Conservation of Charismatic Endangered Species in Wehea Forest, Borneo: Interplay of Ecological and Social Factors in a Community-Based Conservation Project

by

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Abstract

Borneo is blessed with incredible biodiversity, including some of the most charismatic endangered species on the planet. Yet despite being recognized as a biodiversity hotspot, Borneo’s forests, and the biodiversity contained therein, are being lost faster than anywhere else on the planet, with the main threats from habitat loss and hunting. Given the perceived failure of protected areas on Borneo to conserve biodiversity, some NGOs are implementing community-based conservation (CBC) and believe that win-win solutions are possible since biodiversity can be protected and human welfare improved with a single approach. However, on Borneo, where local communities were marginalized and natural resource institutions eroded during the Suharto era, the appropriateness of using CBC to protect biodiversity, especially elusive and low-density species, has not been investigated. In this thesis, I aim to advance our understanding of the conservation of charismatic endangered species on Borneo by examining the interplay of ecological and social factors in conserving the Bornean clouded leopard (*Neofelis diardi borneensis*), Bornean orangutan (*Pongo pygmaeaus morio*), and Miller’s Grizzled Langur (*Presbytis hosei canicrus*), in Wehea Forest, East Kalimantan. I used camera trapping and spatial-capture recapture modeling to estimate density and inferred the vulnerability of each species to threats by using estimates of abundance and conclusions drawn from my camera trapping studies. To help understand critical social factors of the Wehea CBC that could compromise the long-term viability of these three species in Wehea Forest, I used insights from common-pool resource theory and drew on my experience of being immersed with the Wehea Dayak for almost 4 years. Given the specific ecological and social factors found within Wehea, I conclude that a win-win outcome may be not possible. Either the long-term viability of these species may need to be compromised for the sake of human well-being, or the current protected area will have to be maintained at the expense of poverty alleviation. Since the ecological and social factors found within Wehea may be characteristic across Borneo, we should be careful not to automatically assume that CBC is the most effective approach for protecting wide ranging and low-density charismatic endangered species.

Keywords: Conservation; common-pool resource theory; community-based conservation; clouded leopard; orangutan; Miller’s Grizzled Langur; charismatic endangered species; Borneo

I dedicate my thesis to my daughters Tora and Saga. I began this thesis from a desire to make the world a better place. During the process I was blessed to have each of you come into my life and make my world a better place. For that I am eternally thankful.

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List of Acronyms

BCI	Bayesian Credibility Interval
CI	Confidence Interval
CBC	Community Based Conservation
CBNRM	Community Based Natural Resource Management
CPR	Common Pool Resource
CR	Capture Recapture
CSR	Corporate Social Responsibility
FAO	Food and Agriculture Organization
ICDP	Integrated Conservation and Development Project
IFRI	International Forestry Resources and Institutions
IUCN	International Union for the Conservation of Nature
LUCC	Land Use and Cover Change
MLE	Maximum Likelihood Estimation
MVP	Minimum Viable Population
NCS	New Conservation Science
NGO	Non Governmental Organization
PA	Protected Area
REDD	Reduced Emissions from Deforestation and Degradation
SES	Social Ecological System
SESMAD	Social Ecological Systems Meta-Analysis Database
SCR	Spatial Capture Recapture

Chapter 1

Introduction

The contemporary conservation debate

The conceptual framework under which we think about biodiversity conservation has changed dramatically over the past generation. Until the early 1980's conventional wisdom held that central governments should be mainly responsible for conservation through management of large-scale national parks and protected areas (Berkes, 2007). However, in response to the failures of this top-down model to protect biodiversity (e.g. protected areas in tropics and subtropics; Ludwig et al., 1993; Brandon et al., 1998), scholars, practitioners and policymakers began to advocate a more bottom-up approach to conservation (Barrett et al., 2001). Generally known as community-based conservation (CBC), proponents of this strategy argued that indigenous and local non-indigenous people could be conservationists and have traditional ecological knowledge that is essential for managing natural resources (Berkes, 1999; Berkes et al., 2000; Folke, 2004; Sheil & Lawrence, 2004). Despite its initial promise, the success of CBC initiatives was questioned (Terborgh, 1999; Oates, 1999) and there was a resurgence of the "protectionist paradigm" in international biodiversity conservation (Kramer et al., 1997; Rabinowitz, 1999). This led to the emergence of an often contentious "parks vs. people" debate over whether a particular conservation project should emphasize biodiversity protection or development in support of local communities (Terborgh, 2000; Barrett et al., 2001; Brockington, 2002; Sanderson & Redford, 2003; Roe & Elliot, 2004; Wilshusen et al., 2002).

