and poaching (Bennett, 2000; Brodie et al., 2015a; Harrison et al., 2016). Understanding the prevalence and impacts of such disturbance is thus critical to the conservation of Borneo's wildlife.

Large-scale anthropogenic impacts on the forest landscape of Borneo remained relatively low until the advent of industrialised logging in the 1970s. Indeed, as recently as 1973 an estimated 76% (558,060 km^2) of Borneo's land area (737,188 km^2) remained under old-growth forest cover (Gaveau et al., 2014). An increasing global demand for tropical timber and agricultural land coupled with the introduction of new logging technologies in the 1970s, however, led to the selective logging of large tracts of low-lying (< 500 masl) forest on Borneo (Reynolds et al., 2011; Bryan et al., 2013; Gaveau et al., 2014), and much of Borneo's forests now lie within forest concessions. Once opened, many forest areas were subsequently subjected to further degradation and/or eventual deforestation by the actions of illegal logging, droughts and fires (e.g., Beaman et al., 1985; Page et al., 2002; Wooster et al, 2012), and via the conversion to oil palm (*Elaeis guineensis*) and, to a lesser extent, acacia (*Acacia* spp.) and rubber tree (*Hevea brasiliensis*) plantations (Casson, 2000; Carlson et al., 2012). By 2010, Borneo's 1973 forest cover had declined by an estimated 139,333 km^2 (25%), and by 2015 a further 47,174 km (8.5%) was lost (Gaveau et al., 2016). Forest losses varied by region (Bryan et al., 2013), with the highest losses estimated in the Indonesian Kalimantan provinces and the Malaysian states of Sabah and Sarawak, which lost 35.6%, 31.9% and 25.9% of their 1973 forest area by 2015, respectively, whereas Brunei's forest cover declined by around 10.3% over this period (Gaveau et al., 2016).

The drivers of this forest loss also appear to vary by region. In Malaysian Borneo, industrialised plantation industries were responsible for an estimated 57–60% of deforestation from 1973 to 2015, whereas in Indonesian Borneo, plantations were frequently developed on lands cleared before 1973, on highly degraded, burnt lands, and so plantation associated deforestation during this period only amounted to around 15-16% of deforestation (Gaveau et al., 2016). Since 2005, however, Indonesian Borneo has shown a steep rise in the amount of deforestation driven by plantation industries, which is now the principle contributor of forest conversion by area (Gaveau et al., 2016). Cushman et al. (in press) modelled the rates and patterns of recent forest loss on Borneo, and predicted continuing high rates of forest loss in the 2010-2020 period. Forest loss in Malaysian

Borneo is predicted to expand more diffusely throughout the landscape, creating an increasingly patchy and fragmented forest landscape, while patterns of deforestation in Indonesian Borneo is predicted to move along fronts of contagious expansion from previously logged areas, resulting in a "nibbling at the edge" pattern, and a greater retention of much of the interior hill and mountainous forests and increasing loss of the lowlands (Cushman et al., in review).

Responses of wildlife to anthropogenic change on Borneo

Selective logging

The ecological responses of wildlife to selective logging of Borneo's forests have received significant attention in recent years. The majority of studies have compared estimates of abundance, species richness or diversity in differing forest areas, exposed to different forest management approaches, and have focused on a wide range of taxa, including termites (Donovan et al., 2007), butterflies (Dumbrell and Hill, 2005), birds (Lambert, 1992; Edwards et al., 2009), and mammals (e.g., Johns, 1992; Heydon and Bulloh, 1997; Colon, 2002). More recently, meta-analyses have been undertaken to explore general patterns and processes underlying wildlife responses to the logging process (Berry et al., 2010; Bicknell et al., 2014; Costantini et al., 2016). Studies have broadly shown that while the disturbance process typically results in the overall decline of species diversity and richness, selectively logged forests retain many species and a considerable amount of the functional diversity of primary forests (Berry et al., 2010; Edwards et al., 2013, 2014a), particularly when lower yielding and reduced impact logging techniques are applied (Davis, 2000; Bicknell et al., 2014; Edwards et al., 2014b).

The responses to selective logging vary greatly among taxa, with species showing both declines and increases in abundance and species richness. For example, Berry et al. (2010) explored the responses of a range of taxa to selective logging in the Danum Valley region of Sabah, and found that five of the seven animal taxa examined declined in logged forest, but that declines in species richness following logging were typically no greater than around 10%. Costantini et al. (2016) showed that larger bodied birds and mammals were more susceptible to logging than smaller species, and hypothesised that the increased metabolic demands of larger species mean that they require larger foraging areas and higher resource availability, which are two factors likely to be impacted by logging disturbance. Meijaard et al. (2008) proposed that endemic species are less tolerant to habitat modification than those with wider geographic distributions. In terms of phylogenetic age, endemic species tend to be old and have more specialised habitat requirements, whereas species with larger geographic ranges tend to be younger and more ecologically adaptable (Meijaard et al. 2008).

The negative effects of logging may be attenuated and even reversed for some species as forests regenerate over time. Brodie et al. (2015a), for example, showed that the local abundance of 30 species of mammal declined in recently logged areas (≤10-year-old) compared to unlogged forest areas, but that in older logged forest areas (>10-year-old) declines were less substantial for 19 species and 11 species increased in abundance. Edwards et al. (2009) showed that bird species richness and diversity were similar in unlogged forest and enrichment planted logged forest, but significantly lower in naturally regenerating forest, suggesting that management designed to speed recovery of timber species may also deliver conservation gains. The beneficial effects of such enrichment planting were not equal among bird trophic groups, however, with enrichment planting resulting in the rapid recovery of insectivores but the decline of frugivores, an effect which may have reduced the overall abundance of birds within regenerating forest (Edwards et al., 2009).

Thus, while the retention of primary forest is essential for the preservation of some species, selectively logged forests are increasingly valued for conservation, particularly when compared to the more damaging effects of other land use changes, such as the conversion to industrialised plantations (Meijaard et al., 2005a; Meijaard and Sheil, 2008; Edwards et al., 2014a).

Oil palm plantations

The considerably less complex and reduced habitat heterogeneity found within oil palm plantations support only a fraction of the biodiversity found in primary forest, and thus the expansion of oil palm plantations is considered to pose a much greater threat to biodiversity than that of selective logging (Fitzherbert et al., 2008; Danielsen et al., 2009; Yule, 2010; Foster et al., 2011; Savilaakso et al., 2014; Dislich et al., 2016; Drescher et al., 2016). Studies have shown that, compared to forest, oil palm plantations support significantly lower species richness for a range of taxa, including arthropods (e.g., Fayle et al., 2010; Foster etal., 2011; Edwards et al., 2014a), amphibians (Gillespie etal., 2012; Faruk etal., 2013), birds (Edward et al., 2013b), and mammals (Bernard et al., 2009; Yue et al., 2015). Fitzherbert et al. (2008) compiled several studies that investigated the occurrence of a range of taxa in oil palm plantations and found that, across all taxa, a mean of only 15% of species recorded in primary forest was also found in oil palm plantations.

In a meta-analysis of six published studies of bird, beetles and ants, Senior et al. (2012) showed that large-bodied, abundant forest species from higher trophic levels declined most in abundance following conversion of forest to oil palm, whereas among the taxa studied the species able to persist in oil palm plantations tended to be small-bodied species, from lower trophic levels, that had low local abundances in forest. Bernard et al. (2014) compared the mammal species assemblage of a large, contiguous selectively logged forest with that from nearby small, isolated patches of forest within an oil palm plantation. The authors recorded 29 terrestrial mammal species in the large forest, including large bodied, wide ranging species of conservation concern, but only 18 species in the forest patches, consisting mostly of species that are widespread, well-adapted to living in highly modified habitats and of low conservation concern. Functional diversity of dung beetles and birds has also been found to be reduced in oil palm plantations (Edwards et al., 2013b, 2014a), although more studies on functional diversity are needed.

Recent research has explored the potential benefits to biodiversity in oil palm landscapes resulting from the retention of forested riparian reserves following conversion (e.g., Gray et al., 2014a,b; Evans et al., 2016), a legal requirement in Malaysia (Malaysian Ministry of Natural Resources and Environment, 2009). Studies in Sabah have shown that riparian reserves can support similar ant and dung beetle species richness and community composition to that of adjacent logged forest (Gray et al., 2014a,b), and that these narrow, linear forest strips are utilised by a diverse range of small carnivores (Hearn et al., 2010; Evans et al., 2016). It is not known, however, whether these riparian reserves of forest are capable of sustaining populations in the long-term. Nevertheless, such observations suggest that riparian reserves may serve as corridors and facilitate connectivity for species whose dispersal may be otherwise be resisted by the unfavourable habitat of the plantation landscape.

Hunting and poaching

Wildlife has likely been the main source of protein for people on Borneo ever since they first settled there, some 40,000 years ago (Zuraina 1982). Many rural based communities still rely on these resources, while most urban-based people no longer use such wild derived food (Caldecott, 1988; Colfer et al., 2000). Hunters tend to target readily available and common prey, such as mousedeer *Tragulus* spp., muntjac *Muntiacus* spp. and bearded pigs *Sus barbaratus* (e.g., Wadley et al 1997; Wadley and Colfer, 2004). However, hunting often involves non-specific methods such as snares, and an extremely diverse array of smaller species may be taken opportunistically, including rare species (Bennett et al. 2000). Hunting of wildlife has also formed an integral component of many of Borneo's societies and cultures. Skins from Sunda clouded leopards and feathers from Rhinoceros hornbills *Buceros rhinoceros*, for example, have traditionally been worn as personal adornment during ceremonies (Bennett et al., 1997; Rabinowitz et al. 1987).

Hunting of wildlife in all of Borneo's range states is controlled, at least in theory, by legislation. In Sabah, for example, which is typical of Bornean range states, hunting and collection of non-protected species is possible by acquiring a specific permit from the Sabah Wildlife Department. The permit dictates how many individuals of a given species may be taken, the time that harvesting may take place, and the areas permitted. Collection and/or hunting of a range of protected species is prohibited in Sabah, Sarawak, Brunei and Kalimantan, under the Sabah Wildlife Conservation Enactment (1997), Sarawak Wild Life

Protection Ordinance (1998), Brunei Wildlife Protection Act 1978, and the Appendix of The Government of Republic of Indonesia Regulation No. 7 (1999), respectively. Government enforcement personell are in place in all Bornean range states to enforce these protective measures, but resources are often inadequate. Consequently, illegal hunting, or poaching, is likely widespread throughout the island (Bennet et al., 2000).

Throughout the tropics, hunting and poaching of wildlife is thought to present a substantial threat to the conservation of many bird and mammal species (Harrison et al., 2016), yet it is also the most challenging to detect (Wilkie et al., 2011). Hunting and poaching are often associated with, and exacerbated by logging activities. The dense network of logging roads and skids permit greater access and thus hunting opportunities for poachers (Laurance et al., 2009). The negative impacts of hunting and poaching, however, can also operate independently of such activities. Indeed, overexploitation of species can lead to their depletion in otherwise-undisturbed tropical forests, leading to so called "empty forests" (Redford, 1992), devoid of large mammals and birds, and to cascading local extinctions of other plants and animals (Harrison, 2011; Wilkie et al., 2011).

The extent of hunting and poaching in Borneo, and their effects on wildlife remain unclear, but research to date suggests that negative impacts will likely vary considerably depending on the species involved. Brodie et al., 2015a modelled camera trap detection data of medium and large mammals from 7 forest areas in Sabah and Sarawak and found that the negative effects of hunting were stronger for more common than rarer species. Wilson and Johns (1982) found bearded pig densities were lower in logged forest in East Kalimantan, Borneo and attributed this to increased hunting rather than habitat change. The banteng *Bos javanicus* was once a widespread ungulate in Bornean rainforests, but it has been extirpated via hunting from much of its former range due to overexploitation

(Gardner, 2015). Similarly, Sunda Pangolin *Manis javanica* are now experiencing presumably unsustainable levels of harvesting, with vast numbers being smuggled into mainland southeast Asia. Pantel and Anak (2010) reported that >22,000 pangolins were collected for trade in an 18-month period here between 2007 and 2009, and recent confiscations by Malaysian authorities suggest that the pressure remains (Challender et al., 2014). The available evidence, although limited, currently suggests that Borneo is yet to be exposed to the levels of poaching in mainland Southeast Asia (Harrison, 2011), perhaps due to increased geographical isolation restricting the traffic of prized species for emerging markets in China and Vietnam. Nevertheless, the example of the Sunda pangolin clearly shows that trade routes and networks are already present, and so the risk remains.

Sunda clouded leopards and sympatric Bornean felids

The Sunda clouded leopard is an elusive, and little-known felid, found only on the islands of Sumatra and Borneo. On Borneo, the Sunda clouded leopard is the largest member of an assemblage of five wild cats, which includes the bay cat (*Catopuma badia*), marbled cat (*Pardofelis marmorata*), flat-headed cat (*Prionailurus planiceps*), and leopard cat (*Prionailurus bengalensis*). While populations of the leopard cat are widely believed to be stable, and not under threat (Ross et al., 2015), the other four Bornean felids are all thought to exist at low population densities, and be confined to ever shrinking and increasingly fragmented forest habitats, and thus there is significant concern for their continued survival on Borneo (Hearn et al., 2016b,c; Rustam et al., 2016; Wilting et al., 2016). Indeed, in the most recent IUCN Red List assessments the bay cat and flat-headed cat were listed as Endangered (Wilting et al., 2015; Hearn et al., 2016d), two of only six felid species within this threat category, the Sunda clouded leopard listed as Vulnerable (Hearn et al., 2016a) and the marbled cat as Near Threatened (Ross et al., 2016). These assessments, however, despite using the most current data on these felids, equate to best-guesses, for our understanding of these felids' ecology, including their status, habitat associations and distribution, is highly limited, which greatly hinders our ability to understand their possible responses to the rapidly changing landscape on Borneo and, in turn, our ability to conserve them. Enhancing this knowledge, therefore, remains a priority, and is essential to facilitate the development of appropriate conservation action.

In the remainder of this introductory chapter I review the literature to highlight what is known about these each of these felids in the context of understanding the influence of land use change on Borneo, and to identify gaps in our knowledge.

Sunda clouded leopard

The Sunda clouded leopard is a medium sized, Pantherine felid. Males weigh around 24 kg and females 12 kg. The species is restricted to the islands of Borneo and Sumatra, having recently been found to be both genetically and morphologically distinct from the clouded leopard (*Neofelis nebulosa*) populations found on mainland Southeast Asia (Buckley-Beason et al., 2006; Kitchener et al., 2006, 2007; Wilting et al., 2007; Christiansen, 2009). This taxonomic division had important implications to the assessment of the conservation status of these felids (Christiansen, 2009), and this felid is currently listed as Vulnerable on the IUCN Red List as a result of a presumed small and declining population size (Hearn et al., 2016a). However, the robust assessment of this felid's conservation status, identification of threats and development of effective conservation actions are greatly hindered by a lack of understanding regarding this felid's abundance, habitat associations, distribution and responses to habitat alteration and poaching (Hearn et al, 2016b). Remedying these unknowns are thus of the utmost importance for the conservation of this felid.

Central to this uncertainty is the lack of knowledge regarding the Sunda clouded leopard's habitat preferences, and in particular, their use of degraded forest and non-forest habitats. Records of Sunda clouded leopards stem from a diverse range of forest types, including both pristine (Brodie and Giordano, 2012a) and selectively logged dipterocarp forests (Wilting et al., 2006; 2012; Cheyne et al., 2016; Haidir et al., 2013; Sollmann et al., 2014; McCarthy et al., 2015; Hearn et al., 2016b), mangroves (Selous and Banks, 1935; Davis, 1962) and peat swamp forest (Cheyne and Macdonald, 2011; Cheyne et al., 2013), but this felid's use of plantation habitats remains largely unknown. In one of the few studies to investigate Bornean mammal occurrence in oil palm plantation habitats, Yue et al. (2015) and Maddox (2007) found no evidence of this felid using oil palm plantations in Sabah and Sumatra, respectively, although their survey effort was limited. Bernard et al., (2014) failed to record these felids in a number of small forest patches embedded within an oil palm plantation, despite recording them in the large (>1000 km^2), nearby selectively logged forest. Such observations thus support earlier predictions that forest loss and conversion to oil palm plantations present one of this felid's greatest threats (Rabinowitz et al, 1987; Hearn et al, 2016a), but this assumption needs further testing.

If oil palm plantations are indeed avoided by Sunda clouded leopards their increasing prevalence across Borneo is likely resulting in the decrease in size and increase in fragmentation of Sunda clouded leopard habitat. To ensure the conservation of this felid, therefore, it is essential to gain an understanding of the factors that influence the movements and dispersal abilities of Sunda clouded leopards residing in fragmented habitats, yet such data are currently lacking. Indeed, the only empirical movement data available for this species are from a single collared female residing in a large contiguous forest block (Hearn et al., 2013/Appendix I). Models of landscape resistance and connectivity for the Sunda clouded leopard have been recently developed using hierarchical modelling of camera-trap data (Brodie et al. 2015b), but the utility of this prediction is somewhat limited as the authors did not include oil palm as a covariate in the model. Macdonald et al. (submitted) developed a model of the Sunda clouded leopard's connectivity based on an expert opinion assessment of this felid's habitat associations, which requires empirical testing.

The records of Sunda clouded leopards from selectively logged forests suggest that these disturbed habitats, now the dominant form of remaining forest cover on Borneo (Gaveau et al., 2014, 2016), may now form an important habitat for these felids (e.g., Wilting et al., 2006). Exactly how the selective logging process influences these felids, however, is unknown. The first insight into the responses of these felids to such habitat disturbance came from Brodie et al. (2015a), who used camera traps to survey several forest areas in Sarawak and Sabah, and showed that Sunda clouded leopards' local scale abundance was lower in logged forest sites compared to unlogged sites. Whether these patterns remain true across this felid's range and how local scale responses translate into changes to population density of this felid, a key parameter of interest for their conservation, remains unknown.

Brodie and Giordano (2012a) estimated that Sunda clouded leopard density from an area of primary forest was 1.9 individuals per 100 km^2, whereas Wilting et al. (2012) presented densities from two selectively logged forests of around 0.8 and 1.0 individuals per 100 km^2. However, the relatively large, overlapping variances of these density estimates prohibited inference regarding the potential effects of the logging disturbance. Similarly, Sollmann et al. (2014) estimated that Sunda clouded leopard density from two primary and two mixed forest (primary and secondary) sites ranged from around 0.8 to 1.6 individuals per 100 km^2, but found no statistical support for differences in density between the populations. Additional surveys are urgently required both to enable the robust assessment of this felid's conservation status and to contribute to our knowledge of this felid's responses to habitat disturbance.

The potential impact of hunting and poaching on Sunda clouded leopards on Borneo remains unclear. The available evidence suggests that these cats are no longer specifically targeted by poachers, at least within the Malaysian states (Rabinowitz et al., 1987). However, poaching, either directly using snares, or through the reduction of prey availability by the poaching of game species, likely poses a significant threat, both in Sumatra (Holden et al. 2001) and Borneo (Rabinowitz et al. 1987, Wilting et al. 2006, Cheyne et al. 2013).

Bay cat

The elusive bay cat, Borneo's only endemic felid, is known from only twelve specimens and is thought to be one of the world's least known felids (Sunquist and Sunquist, 2002; Kitchener, 2004). The weight of four specimens was between 2 to 2.5 kg, but two of these animals were emaciated, and one's weight was estimated (Sunquist et al., 1994; Kitchener, et al 2004). Visual inspection of images from camera trap surveys in relation to other carnivores of known size suggests that males may be substantially larger than this. Nothing is known regarding this felid's reproductive behaviour, diet, spatial ecology or abundance, and only recently have data emerged regarding its distribution and responses to anthropogenic disturbance. Meijaard (1997), and later Mohd-Azlan and Sanderson (2007), gathered historic and contemporary records of the bay cat and, although hindered by small sample sizes (n=19 and 15, respectively), speculated that the bay cat is widely distributed on Borneo. Such historic records and incidental observations (Sunquist et al., 1994; Meijaard, 1997; Meijaard et al., 2005b; Bricknell, 2003; Hearn, 2003) suggested that this elusive felid exhibits habitat plasticity, and this was later confirmed with the use of camera traps. Recent camera trap records stem from hill and lowland Dipterocarp forest, including both primary (Yasuda et al., 2007; Mohd-Azlan et al., 2003; Brodie and Giordano, 2012b) and selectively logged forest (Mohamed et al., 2009; Bernard et al, 2012; Hon, 2011; Mathai et al., 2014; Cheyne et al., 2016;), which suggests that this felid exhibits some tolerance to disturbance. Brodie et al. (2015a), however, estimated that its local abundance was lower in logged than in unlogged forest. No records have emerged from plantation habitats (Yue et al., 2015). Swamp forest has been identified as habitat for this felid (Payne et al., 1985), but long-term camera trap surveys of the Sabangau National Park's peat swamps did not detect this species (Cheyne and Macdonald, 2011, Cheyne et al., 2016). The bay cat has been recorded up to 1460 m (Brodie and Giordano, 2012b), but there are no data describing this felid's elevational preferences.

No population density estimates exist for the bay cat. The paucity of bay cat specimens collected during the nineteenth and twentieth centuries caused earlier authors to conclude that the species was naturally rare, a stance tentatively supported by the extremely low detection rates of this felid reported from camera trap surveys. Indeed, despite several of these surveys being specifically targeted at felids, bay cat photographic capture rates are typically an order of magnitude below those of the sympatric Sunda clouded leopard. Such observations, and the assumption that this felid is indeed restricted to forest areas, led to the recent IUCN assessment for this species as being Endangered (Hearn et al., 2016a). Clearly, research into the abundance and habitat associations of this apparently rare and elusive felid is of a high priority.

Marbled cat

The marbled cat *Pardofelis marmorata* is a small (2.4–3.7 kg), elusive and little known felid whose wide distribution spans the Indomalayan ecorealm, from Eastern India and Nepal, to Yunnan province, China, and throughout mainland Southeast Asia to the islands of Sumatra and Borneo (Sunquist and Sunquist, 2002; Grassman et al., 2005). Across its range the marbled cat is primarily associated with moist but not dry tropical forests (Nowell and Jackson, 1996). On Borneo, the marbled cat has been recorded in both primary (Bernard et al., 2013) and selectively logged forest (e.g., Mohamed et al., 2009; Cheyne and Macdonald, 2011), suggesting at least some tolerance to disturbance, but this species' use of plantation habitats remains unknown (but see Yue et al., 2015). Nevertheless, the marbled cat is widely believed to be forest dependent (Ross et al., 2015; Rustam et al., 2016), an untested assumption which has important implications for their status and conservation. Indeed, Rustam et al. (2016) used presence-only niche modelling to predict the distribution of this felid on Borneo, and concluded that this felid was found throughout much of forested Borneo.

The marbled cat has long been considered to be a rare felid, whose populations are thought to be declining (Nowell and Jackson, 1996; Sunquist and Sunquist, 2002; Ross et al., 2015). However, despite extensive camera trap programmes throughout range countries, and the patterned pelage enabling the application of mark-recapture techniques of population density estimation, there remain no estimates of its abundance in any part of its range (Hunter, 2015), hampering robust assessment of its conservation status (Ross et al., 2015). Nevertheless, camera trap surveys typically yield exceptionally few photographic captures, even compared to other sympatric felids (e.g., Brodie and Giordano, 2011; Lyngdoh et al., 2011; Bernard et al., 2013; Tempa et al., 2013; Wearn et al., 2013; Chutipong et al., 2014; Coudrat et al., 2014; Gray et al., 2014c; Gumal et al., 2014; Pusparini et al., 2014; Simcharoen et al., 2014; Zaw et al., 2014 McCarthy et al., 2015; Suzuki et al., 2015), and these low rates have hitherto been assumed to result from low population densities. Whether these low capture rates are a result of true rarity, however, or a reflection of biases resulting from camera placement methodologies (Sollmann et al., 2013; Wearn et al., 2013) and this felid's particular behaviour is unclear. Indeed, marbled cats have morphological adaptations for a particularly arboreal lifestyle (Sunquist and Sunquist, 2002), are adept climbers (e.g., Leyhausen, 1979; Mohamed et al., 2009), and have been observed preying on, or attempting to prey on, birds and primates in the canopy (Guggisberg, 1975; Borries et al., 2014).

Flat-headed cat

At around 1.5–2 kg (Sunquist and Sunquist, 2002), the flat-headed cat is the smallest of Borneo's felids, and the one presumed to be facing the greatest risk of extinction (Wilting et al., 2015). The flat-headed cat is found in Southern Thailand, Peninsular Malaysia, Sumatra and Borneo, but no focused studies of this felid's autecology have been undertaken anywhere within its range, and there are no estimates of this felid's density. Morphological adaptations, such as webbed feet and only partially retractable claws (Sunquist and Sunquist, 2002), an excellent swimming ability (Gumal et al., 2010) and incidental sightings of this felid have long suggested that this felid is closely associated with freshwater habitats (e.g., Banks, 1931; Bezuijen, 2000; Cheyne et al., 2009; Mohamed et al., 2009). No studies of this felid's diet have been undertaken, but the stomach contents of an adult flat-headed cat shot in Malaysia contained only fish (Muul and Lim, 1970) and that from a male killed on a road in Kalimantan contained fish scales and shrimp shells, which further supports their presumed wetland association.

Flat-headed cats have been recorded in both primary and logged forests, including within narrow riparian forest strips bordered by oil palm plantations (Hearn et al., 2010), suggesting they may exhibit some degree of tolerance towards disturbance, but sightings from within oil palm or other plantations are unconfirmed. Wilting et al. (2010) used presence-only distribution modelling techniques to assess the flat-headed cat's distribution and confirmed earlier predictions of a close association with wetland forest habitats. Although a historical record exists from 700 m in the Dulit Mountains in Sarawak (Hose, 1893), Wilting et al.'s (2010) study revealed that over 80% of records since 1984 were from below 100 m elevation, suggesting that this felid is highly restricted to low-lying areas, and that over 50% of historical habitat (i.e., that before large-scale human landscape transformation started in the second half of the 20th century) has been converted to land-cover types believed to be unsuitable for flat-headed cats. Furthermore, Wilting et al (2010) showed that only 10–20% of apparently suitable land-cover in the estimated geographic range of this species is fully legally protected, based on IUCN criteria, and that remaining habitats are highly fragmented with few large forest patches (over 1000 km^2)

remaining. A subsequent predictive modelling exercise for this felid, using additional location records obtained up to 2011, and a more robust modelling approach (Kramer-Schadt et al., 2016), closely matched these earlier findings (Wilting et al., 2016).

Leopard cat

Of the five felids found on Borneo, the leopard cat has received the most scholarly attention, although much of the research on this felid's ecology stem from outside of Borneo. It is widely distributed throughout much of central, south, east and southeast Asia, and its range even extends to Siberia (Nowell and Jackson, 1996; Sunquist and Sunquist, 2002, Mohamed et al. 2016). The leopard cat appears to tolerate habitat disturbance well, and in Borneo this felid utilises a diverse range of habitats including selectively logged forest, rubber estates and oil palm plantations (Lim 1999; Rajaratnam et al. 2007, Mohamed et al., 2013). Data from Singapore suggest that leopard cat densities may be higher in oil palm plantations than in neighbouring disturbed forest (Chua et al., 2016). The density of this felid in oil palm plantations has not been assessed in Borneo, but estimates from three selectively logged forests in Sabah confirm earlier suggestions that the leopard cat is an abundant felid, with densities ranging from 9.6 to 16.5 individuals per 100 km^2 (Mohamed et al., 2013). Mohamed et al. (2013) showed that leopard cat encounter rates from off-road camera traps were only 3.6–9.1% of those for on-road traps, which suggests that leopard cats select such disturbed habitat features at the fine-scale. Leopard cats are thus highly tolerant and may even benefit from anthropogenic disturbance, yet further studies to investigate these felid's habitat associations and predictions of their distribution are still required.

Thesis overview

The principal aim of this DPhil thesis is to investigate how anthropogenic disturbance, including selective logging, deforestation and poaching, influences the abundance, distribution, movements and population connectivity of Sunda clouded leopards and other sympatric felids on Borneo. A second aim is to provide some of the first data regarding the ecological interactions and patterns of coexistence among this unique felid assemblage. The underlying theme of this research is thus to advance understanding of the implications of the rapidly changing Bornean landscape to the conservation of these felids, and to contribute to the development of evidence-based conservation recommendations. Below I provide a brief overview of each Chapter.

Chapter 2: Optimizing landscape connectivity and evaluating scenarios of landscape change for Sunda clouded leopards in a human dominated landscape.

In this paper, we conducted the first investigation of the influence of landscape variables on the movements of Sunda clouded leopards. We applied a multi-scale path-level analysis to Sunda clouded leopard movement data and developed resistance surfaces and connectivity predictions for a population of these felids residing within a fragmented landscape. We showed that Sunda clouded leopard movement is facilitated by natural forest habitats with high canopy cover and resisted by non-forest vegetation with low canopy cover. We compared the performance of our empirically optimised model with that of a previously developed expert-opinion model and used our model to predict how connectivity in the local region may change in response to four future scenarios of land use change.

Chapter 3: Predicting connectivity, population size and genetic diversity of Sunda clouded leopards across Sabah, Borneo.

In this paper, we used our local scale Sunda clouded leopard movement model developed in Chapter 2 to develop the first multi-scale, empirically optimised resistance model for Sunda clouded leopards across the whole of the Malaysian state of Sabah. We developed the first movement-based predictions of Sunda clouded leopard population density, genetic diversity, and population connectivity for this species across Sabah to explore how land use changes are impacting these felids. We compared the differences in predictions obtained from expert-opinion derived and empirically derived resistance maps.

Chapter 4: Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning?

In this paper, we draw together and analyse an extensive photographic detection dataset derived from camera trap surveys of multiple areas in Sabah to explore the evidence for resource partitioning as a mechanism to facilitate co-existence within an assemblage of sympatric felids on Borneo. Our analyses provide evidence for partitioning along the spatial and temporal niche axes among Bornean felids.

Chapter 5: The first estimates of marbled cat *Pardofelis marmorata* population density from Bornean primary and selectively logged forest.

In this paper, we develop estimates of marbled cat population density from multiple sites in Sabah by analysing photographic detection data within a spatially-explicit capture-recapture Bayesian modelling framework. Our density estimates are the first for this species, but through comparison with the low detection frequencies recorded from published studies elsewhere in its range, and the absence of previous density estimates for this felid, we caution that our estimates may stem from populations at the higher end of their abundance spectrum. This paper was published in PLoS One (see Appendix II).

Chapter 6: Assessing the responses of Sunda clouded leopard *Neofelis diardi* population density to forest disturbance and refining estimates of their conservation status in Sabah, Malaysian Borneo.

In this paper, we developed estimates of Sunda clouded leopard population density from spatially-explicit capture-recapture analyses of camera trap data from multiple forest sites in Sabah, Malaysian Borneo, to investigate how their density varies across the landscape and in response to anthropogenic disturbance. This paper provides the first, albeit tentative evidence that Sunda clouded leopard population density can be negatively impacted by hunting pressure, forest fragmentation, and recent logging activity, and that well managed selectively logged forest may support higher densities than primary forest. We extrapolate our density estimates to assess this felid's conservation status in Sabah.

Chapter 7: General discussion.

In the concluding chapter I provide a synthesis of the results from Chapters 2 to 6 and discuss them within the context of previous studies. I draw attention to the implications of this body of work to the conservation of wild cats in Sabah, and throughout the island of Borneo. In so doing I identify key questions yet to be answered in the context of conserving these felids and suggest potential avenues of future research.

Appendices

During the timeframe of this D.Phil., I contributed to a number of academic exercises that are directly related to the aims of this thesis, all of which drew upon the emerging data from my DPhil, including both leading and contributing to the most recent Bornean felid IUCN Red List assessments (Ross et al., 2015, 2016; Hearn et al, 2016a,d; Wilting et al., 2015), and several peer reviewed papers. I include some of the most relevant papers as Appendices.

Appendix I.

Hearn, A.J., Ross, J., Pamin, D., Bernard, H., Hunter, L. and Macdonald, D.W. (2013). Insights into the spatial and temporal ecology of the Sunda clouded leopard *Neofelis diardi*. Raffles Bulletin of Zoology, 61(2), 871-875.

Appendix II.

Hearn, A.J., Ross, J., Bernard, H., Bakar, S.A., Hunter, L.T.*B., and* Macdonald, D.W. (2016). The first estimates of marbled cat Pardofelis marmorata population density from Bornean primary and selectively logged forest. PloS one, 11(3), e0151046.

Appendix III.

Ross, J., Hearn, A.J., Johnson, P.J. and Macdonald, D.W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. Journal of Zoology, 290, 96-106.

Appendix IV.

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Appendix V.

Hearn, A.J., Ross, J., Macdonald, D.W., Samejima, H., Heydon, M., Bernard, H., Augeri, D.M., Fredriksson, G., Hon, J., Mathai, J., Azlan, M., Rustam, Meijaard, E., Hunter, L.T.B., Breitenmoser-Würsten, C., Kramer-Schadt, S. and Wilting, A. (2016). Predicted distribution of the bay cat *Catopuma badia* (Mammalia: Carnivora: Felidae) on Borneo. Raffles Bulletin of Zoology, Supplement No. 33, 165-172.

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Chapter 2. Optimizing landscape connectivity and evaluating scenarios of landscape change for Sunda clouded leopards in a human dominated landscape.

Abstract

Estimates of landscape resistance to animal movement are the foundation for predicting population connectivity. Typically, resistance surfaces are parameterised with expert-opinion, habitat suitability or empirical movement data, yet few studies have assessed the relative performance of each approach. Here, we present the first multi-scale, empirical modelling of landscape resistance for Sunda clouded leopards and compare the performance of our empirically optimised movement-based model with that of a previously developed expert-opinion model. We applied a path-level analysis with conditional logistic regression to develop resistance surfaces and connectivity predictions for a population of Sunda clouded leopards residing within a fragmented and human dominated landscape in Malaysian Borneo, the Lower Kinabatangan floodplain, and predict how connectivity may change in response to four future scenarios. We show that Sunda clouded leopard movement through the landscape is facilitated by forest canopy cover and resisted by non-forest vegetation. Open structure oil palm plantation areas in particular, such as recently cleared/planted and underproductive (flooded) plantation areas with low canopy closure, presented the highest resistance to Sunda clouded leopard movements. We predict that clouded leopard connectivity in the region can be greatly enhanced through the protection of privately owned forest patches and the reforestation of underproductive oil palm plantation areas. Conversely, we show that if the region's unprotected forest were to be converted to plantations then connectivity across the Kinabatangan floodplain would be significantly reduced.

Introduction

Landscape resistance is the functional expression of those factors that mediate an organism's movement within its environment (Cushman et al., 2013a). Landscape resistance is usually defined as a function of environmental and anthropogenic variables across a resistance continuum, in which landscape resistance represents the willingness of an organism to cross a particular environment, or the physiological cost or reduction in survival for the organism moving through a particular environment (Spear et al., 2010; Zeller et al., 2012). Reliable estimates of landscape resistance are fundamental when attempting to understand underlying population-level patterns of connectivity and their biological implications (e.g. Spear et al., 2010; Cushman et al., 2006, 2010; Elliot et al., 2014).

To date, the majority of studies measuring resistance surfaces has employed expert-opinion rather than empirical data to parameterize resistance (e.g., Zeller et al., 2013, Macdonald et al., in review). However, while there may often be no alternative data, expert-opinion clearly has shortcomings in comparison to actual animal movement in landscapes. Evaluations of resistance parameterization have shown that the predictive performance of expert-opinion (e.g., Shirk et al. 2010, 2015) or habitat suitability (e.g. Wasserman et al. 2010; Mateo-Sanchez et al. 2015) approaches is often lower than that derived from empirical movement or genetic data. Furthermore, several researchers have recently shown that accurate predictions of landscape resistance from genetic (e.g. Wasserman et al. 2010) or movement (e.g. Elliot et al. 2014; Zeller et al. 2014, 2015; Krishnamurthy et al. 2016) data require a multi-scale approach, to optimize the operative scale at which each landscape variable influences selection of movement routes of the organism in the landscape.

The Sunda clouded leopard (*Neofelis diardi*) is an understudied, threatened felid, which inhabits the Sundaic islands of Borneo and Sumatra (Hearn et al. 2015). On Borneo, this felid appears to be relatively resilient to forest disturbance (Hearn et al. 2016, In press). However, camera trap surveys within an oil palm plantation suggest that this land use may not be readily used by this species (Ross et al., 2010; Yue et al., 2015), and thus the increasing expansion of oil palm plantations across Borneo is likely resulting in a decreasing extent and increasing fragmentation of Sunda clouded leopard habitat (Macdonald et al., in review). Indeed, the rate of forest loss on Borneo, primarily as a consequence of their conversion to oil palm plantations, is one of the highest in the world (Gaveau et al., 2014; Cushman et al., 2017). To ensure the conservation of this felid, it is essential to gain an understanding of the factors that influence the movements and dispersal abilities of Sunda clouded leopards residing in fragmented habitats and to protect and/or restore potential movement corridors to maximise meta-population connectivity.

Little is known regarding the movements, dispersal abilities and population connectivity of Sunda clouded leopards. Currently, the only empirical movement data available for this species are from a single collared female (Hearn et al., 2013). Brodie et al. (2014) used hierarchical modelling of camera-trap data to develop a resistance surface and least-cost connectivity estimates to assess and identify dispersal and corridor locations for Sunda clouded leopards within a transboundary network of protected areas in Borneo. The Brodie et al. (2014) connectivity model used an estimate of time since logging as a variable to parameterize the resistance model, but did not include other land use variables. This limited thematic resolution, and the fact that habitat use patterns are often weak surrogates for landscape resistance (e.g., Wasserman et al. 2010, Mateo-Sanchez et al. 2015), add uncertainty to the robustness of the predictions. Based on a resistance surface developed by a panel of experts, Macdonald et al. (in review) constructed resistant kernel and least-cost path estimates of Sunda clouded leopard connectivity across Borneo and estimated that between 2000 and 2010 the proportion of landscape connected by dispersal fell by approximately 24% leading to a 13% decline in predicted population size. Macdonald et al. (in review) made clear that while their study provided the first step in evaluating broad scale connectivity to guide management decisions for this species, the next priority was to secure the empirical data necessary to test their findings.

Here, we present the first fine-resolution movement data for Sunda clouded leopards and investigate which landscape variables influence their path selection. We applied a path-level analysis (e.g., Cushman et al. 2010; Cushman and Lewis 2010) to parameterize resistance surfaces and develop connectivity predictions for a population of Sunda clouded leopards residing within a fragmented and human dominated landscape in Sabah, Malaysian Borneo, the Lower Kinabatangan floodplain, and to predict how connectivity may change in response to four future scenarios. Our future scenarios reflect changes, both potentially positive and negative for the Sunda clouded leopard, that may realistically occur in this landscape, and include the establishment of riparian buffers, conversion of privately owned forest to oil palm plantations and reforestation of underproductive oil palm plantations. Within the framework of these scenarios, we focus on three hypotheses: (1) forest, including highly disturbed forest types, would facilitate movement of Sunda clouded leopards, while open canopy conditions, in particular recently established oil palm plantations, would express high resistance to movement; (2) consistent with Cushman et al. (2015), we expected that cumulative resistant kernel and factorial least cost path connectivity models applied to the resistance surface would be significantly related to movement path selection, and more so than local landscape resistance alone; and, (3) consistent with intuition, and as confirmed by Shirk et al. (2010) and Mateo-Sanchez et al. (2015), empirically optimised, multi-scale models of Sunda clouded leopard movement would outperform a previous model of connectivity based on expert opinion.

Methods

Study Area

The study area consists of approximately 4,000 km^2 of the Lower Kinabatangan floodplain in eastern Sabah, Malaysian Borneo (Figure 1). Mean monthly temperatures range from 21-34 °C, and mean annual rainfall is around 3,000 mm (Ancrenaz et al. 2004). The region is characterised primarily by seasonal freshwater swamp forest, freshwater swamp forest and severely degraded remnants of mixed dipterocarp forests. Much of the region's forests have been cleared for oil palm development and the remaining forests have been repeatedly logged over the past century, resulting in a fragmented chain of disturbed forest patches along both banks of the Kinabatangan River (Abram et al. 2014). In 2005 approximately 27,900 ha of the region's forests were gazetted as the Lower Kinabatangan Wildlife Sanctuary (LKWS), which is composed of 10 forest blocks (termed 'Lots') which provide a more or less contiguous linkage to around 15,000 ha of protected forests. (Ancrenaz et al. 2004; Figure 1). In addition, in 2010/11 the study area included around 30,000 ha of unprotected forest, much of which is currently allocated for future oil palm conversion (Abram et al. 2014). To the west of the LKWS lies the Central Forest, the largest contiguous area of forest in Sabah, and to the east lies an extensive chain of protected coastal mangrove forest reserves. Oil palm plantations form the predominant land cover in the Lower Kinabatangan floodplain (Abram et al. 2014). The Sandakan to Lahad Datu sealed road (A6) runs north/south through the study area, bisecting the two blocks of the Pin Supu Forest Reserve, and another sealed road runs east/west to the north of the forested areas.

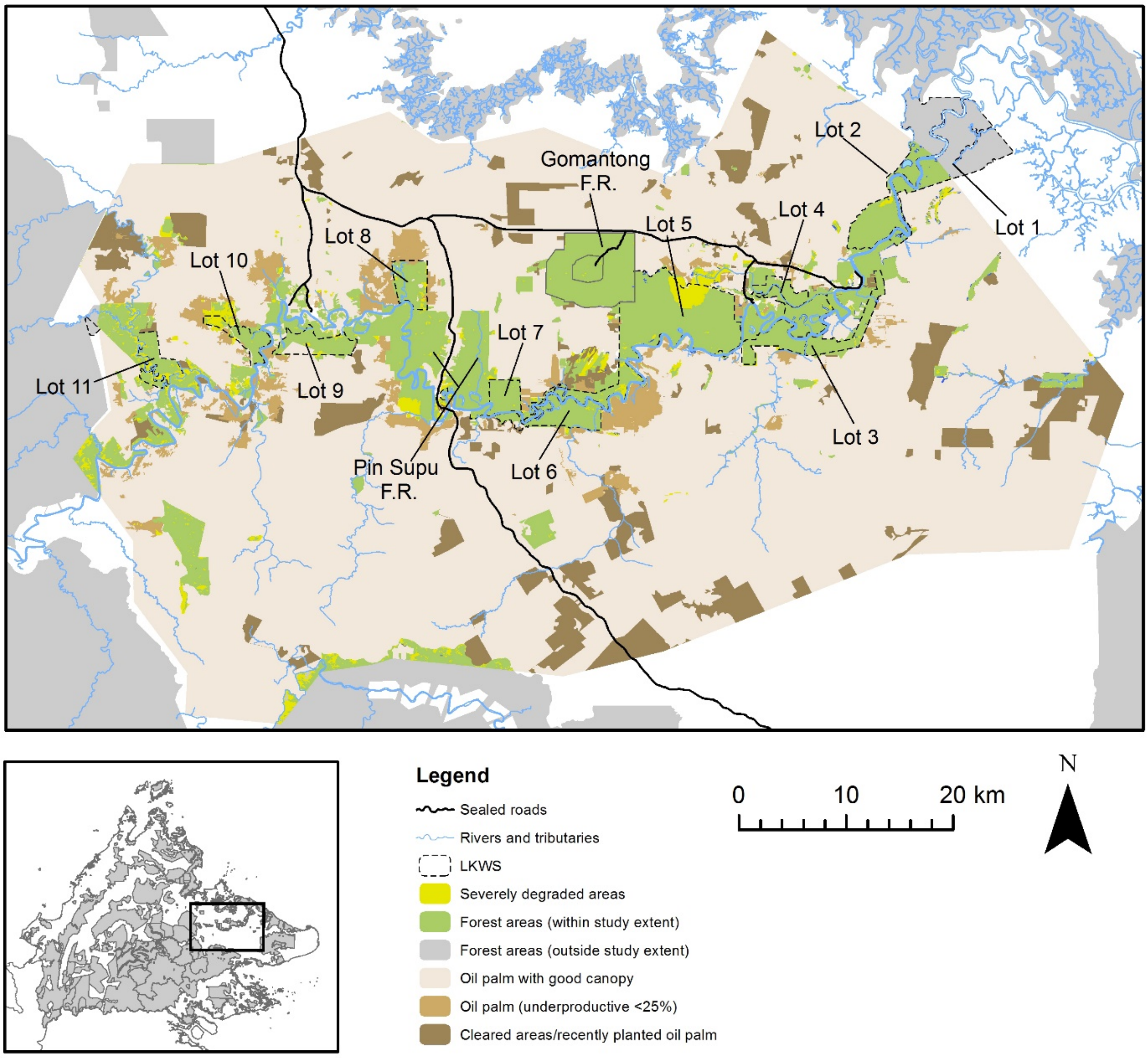

Figure 1. Map of the Lower Kinabatangan floodplain, showing the study extent and land use. Inset map shows the Malaysian state of Sabah, and bounding box shows location of Kinabatangan floodplain. Land cover data modified from Abram et al. (2014).

Sunda clouded leopard telemetry data

From 13 May 2013 to 28 September 2014 we deployed locally constructed, double ended, steel mesh box traps (1 x 1 x 3 m) in Lots 5 and 6 of the LKWS (Figure 1) to capture Sunda clouded leopards and attach GPS collars. For trapping and animal handling, we followed a protocol developed by the Sabah Wildlife Department and approved by the Sabah Biodiversity Centre and the University Complutense's Committee on Animal Care (Department of Animal Physiology, Faculty of Veterinary Medicine) (Nájera et al. submitted). We fitted captured Sunda clouded leopards with GPS/GSM collars (Lotek WildCell SD, Lotek Wireless Inc., Ontario, Canada), which include an automated drop-off device, and scheduled the collars to take a location fix once every 20 minutes. We captured five Sunda clouded leopards (three males, two females) on eight occasions, resulting in six collar deployments on four animals (three males, one female). Of these, five collars failed prematurely, resulting in four usable data sets of varying durations (Table 1). To ensure precision, we only retained location fixes with a Dilution of Precision <8 (e.g., Frair et al. 2010). We subdivided path data for each animal into lengths of 24 hour periods for further analysis (e.g., Zeller et al. 2015).

Table 1. Telemetry data from Sunda clouded leopards captured and tagged within the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysian Borneo.

Animal ID	Sex	Duration of collar data		No. fixes (DOP <8)	No. used paths
		Dates	No. days		
CLM3	Male	15/09/2013 - 27/12/2013	103	5618	96
CLM4	Male	01/02/2014 - 11/3/2014	38	2498	39
CLM1	Male	22/03/2014 - 27/03/2014	5	70	6
CLF4	Female	16/08/2014 - 06/10/2014	51	158	17

Environmental predictor variables

We selected potential predictor variables for the path-level analysis based on existing knowledge of Sunda clouded leopard habitat associations (Hearn et al. 2015, 2016), including land cover, canopy cover, carbon density, and road and major river distribution to parameterize the resistance surface. We used a high resolution (15 m) 2013 land use layer (19 classes), developed by Abram et al. (2014), which was available at the Kinabatangan extent only, a 250 m spatial resolution 2010 land cover map (13 classes) developed by Miettinen et al. (2012), and a 50 m resolution 2010 forest quality and land use cover map of Borneo (9 classes), developed by Gaveau et al. (2014). We used a historic land cover layer, developed by the Sabah Forestry Department, which provides an estimation of forest type cover (24 classes) based on soil and elevation associations at a point in time before anthropogenic modification. We extracted this layer to the Gaveau et al. (2014) 2010 forest cover extent, to account for forest conversion. We used two layers which detail above-ground carbon stock: (1) a fine-scale resolution layer (of six classes) providing carbon data for the Kinabatangan region extent (Abram et al., in press); and, (2) a 1 km spatial resolution global extent layer (Baccini et al. 2012), reclassified to the same six classes used in Abram et al. (submitted). We used a layer developed by Hansen et al. (2013) which depicts canopy cover at a 30 m resolution, and two layers detailing sealed and logging roads in 2013 (unpublished data).