More recently, a related debate has emerged about the proper value and ethical foundations of biodiversity conservation (i.e. "nature-centered" or "people-centered") in the age of sustainability (Miller et al., 2011; Minteer & Miller, 2011). On the one side, proponents of what is called the ‘new conservation science’ (NCS) argue that the only way to protect earth’s biodiversity is through conservation projects that simultaneously preserve biodiversity while improving human well-being (Kareiva et al., 2011; Kareiva & Marvier, 2012). The general idea is that when communities receive direct benefits and achieve a higher standard of living from biodiversity conservation that they will do more to conserve it (Getz et al., 1999; MEA, 2005). Opponents of NCS argue that nature has intrinsic and inherent rights and values and prioritizing the needs and wants of humans de-emphasizes the goal of protecting nature for its own sake (Doak et al., 2014). In addition, opponents claim that the NCS approach dismisses the relationship between species diversity and ecosystem function and that implementing NCS would inevitably exclude keystone species (Soule, 2013). This is especially relevant in places such as Borneo where potential keystone species (e.g. clouded leopards, orangutans, sun bears) are found at extremely low densities and may be sensitive to even small-scale human disturbances of their habitat.

The emergence of NCS may be seen as a response to the emergence of the concept ‘Anthropocene’ (Crutzen & Stoermer, 2000) denoting the present period in which humans are altering many of earth’s geologic and ecological processes. If humans are indeed the dominant ecological force on the planet, then it must also be recognized that ‘humans’ and ‘nature’ cannot be separated in the way that traditional conservation has often done (Berkes & Folke, 1998; Corlett, 2014). The importance of understanding the tight coupling of social and ecological systems (also called social-ecological systems [SESs]) is increasingly being acknowledged and used in fields ranging from conservation planning (Green et al., 2009; Ban et al., 2013) to sustainability science (Ostrom, 2007; 2009) to management of marine protected areas (Basurto et al., 2013; López-Angarita et al., 2014). In this interdisciplinary thesis, I contribute to the growing SES literature by exploring both ecological and social factors in the conservation of charismatic endangered species in a CBC project in Borneo.

Beyond the rhetoric on both sides of the “parks vs. people” and “nature centered vs. human centered” debates, participants appear to share the common goal of protecting earth’s biodiversity. Where the sides diverge is on the emphasis and methods used to achieve conservation goals and objectives, with most individuals falling somewhere along a continuum between the extreme biocentric view to the extreme anthropocentric view of biodiversity conservation (Corlett, 2014). Outside of setting up national parks or protected areas, two of the most common methods used in community-based conservation are integrated conservation and development projects (ICDPs) and community-based natural resource management (CBNRM). ICDPs are more biocentric in that they are essentially biodiversity conservation projects with some emphasis on local community development. CBNRM is more anthropocentric in that it recognizes the rights of local people to manage and benefit from the use of their resources (Blaikie, et al., 2006). However, if we have learned anything from the past generation of conservation paradigms, it's that panaceas do not exist in biodiversity conservation (Ostrom, 2007) and a constructive debate is essential about how protection of biodiversity can and should occur in specific places.

Conservation on Kalimantan, Borneo

Borneo contains the richest and largest expanse of forest in Southeast Asia (~389, 566 km^2; Gaveau et al., 2014) and is widely regarded as one of the hottest of the world's hotspots for biodiversity (Myers et al., 2000). These forests harbor 6% (5000 endemic) of the world's flowering plant species, 6% (37 endemic) of the world's bird species, and 6% (44 endemic) of the world's mammal species including some of the most iconic species (e.g. orangutan and clouded leopard) on the planet (Meijaard & Sheil, 2007). Despite their known conservation value, these forests are being lost at nearly twice the rate as the rest of the world's tropical forests (Margono et al., 2014). This unprecedented transformation of the forest landscape into industrial oil palm plantations and mines is fueling Indonesia's rapid economic growth (5.5% in 2015) and development (ADB, 2015; Gaveau et al., 2013) and lifting millions of people out of poverty.

Past conservation efforts on Kalimantan (i.e. Indonesian Borneo) have focused mainly on creating traditional protected areas (PAs) and about 21% of Kalimantan is currently under nominal strict protection (~110,232 km^2; Gaveau et al., 2013). However, there is growing recognition that Kalimantan's PA network is failing for various ecological, socioeconomic, and political reasons (Jepsen et al., 2002; Meijaard et al., 2006). This is mainly because current PAs are poorly managed, which results in "protected" forests that are increasingly deforested with their buffer zones being degraded (Brun et al., 2015; Curren et al., 2004). In addition, PAs in Kalimantan are small (average size ~ 500 km^2), fragmented and isolated making them not only ineffective in conserving biodiversity but also decreasing their resilience to climate change (Scriven et al., 2015).

In the belief that the protected areas (PAs) oriented approach has failed in Kalimantan, some NGOs, including The Nature Conservancy (TNC), the worlds largest environmental NGO, are arguing for adopting a more "people centered" approach (e.g. CBNRM). However, the efficacy of adopting such an approach on Borneo has yet to be investigated. This is especially important given that indigenous communities in Indonesia recently won rights to their land both from the Indonesian Supreme Court and the former president of Indonesia (Susulo Bambang Yudhoyono). These new legal rulings and regulations have made some conservationists nervous about their long-term impact on biodiversity conservation with some going so far as calling them the "final blow for Indonesia's forests" (Meijaard, 2015) and a "forest destruction time-bomb" (Handadhari, 2015).

Roadmap to the thesis

In this thesis, I aim to advance our understanding of charismatic endangered species conservation on Borneo by examining the interplay of ecological and social factors in a CBC project. To date, most ecological research on Borneo has tended to focus on the ecology of endangered species (e.g. MacKinnon, 1974; Van Schaik et al., 2009), the impact of logging activities on orangutans and other elements of biodiversity (e.g. Wilson et al., 2014; Brodie et al., 2015) and the importance of timber concessions for biodiversity conservation (e.g. Meijaard, 2007; Gaveau et al., 2013). There have also been numerous studies that have looked at the social processes affecting forest and biodiversity loss in Indonesia including local and national governance of Indonesia's forests (e.g. Barr, 1998; Wollenberg et al., 2006), the impacts of decentralization on forest loss (e.g. MaCarthy, 2001; Palmer & Engel, 2007), and international influences that affect forest management (e.g. Peluso, 1992; Tsing, 2005). However, there have been few, if any, studies that have investigated the interactions and challenges of endangered species protection in a CBC initiative. This research is especially important and timely given the recent land rights rulings mentioned above.

My original objective with this thesis was to learn more about Bornean clouded leopard (*Neofelis diardi borneensis*) conservation in East Kalimantan, Indonesia. The clouded leopard is one of the least known cat species in the world and I was hoping to obtain some of the first known density estimates for this species (see chapter 6) and explore conservation related issues surrounding its protection. However, shortly after beginning my research on the clouded leopard in Wehea Forest (see Fig. 1.1), surprisingly, I encountered Miller's Grizzled Langur (*Presbytis hosei canicrus*), a monkey that was previously thought extinct (see chapter 2) and may now be one of the rarest primates in the world. This discovery made international headlines and helped to put Wehea Forest on the map as a tourist destination. In addition, while looking at camera trap photos for clouded leopards, I noticed that I had almost as many pictures of the Bornean orangutan (*Pongo pygmaeaus morio*) as I did of the clouded leopard. This discovery led to the first publication on orangutan terrestriality (see chapter 3). I followed this up by investigating if orangutan terrestriality changed depending on habitat type (primary, secondary and recently logged forest; see chapter 4). Last, I used the camera trap photos of orangutans to explore whether spatial capture-recapture modeling could be used instead of the traditional nest count method to estimate orangutan density (see chapter 5).

Although it was not my original intention to study the orangutan and langur, their inclusion in this thesis is important for understanding charismatic endangered species conservation on Borneo for a number of reasons. First, all three species are found in Wehea Forest, one of the flagship conservation projects in Kalimantan, Borneo. Given the promotion of Wehea Forest as a model of CBC, if there was anywhere on Borneo where these species could be protected it should be in Wehea Forest. Second, these species presents three unique ecologies that require conservation actions at different spatial-scales and possibly even different types of management strategies (e.g. strict protection vs. CBNRM). Third, each species is charismatic and has the potential to serve as a flagship species for this conservation project. Last, very little is known about each species and the high uncertainty in current density estimates highlights a great challenge when developing management plans for species with similar behaviors and ecologies (e.g. elusive, wide-ranging).