Multiple Scale Path-level Modelling

We applied a path-level analysis to model Sunda clouded leopard movement as a function of landscape predictor variables. This approach employs conditional logistic regression to compare landscape characteristics around used paths with that from randomly generated available paths with identical topology (e.g., Cushman and Lewis 2010; Elliot et al. 2014; Krishnamurthy et al. 2016). The underlying ecological drivers of animal movement may operate at a range of spatial scales and so the precision and accuracy of movement models can be improved if scale is accounted for (e.g. Zeller et al. 2013). Thus, for each used path, we created 19 matched available paths of identical topology at each of three scales, by first shifting the x and y coordinates of the available path by a random value (up to the maximum distance specified at each scale of shift), and then rotating its orientation by a random value between 0 and 360° (Cushman and Lewis 2010; Reding et al. 2013; Elliot et al. 2014). We used three spatial scales of shift: (1) no shift, and distances between (2) 0-5 km, and (3) 0-10 km. The retention of the geometrical properties of the used paths and the random rotation and shifting of the available paths helps to avoid potential issues of autocorrelation (Cushman 2010; Cushman et al. 2010).

We used ArcInfo Workstation (ESRI 2010) to derive the environmental predictor variables by calculating the mean value for each GIS variable of all pixels that were aligned along the used and available path trajectories (e.g., Cushman and Lewis 2010; Elliot et al. 2014; Krishnamurthy et al. 2016). We used the clogit function in the Survival package of R (v3.1.2; R Development Team, 2014) to perform the conditional logistic regression analyses, matching each used path with the 19 rotated and shifted available paths at each scale. We performed the conditional logistic regression in three stages. First, we determined the spatial scale at which each variable had the strongest relationship with Sunda clouded leopard path selection by conducting a univariate scaling analysis (e.g. Thompson and McGarigal 2002; Zeller et al. 2014; Elliot et al. 2014; Krishnamurthy et al. 2016). We used Akaike Information Criterion corrected for small sample size (AICc) model selection to identify the most supported scale for each variable, and retained the scale with the lowest AICc ranking for the next step, so long as it had a Wald score *p*-value of <0.05. Second, we evaluated the correlation among the variables and dropped the variable with the greater AICc value in each pair of variables that were correlated greater than Pearson r = 0.70. Third, we conducted an all-subsets analysis and model averaging of the 11 variables with the strongest univariate relationship to clouded leopard path selection, based on Wald Score, using the Dredge function in library MuMin in R. We judged the relative importance of each variable to the final model based on the sum of Akaike weights of models where the variable was included (*wi*), and on the magnitude of the standardized regression coefficient (β).

In our study, there were a number of variables that were developed from higher resolution data (from Abram et al. 2014), and these were of higher accuracy than those available at the regional or national levels. Given our ultimate goal to apply the resistance map beyond the extent of the Kinabatangan study area, we developed resistance surfaces and connectivity models using the 11 best variables overall (Kinabatangan model) and also the 11 best variables that were available at the Sabah state level (Regional model).

Resistance surface and connectivity modelling

We produced resistance surfaces for Sunda clouded leopard movement based on the Kinabatangan and Regional resistance models. We used ArcInfo workstation (v10.2, ESRI 2010) to calculate the Z variable: $z = \beta_1 v_1 + \beta_2 v_2 + \ldots + \beta_n v_n$, where, β_i is the regression coefficient for variable v_i, and converted this to resistance by inverting and adding a constant such that minimum resistance was given value 1 and the maximum was 100.

We used the least-cost resistant kernel (Compton et al. 2007; Cushman et al. 2010) and factorial least cost path approaches (e.g., Cushman et al. 2009; Cushman et al. 2010) to predict Sunda clouded leopard landscape connectivity and to compare the predictions of the two approaches. We implemented the least-cost resistant kernel analysis in UNICOR v2.0 (Landguth et al. 2012), applying a 25,000 cost unit kernel width. This kernel width was chosen since it was approximately the upper bound of the expected radius of a Sunda clouded leopard home range (Hearn et al. 2013). The resistant kernel computes the cost-distance kernel from each of a set of source locations, scaling it such that the volume of the kernel reflects population density at that location, and summing all such kernels to create a cumulative resistant kernel surface, which reflects the incidence function probability of an individual clouded leopard traversing that cell in a given unit of time (Compton et al. 2007). We established source points for the resistant kernel analysis by selecting all forested cells in the study area, and multiplying their resistance value by a uniform random number between 0 and 1 and selecting all cells with the product less than 0.1. This produced a sample of 2405 source points at a density inversely proportional to relative resistance values within closed-canopy forest. The initial expected density was set to 1 for each source cell.

The factorial least cost path approach offers an alternative framework to develop connectivity predictions. Factorial least cost path analysis calculates the density of the least cost path network linking a system of source points across a resistant surface (e.g. Cushman et al. 2009; Cushman et al. 2010; Cushman et al. 2013b). We implemented the factorial least cost path analysis in UNICOR v2.0 (Landguth et al. 2012), using the same set of source points as that used in the resistant kernel analysis, linking each pair of the 2405 points that were within a cost distance threshold of 50,000 cost units with the least cost path between them and then summing the least cost path network to produce a map of least cost path density. This least cost path density map was then smoothed with a 150 m radius moving window before further analysis (e.g., Cushman et al. 2009; Cushman et al. 2010).

Future Scenarios

We evaluated the impacts of four scenarios of possible future landscape change on the extent and fragmentation of the landscape connected by dispersal. We selected future scenarios which reflect changes that are either ongoing or stand a realistic chance of occurring, and which present both potentially positive and negative implications for the Sunda clouded leopard. The four scenarios were: S1 – deforested areas within 50 m of the Kinabatangan River reverted back to forest cover; S2 - non-productive oil palm (identified in Abram et al. (2014)) converted to forest; S3 - both 50 m river buffer and non-productive oil palm converted to forest; S4 - all privately owned unprotected forest converted to oil palm. For each scenario, we created the resistant kernel and factorial least cost path maps using the same methods as for the analyses described above, using only the Kinabatangan resistance model, given that it had higher support based on AIC than the regional model. We compared these maps with each other and with the current condition in two ways. First, we calculated the average and standard deviation of pixel-pixel differences in cumulative resistant kernel value among scenarios to gain an overall quantitative measure of difference in connectivity across the study area. Second, for each scenario, we used FRAGSTATS (v4; McGarigal et al. 2012) to calculate changes in the percentage of the landscape and correlation length connected by dispersal (non-zero cumulative kernel values) and correlation length (non-zero factorial least cost values) of the factorial least cost path network, and compared these values with the current situation.

Performance of connectivity assessment method and resistance surface

We explored the relative performance of three connectivity assessment methods in predicting Sunda clouded leopard movement paths: local resistance, cumulative resistant kernel and factorial least cost path network (e.g., Cushman et al. 2014). We also compared the relative performance of three resistance surfaces developed using different analytical methods: our empirically optimised Kinabatangan and Regional models and an expert-opinion derived Borneo-wide model, developed by Macdonald et al. (submitted), hereafter referred to as expert-opinion model. In this assessment, we randomly rotated the used movement paths between 0 and 360 degrees without any shift in *x* and *y* to produce 19 paired available paths in the vicinity of each used path for each of the connectivity assessment method/resistant surface data combinations. We sampled the values of the local landscape resistance, and the resistant kernel and factorial least cost path surfaces along the length of each of the used and available paths. We calculated the number of standard errors each used path was from the distribution of available matched randomized paths (e.g., Cushman et al. 2010; Cushman et al. 2014). We conducted a two-way analysis of variance to evaluate differences in performance of connectivity assessment methods and resistance surfaces.

Results

Visible inspection of movement paths

Sunda clouded leopard movement paths were almost exclusively restricted to forest cover, including a narrow section (130 m wide) of forest corridor (Figure 2). However, one male (CLM3) traversed oil palm plantation and crossed a busy sealed road. Another male (CLM4) crossed the relatively quiet, sealed access road in Gomantong Forest Reserve. No animals were recorded crossing the Kinabatangan river.

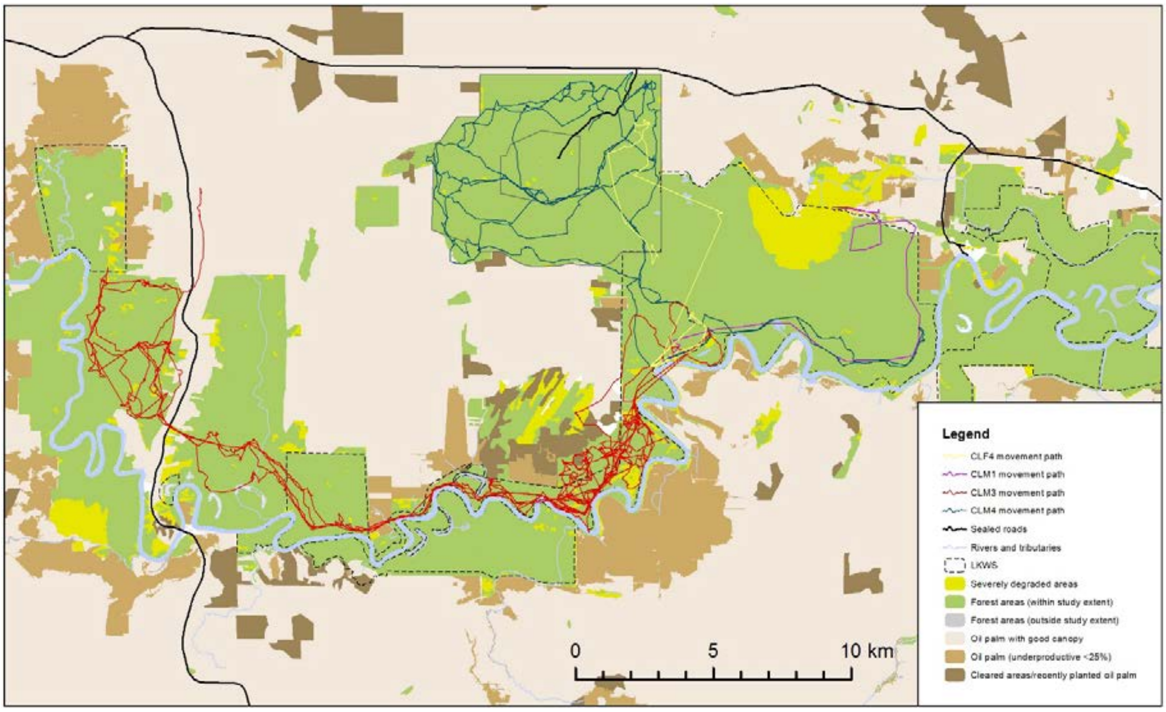

Figure 2. Movement paths of four Sunda clouded leopards in the Lower Kinabatangan Wildlife Sanctuary, Sabah. Land cover data modified from Abram et al. (2014).

Multiple Scale Path-level Modelling

The univariate scaling indicated that twenty-one variables had the strongest relationship with Sunda clouded leopard path selection when shifted between 0-10 km in *x* and *y* and that the relationship was strongest for nine variables at the 0-5 km scale shift (Table 2). The relationships between the predictor variables and Sunda clouded leopard path selection were broadly similar for both the Kinabatangan and Regional models (Table 3). In both models, path selection was positively related to Gaveau: Agroforest/forest regrowth, a range of closed forest type variables and to canopy cover, and negatively related to the river and oil palm plantations.

Resistance surface and connectivity modelling

The Kinabatangan and Regional model resistance surfaces were extremely similar, with a spatial correlation of over 0.95 and average absolute deviation of less than 0.15 (Figure 3). In both surfaces, forest cover with high canopy closure had the lowest resistance, while non-forest areas, such as severely degraded areas and oil palm plantations, had high resistance. Areas of oil palm plantation that were classified by Hansen et al (2013) as having low canopy cover, which were typically areas classified as recently cleared/planted and underproductive (flooded) oil palm areas by Abram et al. (2014), presented the highest levels of resistance. Given the high similarity of the surfaces, we limit further analysis to the Kinabatangan model, given its higher support based on AICc (Table 3).

Table 2. Univariate scaling and Ranking. Univariate Ranking – rank order of variable in terms of its Wald Score at the best spatial scale at which each variable had the strongest relationship with Sunda clouded leopard path selection. 0km-shift Wald Score – Wald Score at scale of no shift; 5km-shift Wald Score – Wald Score of shift of up to 5 km in X and Y; 10 km-shift Wald Score – Wald Score of shift of up to 10 km in x and y. The highest Wald score for each variable in relation to shift is shown in bold.

Univariate Ranking	Variable	0km-shift Wald Score	5km-shift Wald Score	10km-shift Wald Score
1	SFD: Lowland Mixed Dipterocarp Forest	18.07	141.92	**235.79**
2	Abram: Freshwater swamp forest	2.20	101.26	**174.43**
3	Miettinen: Plantation/regrowth	0.37	98.18	**163.52**
4	Abram: Carbon	19.41	93.95	**156.85**
5	Gaveau: Logged forests	2.58	83.66	**156.39**
6	Abram: Dry lowland forest	0.88	60.02	**111.53**
7	SFD: Lowland Freshwater Swamp Forest	0.79	70.89	**108.92**
8	Gaveau: Agroforest/forest regrowth	1.40	41.32	**100.07**
9	Miettinen: Lowland forest	6.66	51.57	**94.02**
10	Hansen: tree cover	24.43	70.82	**88.47**
11	Abram: Oil palm with good canopy	7.79	44.62	**60.75**
12	Gaveau: Oil palm plantations	17.93	39.66	**48.39**
13	Miettinen: Lowland mosaic	4.58	**43.68**	26.44
14	Miettinen: Largescale palm production	3.23	18.39	**25.59**
15	SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	0.50	8.07	**24.90**
16	Abram: Limestone forest	2.00	14.68	**23.53**
17	Miettinen: Lowland open	4.03	**21.98**	11.17
18	River	16.34	**18.06**	14.24
19	Abram: Seasonal freshwater swamp forest	6.64	1.92	**13.21**
20	Abram: Oil palm - underproductive <25%	8.38	**12.65**	10.67
21	Road 2	0.47	4.85	**9.88**
22	SFD: Lowland Seasonal Freshwater Swamp Forest	1.18	**6.66**	1.78
23	Gaveau: Non forest	6.15	**6.48**	4.56
24	Miettinen: Peatswamp forest	0.99	1.18	**5.86**
25	Abram: Cleared areas or planted/young oil palm	4.88	**5.83**	5.52
26	SFD: Lowland Peat Swamp Forest	1.64	**4.42**	0.18
27	SFD: Lowland Mixed Dipterocarp & Kerangas Forest	0.21	2.20	**3.72**
28	Road 1	1.84	**3.66**	1.59
29	Abram: Peat swamp forest	1.05	**3.35**	2.95
30	Abram: Severely degraded areas	0.55	1.40	0.04
31	Baccini: Carbon	0.17	0.57	0.01

Table 3. Regression coefficients (β) and AICc importance for the 11 variables with the strongest univariate relationship to clouded leopard path selection for the Kinabatangan model (includes the 11 best variables overall) and Regional model (includes the 11 best variables that were available at the Sabah state level). SE β: standard error of regression coefficient.

Variable	β	SE β	*AICc importance*	z-score	p-value
Kinabatangan model: AICc 700.56					
River	-12.11	4.85	1.00	2.50	0.013
Gaveau: Agroforest/forest regrowth	3.60	0.86	1.00	4.21	0.000
SFD: Lowland Freshwater Swamp Forest	2.35	0.39	1.00	6.07	$< 2e^{-16}$
SFD: Lowland Mixed Dipterocarp Forest	2.29	0.32	1.00	7.16	$< 2e^{-16}$
Gaveau: Logged forests	2.19	0.88	1.00	2.49	0.013
Abram: Freshwater swamp forest	1.35	0.37	1.00	3.67	0.000
Miettinen: Lowland forest	0.38	0.45	0.63	0.85	0.394
Miettinen: Plantation/regrowth	0.30	0.40	0.46	0.75	0.453
Abram: Carbon	-0.14	0.18	0.55	0.79	0.430
Abram: Dry lowland forest	0.09	0.27	0.30	0.33	0.744
Hansen: tree cover	0.06	0.02	1.00	3.76	0.000
Regional model: AICc 728.08					
River	-13.95	4.92	1.00	2.84	0.005
Gaveau: Agroforest/forest regrowth	2.89	1.90	0.92	1.52	0.128
SFD: Lowland Freshwater Swamp Forest	2.70	0.41	1.00	6.59	$< 2e^{-16}$
Miettinen: Lowland open	-2.38	0.81	1.00	2.93	0.003
SFD: Lowland Mixed Dipterocarp Forest	2.22	0.32	1.00	6.85	$< 2e^{-16}$
Gaveau: Logged forests	1.70	1.89	0.71	0.90	0.369
SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	1.65	0.68	1.00	2.43	0.015
Gaveau: Oil palm plantations	-1.54	1.88	0.56	0.82	0.413
Miettinen: Plantation/regrowth	-0.43	0.36	0.76	1.21	0.227
Miettinen: Lowland mosaic	-0.25	0.43	0.41	0.58	0.561
Hansen: tree cover	0.05	0.01	1.00	3.18	0.001

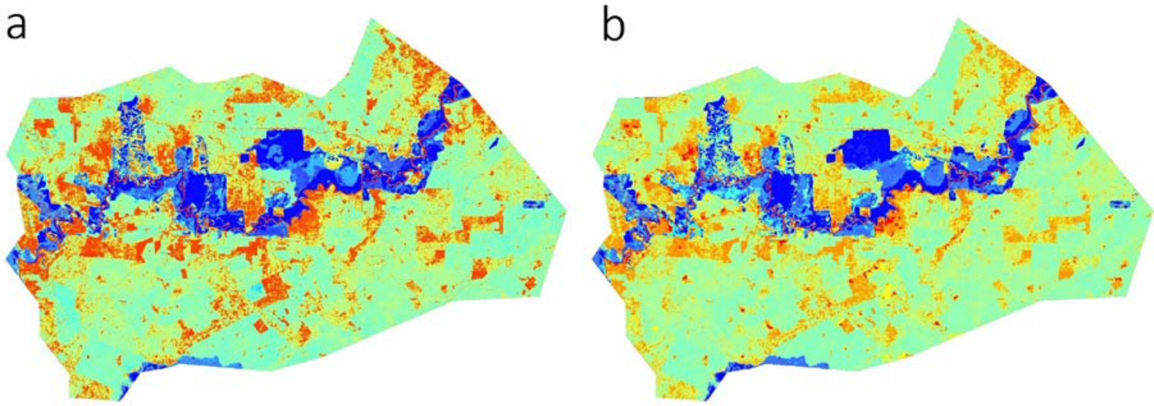

Figure 3. Resistance surfaces produced with: (a) Kinabatangan model; and (b) Regional model, both applied to the extent of the Kinabatangan study area. Low resistance is shown in dark blue (forest with high canopy closure) and high resistance in bright red (oil palm plantations with low canopy closure).

The cumulative resistant kernel surface shows the expected density of clouded leopard movement throughout the study extent (Figure 4). The map shows two core areas of high predicted internal connectivity, which correspond to the two large contiguous forest patches along the Kinabatangan River. Three principal areas of attenuated connectivity are also shown: (i) along the river in the west, between Lots 10 and 11, (ii) between the two core areas, where Lot 5 is reduced to a narrow section of riverine forest, and (iii) where the forest is restricted to a narrow band along the river in Lot 2. The model suggests that a low level of connectivity is retained between the LKWS and the Central Forest Area and the extensive eastern mangrove system, but no direct connectivity between the LKWS and Ulu Segama Forest Reserve.

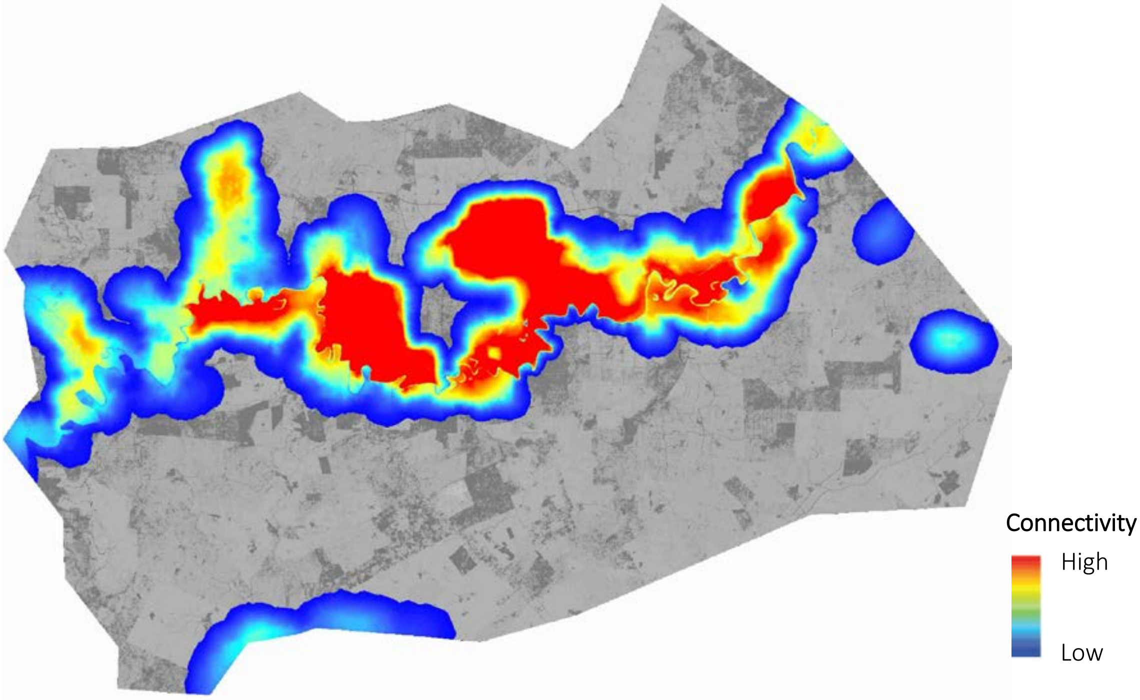

Figure 4. Cumulative resistant kernel surface for the Kinabatangan study area. The cumulative resistant kernel surface shows the expected frequency or density of utilization of each cell by clouded leopard given the source points, the resistance surface and the dispersal threshold chosen. Grey areas are predicted to not be utilized by clouded leopards.

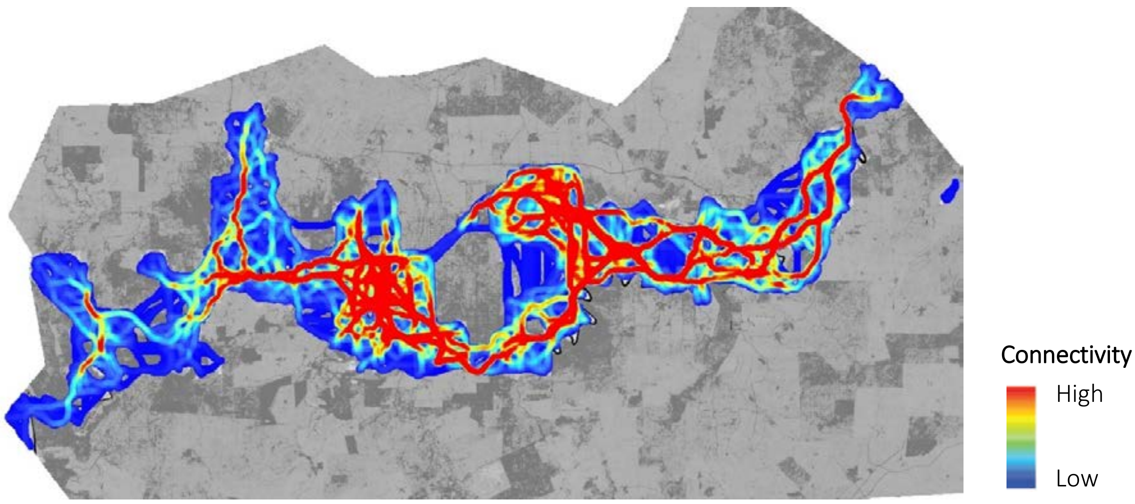

Figure 5. Factorial least cost path density network for the Kinabatangan study area. Red cells contain mainly least cost paths between pairs of source points, while blue areas contain few, and grey areas are predicted not to be utilized by clouded leopards.

The factorial least cost path network map (Figure 5) identifies the same two core areas of high connectivity as the resistant kernel map. However, it does not show the attenuation of connectivity in the narrow bottleneck between these two core patches, nor the area of predicted low connectivity identified in the resistant kernel in the far eastern part of the study area. The factorial least cost path analysis does, however, match the resistant kernel analysis in identifying the reduced connectivity along the river in the far western part of the study area, indicating that this area may be particularly limiting.

Future Scenarios

Scenario 1 (Figure 6a, 7a; Table 4, 5) was quite similar to the pattern and strength of the connectivity predictions for the current landscape, indicating little overall effect of adding a 50 m forest buffer to the rivers. In Scenario 2 (Figure 6b, 7b; Table 5) there was substantially higher connectivity than there is currently as a result of conversion of non-productive oil palm plantation to forest. Scenario 3 (Figure 6c, 7c) was highly similar to Scenario 2, again indicating a relatively small effect of the river buffer. The resistant kernel Scenario 4 (Figure 6d) showed large reductions in connectivity as a result of conversion of private unprotected forest to oil palm, with predicted breakage in connectivity in three places in the western part of the study landscape. Similarly, the least cost Scenario 4 predicted breakage in connectivity at two places in the western part of the study landscape. While the establishment of a 50 m forested riverine buffer in Scenario 1 had relatively little effect on the overall level of connectivity compared to the impacts of a larger scale reforestation in Scenario 2, the percentage change to the correlation length per unit area of reforestation was substantially greater in Scenario 1.

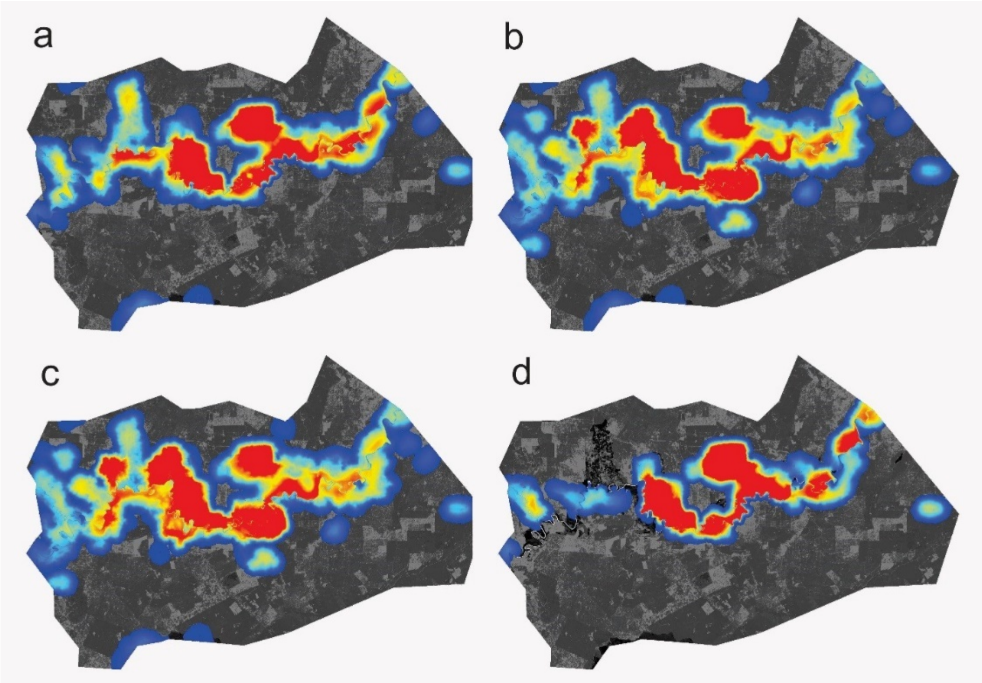

Figure 6. Comparison of cumulative resistant kernels for the four scenarios: (a) S1, areas within 50 m of river are converted to forest cover; (b) S2, non-productive oil palm converted to forest; (c) S3, both a and b; (d) S4, all privately owned unprotected forest converted to oil palm.

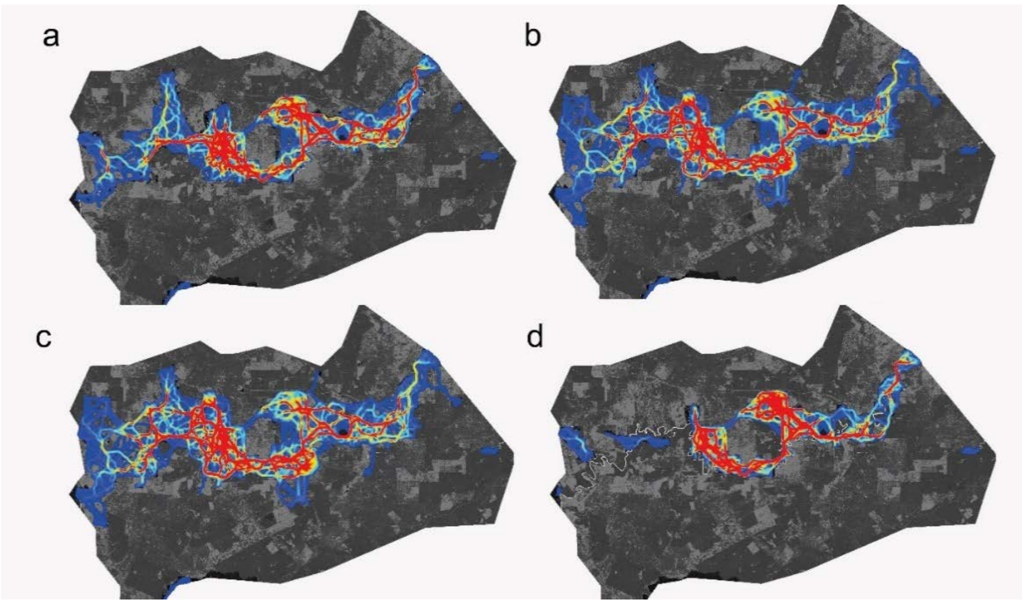

Figure 7. Comparison of factorial least cost path modelling for the four scenarios: (a) areas within 50m of river are converted to forest cover; (b) non-productive oil palm converted to forest; (c) both a and b; and, (d) all privately owned unprotected forest converted to oil palm.

Table 4. Average (lower triangle) and standard deviation (upper triangle) of pixel-pixel differences in cumulative resistant kernel connectivity value and factorial least cost path value across the study area, with differences specified as column scenario minus row scenario, total (upper cell value) and as difference as a percentage of current value (lower cell value).

Scenario	Cumulative resistant kernel					Least cost path				
	Current	S1	S2	S3	S4	Current	S1	S2	S3	S4
Current	x	-3.289	-3.253	-2.683	-11.44	x	35.9	182.04	193.38	67.87
		-19.90%	-16.30%	-13.40%	-57.30%		33.00%	167.11	177.50%	62.30%
S1	-0.098	x	-3.711	-3.126	-10.48	-0.78	x	448.95	474.84	198.8
	-1.10%		-18.57%	-15.64%	-38.30%	-2.89%		412.10%	435.90%	182.50%
S2	-5.72	-5.6	x	-18.245	-0.383	-37.32	-37.23	x	241.59	529.9
	-66.40%	-65.00%				-136.84%	-136.50%		221.80%	486.50%
S3	-6.08	-5.98	4.6	x	0.337	-40.92	-40.91	-3.68	x	556.66
	-70.10%	-69.50%	-53.40%		1.70%	-150.70%	-150.00%	-13.50%		511.00%
S4	3.25	3.35	8.95	9.325	x	14.37	15.45	52.68	46.35	x
	37.70%	38.90%	103.90%	108.30%		52.69%	56.70%	193.19%	170.00%	

Table 5. Percentage of the landscape predicted to be connected by dispersal (non-zero cumulative resistant kernel values) and correlation length (non-zero factorial least cost values) for each scenario, and % change from the current condition of the landscape. S1 - areas within 50m of river are converted to forest cover, S2 - non-productive oil palm converted to forest, S3 - both 50 m river buffer and non-productive oil palm reverted to forest, S4 - all privately owned unprotected forest converted to oil palm, Current – current condition

Scenario	Area reforested (km^2)	Cumulative resistant kernel			Factorial least cost path		
		% landscape connected	% change from current	% change per km^2 of reforestation	Correlation length	% change from current	% change per km^2 of reforestation
S1	3.60	36.01	0.53	0.15	18890	2.42	0.67
S2	140.92	46.12	28.75	0.20	20304	10.04	0.07
S3	144.50	46.1	28.67	0.20	20290	9.96	0.07
S4	-	23.8	-33.59	-	11844	-35.81	-
Current	-	35.82	-	-	18452	-	-

Performance of connectivity assessment method and resistance surface

Standard errors between used paths and the distribution of the available paths were positive and relatively large for both the resistant kernel and factorial least cost path analyses (mean 2.51 and 1.737, respectively) across the three resistant surfaces (Figure 8). A one-sample Z-test indicated that both resistant kernel ($Z = 12.18325$, $p < 0.001$) and factorial least cost path ($Z = 6.6852$, $p < 0.01$) analyses produced distributions of standard errors that were significantly larger than 0, indicating that both methods provide strong performance in predicting used path locations. In contrast, the median number of standard errors the used paths were from the distribution of available paths was negative for the local landscape resistance method across all three resistance surfaces, indicating poor prediction of movement paths by the local value of landscape resistance (Figure 8, Table 6). Tukey multiple-range tests confirmed that both factorial least cost paths and resistant kernel methods outperformed the local landscape resistance ($p < 0.0001$), but there was no difference between the resistant kernel and the factorial least cost path analysis ($p = 0.666$; Table 6). Furthermore, there was no statistically significant difference between any of the resistance surfaces in terms of how many standard errors the used paths were from the distributions of available paths (Kinabatangan-Regional, $p = 0.98$; Kinabatangan-Expert-opinion, $p = 0.802$; Regional-Expert-opinion, $p = 0.786$). The connectivity surfaces for combinations of resistance surface and method, overlain with the used movement paths, are shown in Figure 9, which suggest that the both the empirically optimised connectivity models reflect the same overall pattern as that of the Expert-opinion model, but that the latter appears to be substantially more conservative.

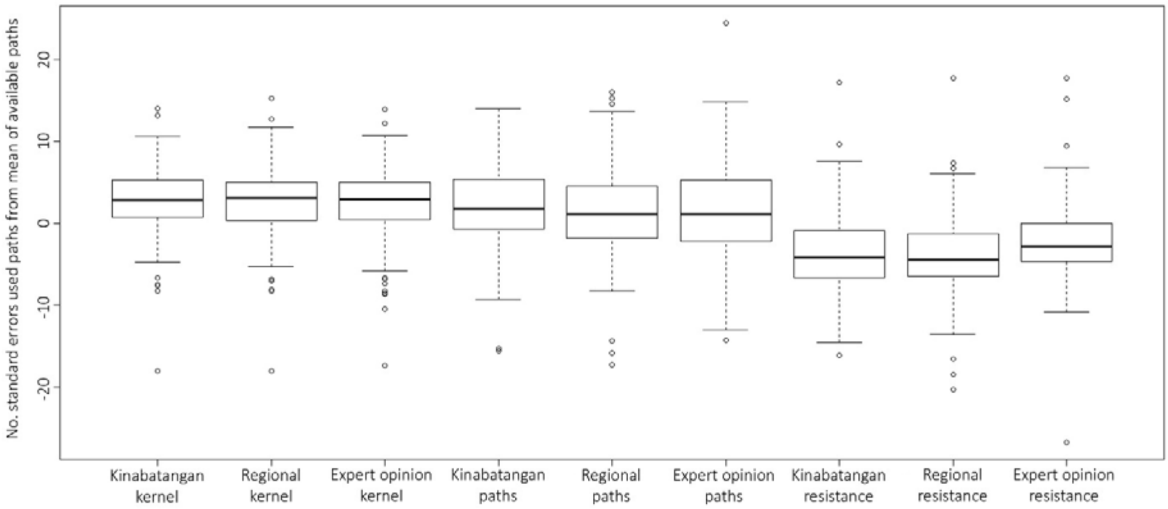

Figure 8. Boxplot of distribution of number of standard errors the used paths were from the distribution of matched randomized available paths for combinations of resistance surfaces (Kinabatangan – resistance surface developed in this paper using locally available high resolution GIS layers; Regional – resistance surface developed in this paper using Sabah-wide GIS layers; Expert opinion – resistance surface developed using expert opinion in Macdonald et al submitted).

Table 6. Analysis of variance table for test differences in performance of method (resistant kernel, factorial least cost path, and local landscape resistance) and resistance surface (Kinabatangan – resistance surface developed in this paper using locally available high resolution GIS layers; Regional – resistance surface developed in this paper using Sabah-wide GIS layers; Macdonald – resistance surface developed using expert opinion in Macdonald et al submitted).

	Df	Sum Sq.	Mean Sq.	F	p-value
Method	2	9109	4554.3	188.76	0.00
Resistance surface	2	88	44.2	1.83	0.16
Method: Resistance surface	4	233	58.2	2.41	0.05

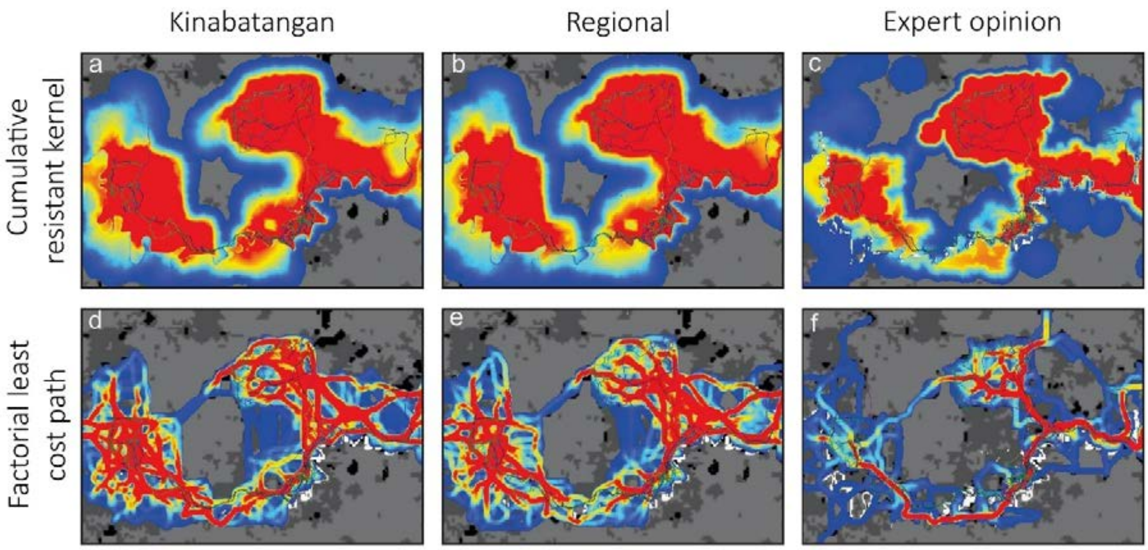

Figure 9. Overlay of used paths (in dark line segments) on top of the predicted connectivity maps for Cumulative resistant kernel (a,b,c) and factorial least cost path (d,e,f), for all three resistance surfaces: Kinabatangan (empirical movement model resistance surface developed in this paper using locally available high resolution GIS layers, a,d); Regional (empirical movement model resistance surface developed in this paper using Sabah-wide GIS layers: b,e); Expert opinion (resistance surface developed using expert opinion in Macdonald et al. submitted: c,f).

Discussion

In this study, we present the first high-resolution data regarding the movements of an understudied, threatened tropical forest felid, the Sunda clouded leopard. Consistent with our first hypothesis, we show that movement is facilitated by forest cover, including disturbed forest, so long as it had high canopy closure, but resisted by non-forest vegetation, such as oil palm plantations. Open structure oil palm plantation areas, such as recently cleared/planted and underproductive (flooded) plantation areas with low canopy closure, presented the highest resistance to Sunda clouded leopard movements. The Sunda clouded leopard has long been considered somewhat resilient to forest disturbance but intolerant of deforestation (e.g., Rabinowitz et al., 1987; Santiapillai and Ashby, 1988), and the conversion of forests to oil palm plantations are widely regarded as one of this species' greatest threats (e.g., Hearn et al. 2015), yet hitherto there has been little empirical evidence to support this view. Our data provide clear support for this forest/non-forest relationship with movement. We also recorded two male Sunda clouded leopards crossing sealed roads on several occasions. Crossings occurred at night, when traffic levels are very low. As traffic levels increase in the future, the relative resistance to movement these roads present, and the threat from vehicle collision, may well increase.

Our analysis is the first to develop landscape resistance surfaces and connectivity models for the Sunda clouded leopard based on empirical movement data. Our connectivity models suggest that all of the protected forest blocks in the Lower Kinabatangan region remain functionally connected for this species, and that these forests in turn retain connectivity with both the main Central Forest to the west and the mangrove system to the east, but that a number of pinch points to movement are evident. Given the small amount of forest cover in the Lower Kinabatangan floodplain (c. 75,000 ha; Ancrenaz et al. 2004; Abram et al., 2014), and the Sunda clouded leopard's apparent low population density in the region (1.5 individuals per 100 km^2; Hearn et al., in press), the Kinabatangan floodplain by itself may be insufficient to support a viable population of these felids over the long-term. To ensure the viability of the Kinabatangan's Sunda clouded leopard population, therefore, it is essential to maintain connectivity through the retention of forest cover. However, around 30,000 ha, or 40% of the region's forest cover lie outside of the protected areas, and at least 64% of these unprotected forests have been allocated for future oil palm cultivation (Abram et al., 2014).

Our future scenarios analyses further highlighted the central role that unprotected forests play in maintaining connectivity between the Lower Kinabatangan region and the

Central Forest area. We showed that conversion of these forests to oil palm plantations would not only significantly reduce the amount of available Sunda clouded leopard habitat but would result in the predicted breakage in connectivity in three places in the western part of the study landscape, which, critically, provides linkage to the Central Forest area. Importantly, however, Abram et al (2014) estimated that a minimum of 54% of the unprotected forests earmarked for conversion in the Lower Kinabatangan floodplain are unsuitable for oil palm cultivation due to the likelihood of flooding, and so such action would not only be detrimental to biodiversity conservation but also unprofitable. We also showed that the conversion of existing underproductive plantations to forest would bring large benefits to Sunda clouded leopards, whilst minimising impacts to the plantation industry. Indeed, Abram et al. (2014) showed that these plantations are not financially viable, and that such areas should be prioritised when selecting areas to be reforested. We predicted that reforestation of areas that had been deforested within 50 m of the Kinabatangan River provided little improvement to region-wide connectivity, although this is likely an artefact of the very small amount of land area involved. However, we predicted that the reforestation of riparian forest close to the river resulted in the highest gains to connectivity per unit area of forest converted, which suggests that narrow riparian corridors may be an important, and cost-effective conservation tool for this felid. Furthermore, riparian areas offer much to the prevention of bank erosion and existing legislation is already in place to reinstate such buffers.

Consistent with our second hypothesis, we showed that our two connectivity modelling approaches outperformed a local measure of landscape connectivity based on the average landscape resistance within a local neighbourhood. This is consistent with the findings of Cushman et al. (2014), who showed that synoptic connectivity modelling approaches (resistant kernel and factorial least cost path) outperformed local landscape resistance when predicting the locations of highway crossings. In our analysis, both synoptic modelling approaches performed statistically equivalently well, but the resistant kernel approach had a higher median and lower variance, suggesting it may be superior when predicting animal movements across a landscape. We also found that resistance surfaces generated from Sabah-wide GIS data performed as well as those which included locally available, high resolution GIS data, which suggests that we can effectively extrapolate the results from our Kinabatangan extent analysis to the entire State of Sabah. There was no difference between the relative performance of resistant kernels and factorial least cost paths developed from the three resistance surfaces. Thus, counter to our third hypothesis, the expert opinion resistance surface, at least in the Kinabatangan region, performed as well as the empirically optimized path-level analysis generated resistance surfaces. Despite their frequent use, few studies have compared the relative performance of expert parameterization of resistance surfaces against those developed using empirical data, but of those that have, the predictive power of expert opinion models was lower than empirically optimized surfaces (e.g., Shirk et al. 2010; Mateo-Sanchez et al. 2014, 2015). Nevertheless, there may often be no alternative data, and our comparative analysis suggests that under certain conditions, expert opinion based predictions of connectivity can potentially produce useful models.

Our model of Sunda clouded leopard landscape resistance and connectivity was developed from a single population, in a specific region of Sabah, which may not necessarily reflect the behavioural ecology of the species elsewhere. Efforts should strive to refine these models of landscape connectivity by obtaining data from a diverse range of locations from across the island. Efforts should also be made to include as many demographic classes as possible, and ideally from dispersing animals (presumably young males), which may show considerable differences in their habitat selection to that of animals with established ranges (Elliot et al., 2014).

Conclusion

Our study demonstrates that forest cover is essential to the movements of Sunda clouded leopards on Borneo and provides important confirmation of the hypothesis that oil palm plantations are highly resistant to the movements of these felids. We confirmed that resistant kernel and factorial least cost path methods of predicting connectivity are effective and superior to local measures of landscape resistance. We found that in this study area, an expert opinion-based resistance surface performed as well as an optimized, multiscale empirical model. Our assessment of future scenarios highlighted the importance of preserving the remaining lowland forest in the region and the large potential benefits of targeted forest restoration. Our next step is to extrapolate the resistance model to the landscape scale.

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Chapter 3. Predicting connectivity, population size and genetic diversity of Sunda clouded leopards across Sabah, Borneo

Abstract

In the face of accelerating global habitat loss and fragmentation there is an increasing need to predict accurately how changes to landscape structure and composition alter the movements and population connectivity of threatened species. Typically, models of connectivity are parameterised with expert-opinion, habitat suitability or empirical movement data, which may vary greatly in their predictive performance, yet few studies have assessed this. In this paper, we developed predictions of population density and genetic diversity, and mapped patterns of population connectivity for a little known, threatened Bornean felid, the Sunda clouded leopard, across the whole extent of Sabah, Malaysian Borneo, and compared the differences in predictions obtained from expert-opinion derived and empirically derived resistance maps. We found that the empirical resistance model produced higher estimates of population size, population density, genetic diversity and overall connectivity than the expert-opinion derived model. Despite their differences, the overall pattern of predicted connectivity was similar in the two models, with both identifying a large patch of core habitat with high predicted connectivity in the Yayasan Forest Management Area and contiguous commercial Forest Reserves, and both models agreed on the location and extent of the main isolated fragments of internally connected habitat, which included the Lower Kinabatangan floodplain, Tabin Wildlife Reserve and Tawau Hills Park as patches of habitat predicted to have extant clouded leopard populations, but predicted to be isolated from other clouded leopard populations. Further research should not only strive to develop more realistic models of landscape connectivity for the Sunda clouded leopard in this state, but also to investigate how different landscape management approaches may best be suited to conserving this felid.

Introduction

In the face of accelerating global habitat loss and fragmentation there is an increasing need to predict accurately how changes to landscape structure affect the population connectivity of threatened species (Spear et al. 2010; Zeller et al. 2012; Cushman et al. 2013a). Such insights can provide a foundation upon which to develop effective conservation action. At its core, population connectivity is the product of the movement of individual organisms across a landscape, the surface of which varies in its resistive qualities. Such movements are shaped by the compounding influences of the composition and structure of the landscape (Zeller et al., 2013), the distribution and density of the population (Cushman, 2006), and the specific dispersal traits of the species (Elliot et al. 2014). Of these, the complex interplay between a species' dispersal characteristics and the effects of how different landscape features combine to attenuate movement is arguably the most important factor mediating landscape resistance and subsequent population connectivity (Spear et al. 2010; Zeller et al. 2012). In most populations, however, there is substantial uncertainty about all of these parameters.

In the vast majority of applications expert-opinion has been used to parameterize resistance surfaces (Spear et al., 2010; Zeller et al., 2012). This has potentially serious limitations given that expert-opinion is of unknown quality and may often fail to reflect accurately the resistance experienced by animals when moving across the landscape (e.g., Shirk et al. 2010; Wasserman et al. 2010). This is particularly true of many threatened species, for which even a basic understanding of their ecology is often lacking. As a consequence, a number of methods have been developed to estimate landscape resistance empirically using genetic (e.g., Cushman et al. 2006; Shirk et al. 2010; Castillo et al. 2014) and movement (e.g., Cushman et al. 2010; Cushman and Lewis 2010; Reding et al. 2013; Elliot et al. 2014) data. These methods have the advantage that they are directly estimated using data from the key processes of interest. Indeed, when they have been compared with expert-opinion or habitat suitability based measures, resistance surfaces directly estimated from movement and genetic data have shown superior performance (e.g., Shirk et al. 2010; Wasserman et al. 2010; Mateo-Sanchez et al. 2014, 2015; but see Chapter 2). Movement and genetic data are often lacking for many threatened species, however, and are typically very costly to acquire. In the absence of such empirical data, expert opinion based estimates of landscape resistance may therefore provide a useful initial prediction of population connectivity, particularly for those species for which a basic understanding of habitat associations is available (e.g., Riordan et al. 2015; Moqanaki and Cushman 2016).