The single-species oriented research presented in chapters 2-6 is essential for helping to understand some basic ecological factors necessary for the conservation of each species. However, by itself, this research provides only one half of the story in a CBC project such as Wehea. To help tell the other side of the story, I draw from common-pool resource (CPR) theory in chapter 7 to help explain possible causes in deforestation in Indonesia from 1965 to present. CPR theory is one of the most prominent contemporary theories of environmental governance (Ostrom et al., 1994; Agrawal, 2001; Fleischman et al., 2014) and was developed from a large body of interdisciplinary research about coordinated resource management successes and failures (Ostrom, 1990). In contrast to Hardin's (1968) "Tragedy of the Commons", Ostrom (1990) showed that individuals could act collectively to manage their resource and proposed a set of design principles (see Table 1.1) that tend to characterize sustainable resource use and management. More recently Ostrom (2007; 2009) proposed the SES framework, which expands upon the initial design principles and recognizes the importance of coupled SESs. Although the scale at which we apply CPR theory in chapter 7 is nation-wide, the lessons learned from its application at this large scale are also useful for studying social factors of endangered species conservation in a CBC project on Borneo.

Table 1.1 Ostrom's design principles of enduring commons institutions

1. Clearly defined boundaries (membership and physical boundaries of resource are clear)
2. Congruence between appropriation and provision rules and local conditions (rules are congruent with local conditions)
3. Collective choice arrangements (individuals affected can participate in modifying operational rules)
4. Monitors are accountable to the resource users
5. Graduated sanctions against violators
6. Ready access to conflict-resolution mechanisms
7. Recognition of rights to organize, by external government authorities
8. Nested enterprises (where the resource is part of a larger system)

CPR theory has also been important to the institutional design of many CBNRM projects, especially in Africa (Saunders, 2014). To support the ‘crafting’ of these projects, the CPR design principles have been adopted by far-reaching international assistance agencies such as the United Nations and World Bank (Esmail, 1997; Agrawal & Gibson, 1999; Steins et al., 2000). International NGOs advocating CBC also take the role of CPR design principles seriously as evidenced by the production of CBNRM manuals that explicitly cite the design principles to inform project interventions (e.g. WWF, 2006). Given that many of these projects have generated disappointing outcomes in practice (Blaikie, 2006; Shackleton et al., 2010), we should learn from these mistakes before replicating them in countries such as Indonesia, where local and indigenous communities have only recently won rights to their land.

Context for the thesis

My motivation for this thesis extends beyond any novelty and scientific importance it may have. The idea originated from the community-based conservation work our NGO (Integrated Conservation) was doing with the Wehea Dayak to help them protect Wehea Forest (38,000 ha), one of the flagship conservation areas for East Kalimantan, Indonesian Borneo (see Fig. 1.1). The Wehea Dayak tribe is divided between six villages located along the Telen and Wahau rivers, however for sake of simplicity I will use “Wehea Dayak” to refer to our work with the community of Nehas Liah Bing, the largest of the six communities. Wehea Forest contains mostly undisturbed forest, surrounded by large tracts of primary and secondary forests either classified as active timber concessions or undesignated forest. Wehea Forest was originally established in 2004 through a coordinated effort that included the Wehea Dayak, The Nature Conservancy (TNC) and regional government and officially designated a protected area (Hutan Lindung) in 2013.