The forests of Borneo host one of the richest biological assemblages on Earth, yet the island is a global hotspot of forest loss and degradation (Bryan et al., 2013; Gaveau et al., 2014; Macdonald et al., submitted). Before the advent of industrial-scale extractive industries in the early 1970s the island's forest cover exceeded 75%, but by 2010 forest cover had declined by a further 30.2%, with the highest proportional losses borne in the Malaysian state of Sabah, at 39.5% (Gaveau et al., 2014). Individual species responses to logging regimes vary, but research is increasingly showing that selectively logged Bornean forests can retain appreciable levels of pre-disturbance biodiversity (e.g., Meijaard et al., 2005; Costantini et al., 2016), as well as the capacity to serve as corridors for less disturbance tolerant species moving between intact forest fragments, while also hosting resident populations of the more resilient species. The establishment of industrial scale plantations of oil palm *Elaeis guineensis*, the principal driver of forest loss on Borneo, however, can lead to dramatic declines in species richness (e.g., Fitzherbert et al., 2008).

Thus, for species of conservation concern on Borneo there is an urgent need for connectivity modelling to assess impacts of landscape change to inform the development of effective conservation strategies. One such species, the threatened Sunda clouded leopard *Neofelis diardi* (Hearn et al., 2015), is charismatic (Macdonald et al., 2015), likely wide-ranging (Hearn et al., 2013), and closely associated with forest (Hearn et al., 2016), and thus serves as both a potential flagship species for Bornean wildlife and as a useful model with which to develop such models of connectivity.

Macdonald et al. (submitted) used spatially synoptic modelling, combining resistant kernel and factorial least cost path analysis (Cushman et al., 2014; Cushman et al., 2013a), and predicted patterns and changes in Sunda clouded leopard connectivity across the entire island of Borneo. They estimated that between 2000 and 2010 the proportion of landscape connected by dispersal had fallen by approximately 24% and the largest patch size had declined by around 30%, leading to a 13% decline in clouded leopard numbers. Macdonald et al.'s (submitted) analysis, however, was based on an expert-opinion derived model of Sunda clouded leopard resistance to movement, and so warranted empirical testing. Hearn et al. (Chapter 2) used a path-level approach (Cushman and Lewis 2010; Cushman et al. 2010) based on movement data from GPS-tagged animals to develop the first multi-scale, empirical connectivity predictions for a population of Sunda clouded leopards in eastern Sabah. Hearn et al. (Chapter 2) evaluated the performance of their empirical model and the Macdonald et al. (submitted) expert-opinion model in predicting the locations of clouded leopard core movement areas and individual movement paths within a small region of Sabah, characterized by a high contrast mosaic of remnant forest patches surrounded by oil palm plantations, and found them to both have equally high predictive ability, although the expert opinion model was slightly more conservative. Given that the Hearn et al. (Chapter 2) empirical model was optimised in a particular location, and that the Macdonald et al. (submitted) expert-opinion model included cover types not present in the Hearn et al. (Chapter 2) study area, and thus may differ from Hearn et al. (Chapter 2) where those cover types are present, it is not known how well these two resistance surfaces predict clouded leopard movement at broader extents and landscapes with a wider range of ecological and topographical conditions, such as the full area of Sabah.

In this paper we had two main objectives. First, we sought to extrapolate the Hearn et al. (Chapter 2) empirical resistance model to predict population density, genetic diversity and population connectivity for clouded leopards across the full extent of Sabah. Second, we wished to quantify the differences in predicted population density, genetic diversity and population connectivity obtained from the Hearn et al. (Chapter 2) empirically optimized and the Macdonald et al. (submitted) expert-opinion resistance surfaces at the full Sabah extent. We had three a priori hypotheses. First, we expected that predictions from the two resistance surfaces would differ much more at broader scales such as the full extent of Sabah than they did at the finer, regional scale, where the empirical resistance model was developed. Second, consistent with the findings of Hearn et al. (Chapter 2), who compared the two resistance models within a relatively small region in Eastern Sabah, we predicted that at the full extent of Sabah the empirical resistance model would produce higher estimates of population size, population density, genetic diversity and overall connectivity than the expert-opinion derived model. Third, consistent with the findings of Hearn et al (Chapter 2), we expected that despite their differences, the overall pattern of predicted connectivity would be the same in the two analyses, identifying the same major core areas and main areas of connectivity between them.

Study Area

The Malaysian state of Sabah occupies an area of 73,631 km^2 in the northernmost portion of Borneo (Figure 1). Akin with the rest of the island, Sabah is characterised by a rugged topography, particularly in central and western areas, which give way to coastal alluvial plains. In 2010 forest accounted for 47.5% of the state's land area (35,006 km^2), following a rapid decline from 78.6% in 1973, representing the highest deforestation rate of all the political units on Borneo during this period (Gaveau et al, 2014). The main driver of forest loss has been the increasing proliferation of mono-culture plantations, chiefly that of oil palm (McMorrow et al., 2001), which accounted for around 21% of land area (15,442 km^2) in 2015 (Malaysian Palm Oil Board, 2016), but also increasing areas of timber plantations, which amounted to 2447 km^2 in 2010 (Reynolds et al., 2011). Considerable areas of highly disturbed, regenerating forests, characterised by areas of scrub and grassland are also present in the state. A number of relatively small (280–1399 km^2) patches of protected primary forest remain in the state, including the Danum Valley, Maliau Basin and Imbak Canyon Conservation Areas, and the Crocker Range, Kinabalu and Tawau Hills Parks (Figure 1), but the vast majority of remaining forest has undergone either one or more rounds of selective logging (Reynolds et al., 2011). The state-owned Permanent Forest Reserve, which includes State Parks, Wildlife Reserves as well as commercial Forest Reserves, now accounts for the majority of remaining forest (Reynolds et al., 2011). The rugged areas along the Crocker and Trusmadi mountain ranges retain large areas of forest in the western and southwestern parts of the state, and sizeable areas in the central areas of the state remain forested, most notably the 10,000 km^2 Yayasan Sabah Forest Management area (YSFMA; Reynolds et al., 2011). Deforestation rates have been significantly higher in the eastern side of Sabah, however, and a number of protected forest areas, including the Tabin Wildlife Reserve, Lower Kinabatangan Wildlife Sanctuary and Tawau Hills Park, are no longer contiguous with the core forest regions.

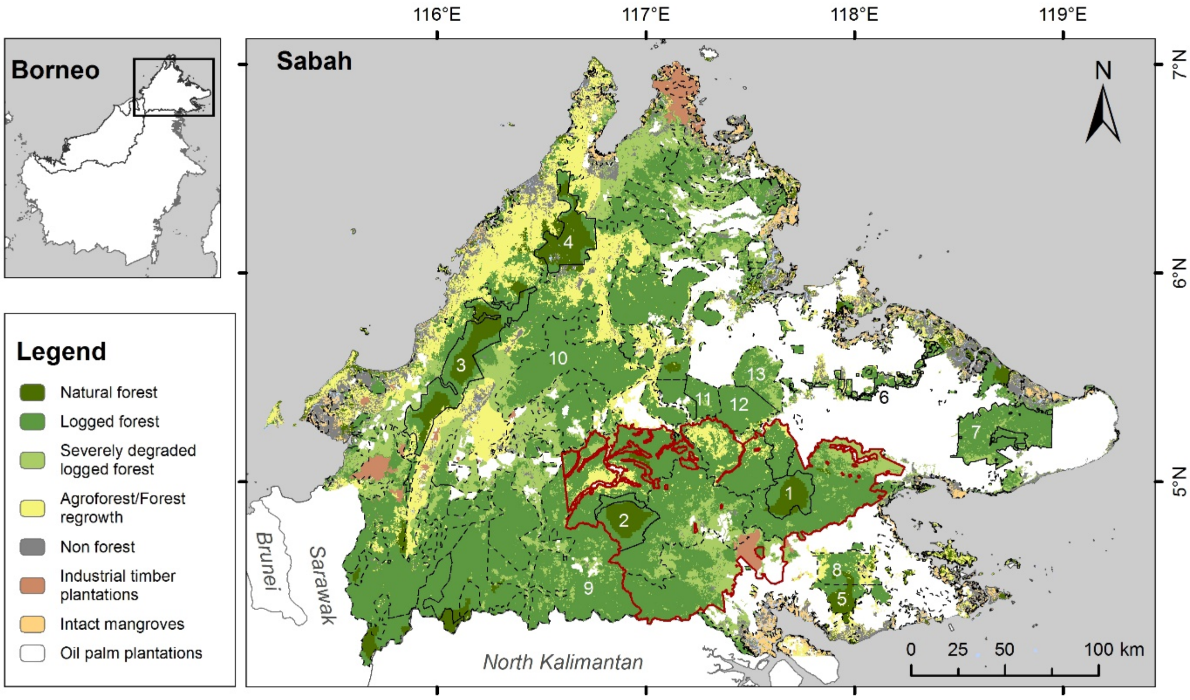

Figure 1. Map of the Malaysian state of Sabah, northern Borneo, showing land use in 2010 (Gaveau et al., 2014). Fully protected forest areas (National Parks, Wildlife Reserves and Conservation Areas) are outlined in solid black lines and include: (1) Danum Valley and (2) Maliau Basin Conservation Areas, (3) Crocker Range, (4) Kinabalu and (5) Tawau Hills Parks, and (6) Lower Kinabatangan and (7) Tabin Wildlife Reserves. Commercial Forest Reserves are outlined in dashed black lines; key areas include (8) Ulu Kalumpang, (9) Sapulut, (10) Trus Madi, (11) Tankulap-Piningah, (12) Deramakot and (13) Segaliud Lokan Forest Reserves. The Yayasan Sabah Forest Management Area is outlined in dark red. Polygons represent the state owned, Permanent Forest Reserve system.

Methods

Development of resistance layers

In this paper we investigated connectivity metrics for Sunda clouded leopards across the full extent of Sabah, based on two resistant surfaces, each developed using different methodological approaches. The two resistance models consisted of Hearn et al's (Chapter 2) empirically optimised, movement based model, and Macdonald et al's (submitted) expert-opinion derived model, hereafter referred to as the Empirical model and Expert-opinion model, respectively. The Empirical model resistance layer was developed by Hearn et al. (Chapter 2) using conditional logistic regression in a path-selection context (e.g., Cushman et al. 2010; Cushman and Lewis 2010), applied to movement data derived from GPS tagged Sunda clouded leopards residing in an approximately 4000 km^2 study extent in eastern Sabah, the Lower Kinabatangan Wildlife Sanctuary and surrounding oil palm matrix. Hearn et al. (in review) used a multiscale approach, and evaluated 3 scales of spatial shift to investigate relationships between clouded leopard movement paths and a range of landscape variables, and developed two models based on different GIS land use data. The first model included high resolution land use variables that were only available at the local study extent (Kinabatangan model), whilst the second model used variables that were available for the whole state (Regional model). For this analysis, we use the resistance layer developed for the full extent of Sabah. At the full extent of Sabah there were several cover types not present in the Hearn et al. (in review) analysis extent. To apply the Hearn et al. (Chapter 2) resistance model to the full extent of Sabah we assumed that all kinds of upland forest were equivalent, reclassifying two classes of montane forest to the same value as lowland tropical forest (which was present in the Hearn et al. (Chapter 2) study area.

The expert-opinion model was developed by Macdonald et al. (submitted) who conducted a survey of the leading experts on Sunda clouded leopard ecology to obtain estimates of resistance values to be assigned to different landcover types. The land cover classes were derived from those developed in a 250m resolution 2010 land cover map of insular Southeast Asia, by Miettinen et al. (2012). Lowland forest and lower montane forest were ranked as the highest quality habitat with mean scores of 4.50 and 4.25 out of 5, respectively, and urban, water and large scale plantation were given the lowest quality scores of 1.0, 1.05 and 1.11, respectively. Lowland Open and Montane Open were also given very low quality scores. These habitat suitability index scores were translated into relative resistances by inverting and scaling from a minimum of 1 to a maximum of 100, and subsequently applied to the Miettinen et al. (2012) map to produce a resistance surface, within the Sabah extent.

Source Points for Connectivity Modelling

For each of the two resistance layers we developed a set of source points for use in connectivity modelling. The resistance layers describe the local cost of moving through any given pixel which is the foundation for connectivity modelling; however, resistance surfaces themselves are insufficient indicators of connectivity (Cushman et al. 2009). Connectivity is a function of the resistance surface and the density, distribution and dispersal ability of the dispersing population (Cushman et al. 2010). Thus, source points that reflect a realistic distribution and density of the population are critical to reliable predictions of connectivity (Cushman et al. 2014). We seeded each of the two resistance layers with source points using the method described in Macdonald et al. (submitted), in which clouded leopard habitat suitability is considered to be directly proportional to the inverse of resistance to movement. Specifically, we generated a raster of identical pixel size and extent as the two resistance layers, but with values randomly varying between 0 and 1. We then multiplied this uniform random map with each of the two resistance layers, and selected all pixels with value less than a constant chosen to produce a set of 4540 points for the empirically optimized resistance layer, which also produced a set of 3811 points for the Expert-opinion resistance layer, since it had higher overall resistance across Sabah and thus lower average suitability for clouded leopard occurrence. It is likely that the true clouded leopard population in Sabah is approximately 1/4 this number (Hearn et al., 2015). We chose this higher number to provide more spatial precision in the estimates of connectivity, given spatial uncertainty in the actual locations of clouded leopard home ranges and the fact that they are mobile animals and may utilize multiple locations in their lifetimes (e.g., Moqanaki and Cushman 2016).

Resistant Kernel Connectivity Modelling

We used the least-cost resistant kernel approach (Compton et al. 2007; Cushman et al. 2010) implemented in UNICOR v2.0 (Landguth et al. 2012) to predict the extent of the landscape connected by dispersal across a 250,000 cost unit kernel width. This kernel width was chosen since it is approximately the upper bound of the expected dispersal ability of clouded leopards (Macdonald et al., submitted). The resistant kernel works by computing the cost-distance kernel from each set of source locations, scaling it such that the volume of the kernel reflects to population density at that location, and summing all such kernels to create a cumulative resistant kernel surface that reflects the incidence function of frequency of movement of the species through each location. Thus, the model calculates the expected relative density of each species in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010). The resistant kernel method of modelling landscape connectivity has a number of advantages; it is spatially synoptic

(Cushman et al. 2014), allowing robust assessment of connectivity at all locations in a landscape relative to all other locations, and is computationally efficient (e.g., Cushman et al. 2012a; 2013a), allowing implementation at broad scales and across multiple scenarios (e.g., Cushman et al. 2015).

We compared the predicted connectivity obtained from the Empirical and Expert-opinion derived resistance surfaces in several ways. First, we visually interpreted the patterns of high and low resistance in each layer, noting the major differences among them. Second, we visually interpreted the patterns of cumulative kernel connectivity value in each layer, noting the major differences in predicted movement rates across the full extent of Sabah. Third, we computed FRAGSTATS (McGarigal et al. 2012) metrics on the mosaic of patches predicted to be connected by dispersal in the cumulative kernel results for each resistance surface, across a range of connectivity thresholds (e.g., Wasserman et al. 2012). We chose two metrics to compute, the percentage of the landscape (PLAND) and the correlation length (GYRATE_AM) predicted to be connected by dispersal at a given connectivity threshold value. The percentage of the landscape is the most basic metric of landscape composition, yet provides a useful quantification of the area predicted to be connected by dispersal. The correlation length measures the distance an organism can travel when placed at a random location in connected habitat and assigned to move in a random direction before reaching the edge of connected habitat (McGarigal et al. 2012), and has been shown to be a strong predictor of functional connectivity (Cushman et al. 2012b). We chose connectivity thresholds at a range of cumulative resistant kernel values, including: 0, 10, 20, 40, 80, 160, 320 and 640, which span the range from including all areas with any level of predicted connectivity among them (0) to only those areas with exceptionally high predicted rates of clouded leopard incidence and movement (640).

Finally, we computed the intersection of the cumulative resistant kernel maps for the Empirical and Expert-opinion resistance models across a range of kernel density thresholds (Cushman et al., 2013b). We calculated the extent of each of the three intersection components (connected in Empirical only, Expert-opinion only, and connected in both.

Predicted Population size and Genetic Diversity

We used simulation modelling (e.g. Shirk et al. 2012; Wasserman et al. 2012) with an individual-based, spatially explicit population dynamics and genetics program (CDPOP version 1.0; Landguth and Cushman 2010) to predict and compare the patterns and causes of differences in the local neighbourhood population density, distribution, and genetic diversity across the two different resistance maps, at two dispersal distances. CDPOP simulates the birth, death, mating and dispersal of individuals in heterogeneous landscapes as probabilistic functions of the cost of movement through them. For each of the two landscape resistance maps, we used the source cells used in the resistant kernel analysis as locations of simulated individual clouded leopards. We used standard simulation parameters widely used in landscape genetics simulation modelling (e.g., Cushman and Landguth, 2010) and stipulated the population to have 30 loci, with 10 alleles per locus, initially randomly assigned among individuals, and a mutation rate of 0.0005. We used an inverse square mating and dispersal probability function, with maximum dispersal cost-weighted distances of 125,000 m and 250,000 m, which reflect the estimated upper and lower range of expected clouded leopard dispersal ability (Macdonald et al., submitted). Reproduction was sexual with non-overlapping generations, and the number of offspring was based on a Poisson probability draw, with mean of 2. We ran 10 Monte Carlo runs in

CDPOP for each of the two landscape resistance maps to assess stochastic variability. We simulated gene flow for 200 non-overlapping generations. Past studies have shown that this is sufficient time to ensure spatial genetic equilibrium (Landguth et al. 2010a,b). We extracted several global measures of population genetic structure for the full study area at generation 200, including total population size, number of alleles in the population, and observed and expected heterozygosity (Macdonald et al., submitted). We analysed the differences in these global measures of genetic structure between the two dispersal abilities.

Results

Landscape resistance and resistant kernel connectivity models

There were striking differences between the Expert-opinion and Empirical resistance layers in predicted resistance to clouded leopard movement across the full extent of Sabah (Figure 2 – top row). Both maps predict low resistance (dark blue) in areas of primary and selectively logged forest, and both predict high resistance (red – yellow) in areas of non-forest, which, in the eastern half of the state, are characterised primarily by oil palm plantations. The main difference between the maps is related to how they treat areas, particularly in the state's western half, that are classified by Miettinen et al. (2012) as Plantation/Regrowth and Lowland Mosaic, and by Gaveau et al., (2014) as Agroforest/Forest regrowth. The Expert-opinion model predicted these areas to be relatively high resistance, while the Empirical model predicted these areas to be relatively low resistance (mid blue). Some areas classified as Severely degraded and logged forest by Gaveau et al., (2014), but as Plantation/Regrowth by Miettinen et al. (2012), such as parts of south eastern Tabin Wildlife Reserve, Ulu Kalumpang Forest Reserve (contiguous with Tawau Hills Park) and the Bukit Pithon Forest Reserve (north east of the YSFMA) were predicted as relatively low resistance in the Empirical map, but as relatively high (yellow-orange) in the Expert-opinion map.

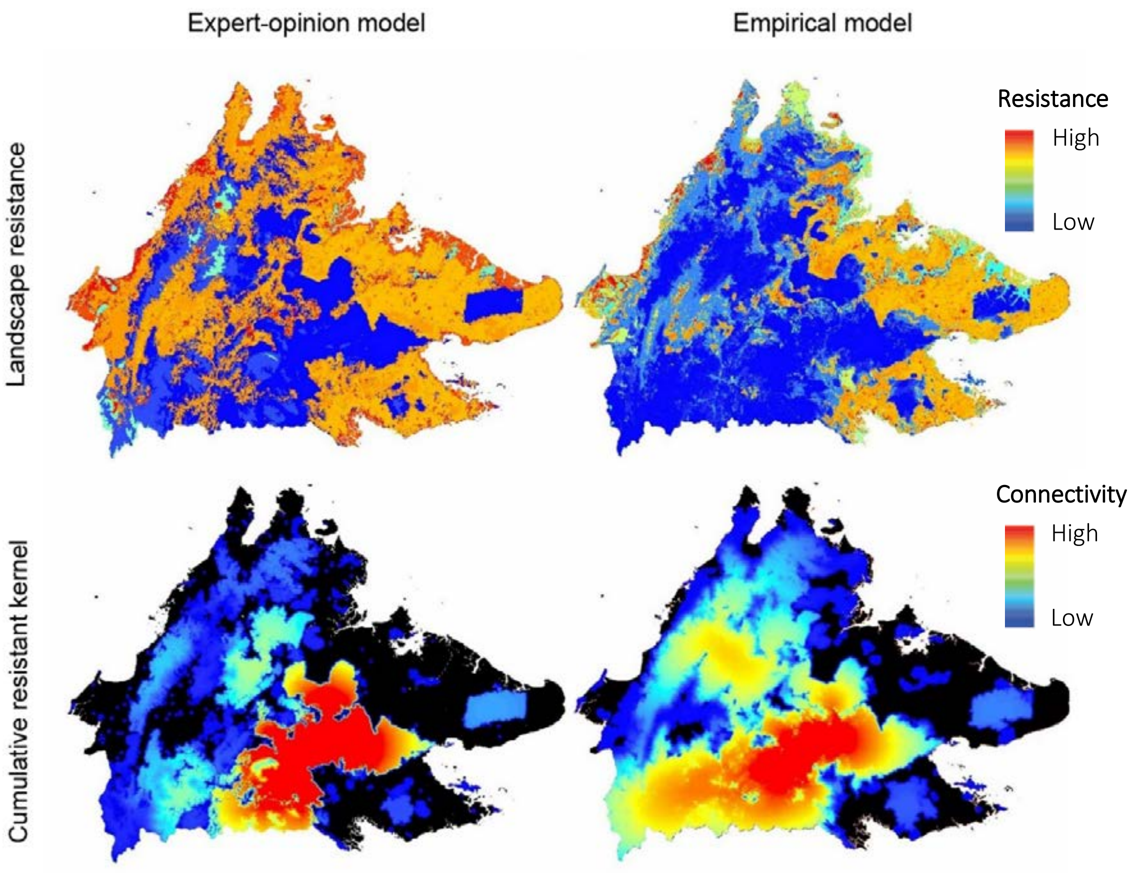

Figure 2. Landscape resistance (top row) and cumulative resistant kernel (bottom row) maps for Sunda clouded leopard movement applied to the full extent of the State of Sabah, Malaysia. Landscape resistance model based on multi-scale optimization of a path-selection function; Resistance ranges from low (1) in dark blue to high (100) in red; Cumulative resistant kernels developed using a 250,000 cost unit dispersal threshold; Red areas are predicted to have high density/frequency of utilization, blue areas low, and black areas are predicted to not be utilized by clouded leopards.

The cumulative resistant kernel prediction of connectivity across Sabah differed substantially between the two resistance models (Figure 2, bottom row). Both cumulative resistant kernel maps showed a major core area of connectivity, which encompasses the YSFMA and contiguous commercial Forest Reserves of Deramakot, Tankulap-Piningah and Segaliud Lokan, to the north, and Sapulut to the southwest. Both approaches predicted losses of functional connectivity between the YSFMA and the Lower Kinabatangan and Tabin Wildlife Reserves and Tawau Hills Park. The two models' main differences were in the western half of the State, where the cumulative resistant kernel map produced on the Expert-opinion resistance surface predicted much less connectivity than the cumulative resistant kernel map produced on the empirical resistance surface. This is a result of the differing resistance assigned to areas classified as Plantation Regrowth and Lowland Mosaic by Miettinen et al. (2012), and as primarily Agroforest/Forest regrowth Plantation Regrowth by Gaveau et al., (2014), as noted above. Despite these differences, both models predicted that these western and northern regions, which include the regionally important Crocker Range and Kinabalu Parks, remained functionally connected to the core areas of connectivity in and around the YSFMA and adjacent commercial Forest Reserves.

We computed FRAGSTATS metrics on the mosaic of patches predicted to be connected by dispersal in the cumulative resistant kernel results for the two resistance surfaces, across a range of connectivity thresholds. The percentage of Sabah predicted to be connected by dispersal across cumulative kernel density thresholds was substantially different between the two resistance layers (Figure 3a). At all dispersal thresholds cumulative resistant kernel surface obtained from the Empirical model had higher extensiveness than that obtained from the Expert-opinion model. The relative difference in the percentage of Sabah connected by dispersal increased as the connectivity threshold increased. At the most liberal threshold (cumulative kernel value greater than 0) the Empirical model cumulative resistant kernel surface had a 16% greater area than the

Expert-opinion model resistant kernel surface. This difference increased at the higher levels of cumulative kernel value, reaching a difference of 20% at cumulative kernel values greater than 320 (Figure 3a). Both maps had low extents predicted to be connected at the very highest connectivity values (less than 10% at cumulative kernel values > 640).

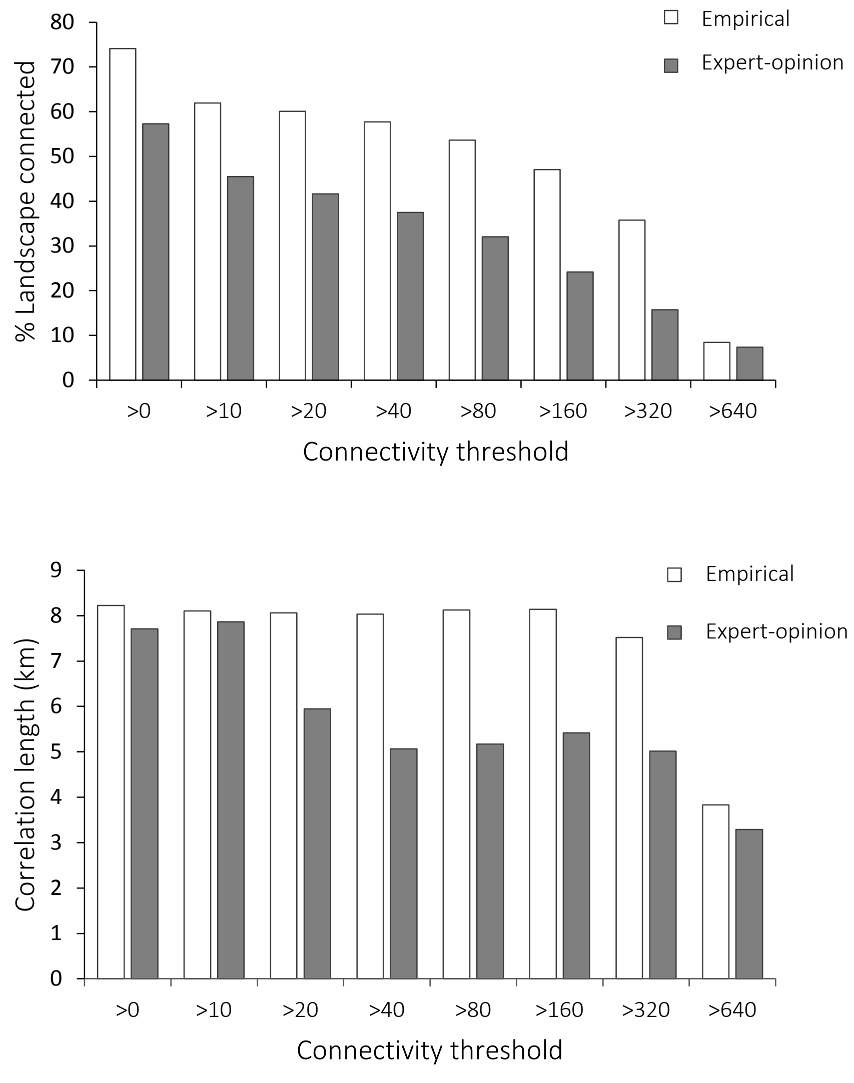

Figure 3. (a) Percentage of the landscape predicted to be connected and (b) Correlation length of connected habitat across a range of cumulative resistant kernel surface thresholds, for the Hearn et al. (Chapter 2) Empirical model and Macdonald et al. (submitted) Expert-opinion model.

Correlation length of connected habitat was nearly the same for all areas connected with cumulative kernel value >0 (Figure 3b). There was a clear threshold at cumulative resistant kernel value of approximately 20, above which the two connectivity surfaces departed in correlation length, with the empirically optimised kernel surface remaining highly connected while the correlation length of the Expert-opinion derived surface declined dramatically (decrease of 29.60 km correlation length, 37% less than the correlation length of the Empirical model at a connectivity threshold of >40 cumulative resistant kernel value). This relative difference in correlation length of connected habitat remained the same up to cumulative resistant kernel threshold of >320, and then declined substantially at the highest connectivity threshold value (>640).

Intersection Analysis

We computed the intersection of the cumulative resistant kernel maps for the Empirical and Expert-opinion resistance maps, across a range of kernel density thresholds (Figure 4). We calculated the extent of each of the three intersection components (connected in the Empirical map only, connected in the Expert-opinion map only, and connected in both maps (Figure 5). At low cumulative kernel thresholds, the vast majority of the area predicted to be connected in either map is connected in both maps (Figure 4a, Figure 5). The proportion of intersection declines as the cumulative resistant kernel threshold increases, such that at high levels of connectivity there is much less overlap between the areas predicted to be connected in the two approaches (Figure 4 e-g). At the very highest level of connectivity value there is much less total area predicted to be connected in either analysis, and only at this very high level of connectivity value does the Expert-opinion analysis predict connectivity in areas not also predicted to be connected in the Empirical analysis.

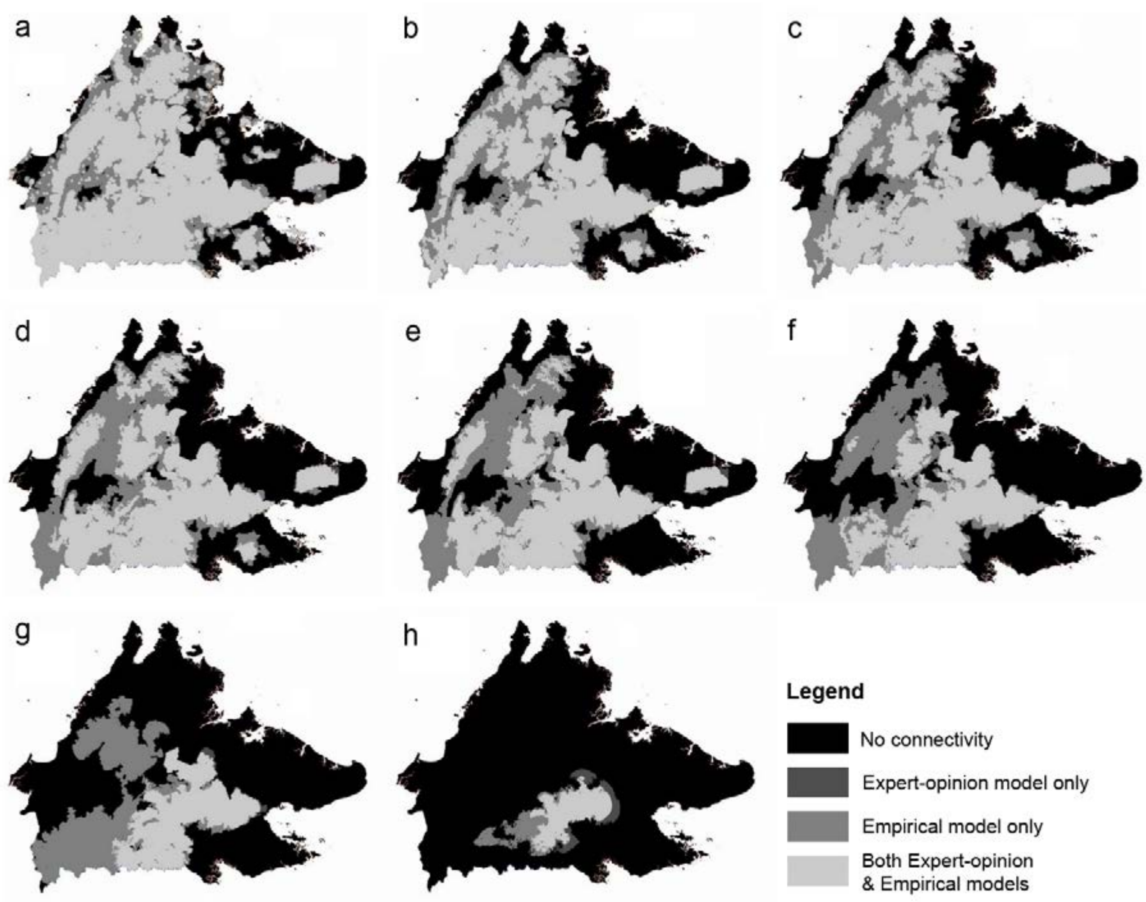

Figure 4. Intersections between the cumulative resistant kernel surfaces produced on the Macdonald et al. (submitted) Expert-opinion model and the Hearn et al. (in prep; Chapter 2) Empirical model resistance maps across eight different cumulative kernel connectivity values: (a) >0, (b) >10, (c) >20, (d) >40, (e) >80, (f) >160, (g) >320, and (h) >640.

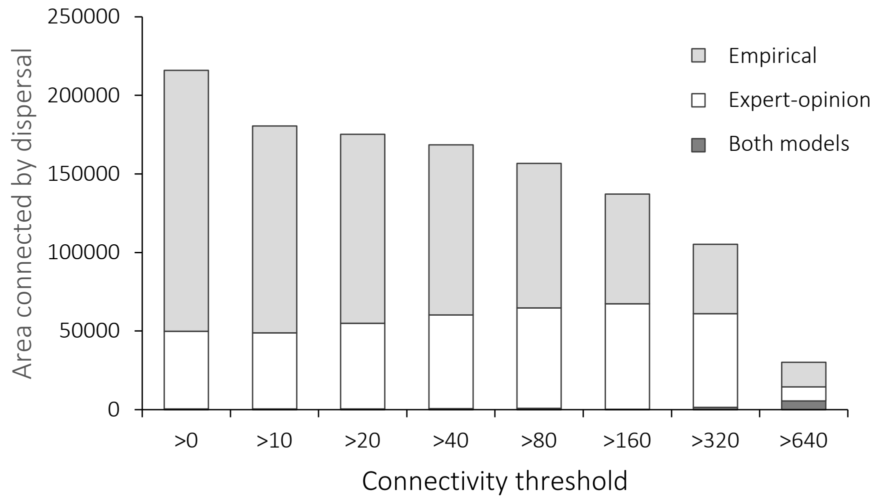

Figure 5. Intersection analysis of areas predicted to be connected by dispersal on the Empirical model map (Chapter 2), Expert-opinion map (Macdonald et al., submitted), and both maps, across a range of cumulative resistant kernel surface thresholds: (>0, >10, >20, >40, >80, >160, >320, >640).

Predicted Population Size and Genetic Diversity

We used the program CDPOP to predict and compare differences in population size, distribution, and genetic diversity across the two different resistance maps. There was considerable local variation in simulated local neighbourhood population density of clouded leopards across Sabah among the four CDPOP scenarios (Figure 6). The general pattern was for broader distribution and larger populations in the Empirical resistance map simulations than the Expert-opinion resistance map simulations, and in the long versus short dispersal ability simulations. We found that the effect of resistance layer on simulated population size across the full extent of Sabah was statistically significant, whereas the effect of dispersal ability was not (Table 1; Figure 7a). All four simulations predicted that population density was highest within a core central area which encompassed the YSFMA and adjacent Deramakot, Tankulap-Piningah and Segaliud Lokan Forest Reserves. The Empirical model scenarios also predicted relatively high population densities in the highland areas of the Crocker and Trus Madi mountain ranges and along the border with Kalimantan and Sarawak, in south-western Sabah, but these areas were predicted as only moderate density in the Expert-opinion model scenarios. All four simulations show populations persisting in the relatively isolated forest patches of the Crocker Range and Kinabalu Parks, and Tabin Wildlife Reserve. In contrast, only the simulations on the Empirical resistance maps show the population persisting in Tawau Hills Park, and Sunda clouded leopards were predicted to persist in the Lower Kinabatangan Wildlife Sanctuary only in the empirical simulation with the high dispersal ability.

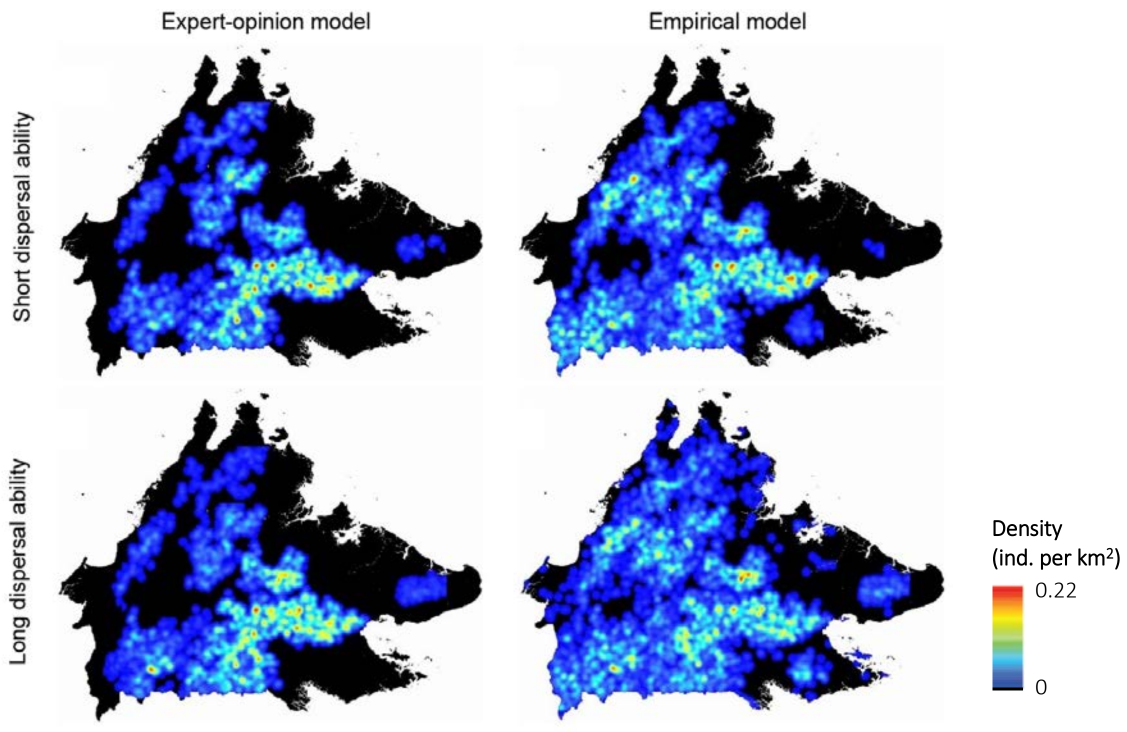

Figure 6. Mean predicted local neighbourhood density of clouded leopards across Sabah under four simulation scenarios: First column: Macdonald et al. (submitted) Expert-opinion model; second column: Hearn et al. (Chapter 2) Empirical model; top row: Short dispersal ability (250,000 cost unit dispersal threshold); bottom row: Long dispersal ability (125,000 cost unit dispersal threshold). Sunda clouded population density is indicated in a colour ramp from 0 (full black) to 0.22 individuals per km^2 (full red).

Table 1. Results of Two-way Analysis of Variance of differences between simulated populations, alleles, and heterozygosity as function of dispersal ability and the resistance map used.

Effect	*Analysis of Variance P*-values		
	Population size	Alleles	Heterozygosity
Dispersal ability	0.533	0.191	0.021
Resistance map	0.010	0.025	0.035
Interaction: Dispersal ability - Resistance map	0.323	0.369	0.730

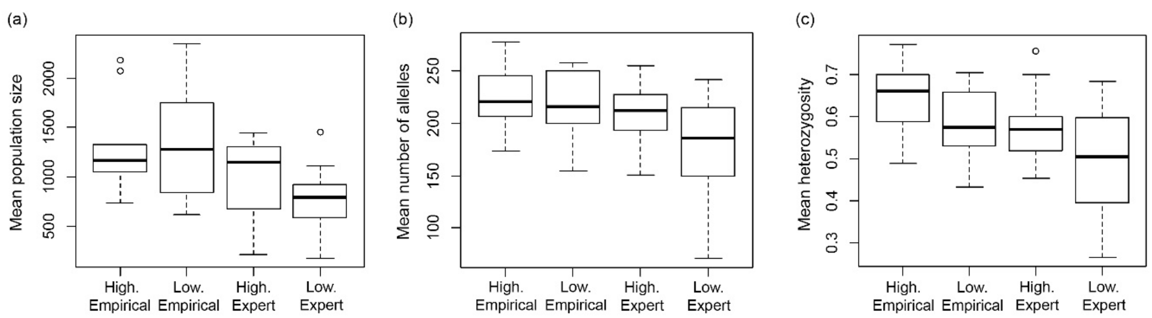

Figure 7. Boxplots of simulated mean (a) Sunda clouded population size across Sabah, (b) number of alleles in the Sabah-wide population of Sunda clouded leopards, (c) heterozygosity for the Sabah-wide population of Sunda clouded leopards, for the Empirical model (Chapter 2) and Expert-opinion model (Macdonald et al. submitted) resistance maps, at 250,000 cost units (High) and 125,000 cost units (Low) dispersal abilities. Error bars represent 95% Confidence intervals and boxes represent interquartile ranges (25%-75%).

There were significant differences in the number of alleles in the Sabah-wide clouded leopard population among resistance maps, but not dispersal abilities or their interaction (Table 1, Figure 7b), with the simulations on the Empirical resistance map producing significantly higher allelic richness than simulations on the Expert-opinion resistance map. There were significant differences in the heterozygosity of the Sabah-wide clouded leopard population among resistance maps and dispersal abilities, but not their interactions (Table

1, Figure 7c). Specifically, heterozygosity was significantly higher in the CDPOP simulations on the Empirical resistance map than on the Expert-opinion resistance map, and significantly higher in simulations with the long dispersal distance than the short dispersal distance.

Discussion

Our goals in this study were to predict the local neighbourhood population density, genetic diversity and map patterns of population connectivity for clouded leopards across Sabah and compare the differences in predictions obtained from expert-opinion and empirically derived resistance maps. Consistent with our first hypothesis, predictions from the two resistance surfaces differed much more at the scale of Sabah than they did at the finer regional scale where the Empirical resistance model was developed. Hearn et al. (Chapter 2) found that at the scale of their Kinabatangan study area (approximately 4,000 km^2 in the eastern Sabah lowlands), which was characterized by a mosaic of remnant native forest patches in a matrix of oil palm plantations, the two resistance maps were very similar and produced extremely similar predictions of regional clouded leopard connectivity. In addition, they found that actual clouded leopard movement paths were well predicted by resistant kernel and factorial least cost path (Cushman et al. 2009) connectivity predictions obtained from both the Empirical and Expert-opinion derived resistance layers. From this they inferred that, at least at the scale of the Kinabatangan study area, the Expert-opinion derived resistance surface performed as well as the Empirically optimized surface. However, there are a number of reasons why we would expect this congruence in performance to deteriorate at broader scales. First, the Expert-opinion based resistance layer produced by Macdonald et al. (submitted) was based on relative suitability estimates for different landcover types, and several landcover types that are common in western Sabah were absent in the Kinabatangan study area; thus the two resistance layers and connectivity predictions obtained from them may differ in areas where these cover types are common. Second, the Expert opinion resistance layer was based solely on the expert opinion weights given to land cover classes, while the Empirical model also included additional variables related to canopy cover. Thus the Empirical model predicted relatively low resistance in some areas with moderately high canopy cover, even if they were in cover types given relatively high resistance in the Expert-opinion model. As a result, we found that the resistance layers, connectivity predictions, population densities and genetic diversities obtained from them differed substantially between the two analyses, with the Expert-opinion model predicting substantially lower population connectivity.

Consistent with our second hypothesis, we found that the Empirical resistance model would produce higher estimates of population size, population density, genetic diversity and overall connectivity than the Expert-opinion derived model. We based this hypothesis on the observation in Hearn et al. (Chapter 2) that in the Kinabatangan study area the Empirical model resistance layer was somewhat less restrictive and produced connectivity predictions somewhat more liberal than the Expert-opinion model. At the scale of the full extent of Sabah this difference is much more pronounced. Specifically, the Expert-opinion model developed by Macdonald et al. (submitted) predicted much higher resistance in a large region of northern and western Sabah, specifically in areas classified as Plantation/Regrowth and Lowland Mosaic by Miettinen et al. (2012) and as Agroforest/Forest regrowth by Gaveau et al., (2014). The Expert-opinion model was parameterised with a single variable, land use, as defined by Miettinen et al. (2012), and

Plantation Regrowth and Lowland Mosaic areas were rated by the expert panel as being of relatively low habitat suitability (2.00 and 2.13 out of 5, respectively). The Empirical resistance surface, however, was parameterised using a range of variables, including a 2010 Borneo wide land use layer developed by Gaveau et al., (2014), the Miettinen et al. (2012) land use layer, and layers depicting canopy cover. In the Gaveau et al. (2014) layer, the areas of discrepancy in the two resistance models were primarily classified as Agroforest/Forest regrowth, which was estimated as moderate resistance in the movement model (See Supplementary file), and these areas also supported a moderate canopy cover, as estimated by Hansen et al. (2013), which was found to have strong inverse relationship with movement resistance (Hearn et al., Chapter 2). Hence, the cumulative summation of these values provided an overall moderate level of resistance in the empirically optimised model. This difference in inferred resistance value in these areas propagated to large differences in predicted population density, genetic diversity and population connectivity, with the Hearn et al. (Chapter 2) analysis predicting higher density, genetic diversity and connectivity in these parts of Sabah. It is impossible to determine based on the analyses in Hearn et al. (Chapter 2) which resistance parameterization is more accurate. Further work will be required to document patterns of density, genetic diversity and movement and/or genetic differentiation as a function of landscape features in this region of Sabah where the predictions described here differ.

Our third hypothesis proposed that, despite their differences, the overall pattern of predicted connectivity would be the same in the two models, identifying the same major core areas and main areas of connectivity between them. Our results largely support this hypothesis. Both analyses identified a large patch of core habitat with high predicted cumulative resistant kernel connectivity value in the YSFMA and contiguous commercial

Forest Reserves. Importantly, however, the analysis based on the Empirical model predicted this core area to extend west along the border with Kalimantan and Sarawak, in south-western Sabah, and also westward, encompassing and linking the mountainous areas of the Trus Madi Forest Reserve and Crocker Range and Kinabalu Parks. In contrast, the Expert-opinion based resistance model predicted these areas to have low connectivity and low rates of predicted movement of clouded leopards through them. So while the models agreed in terms of the location of the most important core area they differed substantially in the extent of that core population.

Despite their differences, both models agreed on the location and extent of the main isolated fragments of internally connected habitat. Namely, they each identified the Lower Kinabatangan floodplain, Tabin Wildlife Reserve and Tawau Hills Park as patches of habitat predicted to have extant clouded leopard populations, but predicted to be isolated from other clouded leopard populations. Efforts should be made to explore mechanisms to increase connectivity between these areas and the main central forest, such establishment of riparian corridors, and identification and/or creation of High Conservation Value forest areas within plantations landscapes.

To apply the Hearn et al. (Chapter 2) resistance model to the full extent of Sabah we assumed that all kinds of upland forest were equivalent, reclassifying two classes of montane forest to the same value as lowland tropical forest (which was present in the Hearn et al. (Chapter 2) study area. Whilst there are no empirical movement data to test these assumptions, occurrence data from camera trap studies support the notion that clouded leopards are found in these forested uplands (Chapter 6). However, in the absence of such empirical data, and since the movement model was based on data from a small number of individuals, we should view this model as preliminary.

Further research should not only strive to develop more realistic models of landscape connectivity for the Sunda clouded leopard in this state, but also to investigate how different landscape management approaches may best be suited to conserving this felid. The best way to resolve the differences between the empirical and expert-opinion predictions would be to obtain additional data on clouded leopard occurrence patterns, genetic structure and movement. Broad-scale monitoring of occurrence patterns would enable empirical estimates of distribution and abundance that could be used to validate the two predictions presented here. In addition, further work with empirical modelling of resistance based on telemetry in other parts of Sabah, ideally targeting the range of different age/sex classes, and focusing on habitat types not included in the current model, would help to generalize the empirical model across the broader extent, enabling more robust comparison of the Empirical vs. Expert-opinion models. This kind of meta-replicated study to generalise ecological relationships across broad scales has been highly useful for other carnivore species (e.g., Short Bull et al. 2011; Shirk et al. 2014), and has been identified as one of the keys to reliable inferences about pattern-process relationships at the landscape level (McGarigal and Cushman 2002). We hope that future work will help to close the gap in understanding through a combination of occurrence, genetics and movement modelling for this species across its range.

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Chapter 4. Spatio-temporal ecology of sympatric felids on Borneo.

Evidence for resource partitioning?

Abstract

Niche differentiation, the partitioning of resources along one or more axes of a species' niche hyper-volume, is widely recognised as an important mechanism whereby ecologically analogous, sympatric species can reduce interspecific competition and predation risk, and thus facilitate co-existence. Such resource partitioning may be facilitated by behavioural mechanisms operating primarily along three main axes of the niche dimension: habitat, food and time. In this study, we investigate the extent to which these mechanisms can explain the coexistence of a unique assemblage of five wild cat species living sympatrically in the forests of Borneo by drawing together and analysing an extensive photographic dataset of species from camera trap surveys of multiple areas in Sabah, Malaysian Borneo. Using multi-scale logistic regression, we show that Bornean felids exhibit differences in both their broad scale and fine scale habitat use. We quantify the temporal activity patterns for Bornean felids and a range of potential prey species, and calculate patterns of overlap between these species, and present evidence for temporal separation within this felid guild. Lastly, we conducted an all-subsets logistic regression to predict the occurrence of each felid species as a function of the occurrence of a range of potential prey species and showed that Bornean felids co-occurred with a range of other species, some of which could be candidate prey. Our study reveals a complex assortment of resource partitioning within the Bornean felid assemblage, operating along all three niche dimension axes.

Introduction

The fundamental mechanisms which facilitate the co-existence of animals and which in turn shape the composition of their communities are a central theme in ecology. Central to this debate is the role of interspecific competition, in which individuals of one species suffer a reduction in fecundity, survivorship and/or growth as a result of exploitative competition for a limited resource with another species, or through direct interference from another species (Miller, 1967). Such competition between species is rarely symmetrical, resulting in a competitive hierarchy within a community, and high levels of interspecific competition may lead to the local extinction of the inferior competitor (Begon et al., 1990). The existence of a large number of species coexisting sympatrically, whilst apparently competing for similar resources, suggests that there are mechanisms in place that enable species to avoid high levels of competition, and thus coexist. Differentiation of a species' niche has long been recognised as an important mechanism whereby ecologically similar, sympatric species may reduce both exploitative and interference interspecific competition, and thus enhance coexistence. Such resource partitioning may be facilitated by the displacement of morphological characters (Dayan and Simberloff, 2005) as well as via behavioural mechanisms, and is thought to operate primarily along three main axes of the niche dimension: habitat, food and time (Pianka, 1974; Schoener, 1974).

The extant members of the Felidae share a remarkably conserved morphology (Kitchener et al., 2010), and as obligate carnivores, typically specialising in mammalian prey, are likely constrained by significant intra-guild competitive forces. In addition, intra-guild killing, an extreme form of interference competition, is thought to be common among felids (Polis et al., 1989; Donadio and Buskirk, 2006). As such, sympatric guilds of felids provide a useful focal group in which to explore hypotheses pertaining to mechanisms of co-existence. Among felids, several authors have provided evidence of behavioural mechanisms which may facilitate co-existence, including differential use of space (e.g., Scognamillo et al., 2003, Palomares et al., 2016), prey species and size classes (e.g., Seidensticker, 1976; Bertram, 1982; Karanth & Sunquist, 2000) and temporal segregation (e.g., Harmsen et al., 2009; Lynam et al., 2013), or a combination of these mechanisms (e.g., Di Bitetti et al., 2010).

As with many ecological relationships, body size and morphological similarity are thought to be key factors influencing the competitive interactions among felids. Felids of comparable size are more likely to take more similar prey and thus interspecific competition should be highest among felid pairs as they become more closely matched in size (Jaksic and Marone, 2007). Conversely, Donadio and Buskirk (2006) explored the empirical evidence for killing events between carnivores and found that species pairs with intermediate differences in body size were more likely to be engaged in intra-guild killing events than those pairs with small or large body size differences, and that both the frequency and intensity of killing peaked when the larger species was 2–5.4 times the mass of the victim.

The forests of Borneo support a unique assemblage of five felids, which includes the Sunda clouded leopard, *Neofelis diardi*, bay cat *Catopuma badia*, marbled cat *Pardofelis marmorata*, leopard cat, *Prionailurus bengalensis* and flat-headed cat, *Prionailurus planiceps*. An understanding of the mechanisms which facilitate co-existence within this threatened wild felid guild may enhance the development of effective management practices, yet a lack of a detailed understanding of any of these felid's ecology has thus far been prohibitive. Nevertheless, incidental observations and preliminary modelling predictions of these felids' distributions on Borneo have begun to identify some possible mechanisms for co-existence within this guild.

While not well studied, the flat-headed cat is known to exhibit morphological adaptations which suggest it has evolved to hunt prey in shallow water, and incidental observations (e.g., Bezuijen, 2000) and presence-only habitat suitability modelling (Wilting et al., 2010, 2016) strongly suggest that this felid is restricted to low lying, wetland forest habitats not heavily utilized by the other guild members. Leopard cats, in contrast, and unlike the other guild members, appear to have an affinity for disturbed forest habitats and oil palm plantations where they seek their primary prey, murid rodents (Rajaratnam et al., 2007; Mohamed et al., 2013, Chua et al., 2016). Presence-only ecological niche modelling of leopard cats on Borneo confirms these associations (Mohamed et al., 2016), while similar predictive models of Sunda clouded leopard, marbled cat and bay cat distributions (Hearn et al., 2016a,b; Rustam et al., 2016) suggest they all select forest habitats and avoid oil palm plantations, but have failed to reveal any further habitat segregation among these felids. However, while Sunda clouded leopards and marbled cats are regularly recorded walking along the ground, morphological adaptations for an arboreal lifestyle (e.g., Sunquist & Sunquist, 2002) and incidental observations of both species hunting arboreal prey (e.g., Davis, 1962; Bories et al., 2014) suggest at least partial habitat segregation from that of the other, presumably terrestrial guild members. Further fine-scale differential use of habitats may also explain co-existence within this felid assemblage. Wearn et al. (2013) showed that detection probabilities in a highly degraded Bornean forest were significantly higher for clouded leopards along logging roads and skid trails, and higher for marbled cats along skid trails only, whereas no such associations were found for bay cats or leopard cats. Conversely, Mohamed et al. (2013) showed that leopard cat encounter rates from off-road camera traps were only 3.6–9.1% of those for on-road traps.

Bornean felids may also be partitioned along the spatial axes by responding differentially to habitat variables at different spatial scales. Several studies that have assessed multi-scale habitat selection optimization have shown that animals respond most strongly to habitat variables associated with human disturbance at relatively course scales, often far exceeding that of the animal's homerange, while typically selecting habitat variables for foraging or resting at fine spatial scales (Thompson and McGarigal, 2002; Wasserman et al., 2012; Mateo-Sanchez et al., 2014).

Telemetry data and camera trap records obtained throughout the diel period show that Sunda clouded leopards and leopard cats are primarily nocturnal (Rajaratnam et al., 2007; Hearn et al., 2013; Mohamed et al., 2013; Ross et al., 2013). Camera trap records have been used to describe activity patterns of the other three felids, but very small sample sizes have prevented robust inference (e.g., Cheyne and Macdonald, 2011; Lynam et al., 2013). It is likely, however, that Bornean felids partition along the temporal axis.

In the absence of further detailed ecological information, examination of body sizes may reveal predictions about potential competitive interactions within the Bornean felid assemblage. The Sunda clouded leopard appears to exhibit a large degree of sexual dimorphism, with males reaching weights of around 24 kg whereas females are around 12 kg (Table 1). The four other members of the felid guild are significantly smaller than this, and thus presumably competitively subordinate, and exhibit largely overlapping body sizes (Table 1). Accordingly, competition for prey should be highest among the four smaller species. Carbone et al. (1999) identified a threshold in carnivore mass of 21.5 - 25.0 kg above which carnivores shift from taking prey of less than half the predator mass to preying on species of equal or greater mass to themselves, and Macdonald et al. (2010) developed this relationship for wild felids. Thus we would expect that the four smaller felids would prey primarily on species <1.5 kg. Indeed, leopard cats are known to be murid rodent specialists (Rajaratnam et al., 2007), and flat-headed cats are specialists of small, aquaticassociated prey (Muul and Lim, 1970), but we have no quantitative data regarding the prey for the other two small felids.

In this study, we draw together the largest dataset collected to date of Bornean felid records derived from extensive camera trap surveys of multiple areas in Sabah, Malaysian Borneo to examine the evidence for resource partitioning and thus potential mechanisms of co-existence within the Bornean felid assemblage. We use the following approaches: 1. Multi-scale habitat modelling, to identify the habitat variables and scales that influence Bornean felid occurrence across the landscape and to refine current predictions of these felids' distribution; 2. All subsets logistical regression to explore the spatial co-occurrence of Bornean felids with other Bornean mammals and birds, to identify potential candidate prey species; 3. Modelling of photo capture events to assess and compare temporal activity patterns within the felid guild and to quantify overlaps in temporal activity between felids and potential candidate prey. We hypothesise that the highest levels of segregation along the spatial, temporal, and prey niche dimensions will be exhibited by species pairs with the greatest overlap in body size (i.e. between the 4 smaller species). We hypothesise that leopard cats will select disturbed areas at fine spatial scales and that, conversely, the Sunda clouded leopard, bay cat, marbled cat and flat-headed cat will all exhibit broad scale avoidance of disturbed habitats but will vary in their selection of optimal foraging habitat at fine scales. We also hypothesise that species that are predicted to incur a higher probability of intra-guild killing (i.e., all four small felids) will exhibit spatio-temporal avoidance of the larger and competitively dominant Sunda clouded leopard, and particularly females, with whom they share an intermediate difference in body size. Lastly, we predict that female Sunda clouded leopards, which will often be accompanied by cubs, will attempt to avoid encounters with male Sunda clouded leopards, and that their smaller body size will restrict them to prey size classes <6 kg, whereas the body size of males may enable them to prey upon a more diverse prey assemblage, including those of an equal mass (in excess of 20 kg).

Table 1. Body weight ratios (heavier/lighter) of adult Bornean felids. Values in bold highlight species pairs with intermediate differences in body size (ratio of 2–5.4), in which the larger of the pair is most likely to kill the smaller (Donadio and Buskirk, 2006). Underlined values highlight species pairs with very similar body sizes (ratio <2), which are predicted to compete for similar prey (Jaksic and Marone, 2007). Felid weight data derived from: [1] Hearn et al, 2003; Hearn unpublished data. [2] Selous and Banks, 1935. [3] Sunquist et al., 1994; Kitchener, et al., 2004. [4] Davis, 1962; [5] Sunquist and Sunquist, 2002; [6] M. Heydon Pers. comm., 2016. [7] Rajaratnam, 2000; Hearn unpublished data.

Species: Mean weight (SE) in kg, sample size	Sunda clouded leopard		bay cat	marbled cat	leopard cat	flat-headed cat
	males	females				
Sunda clouded leopard males: 24.4 (0.9), n=4 [1]	1	2.0	8.7	10.2	11.6	12.8
Sunda clouded leopard females: 12.5 (3.2), n=4 [1,2]		1	**4.5**	**5.2**	6.0	6.6
bay cat: 2.8 (0.6), n=3 [3]			1	<u>1.2</u>	<u>1.3</u>	<u>1.5</u>
marbled cat: 2.4 (0), n=2 [4,5,6]				1	<u>1.1</u>	<u>1.3</u>
leopard cat: 2.1 (0.4), n=19 [7]					1	<u>1.1</u>
flat-headed cat: 1.9 (0.3), n=4 [5]						1

Study Areas

This study was undertaken within eight forest landscapes and two oil palm plantations in the Malaysian state of Sabah, northern Borneo (Fig 1). We selected study areas such that they provided a broadly representative sample of the spectrum of land uses, elevations, anthropogenic disturbance and forest fragmentation present in the state (Table 2). Our study areas included three primary forests, including one predominantly lowland hill (Danum Valley Conservation Area: Danum Valley), and two largely hill dipterocarp and submontane forests (Tawau Hills Park (Tawau) and Crocker Range Park (Crocker)). We surveyed five forest areas which had been exposed to selective logging, including the Lower

Kinabatangan Wildlife Sanctuary (Kinabatangan), Tabin Wildlife Reserve (Tabin), and Kabili-Sepilok, Malua and Ulu Segama Forest Reserves. The selectively logged areas had large variation in respective levels of disturbance, isolation and fragmentation (Table 2). Our study areas also included two relatively mature oil palm plantation areas, Danum Palm and Minat Teguh plantations, both of which adjoined areas of forest.

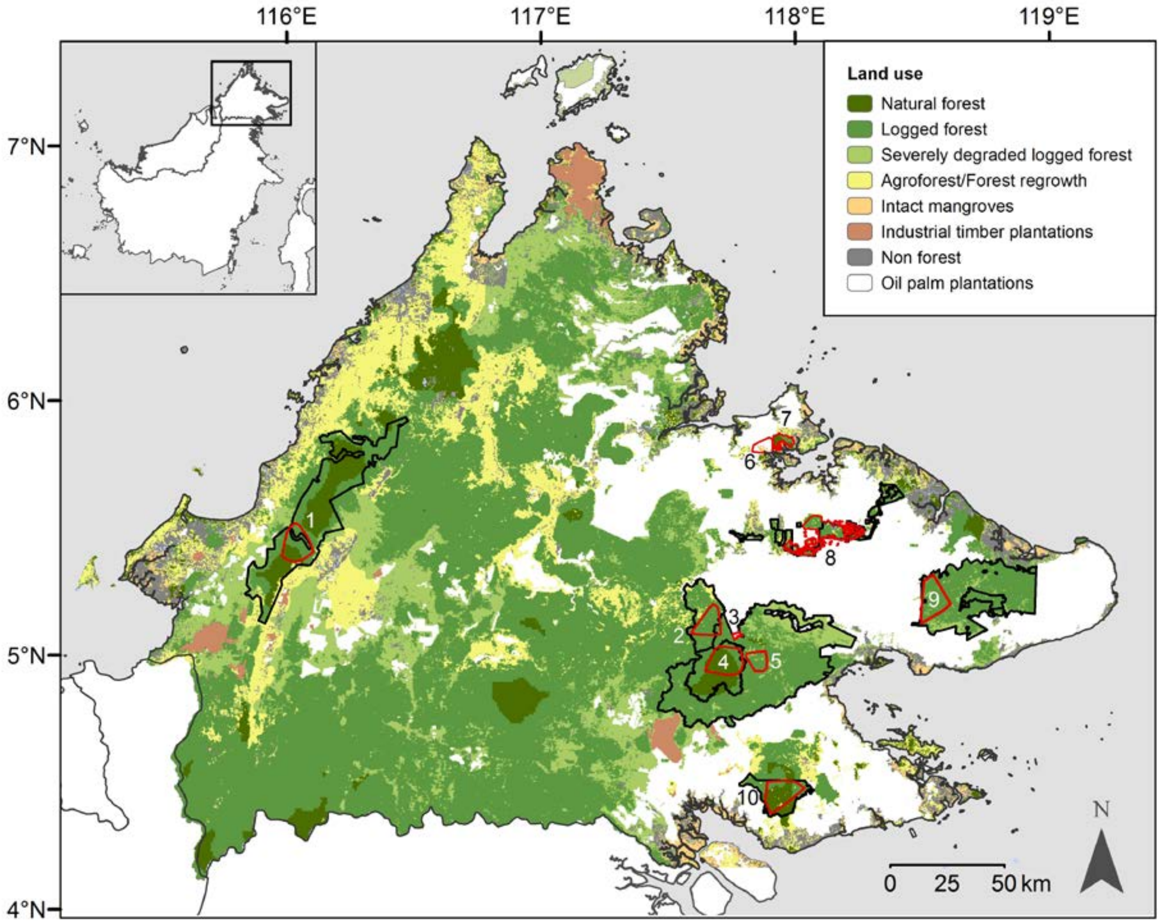

Fig 1. The locations of the eight forest and two oil palm plantation study areas in Sabah, Malaysian Borneo, showing land use in 2010 (Gaveau et al., 2014). Numbered polygons represent the different study areas, defined by the locations of the outermost camera stations: 1. Crocker Range Park; 2. Malua Forest Reserve; 3. Danum Palm Plantation; 4. Danum Valley Conservation Area (surveyed on two separate occasions); 5. Ulu Segama Forest Reserve; 6. Minat Teguh plantation; 7. Kabili-Sepilok Forest Reserve; 8. Lower Kinabatangan Wildlife Sanctuary; 9. Tabin Wildlife Reserve; 10. Tawau Hills Park (surveyed on two separate occasions). Inset shows the island of Borneo.

Table 2. Details of the eight forest and two oil palm plantation study areas in Sabah, Malaysian Borneo. [a] Dominant land cover classes in each study area, derived from data detailed in Gaveau et al. (2014), arranged in decreasing order of occurrence.

Study area	Lat/Lon	General description	Gaveau et al. (2014) landcover classes [a]
Crocker	5° 26′ N, 116° 02′ E	Primary, hill dipterocarp, sub-montane & montane.	Natural forest; Logged forest.
Danum Valley	4° 58′ N, 117° 46′ E	Primary, lowland & hill dipterocarp.	Natural forest; Logged forest.
Kabili-Sepilok	5° 51′ N, 117° 57′ E	Partially selectively logged, lowland Dipterocarp, heath forest & mangrove.	Natural forest; Logged forest; Intact mangrove; Non forest; Agroforest/Forest regrowth.
Kinabatangan	5° 29′ N, 118° 08′ E	Selectively logged, mosaic of forest types, including riparian forest, seasonally flooded forest, swamp forest, limestone forest.	Logged forest; Agroforest/Forest regrowth; Non forest
Malua	5° 08′ N, 117° 40′ E	Twice-logged (1960s & 2006-2007), lowland dipterocarp. High density of open logging roads and skid trails.	Logged forest; Agroforest/Forest regrowth.
Tabin	5° 14′ N, 118° 51′ E	Selectively logged (1969-1989), lowland dipterocarp. Low density of open and semi-closed logging roads.	Logged forest; Severely degraded forest.
Tawau	4° 27′ N, 117° 57′ E	Primary, lowland & hill dipterocarp, sub-montane & montane.	Natural forest, Logged forest; Agroforest/Forest regrowth
Ulu Segama	4° 59′ N, 117° 52′ E	Selectively logged (1978-1991), lowland Dipterocarp. Medium density of open and semi-closed logging roads.	Logged forest; Severely degraded forest.
Danum Palm	5° 05′ N, 117° 46′ E	Semi-mature (planted in 2000), terraced oil palm plantation. Largely open understorey. Semi-natural scrub bordering one large river and one stream.	Oil palm plantations.
Minat Teguh	5° 50′ N, 117° 53′ E	Mature (planted in 1995) oil palm plantation. Largely open understorey. Border fringed with mangrove.	Oil palm plantations; Intact mangroves; Natural forest, Non forest.

Methods

Data collection

Between May 2007 and December 2013, we conducted 12 intensive, systematic camera trap surveys within ten study areas, including repeat surveys of two sites, Danum and

Tawau. Due to financial and logistical constraints, we varied both the number of camera traps used and survey grid size at each survey area (Table 3). We deployed cameras at 578 camera stations over an elevation range of 5–1442m, and accumulated a total of 72,490 trap days (Table 3). We used passive infrared digital camera traps of varying models: Bushnell Trophycam 2010 (Bushnell Corporation, KS, USA), Cuddeback Capture (Non Typical Inc., WI, USA), Panthera V3 (Panthera, NY, USA), Reconyx HC500 and PC800 (Reconyx Inc., WI, USA) and Snapshot Sniper P41 (Snapshot Sniper LLC, OK, USA). We deployed cameras according to one of two protocols, using either a Split-grid approach, where the entire grid is sequentially surveyed in two halves, or a Simultaneous approach, where all camera stations are deployed in a single phase. We primarily deployed cameras along established and newly cut human trails and ridgelines in our forest surveys, and occasionally along old, unsealed logging roads, particularly in two of the selectively logged sites (Malua and Ulu Segama; Table 3). In the two plantation sites, we deployed cameras along access roads, human paths and narrow stretches of terrace (Danum Palm only). For the second survey of Tawau (Tawau 2), cameras were deployed following a stratified random placement approach, at approximately the same spacing as that used in the first survey of Tawau. In all survey areas, camera stations were spaced approximately 1.5–2.0 km apart and cameras were positioned around 40 cm above the ground and arranged in pairs to enable both flanks of the animal to be photographed simultaneously, to facilitate individual identification.

Table 3. Details of camera trap survey protocols for surveys of eight forest study areas and two oil palm plantations in Sabah, Malaysian Borneo. [a] Camera trap grid area is defined by a 100% Minimum Convex Polygon around all camera stations. [b] We followed two survey protocols, Split-grid: where the entire grid was sequentially surveyed in two halves, and Simultaneously (Sim): where all camera stations were deployed in a single phase. [c] values within parentheses represent the number of camera stations situated along forest roads and trails, respectively.

Study area	Camera trap grid				Survey effort	
	Area (km^2) [a]	Protocol [b]	No. cam. stations [c]	Mean elevation and range (m.a.s.l)	Survey dates	No. trap days
Crocker	149.7	Sim.	35 (3, 32)	1029 (383-1452)	6/10/11 - 27/2/12	4059
Danum Valley (1)	66.7	Sim.	23 (2, 21)	285 (175-554)	25/10/07 - 30/12/08	3857
Danum Valley (2)	157.0	Split	79 (0, 79)	384 (153-804)	24/3/12 - 6/10/12	5837
Kabili Sepilok	49.4	Sim.	35 (0, 35)	66 (8-134)	9/2/11 - 25/5/11	2054
Kinabatangan	359.5	Split	68 (0, 68)	35 (5-135)	24/7/10 - 17/12/10	4340
Malua	102.8	Sim.	38 (38, 0)	177 (68-286)	9/7/08 - 12/2/09	3869
Tabin	71.4	Split	37 (1, 36)	140 (11-407)	16/12/09 - 22/4/10	6462
Tawau (1)	149.0	Sim.	77 (0, 77)	706 (209-1195)	21/10/12 - 30/12/13	17397
Tawau (2)	135.7	Sim.	71 (0, 71)	671 (183-1102)	6/7/13 - 11/12/14	17596
Ulu Segama	60.1	Sim.	22 (19, 3)	252 (150-408)	24/5/07 - 18/10/07	2847
Danum Palm	7.8	Sim.	23	210 (120-295)	15/3/09 - 7/7/09	2212
Minat Teguh	44.0	Sim.	33	23 (1-49)	26/5/11 - 18/8/11	1960
Totals:	**1353.0**	-	**578**	-	-	**72490**

Multi-scale habitat modelling

Species respond to habitat variables in a scale dependent manor, and thus failure to incorporate explicit optimisation of spatial scale when examining species-habitat relationships may result in incorrect inferences regarding both the nature and strength of habitat selection (Thompson and McGarigal, 2002; Vergara et al., 2015; McGarigal et al., 2016). As such, we applied a univariate scaling optimization followed by all-subsets logistic regression (e.g., Chambers et al., 2016; McGarigal et al., 2016) to investigate multiple-scale habitat selection by Bornean felids.

We pooled photographic capture detection data of each Bornean felid species from all survey effort, resulting in 578 sampling units for each felid. We reduced our Bornean felid photographic capture dataset to independent detection events by removing all photographs recorded within one hour of a previous photograph of the same species, at the same camera station, and summed the number of independent captures for each felid at each camera station.

We selected several habitat variables we believed may be strongly related to Bornean felid occurrence based on previous research (Hearn et al., 2016a,b; Mohamed et al., 2016; Rustam et al., 2016; Wilting et al., 2016; Chapter 2) (Appendix 1). We used a 250 m spatial resolution 2010 land cover map (13 classes) developed by Miettinen et al. (2012), and a 50 m resolution 2010 forest quality and land use cover map of Borneo (9 classes), developed by Gaveau et al. (2014). We used a historic land cover layer, developed by the Sabah Forestry Department (SFD), which provides an estimation of forest type cover (24 classes) based on soil and elevation associations at a point in time before anthropogenic modification. We extracted this layer to the Gaveau et al. (2014) 2010 forest cover extent, to account for forest conversion. We used a 1 km spatial resolution above-ground carbon layer (Baccini et al., 2012). We used a layer developed by Hansen et al. (2013) which depicts canopy cover at 30 m resolution, and two layers detailing both sealed and logging roads in 2013 (unpublished data).

We performed the logistic regression analyses in three stages. First, we undertook a univariate logistic regression and scaling analysis to identify the spatial scale at which each habitat variable was most strongly related to each Bornean felid's occurrence (e.g., Grand et al., 2004, Wasserman et al., 2012), applying the following spatial scales of analysis: 120, 240, 480, 960, 1920, 3840 and 7680 m focal-radius moving window. We determined the optimal scale at which each variable was most highly related to Bornean felid occurrence by selecting the scale with the lowest AIC value, and excluded all other scales for each variable from further analysis. Due to the clustered nature of the camera trap stations within study areas a Mixed model would have been preferable, but using this approach the models failed to converge and so we used a standard General Linear model (e.g., Zeller et al., 2015). We identified and retained the variables with univariate logistic regression *p*-values of ≤0.2, and excluded all other variables from subsequent analysis. We used the 0.20 *p*-value cut-off for the univariate analysis because variables that are individually non-significant may interact significantly in multivariate models (e.g., Krishnamurthy et al., 2016). In the second stage, we conducted correlation tests between all possible pairs of scale-optimised variables, identifying pairs with a Pearson's correlation value greater than 0.7, and retained the variable in each such pair with the lower AIC value. Lastly, we ran all-subsets logistic regression analyses with Dredge function in MuMIN in R to obtain final model averaged coefficients for each species. We created maps of probability of occurrence across Sabah as a function of the final averaged model for each felid using the equation $p = \exp(z) / (1 + \exp(z))$, where z is the linear combination of coefficients multiplied by the independent variables.

We also used univariate logistic analyses to explore the relationship between Bornean felid occurrence and two fine scale variables that are not available at the regional extent, including whether the cameras were placed on unsealed logging roads and topographical ridgelines. Previous studies have shown significant relationships with logging roads, both positive and negative, among Bornean felids (Wearn et al., 2013; Mohamed et al., 2013) and we hypothesise that ridgelines may be preferentially selected by some Bornean felids to facilitate movement. We were interested in the possible difference between male and female Sunda clouded leopards, and so we undertook separate analyses for each sex. We defined camera stations as being placed on logging roads and ridgelines via observation during camera deployment and by visually inspecting topographical maps.

Felid/candidate prey co-occurrence all-subsets modelling

We conducted an all-subsets logistic regression to explore the co-occurrence of a range of mammalian and avian species with the Bornean felids, as a tool to identify potential candidate prey species. First, we prepared the potential prey variables by reducing all non-felid photographic detection data for each species into independent capture events, following the same procedure as for the felid detection data, and summed the detections per camera station. Two closely related species pairs were not always readily distinguishable from one another, including two mousedeer and two muntjac species, and due to their morphological parallels may present similar prey selectivity for the felids, and so we combined each pair into one variable, as well as including them as separate variables (Appendix 2). Similarly, we produced eight additional potential prey variables by combining data from a number of species with similar morphological and/or ecological niches (Appendix 2). We restricted subsequent analyses to only those species or species groups with samples of ≥ 20 (Appendix 2). Next, we conducted an all-subsets logistic regression modelling with Dredge function in the MuMIN library in R, predicting each felid species as a combination of the abundance of potential prey species co-occurring at camera stations. We produced final model averaged parameter values for the regression models predicting each felid species as functions of co-occurrence of potential prey.

Temporal activity of felids and potential prey

We used our photographic detection dataset to characterise the temporal activity patterns of sympatric Bornean felids and potential prey species and to quantify the extent of temporal overlap between them. We followed the statistical approach developed by Ridout & Linkie (2009) and performed all analyses in R version 3.1.2 (R Development Core Team, 2014) using program Overlap (Linkie & Ridout, 2011; Meredith & Ridout, 2016). First, we assumed that capture times for each species were a random sample of photographs taken at any time of the day (Ridout & Linkie, 2009). Second, we computed each species' or species group's terrestrial activity pattern independently using non-parametric von Mises kernel density estimation, which corresponds to a circular distribution (Ridout & Linkie, 2009), using the default smoothing value of 1.0. For the felid species, we also calculated the proportion of the density that lies within the dawn and dusk (denoted crepuscular), day (denoted diurnal), and night (denoted nocturnal) time periods. We defined dawn (05:00-07:00) and dusk (17:00-19:00) time periods as one hour pre and post sunrise/sunset, and the intervening periods as day (07:00-17:00) and night (19:00-05:00). Lastly, we calculated a measure of overlap between Bornean felids and between the felids and all other species and species groups using the coefficients of overlapping, Δ_1 and Δ_4, which range from 0 (no overlap) to 1 (complete overlap). Following the recommendation of Ridout & Linkie (2009), we used their estimators Δ_1 and Δ_4 when the smaller of the two samples had <75 and ≥75 records, respectively. We obtained confidence intervals as percentile intervals from 10,000 smoothed bootstrap samples. We assessed the significance of temporal activity overlap by computing the 5th and 95th percentiles of the coefficients of overlapping (Δ_1 and Δ_4) values between all possible paired focal species. We identified which species exhibited significantly low overlaps with Bornean felids and those which showed significantly high overlap patterns, which we defined as below the 5th percentile or above the 95th percentile of overlap across all species, respectively. We also identified species which had relatively high and low overlaps with Bornean felids, which we defined as below the 10th percentile and above the 90th percentile of overlap across all species, respectively.

Results

Bornean felid detection dataset

The camera surveys yielded 2883 independent detections of Bornean felids (Table 4). Felid guild composition ranged from 4–5 species for 5 of the forest study areas, dropping to 3 at the higher elevation Crocker, and 1 within the highly fragmented and comparatively small Kabili-Sepliok (Table 4). Sunda clouded leopards and marbled cats were recorded at all but one forest site, Kabili-Sepilok. Leopard cats were recorded at all forest sites and were the only felids to be recorded within our two oil palm plantation areas, although an individual marbled cat was recorded walking along the forest/plantation interface in Danum palm. In contrast, flat-headed cats were recorded within only two study areas, at two cameras stations and on only four occasions. Due to the shortfall in detection data for the flat-headed cat, subsequent analyses focus on the other four Bornean felids. Our survey efforts yielded 65,536 independent detections of non-felid animals, representing at least 148 species. Of these, 58 species or species groupings had detection sample sizes ≥20 and were subsequently used in the prey-all subsets and temporal activity modelling (Appendix 2).

Leopard cats were recorded over the entire elevation range surveyed (5–1452 m), with records from 10 to 1422 m. Comparison of leopard cat kernel density with that of the available survey sites suggests that they had a slight preference for lower elevation sites. Sunda clouded leopards and marbled cats shared a very similar elevational distribution and were recorded over much of the elevation range sampled, with Sunda clouded leopard recorded from 17 to 1452 m, and marbled cats from 32 to 1342 m. Kernel density estimates for both of these felids suggested a preference for higher elevation sites (600–1000 m). Bay cats were recorded over a more restricted elevational range, from 127 to 1051 m, and showed a bimodal kernel density distribution, with peaks at around 250 m and 800 m. We recorded flat-headed cats only in the lowlands, at 18 and 180 m.

Table 4. Bornean felid detection data derived from 12 camera trap surveys of 10 study areas in Sabah, Malaysian Borneo. [a] Number of photographic captures of the same species or different individuals (patterned felids) per camera station, obtained ≥1 hour apart; [b] Number of independent photographic captures per 100 camera trap nights.

Study area	No. independent captures [a] (Detection frequency [b])						
	Sunda clouded Leopard			Leopard cat	Bay cat	Marbled cat	Flat-headed cat
	pooled	males	females				
Danum Valley (1 & 2)	100 (1.032)	90 (0.928)	10 (0.103)	39 (0.402)	11 (0.113)	42 (0.433)	1 (0.010)
Tawau (1 & 2)	339 (0.969)	302 (0.863)	37 (0.106)	128 (0.366)	42 (0.120)	88 (0.251)	0
Crocker	51 (1.256)	46 (1.133)	5 (0.123)	28 (0.690)	0	11 (0.271)	0
Tabin	41 (0.634)	36 (0.557)	5 (0.077)	191 (2.956)	3 (0.046)	42 (0.650)	0
Ulu Segama	83 (2.915)	71 (2.494)	12 (0.421)	494 (17.352)	2 (0.070)	7 (0.246)	0
Malua	11 (0.284)	8 (0.207)	3 (0.078)	272 (7.032)	3 (0.078)	5 (0.129)	0
Kinabatangan	15 (0.730)	8 (0.389)	7 (0.341)	21 (1.022)	0	5 (0.243)	3 (0.146)
Kabili Sepilok	0	0	0	12 (0.276)	0	0 (0)	0
Danum Palm	0	0	0	624 (28.210)	0	5 (0.226)	0
Minat Teguh	0	0	0	164 (8.367)	0	0 (0)	0
Total	**640**	**561**	**79**	**1973**	**61**	**205**	**4**

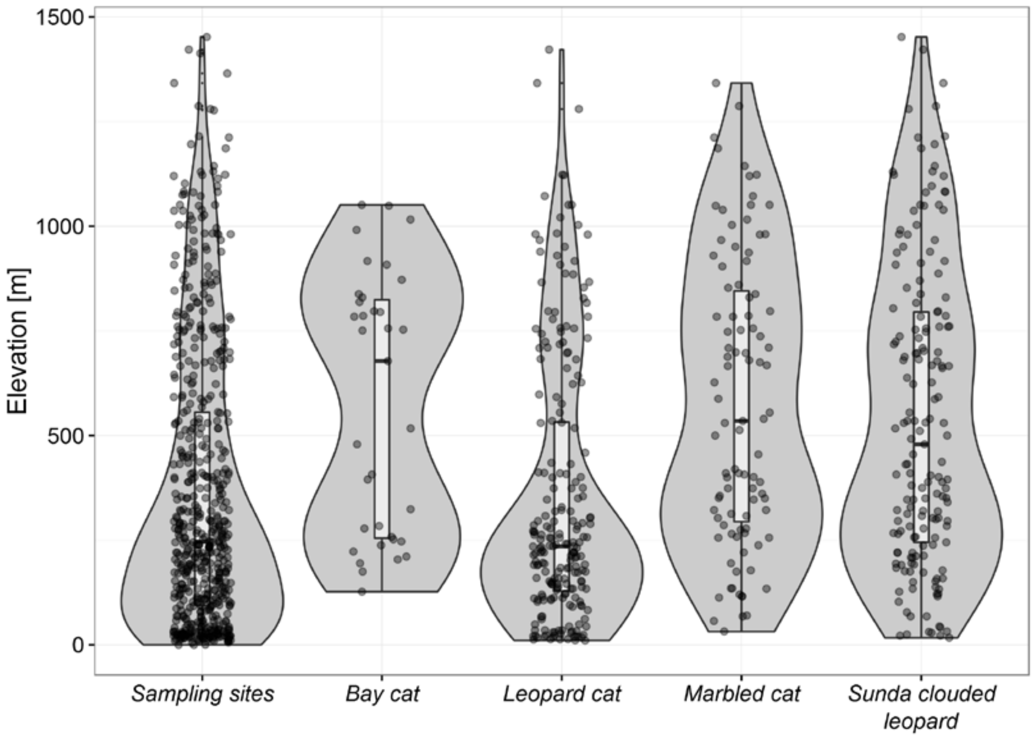

Figure 2. Violin plots displaying the elevational distribution over which Bornean felids were detected by camera traps. The diameter of the plot indicates the kernel density of the elevational range of each species (Hintze & Nelson 1998). The boxplot shows the median elevational value and delineates the 25th and 75th percentile range for each species. The circular dots represent actual records of camera stations at which felids were detected and are arbitrarily assigned to either side of the midline.

Multi-scale habitat modelling

The univariate scaling analyses showed that the strength of the relationship between Bornean felid occurrence and predictor habitat variables was highly dependent on the spatial scale at which each variable is derived, and that directionality of the relationship was reversed under some focal scales (Appendix 3, 4, 5). Following the univariate scaling and variable correlation analyses there were 13, 14, 14, and 13 final habitat covariates for

Sunda clouded leopard, bay cat, marbled cat and leopard cat, respectively, for use in the multivariate analyses.

Bornean felids differed in their respective relationships with habitat covariates (Table 5). Sunda clouded leopard occurrence was positively related to SFD: Lowland Mixed Dipt. Forest at the 480 m focal-radius, and elevation at the 120 m focal-radius, and showed a negative relationship with human footprint, tree cover and Miet: Plantation/regrowth, all at the 7680 m focal-radius. Sunda clouded leopards were most closely associated with areas with high levels of dipterocarp forest at relatively fine spatial scales, at high elevations within broad landscapes with low levels of human footprint, tree cover and areas of plantation and scrub lands at broad spatial scales (Table 5).

Bay cat occurrence was most strongly and negatively influenced by Tree cover SD at the 960 m focal-radius. Human footprint at the 3840 m focal-radius also had a negative relationship with bay cat occurrence, but the effect was less influential. Thus bay cats were most closely associated with areas of low fragmentation and low human footprint at relatively broad scales (Table 5).

Marbled cat occurrence was most strongly and negatively influenced by Tree cover SD at the 3840 m focal-radius, followed by a moderate positive relationship with SFD: Lowland mixed Dipt. forest & limestone veg. at the 120 m focal-radius and roughness at the 960 m focal-radius. This felid was also negatively influenced by Human footprint at the 3840 m focal radius, and showed a weak negative relationship with Miet: Plantation/regrowth at the 3840m and a weak positive relationship with elevation at the 120 m focal-radius. Optimal habitat for marbled cats is therefore areas of higher elevation dipterocarp and limestone forest at fine scales, with rough topography at the moderate scale and with low levels of fragmentation, human footprint and areas of oil palm and scrub lands at the relatively broad scales (Table 5).

The habitat variables influencing leopard cat occurrence differed more starkly than from the other three felids. Leopard cat occurrence was most strongly and positively associated with Gav: Oil palm plantations at the 480 m focal-radius, and was negatively associated with Miet: Lowland mosaic at the 3840 m focal-radius, elevation at the 1920 m focal-radius and Miet: Plantation/regrowth at the 7680 m focal-radius. Optimal habitat for leopard cats is therefore areas of oil palm plantations at relatively fine spatial scales, at lower elevations at relatively broad scales, and with low levels of mosaic and regrowth areas at broad scales (Table 5).

The greatest differences in predicted occurrence were shown between the leopard cat and the other 3 felids, and the highest similarity in predicted occurrence was exhibited between marbled cat and clouded leopard, followed by marbled cat and bay cat (Figure 3). Pearson's correlation between probability of occurrence values across the surfaces and absolute differences in probability of occurrence across the surfaces strongly support this view (Table 6).

Table 5. Results of multivariate analysis. Standardised regression coefficients (β) and AIC importance for habitat variables with significant univariate relationship to Bornean felid occurrence. Adjusted SE β: adjusted standard error of standardised regression coefficient.

Species/variable	Optimal scale (m)	β	Adjusted SE β	z value	AIC imp.	p-value	
Sunda clouded leopard							
(Intercept)	-	-2.2348	0.2573	8.687		2.00E-16	***
Effort	-	0.0077	0.0015	5.036	1	5.00E-07	***
Human footprint	7680	-0.7342	0.2138	3.433	1	0.0006	***
SFD: Lowland Mixed Dipt. forest	480	0.9610	0.2842	3.381	1	7.22E-04	***
Elevation	120	0.4482	0.1395	3.212	1	1.32E-03	**
Tree cover	7680	-0.6267	0.2446	2.562	1	0.0104	*
Miet: Plantation/regrowth	7680	-0.3998	0.1672	2.391	1	0.0168	*
Gav: Agroforest/forest regrowth	7680	0.0802	0.1695	0.473	0.29	0.6359	
Bay cat							
(Intercept)	-	-5.3178	0.9891	5.376		1.00E-07	***
Effort	-	0.0080	0.0020	4.012	1	6.03E-05	***
Tree cover SD	960	-3.1656	1.9542	1.62	1	0.1050	
Human footprint	3840	-0.2944	0.2810	1.048	0.71	0.2950	
Roughness	7680	-0.0846	0.3474	0.244	0.49	0.8080	
Marbled cat							
(Intercept)	-	-2.8765	0.2912	9.877		2.00E-16	***
Effort	-	0.0061	0.0016	3.863	1	0.000112	***
SFD: Lowland mixed Dipt. forest & limestone veg.	120	0.4305	0.1251	3.441	1	0.0006	***
Tree cover SD	3840	-0.5979	0.2805	2.132	0.93	0.0330	*
Roughness	960	0.4234	0.2033	2.083	0.85	0.0372	*
Human footprint	7680	-0.4000	0.2113	1.893	0.82	0.0584	.
Miet: Plantation/regrowth	3840	-0.2668	0.2273	1.174	0.31	0.2404	
Elevation	120	0.1415	0.2073	0.682	0.19	0.4950	
Gav: Agroforest/forest regrowth	7680	-0.0772	0.2034	0.38	0.1	0.7042	
Leopard cat							
(Intercept)	-	-1.2990	0.2051	6.334		2.00E-16	***
Gav: Oil palm plantations	480	0.9168	0.1563	5.866	1	2.00E-16	***
Effort	-	0.0062	0.0014	4.469	1	7.90E-06	***
Miet: Lowland mosaic	3840	-0.6901	0.1654	4.173	1	3.01E-05	***
Elevation	1920	-0.3627	0.1401	2.589	1	0.0096	**
Miet: Plantation/regrowth	7680	-0.2487	0.1240	2.006	0.86	0.0448	*
Gav: Agroforest/forest regrowth	3840	0.1482	0.1350	1.098	0.34	0.2722	
SFD: Lowland mixed Dipt. forest & limestone veg.	7680	-0.1438	0.1748	0.823	0.26	0.4106	
Tree cover SD	240	0.0489	0.1633	0.299	0.15	0.7648	
Human footprint	960	-0.0142	0.1260	0.113	0.14	0.9103	

Table 6. Relationship between occurrence probability map predictions for the four felid species. Lower triangle shows Pearson's correlation between probability of occurrence values across the surfaces. Upper triangle is the mean absolute difference in probability of occurrence across the surfaces.

	Bay Cat	Leopard Cat	Marbled Cat	Clouded Leopard
Bay Cat	x	0.326	0.142	0.224
Leopard Cat	-0.214	x	0.304	0.356
Marbled Cat	0.7242	-0.2315	x	0.104
Clouded Leopard	0.6617	-0.3075	0.878	x

Sunda clouded leopards and marbled cats showed a broadly similar distribution pattern. All of the relatively large and more contiguous forest patches were associated with higher predicted occurrence of these felids, and occurrence tended to be highest within the mid to higher elevation forest areas, and interior areas away from the forest patch edges. The areas of severely degraded logged forest and Agroforest/forest regrowth along the western coastal region, and the oil palm plantation dominated areas in the east presented the lowest predicted probability of occurrence for both Sunda clouded leopard and marbled cat. Sunda clouded leopards, however, exhibited low to moderate predicted occurrence in a number of relatively small forest patches, such as the Kinabatangan, whereas marbled cat occurrence was predicted to be very low, and the occurrence of clouded leopards was more positively influenced by higher elevation. As with Sunda clouded leopards and marbled cats, bay cats showed a very low predicted occurrence throughout all non-forest areas, but unlike the two other felids, areas of moderate to high levels of occurrence for the bay cat were primarily restricted to the core central forest area.

In stark contrast to the three other felids, leopard cats were predicted as having very high occurrence throughout the oil palm dominated lowland landscape in eastern Sabah, and only moderate predictions of occurrence within the more heavily forested regions.

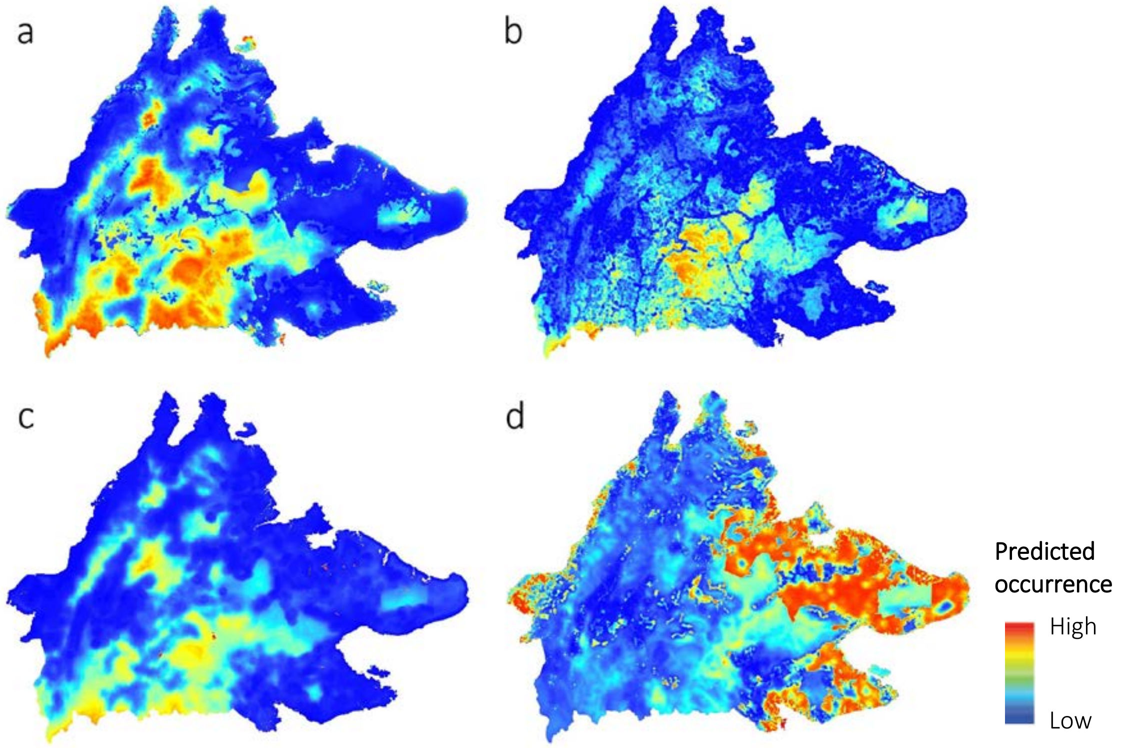

Figure 3. Maps showing the predicted occurrence of 4 species of Bornean felid based on multiscale habitat modelling. a: Sunda clouded leopard; b: Bay cat; c: Marbled cat; d: Leopard cat.

Univariate logistic regression analyses revealed that Bornean felids exhibited large differences in their respective use of roads and ridgelines (Table 7). Male Sunda clouded leopard occurrence was positively associated with roads and strongly and positively associated with ridgelines (Table 7). Conversely, both female Sunda clouded leopard and bay cat occurrence was unrelated to either roads or ridgelines. Leopard cat occurrence was strongly and positively associated with roads but no relationship was found with ridgelines, whereas, contrastingly, marbled cat occurrence was unrelated to roads but strongly and positively associated with ridgelines (Table 7).

Table 7. Univariate logistic regression results for Bornean felid association with roads and ridgelines.

	Variable	Coefficient	AIC	*p*-value
Sunda Clouded leopard (males)	Road	0.5826	605.01	0.0368
	Ridgeline	2.5840	493.06	$< 2E^{-16}$
Sunda Clouded leopard (females)	Road	0.3595	363.32	0.386
	Ridgeline	0.5515	361.04	0.077
Bay cat	Road	0.6518	238.81	0.218
	Ridgeline	0.5065	238.59	0.198
Marbled cat	Road	-0.0175	485.64	0.962
	Ridgeline	1.6415	445.03	$9.53E^{-11}$
Leopard cat	Road	2.7040	680.48	$2.67E^{-14}$
	Ridgeline	0.0305	767.9	0.890

Bornean felid temporal activity patterns

Based on kernel density estimates of temporal activity we found that Bornean felids varied greatly in how they utilised the diel period (Table 8; Figure 4). Male and female Sunda clouded leopards were the most cathemeral, but were particularly active at night and least active at midday. Males showed a clear peak in activity at dawn, whereas females did not, but instead exhibited a peak in activity around midnight. Bay cats and marbled cats exhibited strongly diurnal activity patterns, with both showing little nocturnal activity, particularly bay cats. Both bay cats and marbled cats showed peaks in activity at dawn, and also around or just after midday, although the latter was more markedly so in the bay cat. Activity increased around the dusk period in marbled cats, and decreased sharply after sunset, whereas activity in bay cats fell steadily after peaking during the middle of the day.

Leopard cats were the most nocturnal of all the Bornean felids, and exhibited a sharp fall in activity before and during the dawn period, and a similarly sharp rise in activity during the dusk period. Low numbers of flat-headed cat photographic detections prohibited detailed analysis of activity, but of four records, two were at dawn, and two at night.

Table 8. Probability density mass of temporal activity of Bornean wild cats within four different time periods, expressed as a percentage of the total mass; values within parentheses are the percentage of the total mass that each hour within the respective time period contains. [a] Time periods are as follows: Dawn: 05:00–0700; Day: 07:00–17:00; Dusk: 17:00–19:00; Night: 19:00–05:00.

Species	Probability density mass for time period [a]:			
	Dawn	Day	Dusk	Night
Sunda clouded leopard (males)	13.3 (6.6)	23.9 (2.4)	6.6 (3.3)	56.1 (5.6)
Sunda clouded leopard (females)	8.2 (4.1)	26.3 (2.6)	7.9 (4.0)	57.9 (5.8)
Leopard cat	9.3 (4.7)	4.0 (0.4)	6.2 (3.1)	81.0 (8.1)
Bay cat	8.5 (4.2)	81.0 (8.1)	7.8 (3.9)	2.3 (0.2)
Marbled cat	13.8 (6.9)	62.2 (6.2)	11.9 (6.0)	11.2 (1.1)

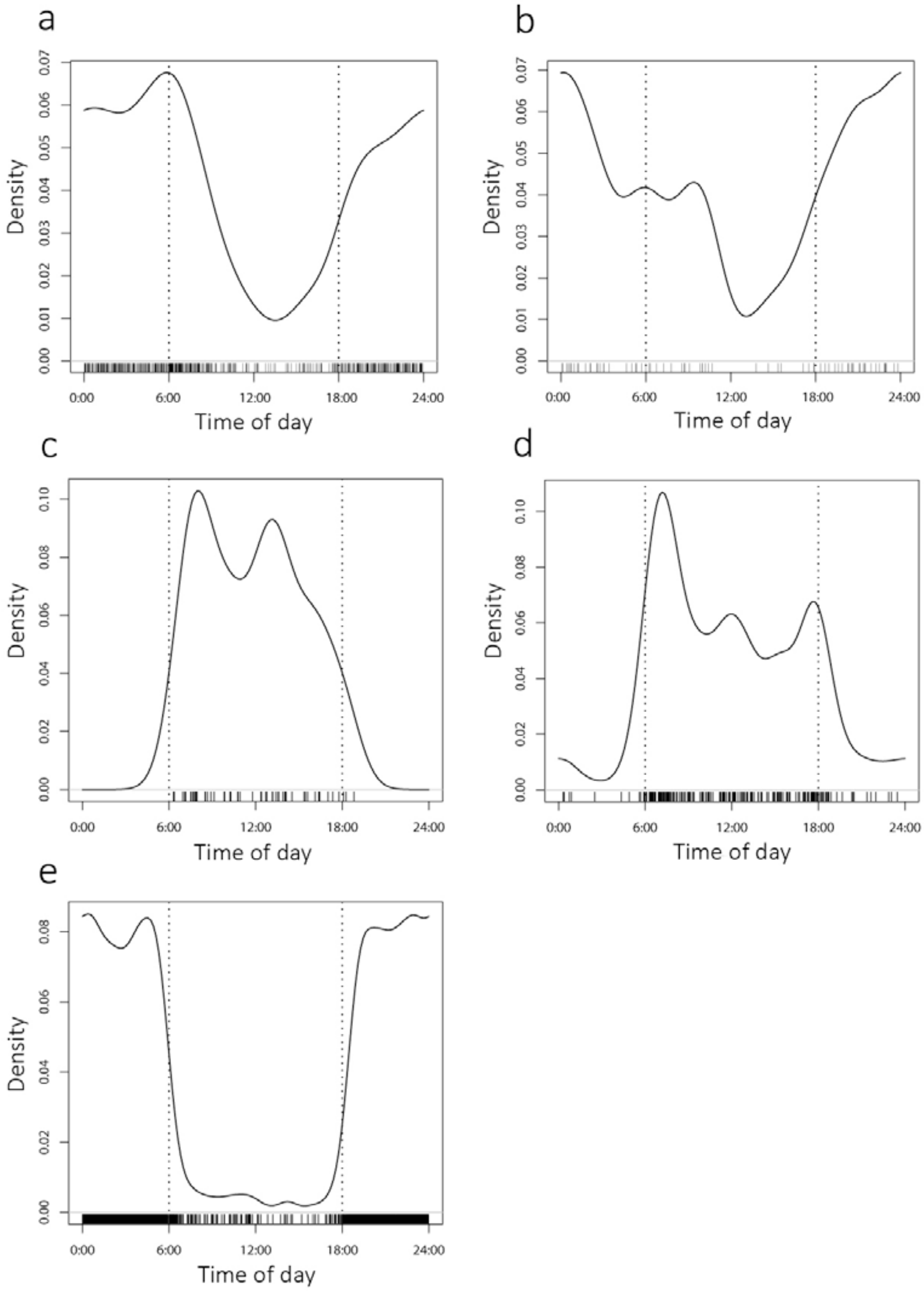

Figure 4. Temporal activity patterns of four sympatric Bornean felid species as estimated by kernel density estimates: a: Sunda clouded leopard males; b: Sunda clouded leopard females; c: bay cat; d: marbled cat; e: leopard cat. Activity data were derived from pooled camera trap surveys of ten study areas in Sabah, Malaysian Borneo. Dotted vertical lines indicate approximate times for dawn and dusk, and individual photographic detection times are indicated by the short vertical lines above the x-axis.

High levels of temporal overlap were exhibited between male and female Sunda clouded leopards (Δ_4 0.873), and between leopard cats and both male (Δ_4 0.739) and female (Δ_4 0.734) Sunda clouded leopards (Figure 5). Temporal overlap between bay cats and marbled cats was also high (Δ_1 0.787), whereas leopard cats exhibited low overlap with both bay cats (Δ_1 0.147) and marbled cats (Δ_4 0.264) (Figure 5). Moderate levels of overlap were exhibited between bay cat and Sunda clouded leopard males (Δ_1 0.396) and females (Δ_1 0.411) and between marbled cat and Sunda clouded leopard males (Δ_4 0.520) and females (Δ_4 0.525) (Figure 5).

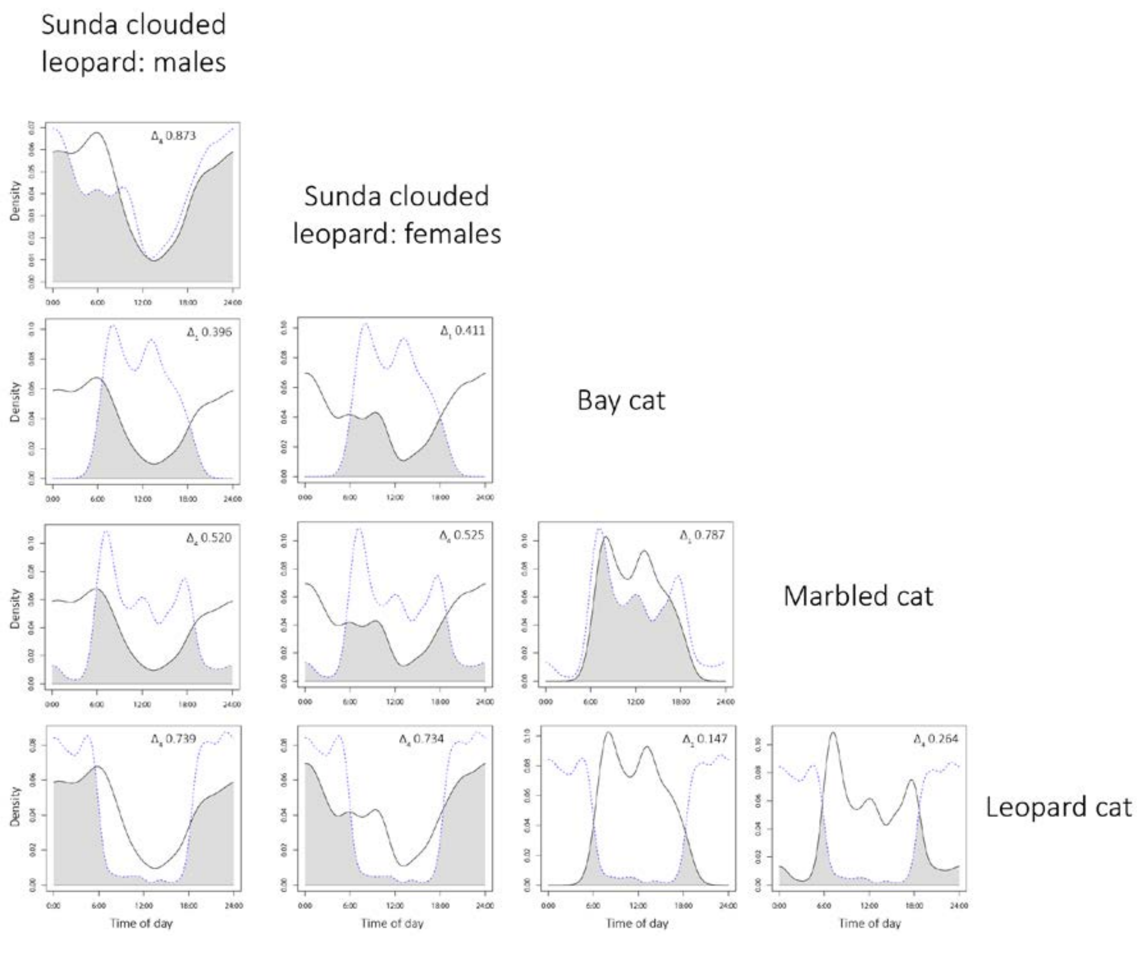

Figure 5. Overlaps of temporal activity patterns between Bornean wild cat species pairs, as estimated by kernel density estimates. The species in each column and each row are represented by solid lines and blue dotted lines, respectively. The coefficient of overlap (Δ_1 and Δ_4) is shown by the grey shaded areas which represent the overlap periods.

Temporal activity relationships between Bornean felids and potential prey

We calculated the temporal overlaps between each Bornean felid and all potential prey species or species groups (Appendix 6). Bornean felids exhibited significantly non-random temporal overlap relationships with a range of different potential prey species or species groups (Figure 6). Male Sunda clouded leopards showed significantly non-random temporal activity associations (above 95th percentile of overlap coefficient values) with sambar deer, female clouded leopard and greater mouse deer, and relatively high temporal associations (above the 90th percentile) with all mousedeer, masked palm civet and leopard cat. Male Sunda clouded leopards also showed significantly non-random temporal separation with pig-tailed macaque, tufted ground squirrel and greater coucal (below the 5th percentile) and relatively high temporal separation (below the 10th percentile) with great argus pheasant, long-tailed macaque and emerald dove (Figure 6).

Female Sunda clouded leopards showed similar temporal overlap relationships with potential prey species as males, except that females also showed relatively high temporal associations with Malay civet, Hose's civet and sun bear, and in females, pig-tailed macaques were below the 10th percentile as opposed to below the 5th (Figure 6).

Bay cats showed significantly non-random temporal activity associations with short-tailed mongoose, pig-tailed macaque, all small birds and pig juveniles, relatively high temporal associations with orang utan and blue-headed pitta, significantly non-random temporal separation with long-tailed and common porcupines, and relatively high temporal separation with banded palm civet, rat spp., Malay badger and common palm civet (Figure 6). Furthermore, while not significant at the level we measured, temporal overlap coefficients were extremely high between bay cat and all partridges, all pheasants, Bulwer's pheasant, crested fireback, crested partridge, great Argus pheasant (Appendix 6).

Marbled cats showed significantly non-random temporal activity associations with all muntjac, Bornean yellow muntjac, pig and pig adult, relatively high temporal associations with red muntjac and crested fireback, significantly non-random temporal separation with long-tailed macaque and rat spp., and relatively high temporal separation with Malay badger, banded palm civet, pangolin and otter civet (Figure 6). Leopard cats showed significantly non-random temporal activity associations with Malay civet, common palm civet, Hose's civet and moon rat, relatively high temporal associations with thick-spined porcupine and banded linsang, significantly non-random temporal separation with greater coucal, tufted ground squirrel and pig-tailed macaque, and relatively high temporal separation with great Argus pheasant, emerald dove and long-tailed macaque.

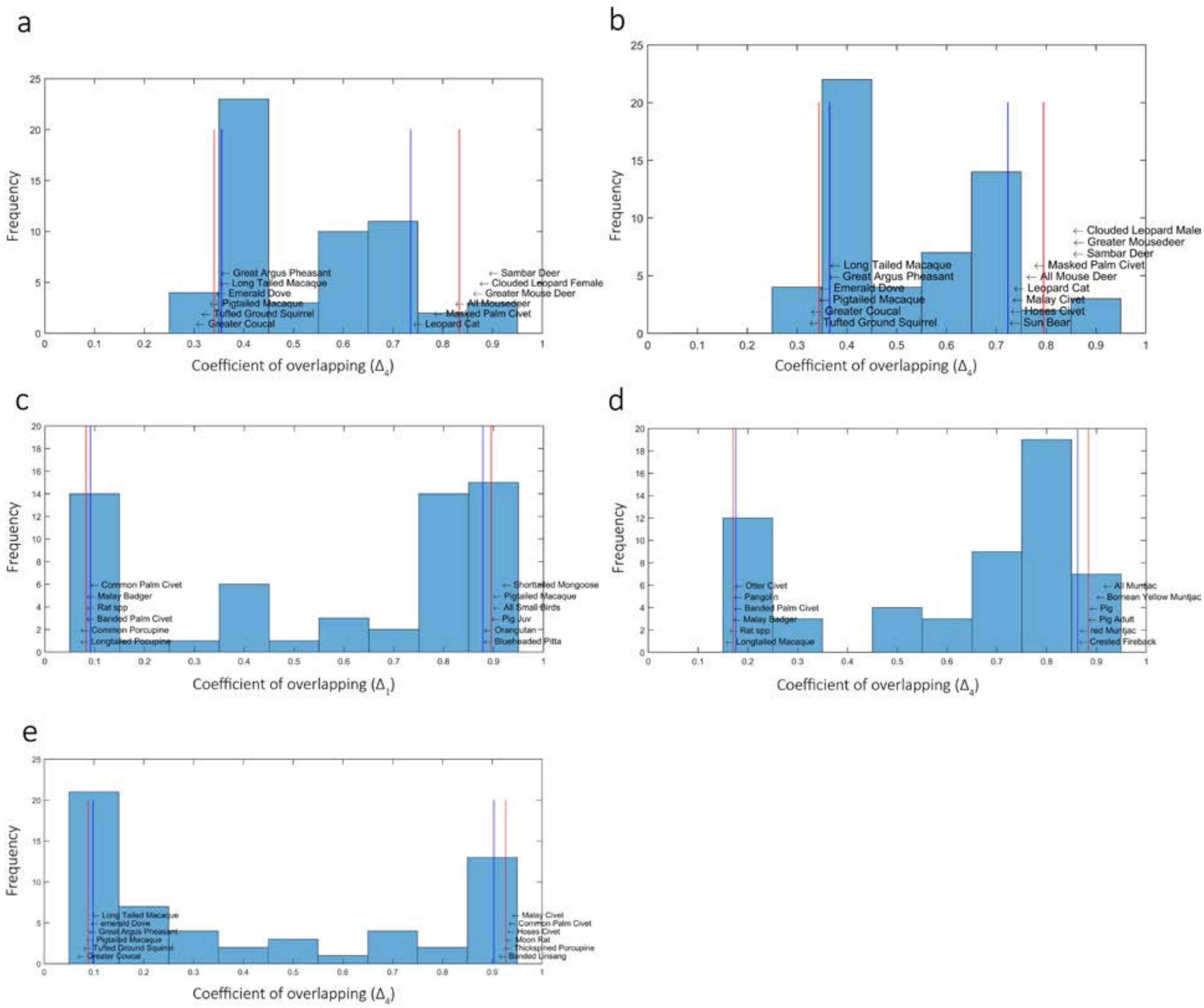

Figure 6. Histogram of the frequency of coefficient of temporal overlap (Δ_1 and Δ_4) values between Bornean felids and all other species and species groups (n= 57): a. Sunda clouded leopard males; b. Sunda clouded leopard females; c. bay cat; d. marbled cat; e. leopard cat. The 5th and 95th percentiles of the Δ_1 and Δ_4 distribution for each felid are shown in vertical red lines, and the 10th and 90th percentiles are shown in vertical blue lines.

Felid/candidate prey co-occurrence all-subsets modelling

The all-subsets logistic regression identified a range of potential prey species that were associated with the occurrence of Bornean felids (Table 9). Four potential prey species variables showed a p-value of ≤0.05 and an AIC relative weight of 1 in relation to male

Sunda clouded leopard occurrence, including Malay civet, common porcupine, sun bear and mongoose spp. (Table 9). All four variables had a positive coefficient, suggesting that they tend to occur at the same locations as male Sunda clouded leopards. Only one variable, sun bear, had a *p*-value of <0.05 in relation to female Sunda clouded leopard occurrence, again with a positive regression coefficient, indicating co-occurrence.

For the bay cat, there were five potential prey variables with a *p*-value of ≤0.05, including sambar deer, all pheasants, all mousedeer and Malay civet. Of these, sambar deer and Malay civet had an AIC relative weight of over 0.9, and all mousedeer and all pheasants had a AIC relative weight of 0.72 and 0.60, respectively. All four prey variables had a positive coefficient, suggesting that they tend to occur at the same locations as bay cat.

For the marbled cat there were four potential prey variables with a *p*-value of ≤0.05 and an AIC relative variable importance of over 0.9, including pig-tailed macaque, banded linsang, Malay civet, and mongoose spp. All of these variables had positive coefficients indicating that they tend to be present at sites where marbled cat was also present.

For the leopard cat, there were six variables with a *p*-value of ≤0.05 and a relative weight of 1, including pig-tailed macaque, common palm civet, all small birds, common porcupine, collared mongoose and Malay civet. Four additional prey species had AIC weight of over 0.9, greater coucal, Malay civet, emerald dove and otter civet, but their *p*-values exceeded 0.05. Greater mousedeer and all pheasants had *p*-values of ≤0.05, but their AIC relative weights were 0.74 and 0.51, respectively. Six of eight of these variables showed positive regression coefficients, meaning that they typically occurred at the same locations as leopard cat, the exception being all pheasants and greater mousedeer, which were negatively associated with leopard cat occurrence.

Table 9. Results of an all-subsets logistic regression analysis to predict the occurrence of Bornean felids as a function of potential prey species. β: standardised regression coefficients; AIC importance: weighted average of models that include prey species variable, weighted by AIC model weight.

		AICc importance	β	Adjusted SE β	z-score	*p*-value	
clouded leopard (males)	(Intercept)		-2.4610	0.2266	10.86	< 2e-16	***
	Malaycivet	1.00	0.0408	0.0093	4.395	0.0000	***
	Commonporcupine	1.00	0.0615	0.0187	3.291	0.0010	***
	Sunbear	1.00	0.1393	0.0442	3.15	0.0016	**
	Mongoosespp	1.00	0.2178	0.1033	2.109	0.0349	*
	Bandedlinsang	0.89	0.2790	0.1464	1.906	0.0567	
	Pig	0.75	0.0085	0.0050	1.693	0.0904	
	Malaybadger	0.29	0.0501	0.0428	1.17	0.2420	
	Binturong	0.30	0.3044	0.2664	1.143	0.2531	
	Yellowthroatedmarten	0.31	0.0865	0.0895	0.966	0.3339	
	Collaredmongoose	0.16	0.0947	0.1062	0.891	0.3727	
	Maskedpalmcivet	0.11	0.0614	0.1021	0.601	0.5476	
	Shorttailedmongoose	0.07	-0.0141	0.0378	0.373	0.7090	
	Bandedpalmcivet	0.07	-0.0061	0.0169	0.362	0.7171	
	Hosescivet	0.06	0.0182	0.0565	0.322	0.7472	
	Effort	1.00	0.0005	0.0016	0.285	0.7757	
clouded leopard (females)	(Intercept)		-3.2000	0.2764	11.578	< 2e-16	***
	Effort	1.00	0.0047	0.0017	2.801	0.0051	**
	Sunbear	1.00	0.0776	0.0331	2.342	0.0192	*
	Hosescivet	0.82	0.0978	0.0531	1.84	0.0657	
	Mongoosespp	0.59	0.1430	0.0866	1.652	0.0986	
	Shorttailedmongoose	0.36	0.0407	0.0278	1.462	0.1436	
	Commonporcupine	0.34	0.0235	0.0184	1.276	0.2018	
	Malaycivet	0.22	0.0078	0.0075	1.032	0.3019	
	Malaybadger	0.22	-0.0812	0.0864	0.939	0.3475	
	Binturong	0.13	0.2662	0.3120	0.853	0.3936	
	Collaredmongoose	0.08	0.0556	0.1060	0.525	0.5998	
	Bandedlinsang	0.07	-0.0968	0.2128	0.455	0.6493	
	Pig	0.07	-0.0017	0.0054	0.309	0.7575	
	Maskedpalmcivet	0.08	0.0316	0.1185	0.266	0.7899	
	Yellowthroatedmarten	0.06	-0.0088	0.0578	0.153	0.8785	
	Bandedpalmcivet	0.06	0.0013	0.0170	0.076	0.9392	
bay cat	(Intercept)		-4.5857	0.4259	10.767	< 2e-16	***
	Sambardeer	1.00	0.0334	0.0133	2.513	0.0120	*
	Allpheasants	0.60	0.0201	0.0095	2.112	0.0347	*
	Allmousedeer	0.72	0.0130	0.0062	2.087	0.0369	*
	Malaycivet	0.91	0.0189	0.0091	2.08	0.0376	*
	GreatArguspheasant	0.44	0.0224	0.0116	1.931	0.0535	
	Commonporcupine	0.59	0.0356	0.0218	1.635	0.1021	
	Effort	1.00	0.0038	0.0024	1.623	0.1047	
	Shorttailedmongoose	0.59	0.0529	0.0365	1.449	0.1473	
	Greatermousedeer	0.33	0.0275	0.0201	1.367	0.1715	
	Lessermousedeer	0.27	0.0187	0.0156	1.202	0.2293	
	Pigsubadult	0.16	-0.0420	0.0515	0.815	0.4150	
	Mongoosespp	0.19	-0.1145	0.1433	0.799	0.4240	
	Crestedfireback	0.10	0.0152	0.0213	0.715	0.4745	
	Borneanyellowmuntjac	0.06	0.0020	0.0048	0.413	0.6797	

Table 9 (Continued).

		AICc importance	β	Adjusted SE β	z-score	p-value	
Marbled cat	(Intercept)		-2.8396	0.2525	11.244	0.0000	***
	Pigtailedmacaque	1.00	0.0241	0.0091	2.656	0.0079	**
	Bandedlinsang	0.98	0.3102	0.1391	2.23	0.0258	*
	Malaycivet	0.98	0.0163	0.0077	2.113	0.0346	*
	Mongoosespp	0.96	0.2007	0.0969	2.072	0.0383	*
	Sunbear	0.97	0.0647	0.0338	1.912	0.0559	
	Commonporcupine	0.77	0.0326	0.0179	1.824	0.0681	
	Hosescivet	0.52	0.0875	0.0558	1.568	0.1169	
	Maskedpalmcivet	0.31	0.1395	0.1028	1.357	0.1748	
	Binturong	0.34	0.3587	0.2814	1.275	0.2025	
	Pig	0.33	0.0061	0.0048	1.265	0.2060	
	TuftedGroundSquirrel	0.25	0.0906	0.0770	1.177	0.2393	
	Bulwerspheasant	0.14	0.0281	0.0320	0.877	0.3803	
	Bandedpalmcivet	0.07	0.0103	0.0164	0.629	0.5291	
	Allpheasants	0.06	0.0035	0.0061	0.58	0.5618	
	Effort	1.00	0.0010	0.0018	0.554	0.5799	
	Ratspp	0.06	0.0051	0.0102	0.497	0.6195	
	Yellowthroatedmarten	0.06	0.0259	0.0525	0.494	0.6212	
	Shorttailedmongoose	0.06	0.0177	0.0389	0.456	0.6483	
Leopard cat	(Intercept)		-1.4863	0.2038	7.292	0.0000	***
	Pigtailedmacaque	1.00	0.0321	0.0095	3.396	0.0007	***
	Commonpalmcivet	1.00	0.2154	0.0655	3.289	0.0010	**
	Allsmallbirds	1.00	0.3250	0.1171	2.775	0.0055	**
	Commonporcupine	1.00	0.0382	0.0164	2.326	0.0200	*
	Collaredmongoose	1.00	0.3832	0.1794	2.136	0.0327	*
	Allpheasants	0.51	-0.0256	0.0128	2	0.0455	*
	Malaycivet	0.93	0.0135	0.0068	1.992	0.0464	*
	Greatermousedeer	0.74	-0.0297	0.0150	1.982	0.0475	*
	Elephant	0.88	0.0907	0.0473	1.916	0.0554	
	GreatArguspheasant	0.60	-0.0343	0.0180	1.906	0.0566	
	Emeralddove	0.92	-0.2480	0.1332	1.863	0.0625	
	Greatercoucal	0.96	1.0237	0.5598	1.829	0.0674	
	Ottercivet	0.90	0.4989	0.2778	1.796	0.0725	
	Allmousedeer	0.39	-0.0093	0.0061	1.534	0.1251	
	Effort	1.00	0.0014	0.0014	0.998	0.3182	
	Pig	0.13	-0.0038	0.0046	0.818	0.4133	
	Sambardeer	0.07	0.0056	0.0116	0.484	0.6284	

Discussion

The extensive survey effort in this study has accumulated the largest Bornean felid detection dataset to date and has revealed evidence of a complex web of niche separation among all felid assemblage members (Table 10). Mechanisms of resource partitioning between individual small felids and the larger Sunda clouded leopard appeared to be as numerous as among the smaller felid members. Consequently, our study provided little support for our a priori hypotheses that resource partitioning would be most pronounced between the four smallest species, which exhibit closely overlapping body sizes and thus may encounter the highest levels of competition. Consistent with our a priori hypothesis, we found that small Bornean felids exhibited spatio-temporal avoidance of the larger and competitively dominant Sunda clouded leopard, which may pose a predation risk, but found no support of greater avoidance of female Sunda clouded leopard. Below, we explore these mechanisms in the context of these core hypotheses, focusing on the four species which our dataset permits, but also drawing on previous studies of flat-headed cats.

Table 10. Potential mechanisms of resource partitioning and coexistence among species pairs from an assemblage of five species of wild felids on Borneo. *possible mechanism, **likely mechanism, *** highly likely mechanism. Underlined species pairs highlight pairs with very similar body sizes which are hypothesised to exhibit the greatest interspecific competition. Species pairs in bold highlight those pairs hypothesised as being most likely to be engaged in intra-guild predation due to differences in body size.

Species pair		No. axes	Elevation	Broad-scale habitat	Fine scale habitat selection			temporal activity	Prey species
					vertical strata	logging road	Ridge		
Clouded leopard ♂	Clouded leopard ♀	4			*	***	***		*
Clouded leopard ♂	Bay cat	5	***			***	***	***	**
Clouded leopard ♀	**Bay cat**	4	***		**			***	**
Clouded leopard ♂	Marbled cat	4			*	***		***	**
Clouded leopard ♀	**Marbled cat**	3					***	***	**
Clouded leopard ♂	Leopard cat	4	***	***			***		***
Clouded leopard ♀	**Leopard cat**	5	***	***	**	***			***
Clouded leopard ♂	Flat-headed cat	6	***	***	*	*	*		***
Clouded leopard ♀	Flat-headed cat	3	***	***	*				
Bay cat	Marbled cat	3			***		***		***
Bay cat	Leopard cat	5	***	***		***		***	***
Bay cat	Flat-headed cat	4	***	***				***	***
Marbled cat	Leopard cat	7	***	***	***	***	***	***	***
Marbled cat	Flat-headed cat	6	*	***	***		***	***	***

Partitioning along the spatial axis

All Bornean felids showed evidence of partitioning along the spatial niche dimension, but the degree of spatial differentiation appeared to vary strongly between different members of the Bornean felid assemblage. Spatial partitioning was lowest between Sunda clouded leopards and marbled cats, and between marbled cats and bay cats, although fine-scale partitioning was evident, whereas leopard cats showed evidence of strong spatial partitioning from that of the other three felids.

Sunda clouded leopards and marbled cats both selected higher elevation forest landscapes at fine scales, and exhibited negative relationships with human dominated, highly disturbed habitat types at broad scales. Unlike Sunda clouded leopards, however, marbled cats showed a particular association with limestone forest at fine scales, and rough topography at moderate scales. Marbled cats showed a strong association with forested ridgelines, but not logging roads, while male clouded leopards, but not females, were associated with both logging roads and ridgelines. Females clouded leopards also use logging roads, but our analysis showed that they do not strongly select them. This may be a mechanism to reduce interactions with males, but conceivably also because they do not have the requirements to traverse over such large areas as their male counterparts, which may exhibit territorial defence and mate guarding behaviours, typical in male felids (e.g., Macdonald et al., 2010). These findings are in accordance with those of Wearn et al. (2013), who showed that detection probabilities along logging roads and skid trails in a highly degraded forest in Sabah were significantly higher for clouded leopards, and higher for marbled cats along skid trails only, but their sample sizes permitted only preliminary conclusions. Our analyses suggest that marbled cats exhibit only partial spatial segregation with clouded leopards at the landscape scale, but interact with certain fine-scale habitat features in the landscape, such as avoidance of logging roads, which may further segregate their spatial niche with these felids.

The bay cat exhibited similar broad scale habitat selection as Sunda clouded leopards and marbled cats selecting areas of low fragmentation and low human footprint at relatively broad scales. Unlike these other felids, however, bay cats did not select higher elevation forest and used neither roads nor ridgelines, potentially indicating avoidance of marbled cats and clouded leopards, particularly male clouded leopards. Unlike bay cats, both marbled cats and Sunda clouded leopards appear to be adapted to arboreal movement and foraging (e.g., Sunquist and Sunquist, 2002). While no quantitative data are available, such arboreal activity could provide further fine-scale spatial segregation between these felids.

Contrastingly, and in accordance with our a-priori hypothesis, leopard cats showed a clear association with disturbed habitats, selecting oil palm plantations at relatively fine spatial scales and exhibiting a preference for lower elevations at relatively broad scales, and also with low levels of mosaic and regrowth areas at broad scales. Mohamed et al. (2013) showed that leopard cat encounter rates from off-road camera traps were only 3.6–9.1% of those for on-road traps and their occupancy models revealed that canopy closure and ratio of climax to pioneer trees had a significantly negative impact on leopard cat occurrence.

Consistent with our hypothesis, and with the results emerging from several studies that have assessed multi-scale habitat selection optimization (Thompson and McGarigal, 2002; Wasserman et al., 2012; Mateo-Sanchez et al., 2014), we show that Bornean felids are selecting habitats at fine spatial scales and avoiding habitats at relatively course scales, often far exceeding that of the animal's homerange. Although not directly comparable, it is noteworthy that analysis of movement resistance from path-level data shows that Sunda clouded leopards invariably responded to habitat variables at broad scales (Chapter 2).

Driven by the differences and similarities in habitat association, the patterns of predicted occurrence showed the same broad pattern of spatial similarity between Sunda clouded leopards and marbled cats, and to a lesser extent bay cats, and clear spatial separation of leopard cats. Predicted occurrence of both Sunda clouded leopards and marbled cats reached a maximum within the higher elevation areas of the main contiguous forest block region in central Sabah; the vast, heavily disturbed coastal areas and oil palm plantation dominated areas in the east presented the lowest predicted probability of occurrence for these felids. These predictions of distribution are broadly similar to those developed from presence only maximum entropy modelling (Hearn et al., 2016a,b; Rustam et al., 2016), but our analyses are an improvement on these earlier models as they provide information about responses to specific habitat variables and the relative influence of scale. Hearn et al. (Chapter 2 & 3) used location data from GPS-tagged Sunda clouded leopards and showed that their movements were closely associated with forest with high canopy closure, and resisted by open habitats such as oil palm plantations. Our current study provides further evidence that very degraded forest areas are possibly not used by Sunda clouded leopards.

The highly contrasting habitat preferences shown by leopard cats resulted in a predicted distribution model that was essentially a polar opposite of the other three felids, with leopard cats predicted to have very high probability of occurrence throughout the oil palm dominated lowland landscape in eastern Sabah, and only moderate predictions of occurrence within the more heavily forested regions. In contrast, Mohamed et al. (2016)

produced a presence only predictive model of occurrence for this felid on Borneo that showed an island-wide, broadly even distribution across habitat types. The Mohamed et al. (2016) model included an expert-opinion component to the assessment, which has been shown to be less reliable than empirically derived predictions of occurrence (e.g., Shirk et al., 2010; Mateo-Sanchez et al., 2015) and, from this expert-opinion, forest habitats were classified as presenting similar habitat suitability to that of plantations. In contrast, our analysis strongly suggests that plantations present a much higher habitat suitability, a view supported by density estimates of this felid from Singapore (Chua et al., 2016). However, it is still not known to what degree leopard cat presence in plantation landscapes is linked to forest cover in the broader landscape, and whether leopard cats still reach such high densities in the interiors of large plantations.

Perhaps the clearest evidence for spatial separation is shown by the flat-headed cat. As shown in this study flat-headed cats are rarely recorded by camera traps, which likely reflects both the comparative rarity of these felids in relation to other Bornean wild cats, but also their highly restricted habitat associations coupled with camera trap deployment strategies. Wilting et al. (2010, 2016) showed that these felids were strongly associated with low-lying riverine and wetland habitats, indicating large divergence in habitat niche from the other fields in the Bornean guild.

Partitioning along the temporal axis

Both the bay cat and the marbled cat exhibited highly overlapping diurnal patterns of activity, and thus showed little evidence of temporal partitioning. On the opposite end of the temporal spectrum, the activity patterns of the primarily nocturnal male and female clouded leopards overlapped greatly both with one another, and with the highly nocturnal leopard cat, suggesting that they too did not differentiate along the temporal niche. Both bay cats and marbled cats, however, showed clear temporal partitioning with leopard cats and with clouded leopards. Our data regarding flat-headed cats did not permit statistical analysis, but the small number of camera trap detections and anecdotal sightings suggest this species too, is nocturnal (e.g. Hearn et al., 2010; Wilting et al., 2010), and thus temporal partitioning would further avoid competition with the diurnal bay cat and marbled cat, but not with the Sunda clouded leopard or leopard cat.

Thus, temporal partitioning may enable competitive displacement between clouded leopards and both marbled cats and bay cats, which have broadly similar spatial niches. Leopard cats are significantly smaller than clouded leopards, hence there is little dietary overlap, and their largely different habitat niches lead to little spatial overlap, and so no temporal displacement would be required to avoid competition among these species. The associations with highly disturbed and freshwater habitats exhibited by leopard cats and flat-headed cats, respectively, reduce the importance of temporal separation between them, but the presence of temporal divergence with the forest-associated bay cats and marbled cats contributes to further niche partitioning among these otherwise closely size-matched felids. However, the lack of temporal divergence between the similarly sized bay cats and marbled cats, which we have shown to also share large similarities in their spatial niche, means that perhaps their persistence is enabled by partitioning on prey.

Differential use of prey

The analytical approach we follow in this study prevents us from drawing firm conclusions regrading Bornean felid prey choice. However, exploration of the co-occurrence of Bornean felids with other mammals and birds, and their temporal patterns of activity, can help identify candidate prey species which can be tested in future studies. Our results demonstrate that male Sunda clouded leopards co-occur with common porcupines, a species which they are known to prey upon (Payne et al., 1985; Gordon and Stewart, 2007). Significant spatial co-occurrence was also exhibited between male Sunda clouded leopard and Malay civet, sun bear and mongoose spp. which are unlikely to be prey animals of male clouded leopards. This association may reflect mutual selection for similar habitat conditions rather than any direct associative behaviour. Both male and female Sunda clouded leopards showed significant temporal activity associations with sambar deer and greater mouse deer. While adult sambar may exceed 200 kg, juveniles and subadults fall within the mass range that clouded leopard males are likely to take based on predator/prey mass allometries (e.g. Carbone et al., 1999; Macdonald et al., 2010), but such theory predicts that only calves would be taken by female Sunda clouded leopards. Nevertheless, these data suggest that sambar may indeed constitute an important resource for these felids. Indeed, Mohamed et al. (2009) reported that a juvenile sambar weighing an estimated 30–35 kg was killed and partially consumed by a Sunda clouded leopard. Interestingly, using a sub-set of the data examined in this paper, Ross et al. (2013) showed that greater mousedeer exhibited shifts in temporal activity in a forest devoid of Sunda clouded leopards (Kabili-Sepilok), which, alongside our findings, suggests that they too may be important prey for Sunda clouded leopards. We found no evidence of co-occurrence or temporal synchronisation of Sunda clouded leopard males or females with that of bearded pigs, but previous studies have shown that they may indeed be important prey. Ross et al. (2013) showed that bearded pigs exhibited a similar shift in activity in the absence of Sunda clouded leopards as that exhibited by greater mousedeer, and Mohamed et al. (2009) detail an observation of a presumed male Sunda clouded leopard killing and subsequently dragging a 20–25 kg bearded pig up to the first storey of a wooden observation tower. These patterns of co-occurrence, in conjunction with previous studies showing temporal interaction among clouded leopards and these species, suggest there may be behavioural responses by clouded leopards to non-randomly associate with these species in both space and time to maximize predation efficiency.

The bay cat remains one of the least known of the world's wild cats, and to our knowledge there are no published data regarding these felids' prey choices. We showed that bay cats exhibited significant spatial co-occurrence with all mousedeer and all pheasant's species-groups, both of which are within the predicted size range of this felid based on predator/prey mass allometries (e.g. Carbone et al., 1999; Macdonald et al., 2010). Bay cats showed significant temporal activity associations with all small birds and blue-headed pitta, and, while not statistically significant, exhibited very high temporal overlap coefficients with a range of terrestrial, large and small bodied birds. Intriguingly, a bay cat was reportedly captured in Sarawak having been attracted to a captive pheasant enclosure (Sunquist and Sunquist, 2002). The strength of these associations is highly suggestive of specialized predation focusing on birds, which could provide a means for niche partitioning with marbled cats, allowing coexistence of these species that appear to be highly similar based on temporal and habitat selection niche axes. Further research on the diet composition of the bay cat is required to verify this hypothesis.

The marbled cat was shown to co-occur significantly non-randomly with pig-tailed macaque, banded linsang, Malay civet, and mongoose spp. Marbled cats have well documented arboreal adaptations (e.g., Leyhausen, 1979; Sunquist and Sunquist, 2002), and so it is likely that these felids actively prey upon arboreal species, which could conceivably include pig-tailed macaques, perhaps targeting young. In Thailand, a marbled cat was suspected of preying on a juvenile Phayre's leaf monkey (*Trachypithecus phayrei*), which, at an estimated weight of around 5 kg, may have exceeded that of the cat (Borries et al., 2004). The stomach contents of a female marbled cat shot on the ground at night in an old logged forest contained a small species of Rattus (Davis, 1962).

The diet of leopard cats is well studied, and is thought to be comprised principally of murid rodents (e.g., Grassman et al., 2005; Rajaratnam et al., 2007; Chua et al., 2016), although, depending on geographical location, they will also take young ungulates, hares, birds, reptiles, insects, eels and fish (Nowell and Jackson, 1996). We did not show evidence for associations with rodents in our study, but this may reflect the reduced ability of camera traps to detect small species.

Our analyses provide some of the first data regarding spatial and temporal associations with potential prey of Bornean felids, and provides tentative evidence that prey selection may vary among Bornean felids to enable co-existence. Similarity in spatial use and/or activity patterns between predator and prey is, by itself, not compelling evidence that a predator relies on any prey species, however. Indeed, felids such as jaguars and pumas may have activity patterns in phase with their main prey (Harmsen et al., 2011) or, as with lions, have cycles that oppose those of their prey (Mills & Shenk, 1992). Nevertheless, these analyses serve to highlight potential prey relationships, which can later be tested via analysis of the composition from stomach contents or scats.

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Wilting, A., Cheyne, S.M., Mohamed, A., Hearn, A.J., Ross, J., Samejima, H., Boonratana, R., Marshall, A.J., Brodie, J.F., Giordiano, A., Eaton, J.A., Hall, J., Pilgrim, J.D., Heydon, M., Semiadi, G., Meijaard, E., Macdonald, D.W., Breitenmoser-Würsten, C. and Kramer-Schadt (2016). Predicted distribution of the flat-headed cat *Prionailurus planiceps* (Mammalia: Carnivora: Felidae) on Borneo. Raffles Bulletin of Zoology, Supplement No. 33, 173-179.

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Appendix 1. Table of variables used in the Prey all-subsets modelling and the felid-prey temporal activity overlap analysis, showing variable description, number of independent photographic records for each species/group of species ([a] 1 record/ species/ camera station/ hour) and IUCN Red List status (CR: Critically endangered; EN: Endangered; VU; Vulnerable; NT: Near threatened; LC Least concern; NA: not applicable; Red List status as of July, 2016).

Variable name	Species records included in variable	No. records [a]	IUCN Red List [b]
Allmousedeer	Combination of Greater mousedeer (*Tragulus napu), Lesser mousedeer* (*T. kanchil*) records, and Mousedeer records which are unidentifiable to the species level.	7314	NA
Allmuntjac	Combination of Bornean Yellow Muntjac (*Muntiacus atherodes*), Southern Red Muntjac (*M. muntjak*) records, and muntjac records which are unidentifiable to the species level.	13447	NA
Allpartridges	Combination of Blue-breasted quail (*Synoicus chinensis*), Sabah Partridge (Arborophila graydoni), Crested partridge (*Rollulus rouloul*), Crimson-headed partridge (*Haematortyx sanguiniceps*), Red-breasted partridge (*Arborophila hyperythra*) and partridge records which are unidentifiable to the species level.	229	NA
Allpheasants	Combination of Bulwer's Pheasant (*Lophura bulweri*), Crested fireback (*L. ignita*), Great Argus (*Argusianus argus*) records, and pheasant records which are unidentifiable to the species level.	4892	NA
Allpittas	Combination of Bornean banded pitta (*Pitta schwaneri*), Black-headed pitta (*P. ussheri*), Blue-banded pitta (*P. arcuata*), Blue-headed pitta (*P. baudii*), Giant pitta (*P. caerulea*) and Hooded pitta (*P. sordida*) records, and pitta records which are unidentifiable to the species level.	342	NA
Allsmallbirds	Combination of all bird records, excluding pheasants, pittas and partridges.	512	NA
Bandedlinsang	Banded Linsang (*Prionodon linsang*)	105	LC
Bandedpalmcivet	Banded palm civet (*Hemigalus derbyanus*)	2237	NT
Bandedpitta	Bornean banded pitta (*Pitta schwaneri*)	266	LC
Bay cat	Borneo bay cat (*Catopuma badia*)	61	EN
Binturong	Binturong (*Arctictis binturong*)	70	VU
Blueheadedpitta	Blue-headed Pitta (*Pitta baudii*)	37	VU
Borneanyellowmuntjac	Bornean Yellow Muntjac (*Muntiacus atherodes*)	7119	VU
Bulwerspheasant	Bulwer's Pheasant (*Lophura bulweri*)	551	VU
Sabah Partridge	Sabah Partridge (*Arborophila graydoni*)	50	VU
Clouded leopard	Sunda clouded leopard (*Neofelis diardi*) (all records)	641	VU
Cloudedleopardmale	Sunda clouded leopard (*Neofelis diardi*) (male records only)	557	VU
Cloudedleopardfemale	Sunda clouded leopard (*Neofelis diardi*) (female records only)	78	VU
Collaredmongoose	Collared mongoose (*Herpestes semitorquatus*)	155	NT
Commonpalmcivet	Common Palm Civet (*Paradoxurus hermaphroditus*)	503	NT
Commonporcupine	Common porcupine (*Hystrix brachyura*)	2013	LC
Crestedfireback	Crested fireback (*Lophura ignita*)	1351	NT
Crestedpartridge	Crested Partridge (*Rollulus rouloul*)	159	NT
elephant	Asian Elephant (*Elephas maximus*)	473	EN

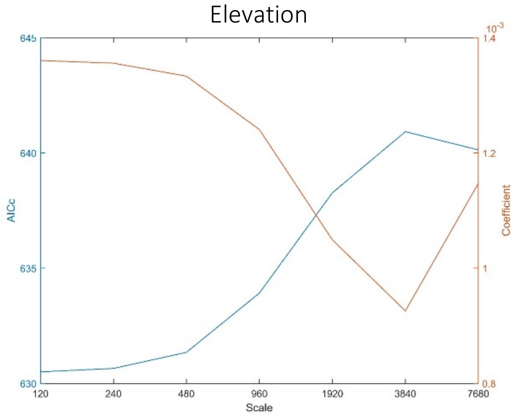
Appendix 1 (continued).

Variable name	Species records included in variable	No. records [a]	IUCN Red List [b]
Emeralddove	Grey-capped emerald dove (C*halcophaps indica*)	363	LC
GreatArguspheasant	Great Argus (*Argusianus argus*)	2976	NT
Greatercoucal	Greater Coucal (*Centropus sinensis*)	20	LC
Greatermousedeer	Greater Mousedeer (*Tragulus napu*)	1882	LC
Hosescivet	Hose's civet (*Diplogale hosei*)	281	VU
Leopard cat	Leopard cat (*Prionailurus bengalensis*)	1973	LC
Lessermousedeer	Lesser mousedeer (*Tragulus kanchil*)	2638	LC
Longtailedmacaque	*Long-tailed macaque (Macaca fascicularis*)	946	LC
Longtailedporcupine	Long-tailed Porcupine (*Trichys fasciculata*)	865	LC
Malaybadger	Malay badger (*Mydaus javanensis*)	437	LC
Malaycivet	Malay civet (*Viverra tangalunga*)	6458	LC
Malayweasel	Malay weasel (*Mustela nudipes*)	29	LC
Marbled cat	Marbled cat (*Pardofelis marmorata*)	205	NT
Maskedpalmcivet	Masked palm civet (*Paguma larvata*)	284	LC
Mongoosespp	Combination of the records of Collared mongoose (Herpestes semitorquatus) and Short-tailed mongoose (Herpestes brachyurus), and mongoose records which are unidentifiable to the species level.	272	NA
Moonrat	Moonrat (*Echinosorex gymnura*)	863	LC
Orangutan	Bornean orangutan (*Pongo pygmaeus*)	254	CR
Ottercivet	Otter civet (*Cynogale bennettii*)	43	EN
Pangolin	Sunda Pangolin (*Manis javanica*)	143	CR
Pig	Bearded Pig (*Sus barbatus*) (all records)	9587	VU
Pigadult	Bearded Pig (*Sus barbatus*) (adult records only)	5977	VU
Pigjuv	Bearded Pig (*Sus barbatus*) (juvenile records only)	1231	VU
Pigsubadult	Bearded Pig (*Sus barbatus*) (subadult records only)	950	VU
Pigtailedmacaque	Southern pig-tailed macaque (*Macaca nemestrina*)	5219	VU
Ratspp	Combination of the records of species within the family Muridae (up to 27 species in 10 genera).	2319	NA
Redmuntjac	Southern Red Muntjac (M*untiacus muntjak*)	5906	LC
Sambardeer	Sambar Deer (*Rusa unicolor*)	2751	VU
Shorttailedmongoose	Short-tailed mongoose (H*erpestes brachyurus*)	817	NT
Sunbear	Malayan Sun Bear (*Helarctos malayanus*)	914	VU
Thickspinedporcupine	Thick-spined porcupine (*Hystrix crassispinis*)	614	LC
Treeshrewspp.	Combination of the records of species within the family Tupaiidae (approx. 6 species).	587	NA
Treesquirrel	Combination of the records of several, largely arboreal squirrel species, including: Horse-tailed squirrel (*Sundasciurus hippurus*), Low's Squirrel (*S. lowii*), Prevost's squirrel (*Callosciurus prevostii*), and Thomas's flying squirrel (*Aeromys thomasi*)	364	NA
TuftedGroundSquirrel	Tufted ground squirrel (*Rheithrosciurus macrotis*)	327	VU
Yellowthroatedmarten	Yellow-throated marten (*Martes flavigula*)	312	LC

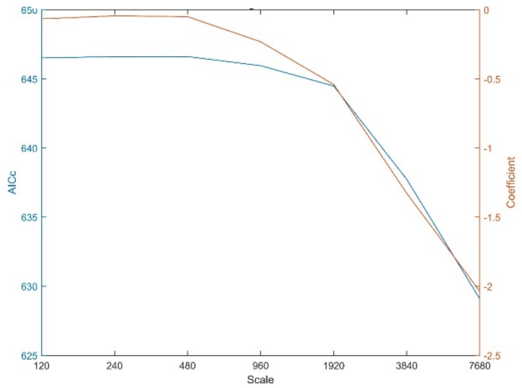
Appendix 2. Scaling plots of AICc values and coefficient values for relationships between Bornean felid species' occurrence and a range of predictor habitat variables cover type across 7 spatial scales. Spatial scales with the lowest AICc were deemed to be optimal, and used for further analysis.

(a) Sunda clouded leopard

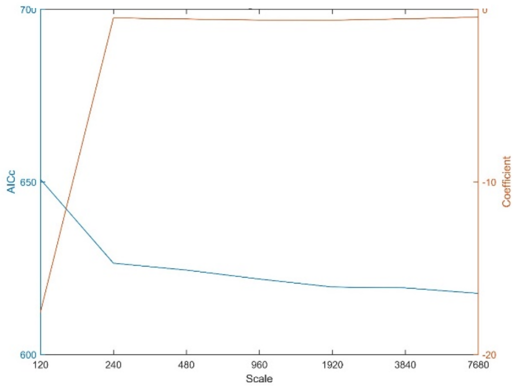
Elevation



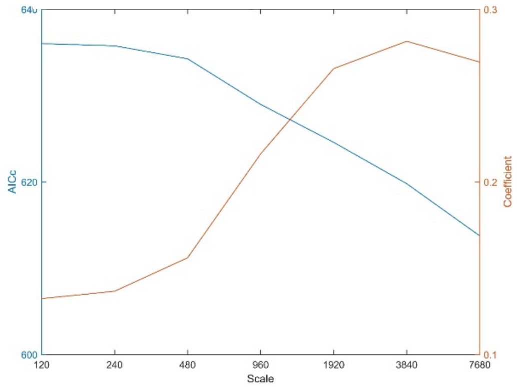
Gaveau: Agroforests / forest regrowth



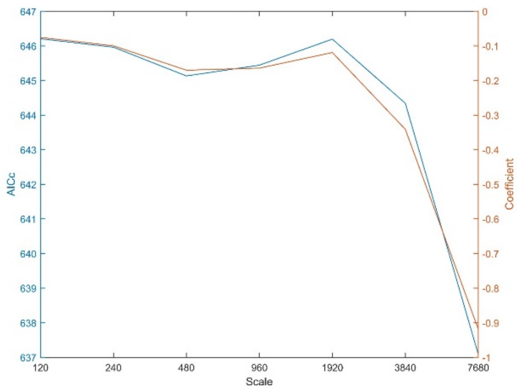
Gaveau: Oil palm plantations



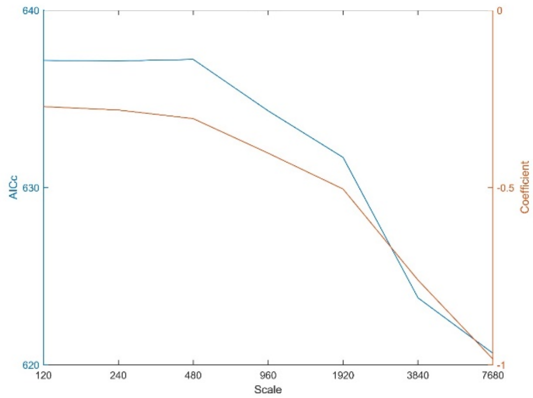
Gaveau: Logged forests



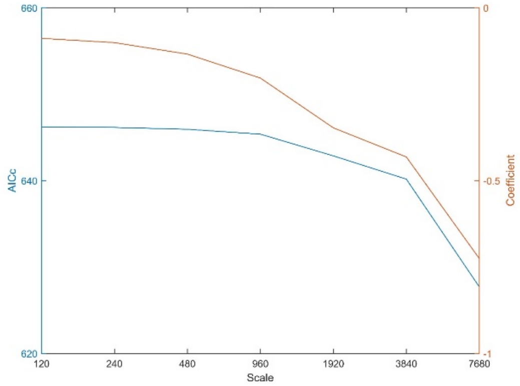
Miet 10



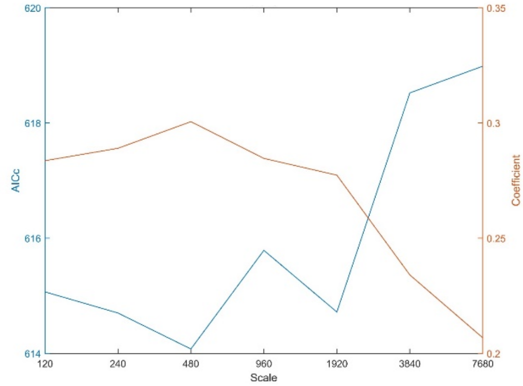
Miet 7



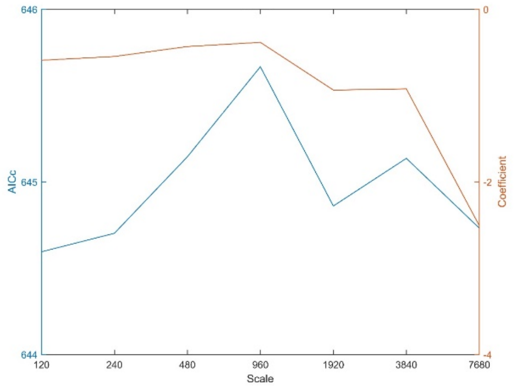
Miet 8



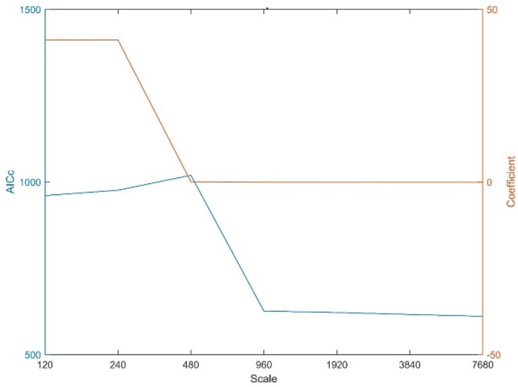
SFD 10



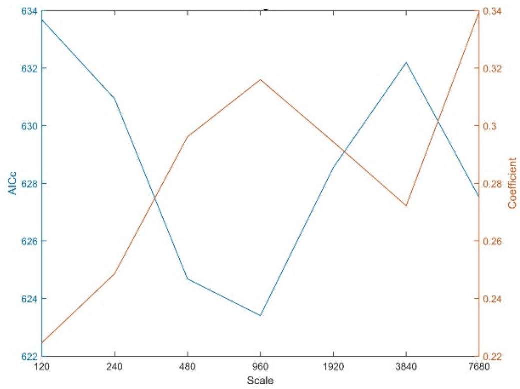
SFD 11



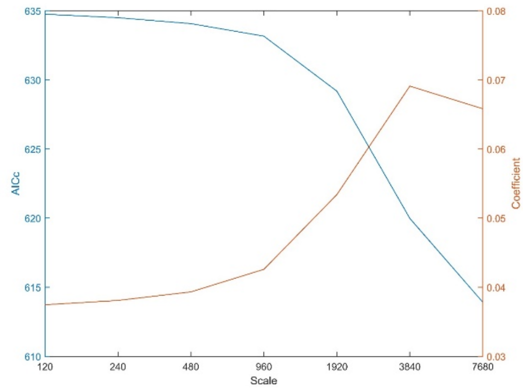
Human footprint



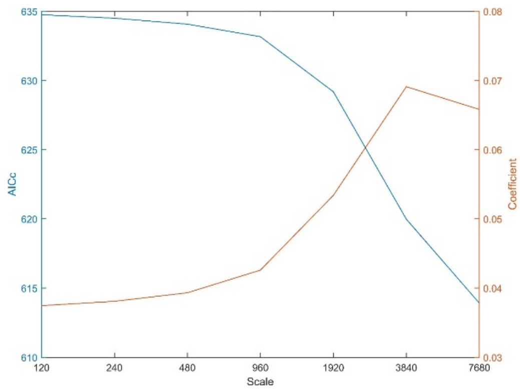
Topographical roughness



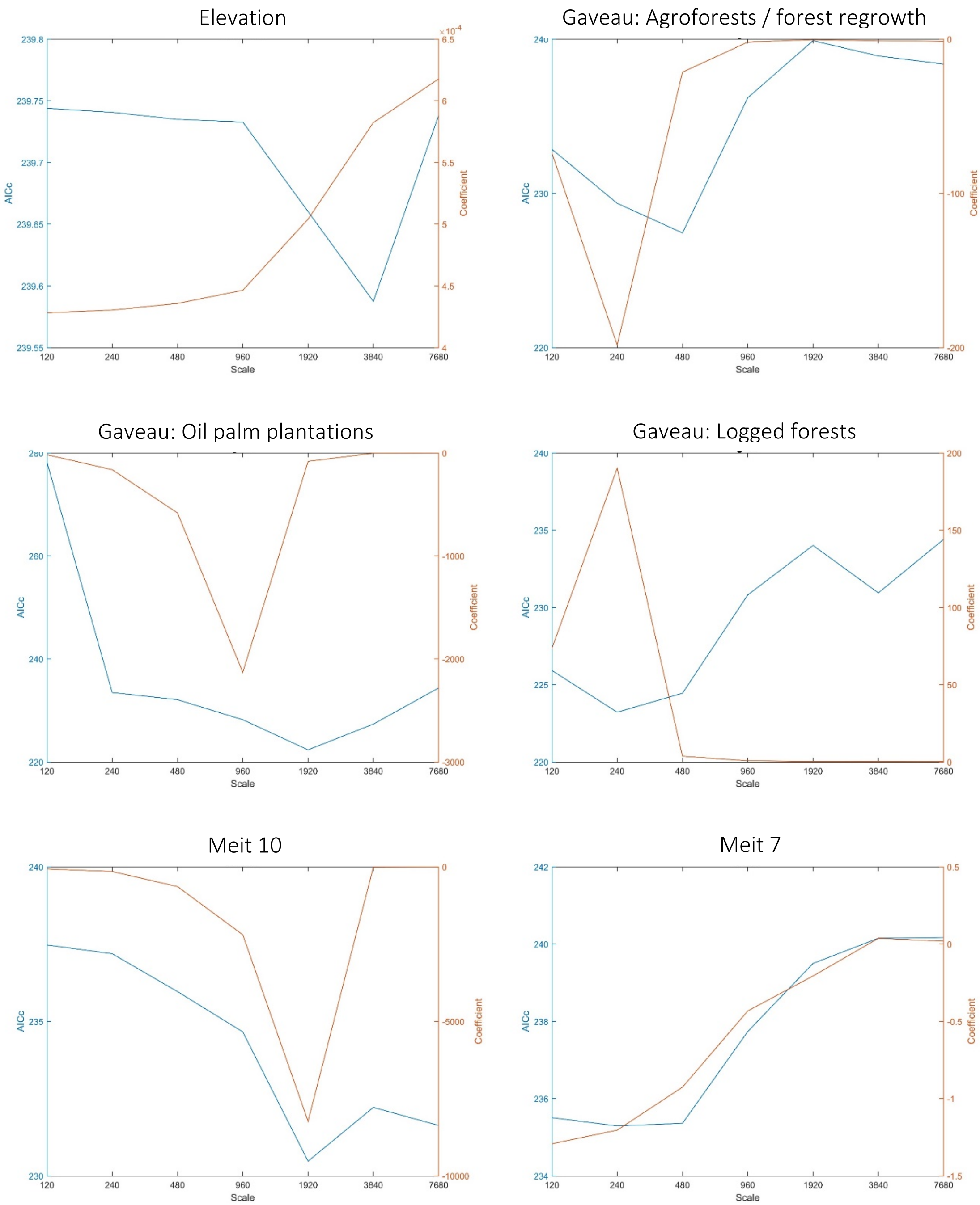
Tree cover



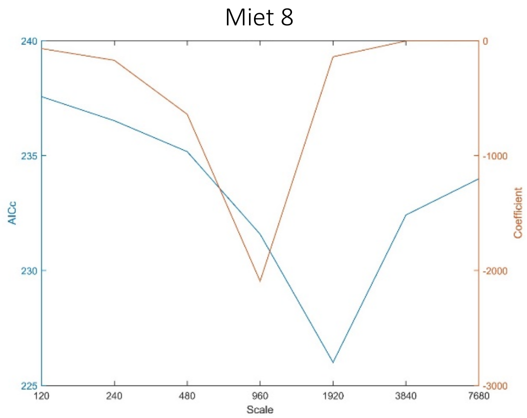
Tree cover SD

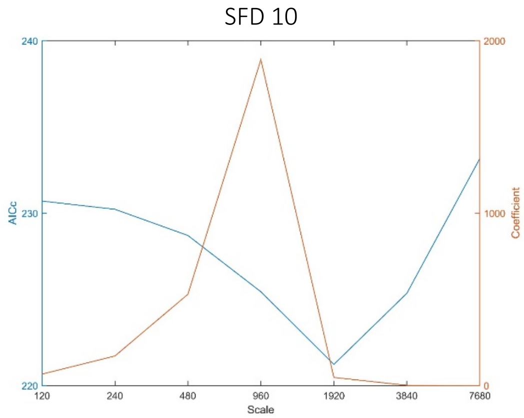


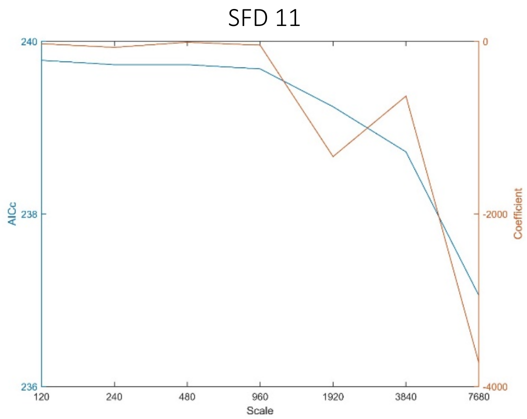
(b) Bay cat

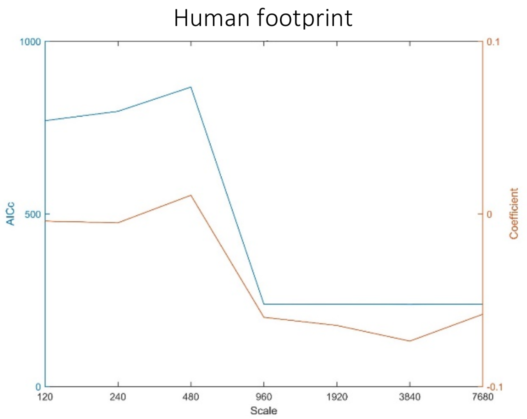


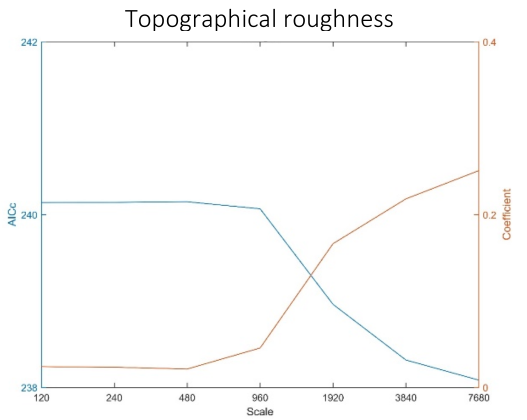
Elevation
Gaveau: Agroforests / forest regrowth
Gaveau: Oil palm plantations
Gaveau: Logged forests
Meit 10
Meit 7
AICc
Coefficient
Scale
120 240 480 960 1920 3840 7680

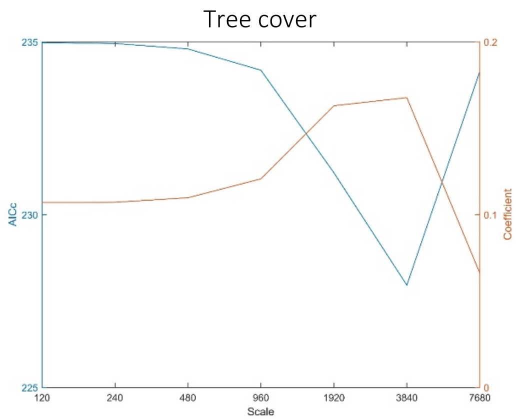

Miet 8
AICc
240
235
230
225
Coefficient
0
-1000
-2000
-3000
120 240 480 960 1920 3840 7680
Scale

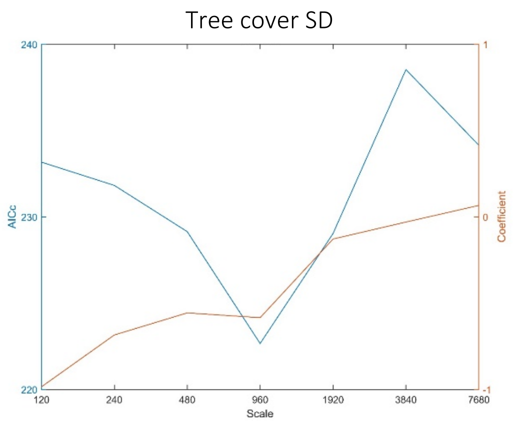

SFD 10
AICc
240
230
220
Coefficient
2000
1000
0
120 240 480 960 1920 3840 7680
Scale


SFD 11
AICc
240
238
236
Coefficient
0
-2000
-4000
120 240 480 960 1920 3840 7680
Scale


Human footprint
AICc
1000
500
0
Coefficient
0.1
0
-0.1
120 240 480 960 1920 3840 7680
Scale

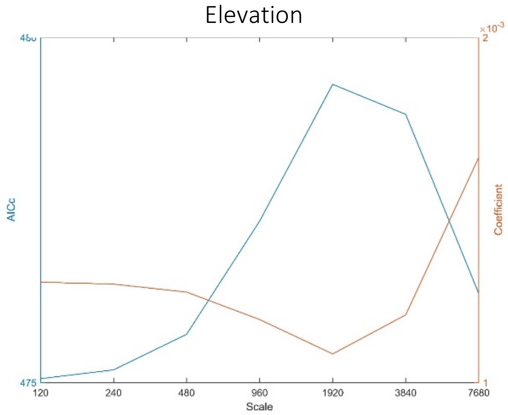

Topographical roughness
AICc
242
240
238
Coefficient
0.4
0.2
0
120 240 480 960 1920 3840 7680
Scale


Tree cover
AICc
235
230
225
Coefficient
0.2
0.1
0
120 240 480 960 1920 3840 7680
Scale

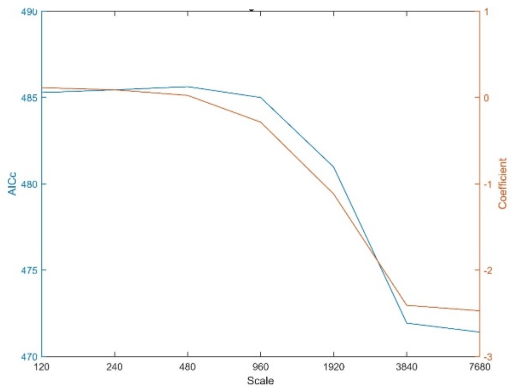

Tree cover SD
AICc
240
230
220
Coefficient
1
0
-1
120 240 480 960 1920 3840 7680
Scale

(c) Marbled cat

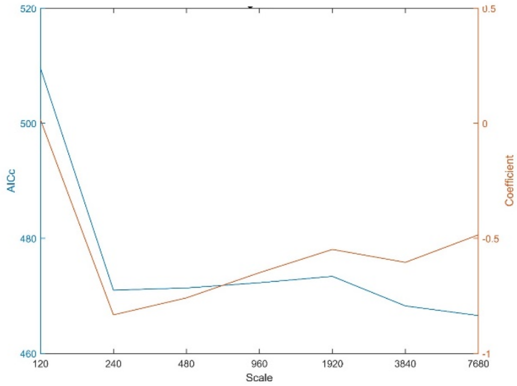
Elevation



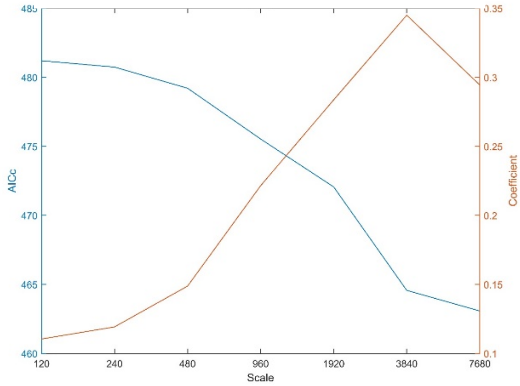
Gaveau: Agroforests / forest regrowth



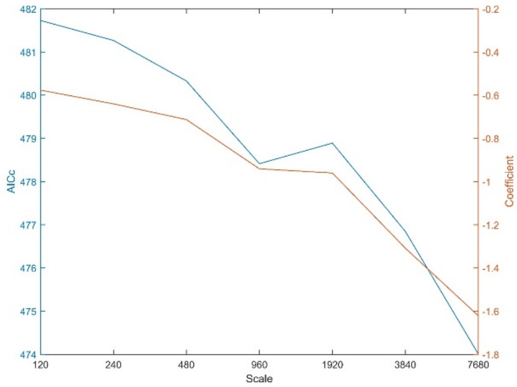
Gaveau: Oil palm plantations



Gaveau: Logged forests



Miet 10



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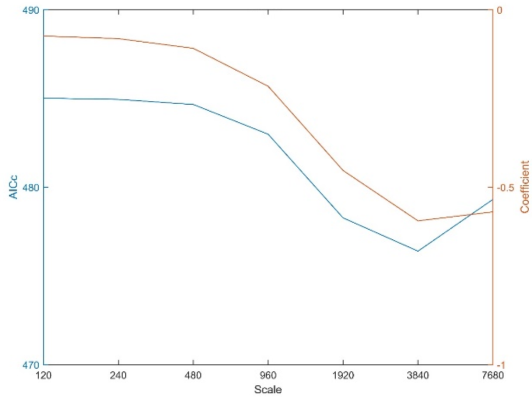
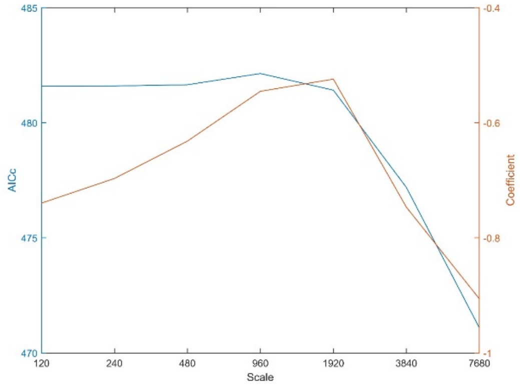
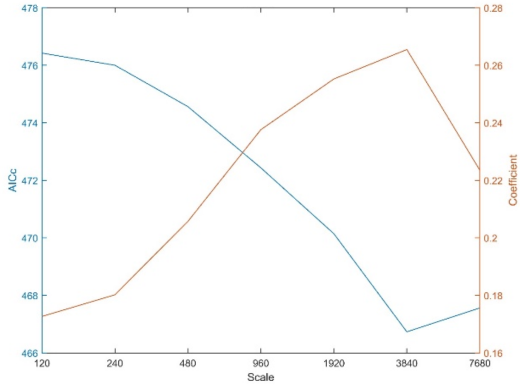


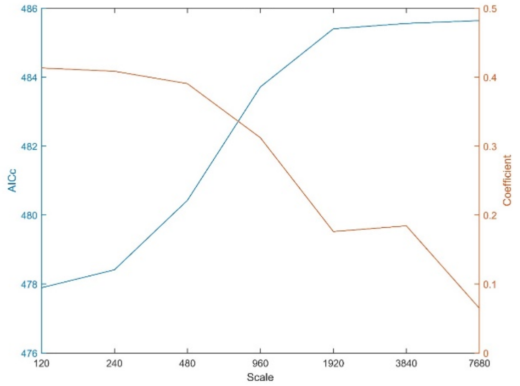
Miet 8



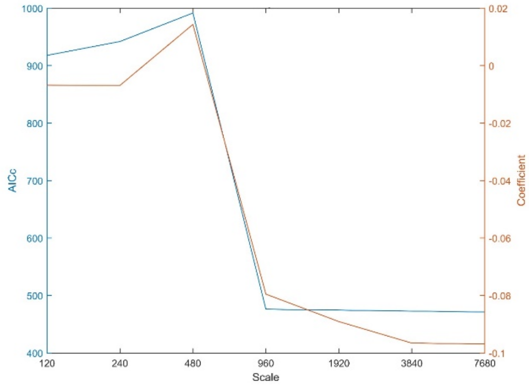
SFD 10



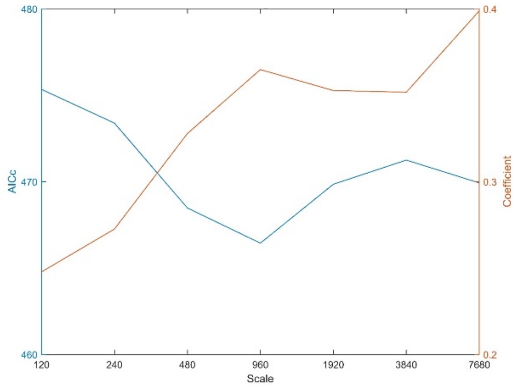
SFD 11



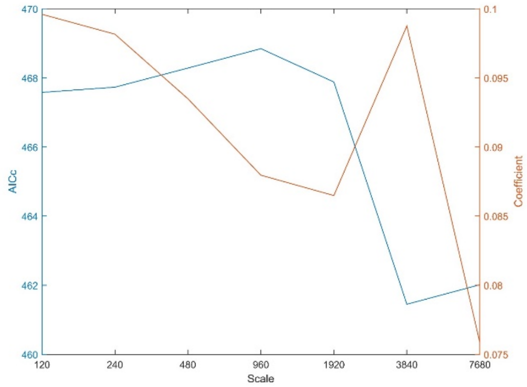
Human footprint



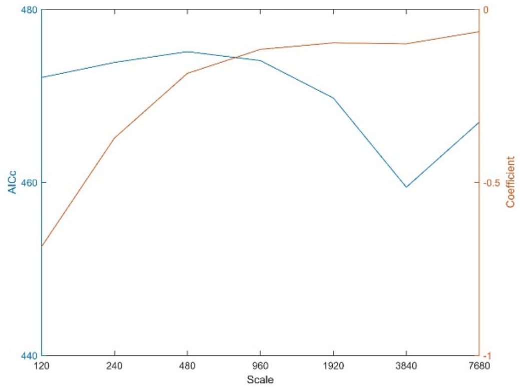
Topographical roughness



Tree cover

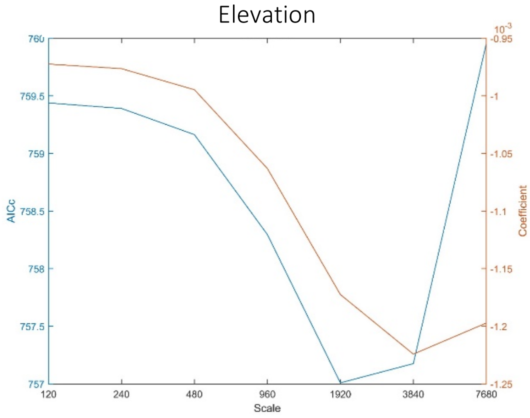


Tree cover SD

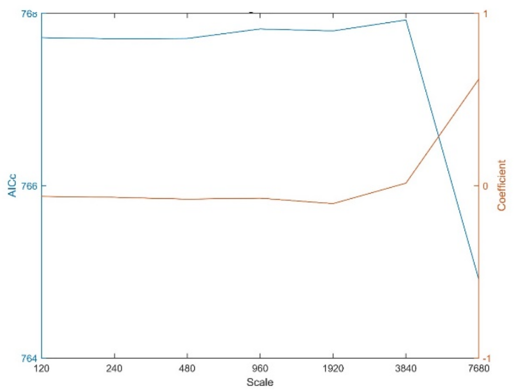


(d) Leopard cat

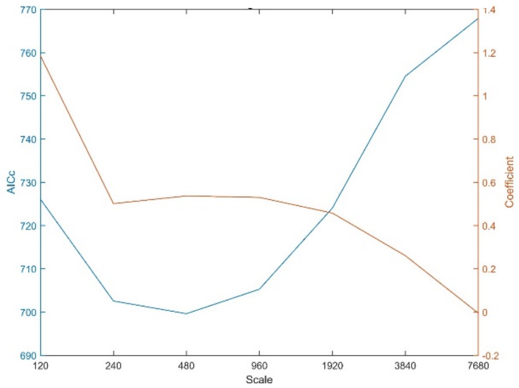
Elevation



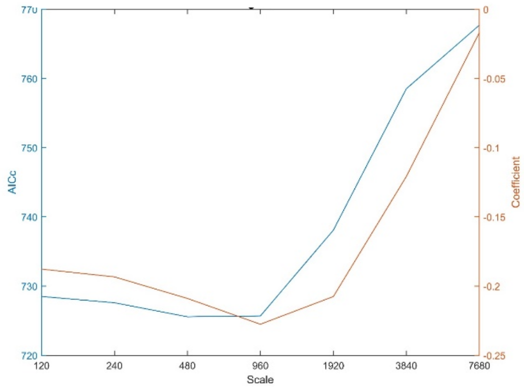
Gaveau: Agroforests / forest regrowth



Gaveau: Oil palm plantations



Gaveau: Logged forests



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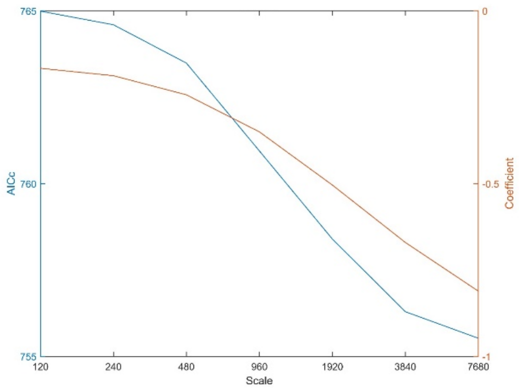
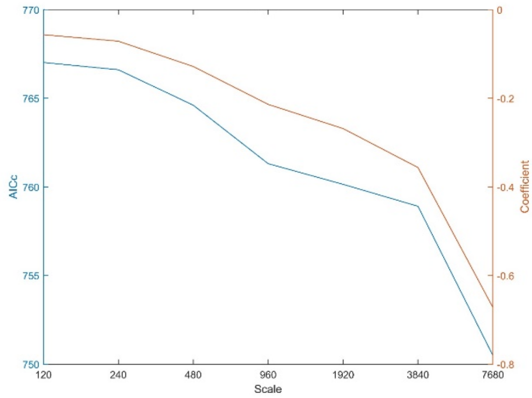


Miet 7



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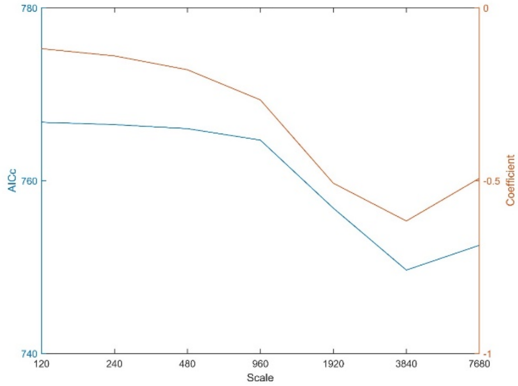
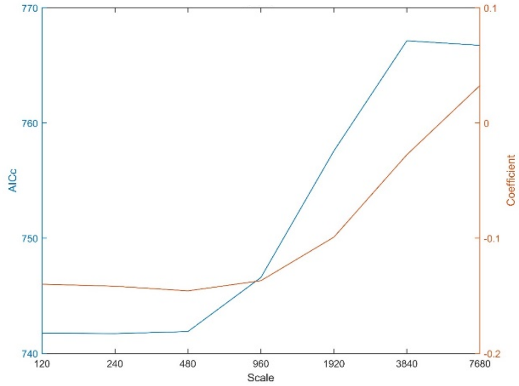
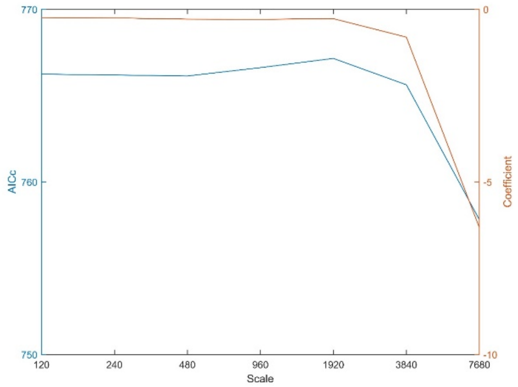


SFD 10



SFD 11



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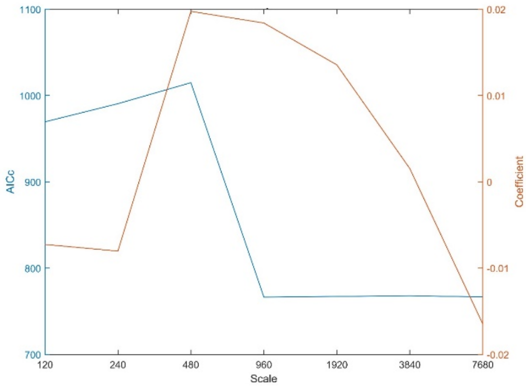
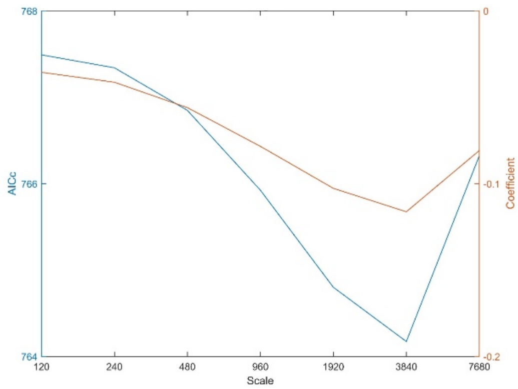
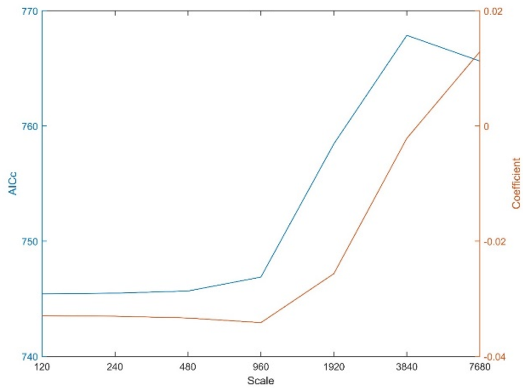


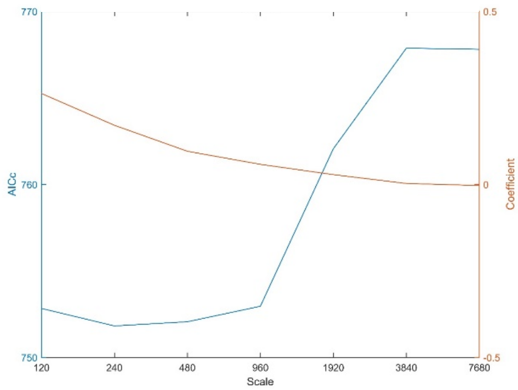
Topographical roughness



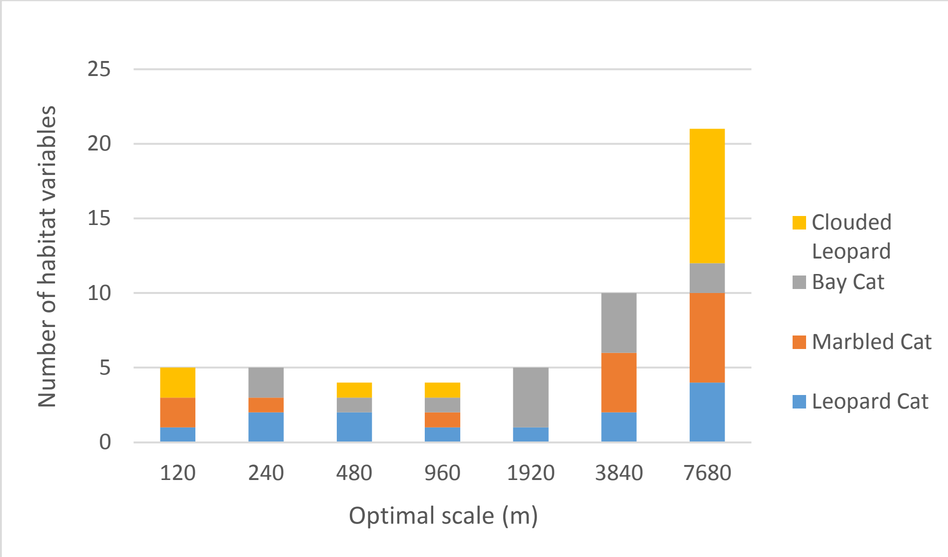
Tree cover



Tree cover SD



Appendix 3. Bar chart showing the optimal scaling of habitat variables in Bornean felids.



Appendix 4. Results of univariate logistic regressions to assess the relative importance of habitat variables in predicting Bornean felid occurrence, showing optimal scale of each habitat variable. Variables showing p values <0.2 were used in the multivariate analyses.

Variable	Optimal scale (m)	Coefficient	AIC	P-Value
Sunda Clouded leopard				
elevation	120	0.00136	630.499	5.25E-05
Gaveau: Agroforest/forest regrowth	7680	-2.03649	629.089	0.00012
Gaveau: Oil palm plantations	7680	-0.45241	617.683	7.52E-07
Gaveau: Logged forests	7680	0.26937	613.737	1.07E-07
Miettinen: Lowland open	7680	-0.91899	637.082	0.00551
Miettinen: Plantation/regrowth	7680	-0.98417	620.645	2.22E-06
Miettinen: Lowland mosaic	7680	-0.72579	627.689	0.00013
SFD: Lowland Mixed Dipterocarp Forest	480	0.30057	614.076	3.72E-05
SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	120	-0.59114	644.595	0.453
Human footprint	7680	-0.12614	610.372	1.26E-07
Roughness	7680	0.33954	627.513	2.41E-05
Canopy cover	7680	0.06582	613.916	2.98E-07
Canopy cover std	7680	-0.07639	606.944	2.24E-09
Bay cat				
elevation	120	-73.83250	232.862	0.505
Gaveau: Agroforest/forest regrowth	480	-21.42180	227.439	0.271
Gaveau: Oil palm plantations	1920	-81.36520	222.353	0.6
Gaveau: Logged forests	240	190.14540	223.22	0.99
Miettinen: Lowland open	1920	-8233.51000	230.473	0.961
Miettinen: Plantation/regrowth	240	-1.20425	235.291	0.332
Miettinen: Lowland mosaic	1920	-139.75500	226.003	0.612
SFD: Lowland Mixed Dipterocarp Forest	1920	46.37472	221.218	0.567
SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	7680	-3728.43000	237.053	0.989
Human footprint	3840	-0.07375	237.425	0.1197
Roughness	7680	0.25091	238.084	0.159
Canopy cover	3840	0.16767	227.957	0.02108
Canopy cover std	960	-0.58446	222.66	0.0859
Marbled cat				
elevation	120	0.00129	475.054	0.00085
Gaveau: Agroforest/forest regrowth	7680	-2.47138	471.408	0.00073
Gaveau: Oil palm plantations	7680	-0.48467	466.581	9.87E-05
Gaveau: Logged forests	7680	0.29443	463.074	2.03E-05
Miettinen: Lowland open	7680	-1.62160	474.008	0.00839
Miettinen: Plantation/regrowth	3840	-0.59497	476.393	0.00679
Miettinen: Lowland mosaic	7680	-0.90594	471.089	0.00176
SFD: Lowland Mixed Dipterocarp Forest	3840	0.26548	466.733	0.00029
SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	120	0.41335	477.891	0.00537
Human footprint	7680	-0.09687	471.215	0.0006
Roughness	960	0.36481	466.437	2.35E-05
Canopy cover	3840	0.09876	461.45	0.00012
Canopy cover std	3840	-0.09975	459.43	1.92E-05

Appendix 4. Continued.

Variable	Optimal scale (m)	Coefficient	AIC	P-Value
Leopard cat				
elevation	1920	-0.00117	757.009	0.00144
Gaveau: Agroforest/forest regrowth	7680	0.61839	764.908	0.08163
Gaveau: Oil palm plantations	480	0.53711	699.623	8.75E-12
Gaveau: Logged forests	480	-0.20891	725.567	3.52E-10
Miettinen: Lowland open	7680	-0.81129	755.524	0.00097
Miettinen: Plantation/regrowth	7680	-0.67206	750.488	5.86E-05
Miettinen: Lowland mosaic	3840	-0.61699	749.64	0.00013
SFD: Lowland Mixed Dipterocarp Forest	240	-0.14167	741.72	4.62E-07
SFD: Lowland Mixed Dipterocarp Forest & Limestone vegetation	7680	-6.32376	757.811	0.0386
Human footprint	960	0.01841	766.399	0.21537
Roughness	3840	-0.11632	764.172	0.0537
Canopy cover	120	-0.03296	745.432	9.72E-06
Canopy cover std	240	0.17063	751.814	9.58E-05

Appendix 5. Table of Overlaps of temporal activity patterns between Bornean wild cat species pairs and between Bornean wild cats and their potential prey species, as estimated by kernel density estimates. The coefficients of overlap (Δ_1 and Δ_4) are accompanied by the upper and lower values of the 95 % confidence limits.

	Clouded leopard			Clouded leopard Males			Clouded leopard Females			Bay cat			Marbled cat			Leopard cat		
	Δ_4	lower	upper	Δ_4	lower	upper	Δ_4	lower	upper	Δ_1	lower	upper	Δ_4	lower	upper	Δ_4	lower	upper
Felids:																		
Clouded leopard	-	-	-	-	-	-	-	-	-	0.398	0.331	0.468	0.521	0.463	0.576	0.742	0.707	0.777
Cloudedleopardmale	-	-	-	-	-	-	0.873	0.789	0.946	0.396	0.327	0.468	0.520	0.459	0.579	0.739	0.701	0.779
Cloudedleopardfemale	-	-	-	0.873	0.789	0.946				0.411	0.307	0.519	0.525	0.413	0.626	0.734	0.646	0.825
Bay cat	0.398	0.331	0.468	0.396	0.327	0.468	0.411	0.307	0.519				0.787	0.695	0.871	0.147	0.091	0.209
Marbled cat	0.521	0.463	0.576	0.520	0.459	0.579	0.525	0.413	0.626	0.787	0.695	0.871				0.264	0.206	0.305
Leopard cat	0.742	0.707	0.777	0.739	0.701	0.779	0.734	0.646	0.825	0.147	0.091	0.209	0.264	0.206	0.305	-	-	-
Potential prey:																		
Allmousedeer	0.803	0.774	0.832	0.824	0.786	0.847	0.759	0.686	0.830	0.428	0.356	0.504	0.609	0.551	0.664	0.581	0.561	0.600
Allmuntjac	0.518	0.483	0.553	0.529	0.492	0.564	0.531	0.435	0.618	0.802	0.733	0.870	0.914	0.878	0.945	0.261	0.248	0.274
Allpartridges	0.378	0.338	0.420	0.379	0.336	0.421	0.383	0.280	0.484	0.761	0.669	0.859	0.769	0.702	0.838	0.109	0.082	0.136
Allpheasants	0.372	0.339	0.405	0.373	0.336	0.408	0.380	0.280	0.473	0.861	0.790	0.933	0.843	0.792	0.889	0.104	0.090	0.117
Allpittas	0.390	0.348	0.430	0.391	0.349	0.431	0.392	0.294	0.490	0.853	0.766	0.930	0.821	0.763	0.877	0.120	0.097	0.145
Allsmallbirds	0.395	0.356	0.433	0.396	0.357	0.434	0.399	0.295	0.501	0.898	0.812	0.968	0.848	0.788	0.902	0.123	0.102	0.144
Bandedlinsang	0.704	0.640	0.768	0.700	0.638	0.765	0.706	0.595	0.807	0.118	0.048	0.196	0.209	0.139	0.280	0.913	0.852	0.962
Bandedpalmcivet	0.629	0.593	0.664	0.624	0.527	0.727	0.653	0.556	0.755	0.082	0.034	0.141	0.171	0.125	0.218	0.859	0.836	0.881
Bandedpitta	0.367	0.324	0.410	0.367	0.325	0.412	0.372	0.274	0.475	0.853	0.767	0.932	0.796	0.737	0.853	0.100	0.075	0.125
Binturong	0.716	0.612	0.815	0.703	0.596	0.806	0.719	0.581	0.839	0.625	0.506	0.731	0.674	0.580	0.762	0.498	0.388	0.604
Blueheadedpitta	0.411	0.334	0.494	0.412	0.332	0.489	0.405	0.293	0.526	0.880	0.738	0.970	0.809	0.702	0.906	0.151	0.086	0.221
Borneanyellowmuntjac	0.462	0.411	0.478	0.445	0.408	0.480	0.447	0.350	0.543	0.443	0.351	0.537	0.899	0.856	0.934	0.175	0.161	0.189
Bulwerspheasant	0.393	0.356	0.431	0.394	0.354	0.432	0.399	0.298	0.497	0.791	0.711	0.876	0.835	0.774	0.888	0.124	0.104	0.144
Chestnutnecklacedpartridge	0.409	0.339	0.484	0.410	0.330	0.489	0.410	0.293	0.524	0.792	0.653	0.914	0.782	0.659	0.894	0.135	0.074	0.200
Collaredmongoose	0.371	0.323	0.420	0.372	0.323	0.425	0.368	0.261	0.468	0.833	0.719	0.927	0.762	0.688	0.831	0.112	0.080	0.148
Commonpalmcivet	0.691	0.651	0.731	0.688	0.643	0.730	0.700	0.600	0.793	0.091	0.051	0.175	0.211	0.159	0.263	0.932	0.901	0.959
Commonporcupine	0.632	0.593	0.670	0.627	0.589	0.665	0.659	0.560	0.761	0.071	0.033	0.145	0.177	0.133	0.226	0.852	0.828	0.876
Crestedfireback	0.397	0.364	0.433	0.399	0.362	0.436	0.400	0.300	0.502	0.800	0.726	0.879	0.864	0.816	0.908	0.127	0.111	0.144
Crestedpartridge	0.380	0.336	0.425	0.381	0.334	0.431	0.384	0.286	0.485	0.761	0.662	0.860	0.763	0.682	0.841	0.111	0.080	0.143
elephant	0.657	0.606	0.709	0.644	0.590	0.692	0.704	0.612	0.795	0.610	0.521	0.698	0.725	0.662	0.789	0.479	0.439	0.521
Emeralddove	0.343	0.302	0.386	0.344	0.303	0.384	0.345	0.238	0.446	0.875	0.797	0.939	0.733	0.670	0.794	0.093	0.072	0.116
GreatArguspheasant	0.353	0.320	0.386	0.353	0.316	0.390	0.363	0.272	0.458	0.863	0.786	0.933	0.797	0.746	0.848	0.089	0.076	0.102

Appendix 5. (Continued).

	Clouded leopard			Clouded leopard Males			Clouded leopard Females			Bay cat			Marbled cat			Leopard cat		
	Dhat4	lower	upper	Dhat4	lower	upper	Dhat4	lower	upper	Dhat1	lower	upper	Dhat4	lower	upper	Dhat4	lower	upper
Potential prey:																		
Greatercoucal	0.306	0.212	0.413	0.303	0.203	0.407	0.327	0.209	0.453	0.839	0.660	0.963	0.685	0.535	0.818	0.065	0.003	0.155
Greatermousedeer	0.869	0.832	0.902	0.860	0.819	0.897	0.854	0.777	0.920	0.305	0.243	0.376	0.457	0.400	0.509	0.795	0.770	0.820
Hosecivet	0.723	0.675	0.768	0.719	0.662	0.769	0.728	0.628	0.824	0.138	0.078	0.204	0.233	0.179	0.292	0.930	0.891	0.964
Lessermousedeer	0.670	0.635	0.707	0.672	0.634	0.711	0.645	0.562	0.727	0.519	0.438	0.600	0.704	0.648	0.754	0.423	0.399	0.445
Longtailedmacaque	0.353	0.317	0.387	0.351	0.313	0.389	0.365	0.269	0.465	0.850	0.754	0.932	0.693	0.622	0.758	0.096	0.080	0.112
Longtailedporcupine	0.633	0.598	0.667	0.630	0.591	0.672	0.645	0.549	0.738	0.071	0.020	0.127	0.154	0.109	0.202	0.867	0.837	0.894
Malaybadger	0.670	0.630	0.711	0.668	0.625	0.710	0.663	0.568	0.753	0.084	0.032	0.144	0.168	0.118	0.224	0.897	0.862	0.927
Malaycivet	0.734	0.703	0.766	0.732	0.699	0.767	0.731	0.645	0.814	0.132	0.074	0.193	0.254	0.208	0.308	0.939	0.920	0.959
Malayweasel	0.396	0.308	0.492	0.396	0.305	0.491	0.405	0.278	0.533	0.777	0.614	0.916	0.770	0.625	0.898	0.140	0.058	0.238
Maskedpalmcivet	0.785	0.739	0.830	0.781	0.733	0.830	0.775	0.686	0.858	0.195	0.125	0.274	0.331	0.272	0.394	0.893	0.846	0.934
Mongoosespp	0.371	0.328	0.415	0.370	0.326	0.419	0.374	0.276	0.471	0.878	0.787	0.939	0.749	0.687	0.815	0.106	0.082	0.134
Moonrat	0.675	0.639	0.712	0.672	0.632	0.712	0.679	0.585	0.772	0.092	0.037	0.150	0.187	0.139	0.240	0.926	0.900	0.951
Orangutan	0.366	0.322	0.408	0.363	0.318	0.409	0.381	0.285	0.480	0.880	0.786	0.953	0.712	0.640	0.780	0.112	0.083	0.142
Ottercivet	0.648	0.563	0.738	0.644	0.564	0.729	0.668	0.564	0.776	0.097	0.020	0.178	0.173	0.095	0.262	0.885	0.787	0.956
Pangolin	0.643	0.578	0.702	0.639	0.572	0.706	0.616	0.507	0.714	0.092	0.031	0.161	0.171	0.110	0.230	0.816	0.759	0.865
Pig	0.611	0.577	0.644	0.611	0.573	0.644	0.612	0.513	0.712	0.763	0.685	0.832	0.885	0.839	0.928	0.349	0.333	0.366
Pigadult	0.595	0.562	0.629	0.594	0.558	0.630	0.598	0.509	0.692	0.787	0.718	0.861	0.883	0.830	0.928	0.334	0.318	0.352
Pigjuv	0.450	0.415	0.485	0.448	0.409	0.490	0.460	0.362	0.570	0.895	0.819	0.949	0.818	0.754	0.876	0.186	0.165	0.208
Pigsubadult	0.477	0.438	0.515	0.474	0.435	0.514	0.492	0.391	0.586	0.863	0.789	0.921	0.861	0.804	0.914	0.220	0.195	0.244
Pigtailedmacaque	0.332	0.298	0.364	0.331	0.296	0.365	0.343	0.258	0.438	0.899	0.832	0.959	0.712	0.659	0.771	0.085	0.073	0.097
Ratspp	0.635	0.602	0.670	0.632	0.595	0.667	0.649	0.548	0.748	0.083	0.037	0.135	0.162	0.119	0.207	0.874	0.853	0.895
Redmuntjac	0.621	0.586	0.658	0.622	0.585	0.659	0.624	0.527	0.718	0.747	0.679	0.806	0.866	0.821	0.905	0.356	0.338	0.373
Sambardeer	0.905	0.874	0.937	0.892	0.856	0.926	0.853	0.770	0.922	0.419	0.359	0.493	0.570	0.525	0.618	0.700	0.677	0.721
Shorttailedmongoose	0.358	0.320	0.395	0.357	0.322	0.394	0.366	0.273	0.461	0.917	0.836	0.976	0.751	0.691	0.812	0.099	0.081	0.116
Sunbear	0.723	0.679	0.765	0.711	0.665	0.755	0.726	0.629	0.814	0.601	0.521	0.682	0.766	0.705	0.823	0.497	0.466	0.529
Thickspinedporcupine	0.680	0.640	0.720	0.677	0.636	0.720	0.681	0.584	0.769	0.096	0.039	0.150	0.189	0.141	0.241	0.923	0.891	0.951
Treeshrewspp.	0.422	0.385	0.460	0.423	0.386	0.462	0.423	0.326	0.526	0.747	0.663	0.835	0.815	0.756	0.873	0.156	0.135	0.179
Treesquirrel	0.425	0.383	0.466	0.427	0.385	0.469	0.428	0.330	0.528	0.750	0.659	0.838	0.837	0.773	0.895	0.159	0.133	0.187
TuftedGroundSquirrel	0.315	0.274	0.356	0.314	0.272	0.357	0.323	0.234	0.421	0.782	0.688	0.872	0.629	0.555	0.699	0.078	0.056	0.102
Yellowthroatedmarten	0.402	0.356	0.447	0.410	0.364	0.458	0.433	0.333	0.537	0.852	0.743	0.939	0.810	0.738	0.876	0.159	0.128	0.191

Chapter 5. The first estimates of marbled cat *Pardofelis marmorata* population density from Bornean primary and selectively Logged Forest

A modified version of this Chapter has been published in *PlosONE* (see Appendix II)

Abstract

The marbled cat *Pardofelis marmorata* is a little studied wild cat that has a broad distribution across much of the Indomalayan ecorealm. This felid is thought to exist at low population densities throughout its range, yet no estimates of its abundance exist, hampering assessment of its conservation status. To investigate the distribution and abundance of marbled cats we conducted intensive, felid-focused camera trap surveys of eight forest areas and two oil palm plantations in Sabah, Malaysian Borneo. Study sites were broadly representative of the range of habitat types and the gradient of anthropogenic disturbance and fragmentation present in contemporary Sabah. We recorded marbled cats from all forest study areas apart from a small, relatively isolated forest patch, although photographic detection frequency varied greatly between areas. No marbled cats were recorded within the plantations, but a single individual was recorded walking along the forest/plantation boundary. We collected sufficient numbers of marbled cat photographic captures at three study areas to permit density estimation based on spatially explicit capture-recapture analyses. Estimates of population density from the primary, lowland Danum Valley Conservation Area and primary upland, Tawau Hills Park, were 19.57 (SD: 8.36) and 7.10 (SD: 1.90) individuals per 100 km^2, respectively, and the selectively logged, lowland Tabin Wildlife Reserve yielded an estimated density of 10.45 (SD: 3.38) individuals per 100 km^2. The low detection frequencies recorded in our other survey sites and from published studies elsewhere in its range, and the absence of previous density estimates for this felid suggest that our density estimates may be from the higher end of their abundance spectrum. We provide recommendations for future marbled cat survey approaches.

Introduction

The marbled cat *Pardofelis marmorata* is a small, elusive, forest-dependent felid whose wide distribution spans the Indomalayan ecorealm, from Eastern India and Nepal, to Yunnan province, China, and throughout mainland Southeast Asia to the islands of Sumatra and Borneo (Ross et al., 2016). This little known wild cat possesses a uniquely marbled coat pattern, from which its name is derived, and a distinctly thick and disproportionately long tail, which is characteristically held in a horizontal fashion when walking. The tail provides a useful counterbalance when climbing, and is likely an adaptation for a particularly arboreal lifestyle (Sunquist and Sunquist, 2002), although, as with much of this species' natural history, this is unconfirmed. In captivity the marbled cat is an adept climber (Leyhausen, 1979), and in the wild it has been observed descending, head-first, down the trunk of a large tree, an ability only previously reported in clouded leopards *Neofelis* spp. and Margays *Leopardus wiedi* (Mohamed et al., 2009). The marbled cat's diet remains unknown (Grassman et al., 2005), but arboreal prey are assumed to be important and there is an observation of an individual stalking birds in the canopy (Guggisberg, 1975) and another potentially preying on a juvenile Phayre's leaf monkey *Trachypithecus phayrei* (Borries et al., 2014). Nevertheless, despite their obvious arboreal adaptations the scientific literature includes camera trapping records of marbled cats walking on the ground (e.g., Grassman and Tewes, 2002; Brodie and Giordano, 2011; Lyngdoh et al., 2011; Bernard et al., 2013), so this felid's activities are clearly not restricted to the trees.

The marbled cat is widely considered to be a rare felid, whose populations are thought to be declining (Nowell and Jackson, 1996; Sunquist and Sunquist, 2002; Ross et al., 2016), yet there are no estimates of its abundance in any part of its range (Hunter, 2015), hampering robust assessment of its conservation status (Ross et al., 2016). Camera trap surveys undertaken within marbled cat range typically yield very few photographic captures (Brodie and Giordano, 2011; Lyngdoh et al., 2011; Bernard et al., 2013; McCarthy et al., 2015). Such low capture success has likely hitherto precluded efforts to estimate this felid's population density through capture-recapture analyses. Whether these low capture rates are a result of true rarity, or a reflection of the species' semi-arboreal nature or habitat use is unclear.

While knowledge of the marbled cat's status remains shrouded in uncertainty, it is clear that the loss of forest across their range continues at an ever increasing rate (Miettinen et al., 2011; Gaveau et al., 2014) and that indiscriminate poaching of these cats continues unabated (Coudrat et al., 2014; Duckworth et al., 2014; Wilcox et al., 2014), presenting a significant potential threat (Ross et al., 2016). As such, there is an increasing need to derive robust, range-wide estimates of the status of the marbled cat to facilitate the development of appropriate conservation measures. Here we use data stemming from intensive, felid-focused camera trapping surveys of a range of habitat types in Sabah, Malaysian Borneo to investigate the distribution and abundance of marbled cats. We produce the first marbled cat population density estimates from both primary and selectively logged forest areas using spatially-explicit capture-recapture modelling within a Bayesian framework.

Study Areas

We systematically surveyed eight forest areas and two oil palm plantations in Sabah, Malaysian Borneo with camera traps between May 2007 and December 2013 (Fig 1). The survey areas were broadly representative of the range of habitat types and the gradient of anthropogenic disturbance and fragmentation present in contemporary Sabah (Reynolds et al., 2011; Table 1). Survey areas included three primary forests: Danum Valley Conservation Area (Danum Valley); Tawau Hills Park (Tawau) and Crocker Range Park (Crocker), which range in elevation from lowland and hill dipterocarp to montane forest. We surveyed five selectively logged areas: Lower Kinabatangan Wildlife Sanctuary (Kinabatangan), Tabin Wildlife Reserve (sub-divided into two areas, Tabin North and South, see below), and Kabili-Sepilok, Malua and Ulu Segama Forest Reserves, which vary both in the degree of logging disturbance they were exposed to and in their levels of isolation and fragmentation. We also surveyed two oil palm plantations: Danum Palm and Minat Teguh plantations, which were both contiguous with areas of forest.

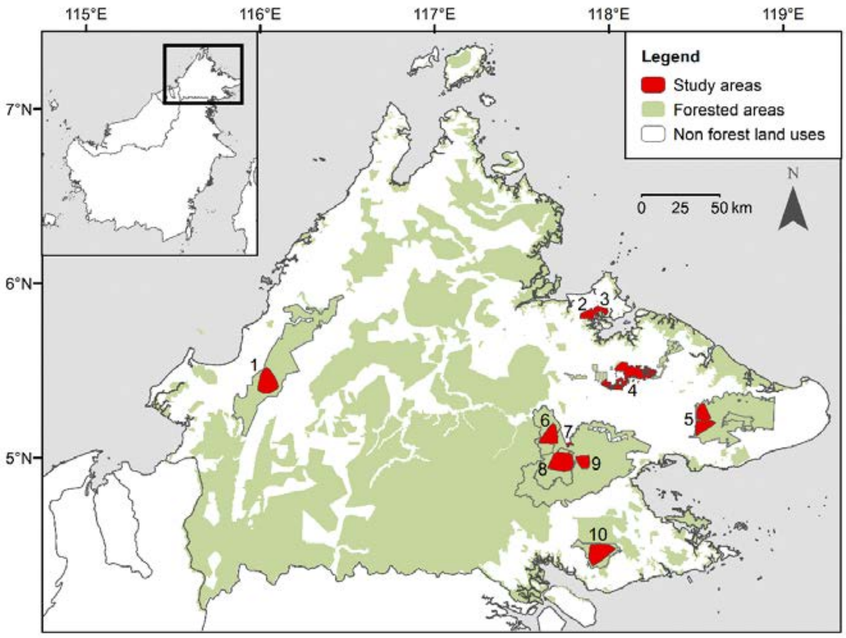


Fig 1. Locations of the eight forest and two oil palm plantation survey areas for marbled cats in Sabah, Malaysian Borneo. Inset shows the island of Borneo, and the main map shows the Malaysian state of Sabah. Numbered polygons represent the different study areas: 1. Crocker Range Park; 2. Minat Teguh plantation; 3. Kabili-Sepilok Forest Reserve; 4. Lower Kinabatangan Wildlife Sanctuary; 5. Tabin Wildlife Reserve (North and South); 6. Malua Forest Reserve; 7. Danum Palm plantation; 8. Danum Valley Conservation Area; 9. Ulu Segama Forest Reserve; 10. Tawau Hills Park. Density estimation using SECR analysis was possible in three of these areas: Danum Valley, Tabin and Tawau.

Table 1. Details of the eight forest and two oil palm plantation study areas in Sabah, Malaysian Borneo. FMU: Forest Management Unit.

Study area	FMU size (km^2)	Location (Lat/ Lon)	Dominant landcover type(s)	Level of fragmentation
Crocker	1399	5° 26′ N, 116° 02′ E	Primary, hill dipterocarp, sub-montane & montane.	Large, relatively isolated forest block.
Danum Valley	438	4° 58′ N, 117° 46′ E	Primary, lowland & hill dipterocarp.	Part of ca. 1 million ha Central Sabah Forest complex.
Kabili-Sepilok	42.9	5° 51′ N, 117° 57′ E	Partially selectively logged, lowland dipterocarp, heath forest & mangrove.	Small, isolated fragment. Possible connectivity along coastal mangrove system
Kinabatangan	260	5° 29′ N, 118° 08′ E	Selectively logged, mosaic of forest types, including riparian forest, seasonally flooded forest, swamp forest, limestone forest.	Highly fragmented. Contiguous with 250 km^2 state owned Forest Reserves and privately owned forest patches.
Malua	340	5° 08′ N, 117° 40′ E	Twice-logged (1960s & 2006–2007), lowland dipterocarp. High density of open logging roads and skid trails.	Part of ca. 1 million ha Central Sabah Forest complex.
Tabin (North and South)	1,205	5° 14′ N, 118° 51′ E	Selectively logged (1969–1989), lowland dipterocarp. Low density of open and semi-closed logging roads.	Large, relatively isolated forest block. Possible connectivity with coastal mangrove to north.
Tawau	280	4° 27′ N, 117° 57′ E	Primary, lowland & hill dipterocarp, sub-montane & montane.	Large, relatively isolated forest block, contiguous with commercial Forest Reserve to north.
Ulu Segama	2029	4° 59′ N, 117° 52′ E	Selectively logged (1978–1991), lowland dipterocarp. Rehabilitation planting ongoing. Medium density of open and semi-closed logging roads.	Part of ca. 1 million ha Central Sabah Forest complex.
Danum Palm	NA	5° 05′ N, 117° 46′ E	Semi-mature (planted in 2000), terraced oil palm plantation. Largely open understorey. Semi-natural scrub bordering one large river and one stream.	Shares eastern and western borders with ca. 1 million ha Central Sabah Forest complex.
Minat Teguh	NA	5° 50′ N, 117° 53′ E	Mature (planted in 1995), oil palm plantation. Largely open understorey. Border fringed with mangrove.	Shares eastern border with Kabili-Sepilok Forest Reserve

Methods

We used passive infrared digital camera traps of varying models: Bushnell Trophycam 2010 (Bushnell Corporation, KS, USA), Cuddeback Capture (Non Typical Inc., WI, USA), Panthera V3 (Panthera, NY, USA), Reconyx HC500 and PC800 (Reconyx Inc., WI, USA) and Snapshot Sniper P41 (Snapshot Sniper LLC, OK, USA). Due to varying equipment and logistical constraints, camera trap grids differed in size and effort, and cameras were deployed according to one of two protocols, (i) Split-grid, where the entire grid is sequentially surveyed in two halves and (ii) Simultaneous, where all camera stations are deployed in a single phase (Table 2). Camera stations were un-baited and separated by approximately 1.5–2.0 km. In our forest surveys we preferentially deployed camera stations along established human trails, newly cut trails and ridgelines. In the absence of an existing human trail we attempted to recreate an established trail by clearing an approximately 0.6 m wide section of trail free of dense vegetation, woody saplings and leaf litter, for approximately 50 m either side of the camera station. Established trails were also cleared in this fashion in the vicinity of the camera station, particularly those that were not well used. Where available, camera stations were also situated along old, unsealed logging roads. Such roads formed the majority of camera stations in two of the selectively logged sites (Malua and Ulu Segama), but formed a small proportion of camera stations or were absent in the other five forest sites (Table 2). For the plantation surveys we deployed cameras along access roads, human paths and narrow stretches of terrace (Danum Palm only). In all survey areas, cameras were positioned around 40–50 cm above the ground and arranged in pairs to enable both flanks of the animal to be photographed simultaneously, to permit subsequent identification of individuals based on their unique pelage patternation.

Table 2. Camera trap survey specifications and marbled cat photographic capture data derived from intensive camera trap surveys of multiple study areas in Sabah, Malaysian Borneo. a Camera trap grid area is defined by a 100% Minimum Convex Polygon around all camera stations. [b] We followed two survey protocols, Split-grid: where the entire grid was sequentially surveyed in two halves, and Sim.: Simultaneous, where all camera stations were deployed in a single phase. [c] Number of photographic captures of different individuals or images obtained more than 1 hour apart. [d] The number of independent adult photographic captures per 100 trap days. [e] Values within parentheses represent the number of independent photographic captures that did not permit identification to individual. [f] SECR density estimation was possible at these sites.

	Camera trap grid					Survey effort and marbled cat capture data						
Study area	Area (km^2)[a]	Protocol [b]	No. cam. stations	No. cam. stations on road / trail	Mean elevation and range (m.a.s.l)	Survey Dates	No. trap days	No. independent captures [c]		Detection frequency [d]	No. different animals recorded [e]	
								Adults	cubs		Adults	cubs
Danum Valley [f]	157.0	Split	79	0 / 79	384 (153–804)	24/3/12 – 6/10/12	5837	39	0	0.67	17 (10)	0
Tabin North [f]	71.4		37	1 / 36	140 (11–407)	16/12/09 – 22/4/10	3300	27	1	0.82	8 (2)	1
Tabin South	72.9		37	11 / 27	209 (62–431)	18/9/09 – 11/1/10	3162	15	0	0.47	4 (1)	0
Tawau [f]	149.0	Sim.	77	0 / 77	706 (209–1195)	21/10/12 – 30/12/13	17397	72	1	0.41	28 (4)	1
Crocker	149.7	Sim.	35	3 / 32	1029 (383–1452)	6/10/11 – 27/2/12	4059	11	0	0.27	5 (3)	0
Kabili Sepilok	49.4	Sim.	35	0 / 35	66 (8–134)	9/2/11 – 25/5/11	2054	0	0	0	0	0
Kinabatangan	359.5	Split	66	0 / 66	35 (5–135)	24/7/10 – 17/12/10	4340	5	0	0.12	3 (2)	0
Malua	102.8	Sim.	38	38 / 0	177 (68–286)	9/7/08 – 12/2/09	3869	5	0	0.13	3 (2)	0
Ulu Segama	60.1	Sim.	22	19 / 3	252 (150–408)	24/5/07 – 18/10/07	2847	7	1	0.25	5 (2)	1
Danum Palm	7.8	Sim.	23	NA	210 (120–295)	15/3/09 – 7/7/09	2212	5	0	0.23	1	0
Minat Teguh	44.0	Sim.	33	NA	23 (1–49)	26/5/11 – 18/8/11	1960	0	0	0	0	0

Where resulting photographic capture data from each site permitted, we estimated population densities of marbled cats using a Spatially Explicit Capture Recapture (SECR) model undertaken within a Bayesian framework (Royle et al., 2009), implemented in the R (version 3.1.2; R Development Team, 2014) package SPACECAP (version 1.1.0; Gopalaswamy et al., 2012). This approach incorporates a model of individual movements with one that describes detection by camera traps (Efford, 2004; Royle and Young, 2008). For each study site we compiled the number of photographs of each individual at each camera station and developed a capture history for each identified animal. Identification of animals was independently undertaken by a minimum of two people. We were unable to reliably distinguish the sex of marbled cats from all photographs, and so both sexes were analysed together. Finer sampling interval lengths may improve precision of density estimates in SECR analyses (Goldberg et al., 2015) and so we considered each 24-hour period as a sampling occasion. We limited our sampling duration to approximately 4 months (100–120 days, Table 2), which is a duration applied in similar studies to approximate population closure (e.g., Royle et al., 2011; Wilting et al., 2012). Surveys typically included lengthy camera set-up, transition (Split-grid protocol only) and collection phases, thus the total survey duration of each study site exceeded these closed periods. As a consequence, we selected closed survey periods during which camera trap effort, and, in turn, marbled cat photographic capture rates were maximised. Due to logistical constraints during our Tabin survey, which followed a Split-grid protocol, the transition phase in Tabin exceeded 50 days, and so we present these two sub-areas as two distinct surveys: Tabin North and South.

We generated potential home range centres by delineating a grid of regularly spaced points, with a mesh size of 0.16 km^2, within a polygon defined by the addition of a buffer to the outermost coordinates of the three trapping grids. This is known as the state space. We systematically increased buffer size during a sequence of preliminary runs until detection probability at the edge of the state space was negligible; we deemed a buffer size of 10 km sufficient for all sites. We classified each potential home range centre as either habitat or unsuitable-habitat using a GIS (ArcMap 10.2, ESRI, Redlands, California, USA) in conjunction with habitat data derived from field knowledge and hi-resolution aerial images from Google Earth (Images: DigitalGlobe). Marbled cats are thought to be forest dependent and not found in oil palm plantations (Ross et al., 2016) and so we considered forested areas (both pristine and disturbed) as habitat and all other non-forest land uses as unsuitable. For all analyses SPACECAP was run using a half normal model, with 100,000 iterations, a burn-in of 15,000 and a thinning rate of 1. We set data augmentation to 180, 800 and 140 for our Tabin, Danum Valley and Tawau analyses, respectively, following a series of preliminary runs, increasing data augmentation where necessary to ensure that ψ, the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value, did not exceed 0.8. We assessed model parameter convergence by means of Geweke tests; z scores falling between -1.64 and 1.64 were deemed acceptable.

Results

We recorded marbled cats in all forest study sites apart from Kabili-Sepilok, although photographic capture success varied greatly between areas (Table 2). We only obtained sufficiently high marbled cat detection frequencies to permit density estimation from Danum Valley, Tabin North and Tawau (Table 3). We recorded a single cub, on one occasion, in each of Tabin North, Tawau and Ulu Segama. We did not detect any marbled cats in Minat Teguh but an individual marbled cat was recorded on five occasions at a single camera station in Danum Palm, which was located at the very border of the plantation/interface with the Ulu Segama Forest Reserve.

Table 3. Sampling specifications and marbled cat capture data from the closed survey periods in Danum Valley, Tabin North and Tawau. [a] Number of independent photographic captures that were used in the SECR analysis. Values in parentheses represent the number of independent captures that were obtained within the closed period but did not permit individual identification and so were excluded from the analysis. [b] Values in parentheses represent the number of different camera stations that each individual was recorded at during the closed survey period.

Study area	Closed survey period	No. sampling occasions	No. trap days	No. captures[a]		No. different animals		No. captures per individual[b]
				Adults	cubs	Adults	cubs	
Danum Valley	25/05/2012 – 21/09/2012	120	4319	22 (4)	0	15	0	5(2), 2(2), 2(1), 2(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1)
Tabin North	11/01/2010 – 20/04/2010	100	2815	25 (3)	1	8	1	8(1), 6(1), 5(2), 2(2), 1(1), 1(1), 1(1), 1(1)
Tawau	14/12/2012 – 12/04/2013	120	6641	35 (1)	0	15	0	8(5), 6(4), 4(3), 4(2), 2(2), 2(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1), 1(1)

Posterior SECR summaries of the model parameters from our three study sites that provided sufficient data for density estimation are provided in Table 4. The mean estimated marbled cat densities for Tabin North, Danum Valley and Tawau were 10.45 (SD: 3.38), 19.57 (SD: 8.35), and 7.10 (SD: 1.90) individuals per 100 km^2, respectively, with 95% intervals of 4.01–17.37, 6.87–36.65 and 3.49–10.73 individuals per 100 km^2, respectively. Bayesian *p*-values of our SECR models indicated that the models were of an adequate fit, and Geweke tests indicated that all model parameters converged. The movement parameters were similar for both Tabin and Danum Valley, but were substantially larger in Tawau, indicating that the home ranges of animals in that population are likely larger.

Despite legislation prohibiting any hunting activity we found spent shotgun cartridges in seven of the forests we surveyed, Danum Valley being the only exception. We made no effort systematically to quantify poaching intensity but this is indicative that illegal poaching activities are widespread. No evidence of direct poaching of marbled cats was found.

Table 4. Posterior summaries from the Bayesian-SECR model parameters of camera trap data from Danum Valley, Tabin North and Tawau. σ: movement parameter, related to home range radius; λ_0: baseline trap encounter rate, the detection parameter of the spatial explicit capture-recapture model; ψ: the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value; *N*: number of individuals in the state space; *D*: density (individuals per 100 km^2).

Parameter	Tabin North		Danum Valley		Tawau	
	Mean (SD)	95% Lower - Upper HPD	Mean (SD)	95% Lower - Upper HPD	Mean (SD)	95% Lower - Upper HPD
σ	643 (97)	470 – 832	764 (215)	432 – 1155	2619 (511)	1777 – 3615
λ_0	0.036 (0.014)	0.013 – 0.065	0.009 (0.006)	0.002 – 0.02	0.002 (0.001)	0.001 – 0.004
ψ	0.275 (0.093)	0.107 – 0.457	0.284 (0.121)	0.097 – 0.533	0.267 (0.078)	0.127 – 0.423
N	51.3 (16.6)	21 – 83	230.7 (98.5)	81 – 432	41 (11)	22 –62
D	10.45 (3.38)	4.28 – 16.91	19.57 (8.35)	6.87 – 36.65	7.1 (1.9)	3.81 – 10.73
p-value	0.690		0.753		0.702	

Discussion

We present the first published density estimates for the marbled cat from any part of its range. Typical of camera surveys of cryptic forest felids, our recapture rates were relatively low for many individuals, particularly in Danum Valley and Tabin North, limiting our ability to derive estimates of movement parameters, and so our estimates of density at these sites may be high. Our highest estimate of density was the primary, lowland hill dipterocarp forest of Danum Valley Conservation Area, which was approximately two times greater than that of both the lowland, selectively logged Tabin Wildlife Reserve and the primary, uplands of Tawau Hills Park. As there is both a considerable overlap in our 95% intervals and a lack of replicates our ability to make robust conclusions about the possible influence of habitat type and anthropogenic disturbance on marbled cat densities is limited. Nevertheless, our study provides tentative evidence that undisturbed, lowland hill forest may support higher densities than both disturbed lowland and undisturbed higher elevation forests in northern Borneo.

No estimates of marbled cat density are available to compare against those derived from the current study. Our marbled cat density estimates were higher than that of the Sunda clouded leopard *Neofelis diardi* in central Sabah (0.8–1.9 individuals per 100 km^2), which were obtained using a SECR approach (Brodie and Giordano, 2012; Wilting et al., 2012), but similar to estimates of leopard cat *Prionailurus bengalensis* density from the same area (9.6–16.5 individuals per 100 km^2), which were also derived using an SECR approach (Mohamed et al., 2013). The latter finding is unexpected given the presumed high abundance and rarity of the leopard cat and marbled cat, respectively, although such assumptions may be based on the leopard cat's close association with logging roads leading to high observer encounter rates (Mohamed et al., 2013) and the marbled cat's avoidance of such features. Indeed, McCarthy et al., (2015) used camera traps to survey the Bukit Barisan Selatan National Park, Sumatra, and found that marbled cat occupancy peaked at moderate distances from roads (sealed and un-sealed).

Our density estimates may not be representative of other areas, and they may all stem from high density populations. Indeed, the relatively high capture frequencies of marbled cats in Danum Valley, Tabin North and Tawau, were approximately 2 to 6 times greater than that recorded in our other study sites and in previous intensive camera trap surveys elsewhere (Brodie and Giordano, 2011; Lyngdoh et al., 2011; Bernard et al., 2013; Tempa et al., 2013; Wearn et al., 2013; Chutipong et al., 2014; Coudrat et al., 2014; Gray et al., 2014; Gumal et al., 2014; Pusparini et al., 2014; Simcharoen et al., 2014; Zaw et al., 2014

McCarthey et al., 2015; Suzuki et al., 2015). Although we found evidence of poaching activities in Tabin and Tawau, all these sites are protected areas with limited access. Thus, poaching intensity is likely to be low relative to other sites in Sabah, and indeed elsewhere in the marbled cat's range. While we acknowledge the methodological limitations of comparing such indices of abundance across survey sites (Sollmann et al., 2013) the populations we surveyed in northern Borneo are likely to be from the higher end of their abundance spectrum.

The records of marbled cat presence in our four selectively logged survey sites, two of which provide confirmation of breeding activity, adds to the growing body of evidence that the species is able to tolerate some degree of habitat disturbance, e.g., (Wearn et al., 2013), and highlights the potential conservation values of these forests to this felid. Our surveys of Kinabatangan, Tabin and Ulu Segama took place approximately 16–20 years' post-harvest disturbance, and so these forests would have undergone substantial regrowth and recovery by this time. This is particularly true of Ulu Segama, where there has been intensive rehabilitation planting (Moura Costa, 1996; Reynolds et al., 2011). However, we also detected marbled cats in Malua, a particularly disturbed forest, less than one-year post harvest. We recorded few marbled cats in the highly fragmented Kinabatangan, although we were unable to disentangle the potential interplay between forest disturbance, poaching intensity and fragmentation, from that of habitat association. While the absence of marbled cat captures from Kabili-Sepilok cannot be used to infer that the species has been extirpated, this forest patch may be too small and/or isolated for a population to persist. We did not detect any marbled cat activity within either plantation area, but we did record one individual walking along the forest/plantation interface in Danum Palm. While our plantation surveys were of limited scope, our data tend to support the view that oil palm plantations are rarely used by marbled cats (Ross et al., 2016), although the periphery may be utilised.

Indiscriminate hunting and poaching appears to be increasing region-wide, particularly in Lao PDR and Vietnam, where trade-driven intensive snaring is likely impacting wild felids, including the marbled cat (Coudrat et al., 2014; Duckworth et al., 2014; Wilcox et al., 2014). It is becoming increasing important to gauge the status and monitor populations of threatened, non-*Panthera* felids, which currently lack such programmes and are rarely the focus of conservation effort and funding (Duckworth et al., 2014). Although generating estimates of marbled cat density poses a significant challenge, we show that well designed surveys using well established techniques produce rigorous data useful for such. Of those surveys that yielded sufficient capture rates to permit density estimation, camera stations were primarily situated along existing and newly created human trails, and included very few stations along logging roads. It is possible that this contributed to our ability to detect this felid and so the efficacy of future marbled cat focused surveys may be improved by maximising off-road camera deployment. There are a number of equally intensive camera trapping studies now being undertaken within marbled cat range, most targeting the estimation of tiger *Panthera tigris* and clouded leopard population density. As these data become available further estimates of the density of marbled cat will better underpin ecological understanding and conservation planning of one of Asia's most widely distributed, yet particularly elusive wild cats.

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Chapter 6. Responses of Sunda clouded leopard population density to anthropogenic disturbance and refining estimates of their conservation status in Sabah

Abstract

Abstract Extensive areas of tropical forests have been, and continue to be, disturbed as a result of selective timber extraction. Although such anthropogenic disturbance typically results in the loss of biodiversity, many species persist, and their conservation in production landscapes could be enhanced by a greater understanding of how biodiversity responds to forest management practices. We conducted intensive camera-trap surveys of eight protected forest areas in Sabah, Malaysian Borneo, and developed estimates of Sunda clouded leopard Neofelis diardi population density from spatially explicit capture–recapture analyses of detection data to investigate how the species' abundance varies across the landscape and in response to anthropogenic disturbance. Estimates of population density from six forest areas were 1.39–3.10 individuals per 100 km^2. Our study provides the first evidence that the population density of the Sunda clouded leopard is negatively affected by hunting pressure and forest fragmentation, and that among selectively logged forests, time since logging is positively associated with abundance. We argue that these negative anthropogenic impacts could be mitigated with improved logging practices, such as reducing the access of poachers by effective gating and destruction of road access points, and by the deployment of anti-poaching patrols. By calculating a weighted mean population density estimate from estimates developed here and from the literature, and by extrapolating this value to an estimate of current available habitat, we estimate there are 754 (95% posterior interval 325–1,337) Sunda clouded leopards in Sabah.

Introduction

While still containing some of the largest contiguous tracts of forested land in Southeast Asia, the rainforests of Borneo are experiencing amongst the highest global levels of forest degradation and loss, principally as a result of selective timber extraction and subsequent conversion to oil palm, *Elaeis guineensis*, plantations (Gaveau et al., 2014, 2016; Cushman et al., 2017). The intricate ecological responses to selective logging of Borneo's forests remain unclear for most species, yet several studies have indicated that many can persist after such management, with only a minority of species studied so far exhibiting markedly reduced post logging densities (e.g., Meijaard et al., 2005; Costantini et al., 2016). In comparison, the conversion of these forests to oil palm production has been shown to result in a very substantial reduction in biodiversity and functional diversity (Fitzherbert et al., 2008; Yue et al., 2015), a pattern mirrored region-wide (Wilcove et al., 2013). Thus, while logged forest undoubtedly has lower intrinsic value to biodiversity conservation than pristine forest, it is becoming increasingly clear that further gains to conservation could be achieved if management of production forests was improved to minimise negative impacts on biodiversity (Meijaard and Scheil, 2008). However, such an optimisation approach, based on an understanding of how biodiversity responds to forest management practices and other anthropogenic disturbances, is currently lacking for many species, and remedying this knowledge gap remains a priority.

The Sunda clouded leopard, *Neofelis diardi*, is a medium-sized felid, endemic to the islands of Borneo - where it is the terrestrial apex predator - and Sumatra. This species is currently listed as Vulnerable on the IUCN Red List as a result of a presumed small and declining population size (Hearn et al., 2016a). Assessment of its conservation status and development of effective conservation actions, however, are hindered by a lack of understanding regarding their abundance, distribution and responses to anthropogenic disturbance (Hearn et al., 2016b). Records of Sunda clouded leopards inhabiting a diverse range of forest types, including both pristine and selectively logged forests (e.g., Brodie & Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013, 2016; Sollmann et al., 2014; McCarthy et al., 2015; Hearn et al., 2016a), indicate that they exhibit some capacity to tolerate anthropogenic disturbance. Brodie et al. (2015a), however, showed that Sunda clouded leopard local scale abundance was lower in logged forest sites compared to unlogged sites. In addition, the movements of Sunda clouded leopards from a fragmented landscape were shown to be positively and strongly associated with forest, including highly disturbed forest types, but negatively associated with a range of non-forest vegetation (Hearn, 2016: Chapter 3), thus confirming earlier predictions that forest loss and conversion to oil palm plantations present one of this felid's greatest threats (Rabinowitz et al., 1987; Hearn et al., 2016a,b). Indeed, the increasing prevalence of vast tracts of oil palm plantations throughout this species' range is likely resulting in the fragmentation of habitat and the consequent isolation of individual populations, potentially making them increasingly vulnerable to demographic stochastic processes and inbreeding depression. Robust spatial ecology data are lacking for the Sunda clouded leopard, but preliminary analyses suggest that they have relatively large home ranges (Hearn et al., 2013). It is thus conceivable that as forests become increasingly fragmented, and forest patches decline in size, they become less able to support viable populations, resulting in reduced population densities, and, ultimately, local extirpation.

While recent research has provided new insights into how anthropogenic pressures influence Sunda clouded leopard abundance and habitat selection at a local scale, how these responses translate into changes to their population density remains unknown. Sollmann et al. (2014) estimated that Sunda clouded leopard density from two primary and two mixed forest (primary and secondary) areas in Sumatra ranged from around 0.8 to 1.6 individuals per 100 km^2, but found no statistical support for differences in density between the populations. In the Malaysian state of Sabah, northern Borneo, Brodie & Giordano (2012) estimated that Sunda clouded leopard density from an area of primary forest was 1.9 individuals per 100 km^2, whereas Wilting et al. (2012) presented densities from two selectively logged forests of around 0.8 and 1.0 individuals per 100 km^2. However, akin with Sollmann et al. (2014), the relatively large, overlapping variances of the Sabah-derived estimates suggest that the population densities were not significantly different. Such low precision estimates are a reflection of the difficulty of obtaining sufficiently large sample sizes. This is typical of studies of elusive forest felids (Foster & Harmsen, 2012) and hinders our ability to draw robust conclusions regarding the Sunda clouded leopard's responses to disturbance, potentially masking any underlying problems.

As obligate carnivores, large felid abundance is directly affected by prey density under a wide range of ecological conditions (Carbone & Gittleman, 2002; Karanth et al., 2004), and so it is reasonable to assume that prey densities are a key limiting factor for Sunda clouded leopards. Quantitative data regarding Sunda clouded leopard diet preferences are lacking, but incidental reports and observations from Borneo (e.g., Rabinowitz et al., 1987; Yeager, 1991; Matsuda et al., 2008) suggest that they exploit a diverse array of mammals, and studies of temporal activity overlaps and patterns of co-occurrence with potential prey (Ross et al., 2013) indicate that ungulates may be a key resource. Thus, the response of Sunda clouded leopards to anthropogenic disturbance may be mediated largely by the responses of their prey to such habitat modification. Bornean mammalian responses to selective logging vary greatly, but their sensitivity to disturbance is positively correlated with their phylogenetic age and dietary specificity, and negatively correlated with their ecological niche width (Meijaard & Sheil, 2008; Meijaard et al., 2008). Brodie et al. (2015a) showed that, compared to estimates in unlogged forest, muntjac (*Muntiacus* spp.) and mousedeer (*Tragulus* spp.) abundance declined, and bearded pig (*Sus barbatus*) and sambar deer (*Rusa unicolor*) increased in old logged forests. The abundance of all four ungulates was lower in recently logged forests. An increased abundance of some species in logged forest may benefit the Sunda clouded leopard and result in elevated abundances compared to primary forest. Conversely, the dense network of logging roads and skids present in production forests permit greater access and thus hunting opportunities for poachers (Laurance et al., 2009), of which ungulates are a favoured quarry (Corlett, 2007). In this balance, increased exploitative competition with humans in selectively logged forests without adequate protection against such threats could result in reduced Sunda clouded leopard densities.

Here, we develop estimates of Sunda clouded leopard population density using spatially explicit capture-recapture analyses of camera trap data from multiple forest areas in Sabah to investigate how density varies across the landscape and in response to anthropogenic disturbance. We test our *a-priori* hypotheses that Sunda clouded leopard population density will be lower in forests with (i) higher hunting pressure and (ii) higher levels of forest fragmentation. We also hypothesise that (iii) among selectively logged forests, time since logging will be positively associated with Sunda clouded leopard density. We combine our results with those from previously published studies to develop an estimate of Sunda clouded leopard population size in Sabah.

Study Areas

Between May 2007 and December 2013, we conducted intensive, systematic camera trap surveys of eight protected forest areas in the Malaysian state of Sabah, northern Borneo (Fig 1, Table 1). We selected survey areas such that they provided a broadly representative sample of the spectrum of forest types, elevations, anthropogenic disturbance and fragmentation present in the state. We surveyed three primary forests, including one predominantly lowland hill (Danum Valley Conservation Area: Danum Valley), and two largely hill dipterocarp and submontane forests (Tawau Hills Park (Tawau) and Crocker Range Park (Crocker)). We surveyed five forest areas which had been exposed to selective logging, including the Lower Kinabatangan Wildlife Sanctuary (Kinabatangan), Tabin Wildlife Reserve (Tabin), and Kabili-Sepilok, Malua and Ulu Segama Forest Reserves.

Methods

Camera survey protocol

We undertook camera trap surveys designed specifically to estimate Bornean felid population density (Hearn et al., 2016c). Depending on logistical constraints, we deployed cameras according to one of two protocols, applying either a split-grid approach, where the entire grid is sequentially surveyed in two halves, or a simultaneous approach, where all camera stations are deployed in a single phase (Table 2). We deployed cameras primarily along established and newly cut human trails and ridgelines, and occasionally along old, unsealed logging roads, particularly in two of the selectively logged sites (Malua and Ulu Segama; Table 2). Camera stations were spaced approximately 1.5–2.0 km apart, to balance the need for a sufficiently large sampling grid with the need to ensure that each animal's homerange contains several stations (e.g., Foster & Harmsen, 2012). Cameras were positioned around 40–50 cm above the ground and arranged in pairs to enable both flanks of the animal to be photographed simultaneously, to facilitate individual identification.

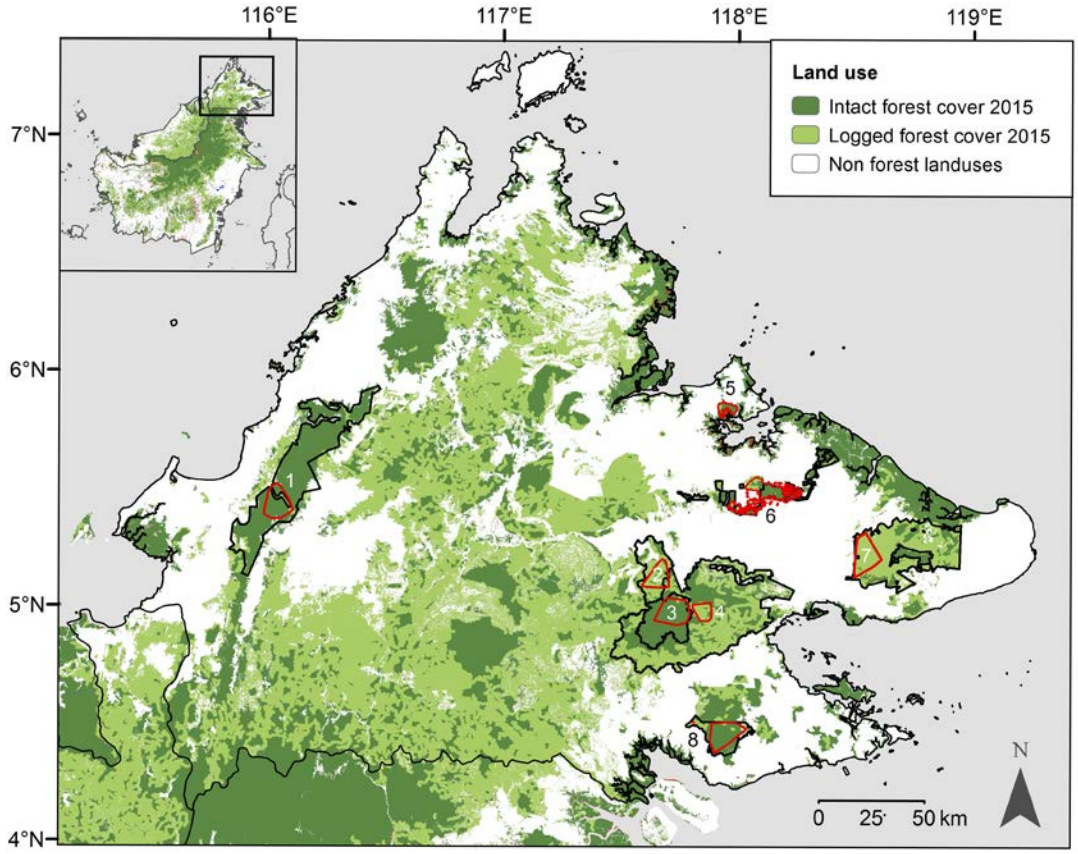

Fig 1. The locations of the eight camera trap survey areas in Sabah, Malaysian Borneo, showing land use in 2015. Numbered polygons represent the different study areas: 1. Crocker Range Park; 2. Malua Forest Reserve; 3. Danum Valley Conservation Area; 4. Ulu Segama Forest Reserve; 5. Kabili-Sepilok Forest Reserve; 6. Lower Kinabatangan Wildlife Sanctuary; 7. Tabin Wildlife Reserve; 8. Tawau Hills Park. Inset shows the island of Borneo. Land use data derived from Gaveau et al (2016). Note, Intact forest includes both primary forest as well as previously logged forest, the impacts of which were no longer visible via analysis of satellite images in 2015; see Gaveau et al (2016) for further details

Table 1. Details of the eight forest study areas in Sabah, Malaysian Borneo. Study areas are arranged in approximate order of increasing disturbance (level of fragmentation and exposure to selective logging practices).

Study area	Location (Lat/ Lon)	Size (km^2)	Level of isolation /fragmentation of forest patch	Dominant landcover type(s) / logging exposure	Time since logging (Years)
Danum Valley	4° 58′ N, 117° 46′ E	438	Low. Part of ca. 1 million ha Central Sabah Forest complex	Primary, lowland & hill dipterocarp.	N/A
Tawau	4° 27′ N, 117° 57′ E	280	Medium. Large, relatively isolated forest block, contiguous with commercial Forest Reserve to North.	Primary, lowland & hill dipterocarp, sub-montane & montane.	N/A
Crocker	5° 26′ N, 116° 02′ E	1399	Medium. Large, relatively isolated forest block.	Primary, hill dipterocarp, sub-montane & montane.	N/A
Ulu Segama	4° 59′ N, 117° 52′ E	2029	Low. Part of ca. 1 million ha Central Sabah Forest complex	Selectively logged (1978-1991), lowland Dipterocarp. Medium density of open and semi-closed logging roads.	16
Tabin	5° 14′ N, 118° 51′ E	1,205	Medium. Large, relatively isolated forest block. Possible connectivity with coastal mangrove to North.	Selectively logged (1969-1989), lowland dipterocarp. Low density of open and semi-closed logging roads.	20
Kabili-Sepilok	5° 51′ N, 117° 57′ E	43	High. Small, isolated fragment. Possible connectivity along coastal mangrove system	Partially selectively logged (low impact, ceased 1957), lowland Dipterocarp, heath forest & mangrove.	>50
Kinabatangan	5° 29′ N, 118° 08′ E	260	High. Relatively isolated, highly degraded patches of forest along large river.	Selectively logged, mosaic of forest types, including riparian forest, seasonally flooded forest, swamp forest, limestone forest.	>20
Malua	5° 08′ N, 117° 40′ E	340	Low. Part of ca. 1 million ha Central Sabah Forest complex	Twice-logged (1960s & 2006-2007), lowland dipterocarp. High density of open logging roads and skid trails.	1

Table 2. Details of camera trap sampling regimes and Sunda clouded leopard photographic capture data derived from surveys of eight forest study areas in Sabah, Malaysian Borneo. [a] Camera trap grid area is defined by a 100% Minimum Convex Polygon around all camera stations. [b] We followed two survey protocols, Split-grid: where the entire grid was sequentially surveyed in two halves, and Simultaneously (Sim): where all camera stations were deployed in a single phase. [c] Number of photographic captures of different individuals or images obtained more than 1 hour apart. [d] values within parentheses represent capture data for male, females and cubs, respectively.

Study area	Camera trap grid					Survey effort and Sunda clouded leopard capture data			
	Area (km^2) [a]	Protocol [b]	No. cam. stations	No. cam. stations on road / trail	Mean elevation and range (m.a.s.l)	Survey dates	No. trap days	No. independent captures [c, d]	No. different animals recorded [d]
Danum Valley	157.0	Split	79	0 / 79	384 (153–804)	24/3/12–6/10/12	5837	88 (82,6,0)	9 (6,3,0)
Tawau	149.0	Sim.	77	0 / 77	706 (209–1195)	21/10/12–30/12/13	17397	239 (219,20,1)	12 (7,5,1)
Crocker	149.7	Sim.	35	3 / 32	1029 (383–1452)	6/10/11–27/2/12	4059	51 (46,5,2)	8 (4,4,2)
Ulu Segama	60.1	Sim.	22	19 / 3	252 (150–408)	24/5/07–18/10/07	2847	83 (70,13,0)	11 (6,5,0)
Tabin	159.0	Split	74	12 / 62	175 (11–431)	18/09/09–22/4/10	6462	41 (36,5,0)	9 (5,4,0)
Kabili Sepilok	49.4	Sim.	35	0 / 35	66 (8–134)	9/2/11–25/5/11	2054	0	0
Kinabatangan	359.5	Split	66	0 / 66	35 (5–135)	24/7/10–17/12/10	4340	15 (8,7,0)	5 (2,3,0)
Malua	102.8	Sim.	38	38 / 0	177 (68–286)	9/7/08–12/2/09	3869	11 (9,2,1)	6 (4,2,1)

Assessment of poaching pressure

We followed the approach of Brodie et al. (2015a) and analysed our camera trap data to provide an estimate of poaching pressure for each study area and to enable comparison with estimates of poaching pressure recorded in their previous studies. Our assessment was based on the photographic encounter rate of presumed poachers, calculated as the mean proportion of days that ≥1 poacher was recorded at each camera station. Hunting of birds or mammals of any species is prohibited by law in all our study areas, and people did not live in, or use the forest for any legal purpose other than limited tourism, research and forest management at any of our sites. Excluding obvious records of unarmed park staff, field personnel and tourists, we assumed that any person photographed within the forest was a poacher. In most (86%) cases, people in the forest illegally were photographed carrying shotguns or spears, and/or accompanied by dogs. This approach does not permit assessment of historical poaching pressure, which may arguably be a more important parameter to measure, but does provide a useful, non-subjective assessment of current poaching levels.

SECR analyses

We developed estimates of Sunda clouded leopard population density using a Spatially Explicit Capture Recapture (SECR) approach (Efford, 2004; Royle & Young, 2008), undertaken within a Bayesian framework (Royale et al., 2009). We used the R (version 3.1.2; R Development Team, 2014) package SPACECAP (version 1.1.0; Gopalaswamy et al., 2012) to conduct all SECR analyses. We used pelage markings and morphology to identify and sex individual animals and developed a unique capture history for each animal. Detections of cubs were recorded but only adult animals were included in the analysis. While it has been shown that gender can affect detection parameters in felids, and inclusion of sex as a covariate can consequently improve parameter estimation precision (e.g. Sollmann et al., 2011), we were unable to model sex-specific detection parameters because of the low number of female recaptures and so data for both sexes were pooled and analysed together. We assigned each 24-hour period as a unique sampling occasion, as short sampling interval lengths may improve model precision (Goldberg et al., 2015). We limited our sampling duration to 90 days, apart from one site (Tabin), where the lengthy transition period, and consequent reduction in camera trapping effort, necessitated a period of 120 days to provide sufficient detection frequencies. Such sampling durations are in-line with similar studies to approximate population closure (e.g., Royle et al., 2011; Wilting et al., 2012).

We developed a state space, a polygon defined by the addition of a buffer to the outermost coordinates of each trapping grid, within which we established potential home range centres by delineating a grid of regularly spaced points, with a mesh size of 0.25 km2. Following Gopalaswamy et al. (2012) we eliminated potential home-range centres from areas predicted to be unsuitable for Sunda clouded leopards using a GIS (ArcMap 10.2, ESRI, Redlands, California, USA) in conjunction with habitat data derived from field knowledge and hi-resolution aerial images from Google Earth (Images: DigitalGlobe). We assumed that Sunda clouded leopards are restricted to forest cover and not found in oil palm plantations (Hearn et al., 2016b) and so we considered forested areas (both pristine and disturbed) as habitat and all other non-forest land uses, as unsuitable. During a sequence of preliminary runs, we systematically increased buffer size until the probability of detection at the state space boundary was negligible. Accordingly, buffer size varied from 12 to 30 km.

We ran all SPACECAP density estimation analyses using a half normal detection and Bernoulli's encounter model, with 100,000 Markov-Chain Monte Carlo (MCMC) iterations and a thinning rate of 1. We varied burn-in for each survey until adequate parameter convergence was attained, which we assessed by means of Geweke tests; z scores falling between -1.64 and 1.64 were deemed acceptable. Program SPACECAP applies a data augmentation process in which a theoretical population of zero-encounter history individuals is added to the dataset of known animals (Gopalaswamy et al., 2012). We varied data augmentation values for each survey, assigning a final value following a series of preliminary runs, increasing data augmentation where necessary to ensure that ψ, the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value, did not exceed 0.8. Finally, we examined the Bayesian p-value provided by program SPACECAP, which measures the discrepancy between observed data and expected values, to assess the goodness-of-fit of the model; models presenting p-values of around either 0 or 1 were considered inadequate (Gelman et al., 1996; Gopalaswamy et al., 2012). For each parameter estimated, we present the posterior mean, standard deviation, and 95% Bayesian highest posterior density (HPD) interval. The HPD is the shortest interval enclosing 95% of the posterior distribution. Following Sollmann et al. (2014) we consider parameters from each site to be significantly different if the 95% HPD of one does not include the mean of the other.

Estimation of population size in Sabah

We developed an estimate of Sunda clouded leopard population size for Sabah based on extrapolation of an estimate of this species' density to an estimate of current available habitat. Following a meta-analysis approach, we calculated a weighted mean population density estimate from estimates developed in this paper (n=6) and from previous published estimates from Sabah (Brodie and Giordano, 2012, n=1; Wilting et al., 2012; n=2), by weighting each unique value by the inverse of their coefficient of variation, based on their respective 95% HPD values. Using the same weighted approach, we calculated a mean upper and lower density estimate, based on each value's upper and lower quantiles. For an approximation of available Sunda clouded leopard habitat, we assumed that these felids are restricted to forest habitats and used an estimate of Sabah forest cover for the year 2015 developed by Gaveau et al. (2016), based on analysis of LANDSAT imagery. Gaveau et al.'s (2016) definition of forest included closed-canopy, old-growth and selectively logged dipterocarp, heath, fresh-water and peat swamp forests and mangrove forests, but excluded young forest regrowth, scrublands, tree plantations, agricultural land, and non-vegetated areas, and thus closely matches current predictions for clouded leopard habitat associations (Hearn et al., 2016b). It is important to note that this definition of available habitat includes forest types from which no robust density estimates are currently available (i.e., heath forests, peat swamp forests and mangrove), and so our population estimate should be treated with appropriate caution.

Results

Photographic capture success

We recorded 528 independent photographic captures of Sunda clouded leopards, with records stemming from all survey areas apart from Kabili-Sepilok (Table 2). We found evidence of breeding activity at three sites, recording two different cubs in Crocker and one in both Malua and Tawau (Table 2). The number of independent photographic captures within the closed survey period varied greatly across the different sites, ranging from 10 to 101 (mean = 41), and the number of different individual animals recorded within this period ranged from 5 to 10 (Table 3). We could assign individual identity to all but one of the photographic captures, a female from Malua. At most sites, we recorded more individual males than females, and males typically had higher recapture rates than did females (Table 3).

Table 3. Sampling specifications and Sunda clouded leopard capture data from the closed survey periods from seven study areas in Sabah, Malaysian Borneo. [a] Number of independent photographic captures that were used in the SECR analysis. [b] Values in parentheses represent values for males, females and cubs, respectively. [c] Values in parentheses represent the number of different camera stations that each individual was recorded at during the closed survey period.

Study area	Closed survey period	No. sampling occasions	No. trap days	No. captures [a,b]	No. different animals recorded [b]	No. captures per individual [c]	
						Males	Females
Danum Valley	23/06/2012 – 20/09/2012	90	3376	46 (43,3,0)	8 (6,2,0)	23(13), 8(5), 7(4), 2(2), 2(1), 1(1)	2(2), 1(1)
Tawau	11/3/2013 – 8/6/2013	90	6471	101 (92,9,0)	10 (5,5,0)	49(24), 30(17), 7(4), 4(3), 2(2)	3(3), 3(2), 1(1), 1(1), 1(1)
Crocker	17/11/2011 – 14/02/2012	90	3005	37 (34,3,2)	6 (3,3,2)	21(11), 9(3), 4(1)	1(1), 1(1), 1(1)
Ulu Segama	21/06/2007 – 18/09/2007	90	1980	59 (48,11,0)	10 (6,4,0)	22(6), 10(6), 6(4), 5(3), 3(1), 2(1)	5(4), 2(2), 2(1), 1(1)
Tabin	11/11/2009 – 10/3/2010	120	3677	21 (18,3,0)	8 (5,3,0)	10(6), 4(4), 2(2), 1(1), 1(1)	1(1), 1(1), 1(1)
Kinabatangan	20/8/2010 – 17/11/2010	90	3060	13 (7,6,0)	5 (2,3,0)	6(3), 1(1)	4(4), 1(1), 1(1)
Malua	30/9/2008 – 28/12/2008	90	2577	10 (8,2,1)	6 (4,2,1)	3(2), 2(2), 2(1), 1(1)	1(1), 1(1)

Assessment of poaching pressure

We found evidence of probable poaching activity in all forest areas, apart from Danum (Table 4). The lowest poacher detection rates were found in Danum, Ulu Segama and Tawau, where camera theft was also low, and the highest in Kinabatangan and Malua, where camera theft was high. Camera theft from Crocker was also relatively high. Tabin had a relatively high poacher detection rate but a relatively low incidence of camera theft.

Table 4. Indication of relative poaching pressure in each study area based on photographic detection rate of presumed poachers and percentage of camera traps stolen; see methods for full description.

Study area	Mean hunter encounter rate ±SD	% camera stolen
Danum Valley	0.000 ±0.000	0
Ulu Segama	0.071 ±0.228	0
Tawau	0.090 ±0.455	1.3
Kabili-Sepilok	0.144 ±0.704	5.7
Crocker	0.288 ±0.642	11.1
Tabin	0.381 ±2.366	2.7
Kinabatangan	0.434 ±1.138	6.1
Malua	0.576 ±0.899	26.3

Density estimates

We developed estimates of Sunda clouded leopard density at all study sites at which they were detected apart from Malua, in which low numbers of photographic captures prevented SECR model convergence, and so was removed from subsequent analyses. At all other sites Bayesian *p*-values indicated that the models were of an adequate fit (Table 5) and Geweke tests indicated that all model parameters converged. Sunda clouded leopard density across these six sites varied from 1.39 to 3.10 individuals per 100 km^2 (Table 5). The two highest density estimates stemmed from the enrichment-planted Ulu Segama (3.10 individuals per 100 km2 ± SD 1.11) and selectively logged Tabin (2.66 ± SD 1.11), and the lowest from the primary upland Crocker (1.39 ± SD 0.41) and the highly degraded and fragmented Kinabatangan (1.54 ± SD 0.70). Sunda clouded leopard density was significantly higher in Ulu Segama than Crocker, Danum and Kinabatangan, and density in Tabin was significantly higher than in Crocker and Kinabatangan, but we otherwise found no statistical support for differences in density between any other sites. The movement parameters from

Kinabatangan and Tabin were significantly larger than that from all other sites, and the estimate from Kinabatangan was significantly larger than that from Tabin, by almost a factor of two (Table 5).

Estimation of population size in Sabah

The weighted mean population density developed from nine available density estimates was 1.90 individuals per 100 km2, and the weighted lower and upper 95% posterior intervals were 0.82 and 3.37 individuals per 100 km2, respectively. Based on data derived from Gaveau et al. (2016), the amount of available habitat in Sabah in 2015 was 39,693 km2. Extrapolation of the weighted density estimate to this habitat assessment produced an estimated population size of 754 (95% posterior interval 325–1337) individuals for Sabah.

Table 5. Posterior summaries of the Bayesian-SECR model parameters of camera trap data of the Sunda clouded leopard from six study areas in Sabah, Malaysian Borneo. 95% HPD: the Bayesian highest posterior density interval; σ: movement parameter, related to home range radius; λ_0: baseline trap encounter rate, the number of independent photographic detections per day; ψ: the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value; *N*: number of individuals in the state space; *D*: density ±SD (individuals per 100 km^2).

Study area	σ	λ_0	ψ	*N*	*D*	*p*-value
Danum Valley	3074 ±432 (2341–3937)	0.017 ±0.004 (0.009–0.025)	0.353 ±0.118 (0.142–0.591)	25.5 ±8.0 (12.0–41.0)	1.73 ±0.54 (0.81–2.78)	0.523
Tawau Hills	3915 ±354 (3284–4625)	0.01 ±0.002 (0.009–0.017)	0.400 ±0.111 (0.194–0.619)	19.8±4.6 (11.0–28.0)	2.23 ±0.52 (1.35–3.27)	0.573
Crocker	3688 ±479 (2815–4638)	0.023 ±0.006 (0.012–0.035)	0.283 ±0.100 (0.100–0.111)	12.6 ±3.7 (7.0–20.0)	1.39 ±0.41 (0.77–2.21)	0.501
Ulu Segama	2692 ±408 (1970–3470)	0.043 ±0.015 (0.020–0.072)	0.319 ±0.118 (0.114–0.555)	44.3 ±15.9 (18.0–76.0)	3.10 ±1.11 (1.26–5.32)	0.496
Tabin	4649 ±1616 (2325–7575)	0.004 ±0.002 (0.001–0.007)	0.284 ±0.122 (0.084–0.529)	30.3 ±12.6 (9.0–54.0)	2.66 ±1.11 (0.79–4.74)	0.697
Kinabatangan	9104 ±2672 (5151–13986)	0.003 ±0.002 (0.001–0.007)	0.316 ±0.146 (0.072–0.609)	26.5 ±12.0 (7.0–50.0)	1.54 ±0.70 (0.41–2.90)	0.606

Discussion

Influence of anthropogenic disturbance on Sunda clouded leopard density

We present estimates of Sunda clouded leopard population density from six of eight forest areas we surveyed in Sabah, Borneo, including the first for this species from enrichment-planted, highly fragmented, and submontane forest types. Our estimates of density from forest areas exposed to varying levels of anthropogenic disturbance ranged from 1.39 to 3.10 individuals per 100 km^2, and are thus comparable with those from previous studies in Sabah (0.84–1.9: Brodie and Giordano, 2012; Wilting et al., 2012), the Indonesian province of Central Kalimantan (0.72–4.41: Cheyne et al., 2013) and Sumatra (0.8–1.6: Sollmann et al., 2014). Nevertheless, statistically significant differences in Sunda clouded leopard population density were evident between several of our study areas.

While the absence of replication in our study approach limits our ability to draw robust conclusions about the possible influence of anthropogenic disturbance on Sunda clouded leopard densities, our results support our first *a priori* hypothesis that population density is negatively impacted by poaching pressure. Indeed, the two areas with the lowest estimates, the primary uplands of the Crocker Range Park and the low lying logged forests of the Lower Kinabatangan, were subject to some of the highest levels of poaching pressure, whereas forest areas with a relatively low incidence of poaching, e.g., Danum Valley, Ulu Segama and Tawau, yielded some of the highest densities. In the case of Ulu Segama, the estimate of density was statistically higher than that of the two lowest density sites. It is worth noting that the comparatively low density found in Crocker Range may also be a reflection of higher elevation forest supporting lower productivity. While we are unable to disentangle the possible influence of low detection probabilities as a result of other factors unrelated to abundance (Sollmann et al., 2013), the very low photographic capture success from Malua Forest Reserve, where poaching intensity was the highest of our study areas, is indicative of a low population density relative to our other sites. The high density estimate from Tabin Wildlife Reserve, which was also significantly higher than that of our two lowest density sites, yet was subject to moderate levels of poaching, appears to contradict this trend. However, unlike other areas where poaching activity was more diffuse, most records of poaching activity in Tabin typically involved poachers spot-lighting from four-wheel-drive vehicles along the single access road within the reserve, or occasionally along the western border with an oil palm plantation. It is, therefore, possible that the impact of poaching was not widespread throughout the study area.

Our data also tentatively support our second *a priori* hypothesis that Sunda clouded leopard population density will be lower in forests with higher levels of forest fragmentation. Firstly, the Lower Kinabatangan, which is composed of several relatively small forest patches embedded within a largely oil palm plantation landscape, supported the second to lowest density of all our areas. Secondly, we found no evidence of Sunda clouded leopards within the Kabili-Sepilok Forest Reserve, a small (42.76 km2), potentially isolated dipterocarp forest fragment contiguous with a coastal chain of mangrove and nipah palm, but otherwise surrounded by oil palm plantations. Forestry Department staff stationed in the area report that the species had been recorded there in the past, so it is likely that gradual loss of surrounding forest and conversion to oil palm plantations has led to local extirpation. Kabili-Sepilok Forest Reserve is a probable harbinger of the effects of ongoing fragmentation which will be detrimental to Sunda clouded leopard populations across much of its remaining range.

The low number of photographic captures from Malua Forest Reserve, which was surveyed just one year after selective logging operations ceased, provides tentative support for our third *a-priori* hypothesis, that time since logging is positively related to Sunda clouded leopard density in selectively logged forests. Furthermore, our two highest density estimates stemmed from two forests surveyed 16 and 20 years post logging activities, of which one, the enrichment-planted Ulu Segama Forest Reserve, was statistically higher than that from the primary Danum Valley Conservation Area. It is noteworthy that Wilting et al's (2012) survey of the Tangkulap-Pinangah Forest Reserve in Sabah, just eight years after logging operations stopped, yielded a density of 0.84 individuals per 100 km2, which is lower than any of our estimates. Brodie et al. (2015a) showed that, compared to unlogged forest areas, the abundance of four ungulate species was lower in recently logged areas, whereas bearded pig and sambar deer were more abundant, and muntjac and mousedeer less abundant in old logged areas. Thus, while we cannot be sure by what mechanism the effect may operate, one hypothesis is that following recent logging there is a direct negative effect on prey abundance and or availability, which declines over time. Another, not mutually exclusive, hypothesis is that the logging operations, and associated proliferation of roads, increases both the number of poachers and their penetration of the forest, reducing prey populations and perhaps also inflicting a by-catch on the Sunda clouded leopards themselves, and that the relative impact of these roads diminishes over time as the roads become unnavigable. Brodie et al. (2015b) found that an increase in road density on Borneo is associated with reduced local occurrence of Sunda clouded leopards, and in Sumatra, Haidir et al. (2013) found that this felid's habitat use was positively affected by distance to forest edge. In another Sumatran study, McCarthy et al. (2015) reported that this species occurred most commonly at moderate distances from roads, rivers and forest edges, all features which assist the movement of people.

Our results confirm earlier suggestions (e.g., Wilting et al., 2006; Hearn et al., 2016a,b) that selectively logged forest provides an important resource for Sunda clouded leopards, and suggests that appropriate management of these commercial forests could further enhance their conservation value. Our results suggest that the overriding priority is to reduce poaching pressure, both on these felids and their prey, by reducing access to the forest interior along logging roads. Reduction of vehicular access could be achieved through the installation of gates and the destruction of bridges following the cessation of logging activities. This is particularly important in more recently logged forests, which will have a more extensive network of gravel roads that are still passable. Such efforts will not prevent access on foot, and so measures such as anti-poaching patrols, while expensive, are also an essential tool to reduce the threat from poaching in these forests.

Estimation of population size in Sabah

We provide the first estimate of Sunda clouded leopard population size for the Malaysian state of Sabah based on robust spatially explicit capture recapture density estimates from nine forest areas within the state. Our estimated population size of around 754 (95% posterior interval 327–1337) individuals is a significant methodological improvement on the very approximate estimate of 1500–3200 individuals provided by Wilting et al. (2006), based on extrapolation of a track-based assessment of density from Tabin Wildlife Reserve. Our basic model of population size does not include a minimum patch size or measure of proximity to other patches in its calculation, as such data are currently lacking. Nevertheless, their apparent absence from the relatively small forest fragment of Kabili-Sepilok suggests that our estimate of available habitat may be slightly inflated, and with it our population estimate. In addition, while we made efforts to survey a range of forest types and levels of anthropogenic disturbance, there are a number of forest types that were not included. Of these, mangrove forest, given its potential importance in connecting otherwise isolated populations, is particularly important. Surveys within these habitats and efforts to determine minimum patch sizes for this felid are therefore a priority.

As forest cover on Borneo declines, there is an increasing need to assess the population size of this felid across the entire island, and thus the conservation status of the Bornean sub species, Neofelis diardi ssp. borneensis. The Sabah bias of our data, and the lack of robust spatially explicit density estimates from outside this region currently hinders such assessment. While the overall nature of the forests within Sabah broadly parallels those of the island as a whole, outside of this state there are stark differences in forest management and patterns of deforestation (Cushman et al., 2017). Furthermore, the threat from hunting and/or poaching, which we have shown to be a potentially important factor influencing Sunda clouded leopard density, is likely to vary considerably throughout the island. There is increasing evidence that Sabah's forests have hitherto been subjected to lower influences of hunting and poaching than elsewhere and that populations densities may be far lower outside of this region. Indeed, the mean encounter rate of hunters/poachers from five areas in Sarawak were more than an order of magnitude higher than that described in this paper (Brodie et al., 2015a). Furthermore, Cheyne et al. (2016) surveyed eight forest areas in Kalimantan with a comparable effort and approach to that used in our study, and recorded an exceptionally low number of Sunda clouded leopard records (≤3) from each of six of these forests, which could be indicative of low population densities. Efforts should thus be made both to establish the incidence of poaching across this felid’s range, and to derive robust, spatially explicit estimates of their density outside of Sabah to help better inform the conservation of this elusive wild cat.

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Chapter 7. General discussion

Aims and motivations

For decades, Borneo's once extensive and pristine forests have been increasingly exposed to a suite of anthropogenic disturbance and deforestation processes as a cumulative result of selective and illegal logging, hunting, droughts, fires and the conversion to plantations, chiefly oil palm (Beaman et al. 1985; Casson, 2000; Page et al., 2002; Wooster et al, 2012; Carlson et al., 2012, Gaveau et al., 2014, 2016). Such forest disturbance, and expansion of plantations at their expense, is of great concern to environmentalists and other observers (e.g., Fitzherbert et al., 2008; Sheil et al., 2009), prompting the investigation of the possible impacts of these landscape changes to Bornean biodiversity (e.g., Berry et al., 2010; Senior et al., 2012; Bernard et al., 2014 Edwards et al., 2013, 2014). It remains unclear, however, how such anthropogenic disturbance impacts the Sunda clouded leopard and other threatened, sympatric Bornean felids.

Understanding of the Bornean felid's statuses, habitat associations, distributions and movements are broadly lacking or otherwise underpinned by studies based largely on expert opinion (Ross et al., 2015, 2016; Hearn et al., 2016a,b,c,d; Wilting et al., 2015; 2016; Mohamed et al., 2016; Rustam et al., 2016), as opposed to empirical analysis, and thus require further testing. For example, while records of the Sunda clouded leopard, bay cat, marbled cat and flat-headed cat from selectively logged forests (e.g., Wilting et al., 2006; 2012; Cheyne et al., 2016; Haidir et al., 2013; Sollmann et al., 2014; McCarthy et al., 2015; Mohamed et al., 2009; Bernard et al, 2012; Hon, 2011; Mathai et al., 2014) broadly support the hypothesis that these felids are tolerant to this form of anthropogenic disturbance, the widely held view that these felids avoid non-forest areas remains untested, yet this has important implications to the amount of remaining habitat available to these felids, and thus their population size, as well as levels of populations connectivity. Furthermore, it remains unclear how anthropogenic disturbance influences these felids' population densities.

This thesis investigated how anthropogenic disturbance, including selective logging, deforestation and poaching, influences the distribution, movements, population connectivity and abundance of Sunda clouded leopards and other sympatric felids on Borneo, explored how inferences of these felids' distribution and connectivity differ between analyses based on expert opinion and empirical data, and provided some of the first data regarding the ecological interactions and patterns of coexistence among this felid assemblage. The underlying theme of this research was thus to advance understanding of the implications of the rapidly changing Bornean landscape to the conservation of these felids, and to contribute to the development of evidence-based conservation recommendations.

Synthesis

Influence of disturbance on Sunda clouded leopards

Insight into the ways in which landscape composition influences the movement of animals can greatly improve understanding of a given species' responses to anthropogenic disturbance, and the development of effective conservation management. As such, this thesis begins in Chapter 2 by exploring the effects of multiple landscape features on Sunda clouded leopard movement in a human dominated landscape – the Lower Kinabatangan Wildlife Sanctuary (LKWS) – a cluster of small, linear forest patches embedded within a matrix of oil palm plantations. Within this landscape, we showed that Sunda clouded leopard path selection was positively and strongly associated with a range of forest habitats, including highly disturbed forest types, so long as they had high canopy closure, and we showed that these closed canopy habitats facilitated the movements of these felids. Conversely, and in accordance with long-standing yet largely untested assumptions that the Sunda clouded leopard is intolerant of deforestation (e.g., Rabinowitz et al., 1987; Santiapillai and Ashby, 1988), we showed that Sunda clouded leopard movement was most highly resisted by oil palm plantations, particularly by recently cleared/planted and underproductive (frequently flooded) plantations with low canopy closure.

We developed predictions of Sunda clouded leopard connectivity in the LKWS, and showed that all of the core protected forest blocks in the region remain functionally connected with each other and with adjacent forest blocks elsewhere in Sabah. We also showed how small changes to the amount of forest cover in this landscape had large effects on this felid's connectivity; small increases, such as via the restoration of underproductive plantation areas, greatly improve connectivity, while loss of the region's unprotected forest led to significantly reduced levels of connectivity.

In Chapter 3 we sought to extrapolate the resistance and connectivity model developed in Chapter 2 to predict population density, genetic diversity and population connectivity for clouded leopards across the full extent of Sabah. We predicted that the large, contiguous Central Forest block in Sabah, which is largely composed of the ca. 1 million ha state owned Yayasan Sabah Foundation Area, exhibited the highest levels of connectivity, populations size and genetic diversity (Figure 1a,b). We also identified a number of isolated fragments of internally connected habitat, including the LKWS, Tabin Wildlife Reserve and Tawau Hills Park as patches of habitat predicted to have extant clouded leopard populations, but predicted to be isolated from other clouded leopard populations. All three of these areas are important protected areas, yet, as I discuss further below, the

Sunda clouded leopard populations that they support are potentially threatened by both isolation and low populations size.

Our model of Sunda clouded leopard landscape resistance and connectivity was developed from a single population, in a specific region of Sabah, which may not necessarily reflect the behavioural ecology of the species elsewhere. Furthermore, the data stem from animals that may have established homeranges, and thus may exhibit a more conservative use of the landscape than that of dispersing animals (presumably young males), as has been shown in lions (Elliot et al., 2014). In turn, our model of connectivity in Sabah may be too conservative. It is arguably prudent when developing conservation plans to air on the side of caution and follow a more conservative approach when there are unknowns. Nevertheless, future research should attempt to refine these models (see below).

In Chapter 4, as part of a study to explore the mechanisms of niche separation within the Bornean felid assemblage, we develop predictions of Sunda clouded leopard occurrence and distribution in Sabah derived from analysis of extensive camera trap surveys throughout the state. We showed that Sunda clouded leopards selected areas with high levels of dipterocarp forest at relatively fine spatial scales, within broad landscapes with low levels of human footprint, plantations and scrub lands. Our analysis also highlighted that higher Sunda clouded leopard occurrence was positively associated with higher elevation forest, which accords with the findings from studies of these felids in Sumatra (Haidir et al., 2013; McCarthy et al., 2015; Sunarto et al., 2015), and with the presence of logging roads (males only), as shown by Wearn et al. (2013), and ridgelines (both sexes), which has not been demonstrated before. We developed a map of Sunda clouded leopard occurrence for Sabah (Figure 1c), which predicted that these felids' occurrence reached a maximum within the higher elevation areas of the main contiguous forest block region in central Sabah, whereas the vast, heavily disturbed coastal areas and oil palm plantation dominated areas in the east presented the lowest predicted probability of occurrence for these felids. These predictions of distribution are broadly similar to that developed from presence only maximum entropy modelling (Hearn et al, 2016c), but our analyses are an improvement on these earlier models as they provide information about responses to specific habitat variables and the relative influence of scale. Comparison of the patterns of utilisation based on our path level model and predictions of genetic diversity in Sabah with our occurrence predictions derived from the camera trap data show a broadly similar pattern, and confirms earlier predictions of population isolation (Figure 1).

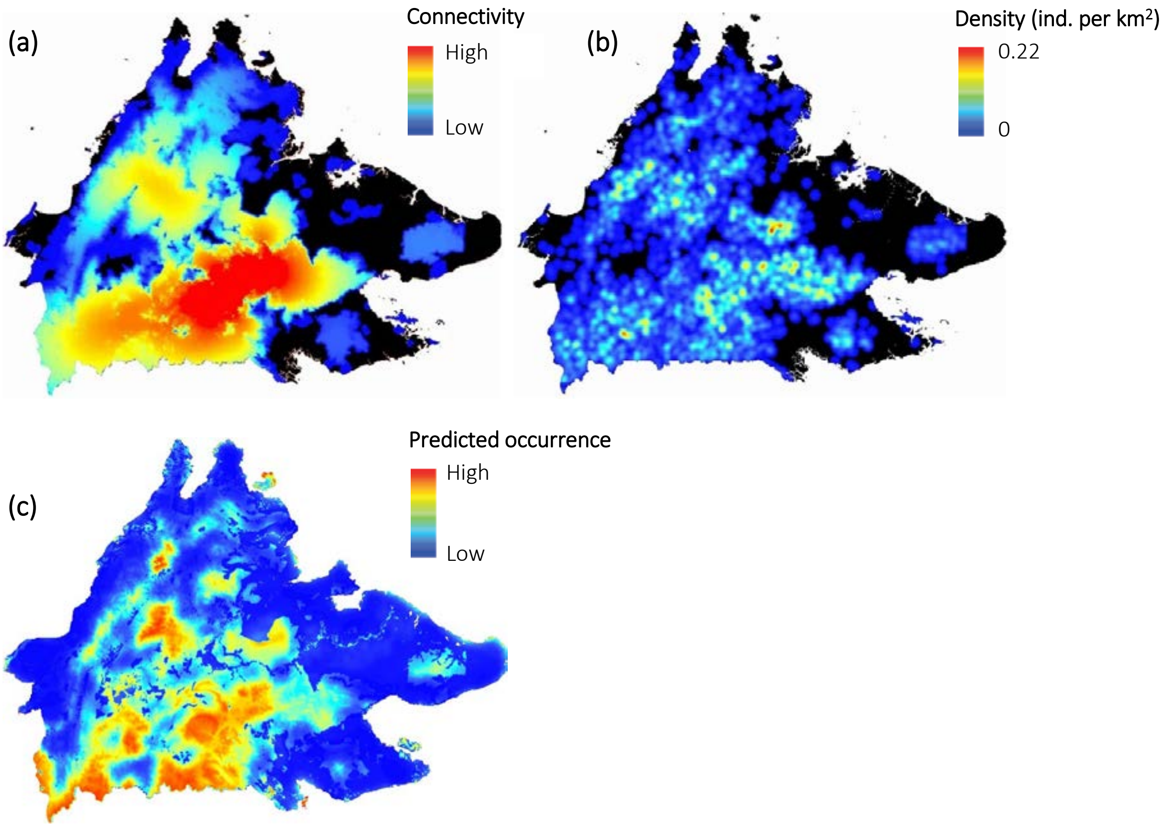

Figure 1. (a). cumulative resistant kernel prediction of clouded leopard connectivity based on path level analysis of movement data (see Chapter 3); (b) Mean predicted local neighbourhood density of clouded leopard in a 5000m focal area across Sabah under calculated using long dispersal ability (125,000 cost unit dispersal threshold; see Chapter 3); (c) Predicted occurrence of Sunda clouded leopards based on multiscale habitat modelling of camera trap detection data (see Chapter 4).

In Chapter 6, we analysed the Sunda clouded leopard detection dataset used in Chapter 4 within a spatially explicit capture recapture analytical framework and showed that Sunda clouded leopard density from 6 forest areas exposed to varying levels of anthropogenic disturbance ranged from 1.39 to 3.10 (mean 2.11) individuals per 100 km^2. These estimates are comparable with those from previous studies in Sabah (0.84–1.9: Brodie and Giordano, 2012a; Wilting et al, 2012), the Indonesian province of Central Kalimantan (0.72–4.41: Cheyne et al, 2013) and Sumatra (0.8–1.6: Sollmann et al., 2014). We showed that Sunda clouded leopard population density can be negatively impacted by hunting pressure, forest fragmentation, and recent logging activity, and that well recovered, selectively logged forest may support higher densities than primary forest. This is consistent with Brodie et al. (2015) who found that local scale abundance of Sunda clouded leopard was negatively related to hunting pressure, and that the negative effects exhibited by a range of species following selectively logging, many of which will form the prey base of this felid, may be attenuated and even reversed as forests regenerate over time. We estimated that the Sunda clouded leopard population size in Sabah is currently around 754 individuals (325-1337 individuals 95% CI), which provides a significant methodological improvement upon the very approximate estimate of 1500–3200 individuals provided by Wilting et al (2006), based on extrapolation of a track-based assessment of density from one forest area.

Other Pantherine felids have shown broadly similar responses to anthropogenic disturbance to that of the Sunda clouded leopard. Jaguars *Panthera onca* tend to be very closely associated with closed forest habitats (e.g., Maffei et al. 2004), although some open habitats such as the grassy Pantanal also support relatively high densities of these cats (Soisalo et al. 2006). In comparison, leopards *Panthera pardus*, the most widely distributed large felid, can not only persist but thrive in human dominated areas. Athreya et al. (2013)

found a relatively high density of leopards in India inhabiting a cropland landscape devoid of wilderness and wild herbivore prey, and Odden et al. (2014) studied the movements of leopards in India and found that these felids were often closely associated with human settlements. Although not well studied, there is also evidence that the closely related mainland clouded leopard is more tolerant of human dominated areas than the Sunda species. Grassman et al (2005) used VHF telemetry to study the movements of mainland clouded leopards in Thailand, and found that one individual regularly used open forest-grassland to seek their primary prey, hog deer *Axis porcinus* and muntjak *Muntiacus muntjak*. This possible differential response to open habitats may have contributed to the speciation. he responses Unlike Sunda clouded leopards, leopard *Panthera pardus* in India have been shown to oil palm plantations and other human dominated landscapes

Our basic model of population size did not include a minimum patch size or measure of proximity to other patches in its calculation, as such data are currently lacking. Our camera survey found no evidence of clouded leopards within a relatively small forest fragment in Sabah, the Kabili-Sepilok Forest Reserve, yet reports suggest that they were found there only a decade earlier. It is possible, therefore, that they are many more such small, isolate forest patches that do not support this felid, and that our estimate of population size may be slightly inflated. In addition, while we made efforts to survey a range of forest types and levels of anthropogenic disturbance, there are a number of forest types that were not included, including mangrove and agroforest areas. Surveys of these habitat types and efforts to determine minimum patch sizes for this felid are therefore a priority.

The estimates of Sunda clouded leopard density, connectivity, habitat use and distribution described in this thesis were a key resource in the development of the most recent IUCN assessment for this species (Hearn et al., 2016a).

Influence of disturbance on small Bornean felids

With the exception of the leopard cat, which has a large geographical distribution and has been the focus of numerous ecological investigations (e.g., Lim 1999; Rajaratnam et al. 2007, Mohamed et al., 2013; Chua et al., 2016), the three, small, threatened Bornean felids remain some of the least studied of the world's wild cats (Brodie, 2009; Zanin et al., 2015), and we know almost nothing about their possible responses to habitat disturbance. This thesis thus provides some of the first data regarding the ecology and responses to disturbance among these largely unknown felids. As such, this thesis was a key resource in the development of the most recent IUCN assessments for the bay cat (Hearn et al. 2016b), marbled cat (Ross et al. 2016), leopard cat (Ross et al. 2015) and flat-headed cat (Wilting et al. 2015).

In Chapter 4 we showed that the occurrence of both bay cats and marbled cats across the Sabah landscape was negatively associated with anthropogenic disturbance and positively associated with forest, confirming earlier untested assumptions of a close forest association in these felids (Meijaard, 1997; Sunquist and Sunquist, 2002; Mohd-Azlan and Sanderson, 2007; Ross et al., 2015; Hearn et al., 2016b; Rustam et al., 2016). Specifically, we showed that bay cats exhibited broad scale avoidance of fragmented forest landscapes and human footprint, and that marbled cats were positively associated with forest cover, particularly at higher elevations and with rough topography. Marbled cats showed a strong association with forested ridgelines, but not logging roads, while bay cats showed no such patterns of association. Similarly, Wearn et al (2013), although limited by small sample sizes, showed that bay cat detection probabilities in a highly degraded forest in Sabah were not influenced by the presence of logging roads and skid trails, but that marbled cats preferentially selected skid trails.

We found that marbled cats, and to a lesser extent bay cats, showed similar predicted occurrence patterns in Sabah to that of Sunda clouded leopards, suggesting broadly similar habitat niche selection with this felid. Marbled cat occurrence reached a maximum within the higher elevation areas of the main contiguous forest block region in central Sabah, and the vast, heavily disturbed coastal areas and oil palm plantation dominated areas in the east presented the lowest predicted probability of occurrence for these felids. Bay cats also presented a similar overall predicted distribution pattern. These results support earlier findings based on presence only niche distribution modelling that marbled cats and bay cats have broad distributions across Sabah, and indeed Borneo, but that they are closely associated with forest (Hearn et al., 2016c,d; Rustam et al., 2016; Wilting et al., 2016).

As predicted, and in accordance with previous studies of the leopard cat (Lim 1999; Rajaratnam et al. 2007, Mohamed et al., 2013), we show that this species' occurrence is positively associated with disturbed habitats, and likely benefits from habitat disturbance. The highly contrasting habitat preferences shown by leopard cats resulted in a predicted distribution model that was essentially a polar opposite of the other three felids, with leopard cats predicted as having very high occurrence throughout the oil palm dominated lowland landscape in eastern Sabah, and only moderate predictions of occurrence within the more heavily forested regions. In contrast, Mohamed et al. (2016) produced a presence only predictive model of occurrence for this felid on Borneo that showed an island-wide, broadly even distribution across habitat types. The Mohamed et al. (2016) model included an expert-opinion component to the assessment, which has been shown to be less reliable than empirically derived predictions of occurrence (e.g., Shirk et al. 2010; Mateo-Sanchez et al. 2015, Chapter 2, 3), and forest habitats were classified as presenting similar habitat suitability to that of forests. In contrast, our analysis strongly suggests that plantations are selected preferentially over forest. These finding supports the results of Chua et al. (2016) who showed that these felids were more abundant in an oil palm plantation compared to an adjacent area of secondary forest

We did not specifically investigate the influence of habitat disturbance on bay cat population density, or attempt to derive estimates of their population size. Brodie et al. (2015) estimated that this felid's local scale abundance was lower in logged than in unlogged areas, and our predictions of occurrence support this finding. The paucity of bay cat specimens collected during the nineteenth and twentieth centuries, and the extremely low detection rates of this felid from camera trap surveys (Mohd-Azlan et al., 2003; Yasuda et al., 2007; Brodie and Giordano, 2012b) and selectively logged forest (Mohamed et al., 2009; Bernard et al, 2012; Hon, 2011; Mathai et al., 2014; Cheyne et al., 2016;) has led to the conclusion that the bay cat is naturally rare, prompting its classification as Endangered on the IUCN Red List (Hearn et al., 2016e). The low detection rates found in this study tend to support this assessment. Wearn et al., (2013), however, question the link between low detection rates and low abundance. These authors showed that their random placement of camera traps in a heavily disturbed forest in Sabah yielded significantly higher detection rates than previous studies, and suggested that targeted placement of camera traps along roads, ridgelines and trails, and the bay cat's avoidance of such features mean that previous researchers have greatly underestimated this felid's abundance. However, our multi-scale logistic regression analysis predicted a substantially lower occurrence of bay cats in more disturbed areas. Wearn et al. (2013) based their findings on a very small photographic detection size sample (n = 8) and surveyed over a relatively small area (c. 3 km^2), which likely only encompassed a very small number of individuals, and so their hypothesis needs further testing.

In Chapter 5 we used spatially explicit capture recapture analysis to provide the first ever estimates of population density for this species from anywhere in their range. Our density estimates ranged from around 7.1 to 19.6 individuals per 100 km^2 and provided tentative evidence that undisturbed, lowland hill forest may support higher densities than both disturbed lowland and undisturbed higher elevation forests in northern Borneo. Capture frequencies from the three areas which permitted density estimation were approximately 2 to 6 times greater than that recorded in our other study sites and in previous intensive camera trap surveys elsewhere on Borneo (e.g., Brodie and Giordano, 2011; Bernard et al., 2013; Wearn et al., 2013) and elsewhere in their range (Lyngdoh et al., 2011; Tempa et al., 2013; Chutipong et al., 2014; Coudrat et al., 2014), which suggests that they that they may all stem from high density populations and are thus not necessarily representative of other areas. Nevertheless, our findings support the recent downgrading of the marbled cat's Red List status from Vulnerable to Near Threatened (Ross et al., 2016), although further studies are clearly needed before a robust conclusion can be drawn. Our analyses have shown that this is indeed possible, and the results of our fine-scale habitat use on Chapter 4 suggest that such surveys should preferentially deploy cameras along ridgelines and avoid logging road placement. The deployment of camera traps along logging roads may be at least partially responsible for the exceptional low detection rate of marbled cats in surveys in mainland Asia (e.g., (Lyngdoh et al., 2011; Tempa et al., 2013; Chutipong et al., 2014; Coudrat et al., 2014).

Future research

As discussed above, there are limitations to the models of Sunda clouded leopard connectivity due to the restricted empirical movement data used to parameterise the models. As such, efforts should strive to refine our models of landscape resistance and connectivity by obtaining data from a diverse range of locations and habitat types from across the island. Research to determine the degree to which clouded leopards use Agroforest areas, and how this land use influences their movements, is of a high priority. Future collaring efforts should also attempt to include as many demographic classes as possible, and ideally from dispersing animals. Meeting this challenge, however, will be difficult.

Both Sunda and mainland clouded leopards are notoriously difficult to capture, and previous efforts to capture them have resulted in either no captures, or very low sample sizes (e.g., Grassman et al., 2005; Austin et al., 2007; Rajaratnam, 2000; Ross et al., 2010; Hearn et al., 2013). Efforts to improve capture protocols (see below) are needed to increase the efficacy of future collaring work, but alternative approaches should also be considered. Working in partnership with local authorities to monitor the post-release movements of translocated 'conflict' animals, for example, could provide vital movement data whilst also investigating the efficacy of this increasingly used management approach.

Live capture of felids in tropical forests typically involves some form of leg-hold trap or snare, or box traps (for a review see McCarthy et al. 2013). Previous live trapping programmes targeting both mainland and Sunda clouded leopards have deployed metal or wooden box traps, with a single-entry door, baited with carrion or live chickens (Grassman et al., 2005; Austin et al., 2007; Rajaratnam, 2000; Ross et al., 2010; Hearn et al., 2013). In this study, we developed a more open, and potentially less threatening live-trap design, which may have helped trap improve capture efficacy. Our relatively large traps (1 m width and height, and 3 m long) were constructed locally, using a 5 cm steel wire mesh, and had two vertically sliding doors, triggered by a central wooden treadle. The double door design allows the target animal to see straight through the trap, and may appear less threatening. Rather than using live bait, which is logistically demanding to maintain and which may contravene animal welfare legislation or University protocols, we deployed the traps directly upon the predicted movement path of the target animal, along key ridgeline trails, which we identified using camera traps. To further encourage the animal to move through the trap, we blocked passage either side of the trap, and attempted to funnel the animal to the trap entry points using a line of fallen branches and other vegetative material. We did not explicitly compare this approach with other trap designs, but we successfully captured 5 of the 7 individuals that had been recorded by camera traps in the study area, which suggests this may be an effective trap design. In addition, trap injuries were minimal, or absent (Nájera et al, submitted). It would be useful to compare and assess the efficacy of live trap protocols for these felids.

To date, investigation of the movements of marbled cats stem from only a short-term study of a single collared individual in Thailand (Grassman et al., 2005), while no studies have investigated the spatial ecology of either the bay cat or flat-headed cat. As such, targeted telemetry programmes for these felids in carefully selected study areas remain of the highest priority (Nowell and Jackson, 1996; Mohd-Azlan and Sanderson, 2007). An alternative, or complimentary approach to develop predictions of landscape resistance and connectivity is that of genetic analysis of scat or hair samples from across the landscape (e.g. Wasserman et al. 2010). The collection of sufficient Bornean felid scat samples would be challenging (e.g., see Wilting et al., 2006), however, particularly that of the wetland associated flat-headed cats, and so scat dogs would be a useful, although potentially expensive tool. The samples obtained would also provide the means to investigate the diet of these felids, potentially using molecular techniques (e.g., Kohn and Wayne, 1997), and to compare and validate the movement-based models of Sunda clouded leopard connectivity developed in this thesis.

Future research should strive to develop more cost effective ways of monitoring these felids with camera traps, perhaps assisted by fine-scale habitat data emerging from future telemetry studies. One approach worthy of consideration is to explore the detection probabilities of single, vertically orientated (over the predicted travel route) camera deployment at camera stations, which could either halve camera costs or double the sampling effort. Field testing in Australia showed that such vertical orientation over roads results in lowered small carnivore detection probabilities (Meek et al., 2016). However, this approach may still prove effective for larger bodied carnivores, which are more easily detected by the passive infrared receivers (PIR) used in most camera traps (Tobler et al. 2008), or if the researcher is able to determine the travel route more precisely – such as narrow ridge deployment (as highlighted in Chapter 4), or through the development of optimised PIR lens assemblies as opposed to off-the-shelf camera traps, which are specifically designed for horizontal orientation.

Conventional camera based capture recapture approaches (e.g., Karanth, 1995, Karanth and Nichols 1998, 2002) require the identification of individual animals, for example using pelage markings, and thus are not appropriate for bay cat or flat-headed cat. Rowcliffe et al. (2008) developed an analytical approach for density estimation which models the process of contact between animals and cameras, and does not require individual recognition. The model assumes that the animals move randomly through the landscape, and thus is not appropriate for species which respond strongly to habitat features, such as roads, trails and ridges (Foster and Harmsen, 2012), but may be suitable for bay cats and flat-headed cats. The approach requires the calibration of distance within the frame of the detection zone/camera image, typically by the placement of objects at measured distances apart, but it may be possible to develop such calibration post-survey, and thus enable the use of existing camera trap data.

This thesis has generated an enormous amount of photographic data, opening up possibilities of investigating the ecology of a vast range of species. Future studies should strive to combine data sets from multiple researchers to vastly increase sample sizes, such as occurred during the Borneo Carnivore Symposium in 2011 (Kramer-Schadt et al, 2016), but this time applying a more sophisticated modelling approach to disentangle the habitat ecology of the Sunda clouded leopard and their community.

Conclusion

This study presents some of the first, empirical data to support the hypothesis that three of Borneo's threatened felids - the Sunda clouded leopard, bay cat, and marbled cat - are adversely impacted by anthropogenic disturbance of forest. While these felids were found to select habitats with low levels of disturbance at broad scales, and evidence of reduced populations densities in recently selectively logged forests and areas exposed to higher poaching pressures, this study shows that all three of these felids are able to persist, and can even thrive, in forests exposed to selective timber harvesting. As such, and in accordance with a growing body of evidence which shows that selectively logged forests remain as important conservation resources, it is likely that the continued survival of these felids will be underpinned by the careful management of this forest resource, and not necessarily by the preservation of vast tracks of undisturbed forest, which is no longer possible. We show how even small patches of forest can prove vital to the movements of Sunda clouded leopards, and is likely that the other threatened felids are similarly affected. This study has shown that oil palm habitats, a vital resource for the developing nations of Malaysia and Indonesia, greatly resist the movements of Sunda clouded leopards, and that the conversion of forest likely forms the greatest threat to these felids. However, this study has also shown that these felids are willing to move, albeit small distances, across such anthropogenically dominated landscapes, and so there remains hope that plantations may be better managed to promote such movements. The identification of High Conservation Value (HCV) forest patches (e.g., Senior et al. 2015) within plantation areas is of a high priority, as is the creation of new forest corridors and the reestablishment of forested Riparian buffers. Within Sabah, we show that such approaches are particularly needed to increase connectivity between the main forest block and the isolated protected areas of Tabin Wildlife Reserve, Tawau Hills National Park, and Lower Kinabatangan Wildlife Reserve. The assemblage of Bornean felids is a unique treasure of this island. With careful management of the island of Borneo there is every hope that they will remain so.

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Appendix I.

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Appendix II.

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Appendix III.

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Appendix IV.

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Appendix V.

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