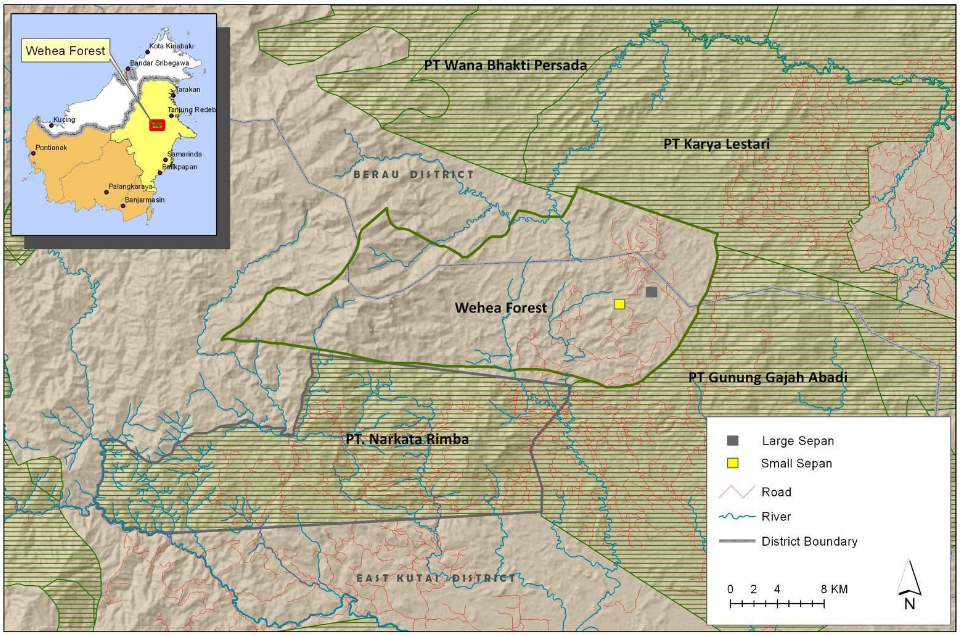

Figure 1.1 **Map of Wehea Forest and surrounding logging concessions. Inset shows Wehea Forest in relation to the island of Borneo.**

In 2009, during my first trip to Wehea, I was approached by the *kepala adat* (i.e. chief of the village), Ledjie Taq, and asked if our NGO would consider helping his community in protecting Wehea Forest. He was worried about the capacity of his community to manage the forest given that TNC had stopped their activities in Wehea to focus on their REDD+ projects in another part of East Kalimantan. We agreed to help and this led to a number of studies organized or led by myself and others on the ecological and social dimensions of the Wehea SES. In addition, and in collaboration with the community, we organized economic development projects, environmental education activities, and university field courses, supported university scholarships, coordinated outreach opportunities and provided training and support to Wehea Forest Guardians.

Although we had some great achievements, some of which are highlighted in this thesis, we also faced tremendous challenges. Wehea and the forests surrounding it are a biodiversity "hotspot" and home to some of the most charismatic and endangered species on the island, three of which are discussed in some detail in this thesis. However, this region of East Kalimantan is also characterized by extreme anthropogenic disturbances including deforestation and rapid development for oil palm plantations, coal and gold mines. There is a large population of “transmigrants” from other areas of Indonesia who were resettled by the Indonesian government and who feel that standing forest areas are “wasted and unused land.” Competition for resources between local communities is fierce and there is a “development fever” that pervades the district. In addition, there is heavy investment in development projects from foreign governments and multi-national companies. In this thesis, I will draw conclusions that are based on the scientific knowledge I gained during my 4 years of doctoral research in Wehea Forest and also from my personal experience of working with the Wehea Dayak from 2009 to 2014. I hope that both this knowledge and experience contributes to the debate about how protection of biodiversity can and should occur in specific places and also to the conservation of charismatic endangered species on Borneo.

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Chapter 2.

Discovery of Miller's Grizzled Langur (*Presbytis hosei* canicrus) in Wehea Forest confirms the continued existence and extends known geographical range of an endanged primate

This chapter was previously published in the article "Discovery of Miller's Grizzled Langur (Presbytis hosei canicrus) in Wehea Forest confirms the continued existence and extends known geographical range of an endangered primate", co-authored by Lhota, S., Loken, B.R., Spehar, S., Fell, E., Pospech, A., and Kasyanto, N. in the American Journal of Primatology and has been reprinted with permission from © 2012 Wiley Periodicals, Inc. I authored the majority of the text and exclusively completed and authored the data analysis, tables and figures. In addition, I conducted the fieldwork that made the initial discovery.

Abstract

Miller's Gizzled Langur (*Presbytis hosei canicrus*) is one of the least known and rarest primates in Borneo. With a limited geographic range along the central coast of East Kalimantan and the highly degraded Kutai National Park its former stronghold, this subspecies is now extremely rare and has been listed as one of the world's 25 most endangered primates. From June 6 to August 2, 2011, we carried out both direct observation and camera trapping surveys at two mineral springs (sepans) in the Wehea Forest, East Kutai District, East Kalimantan. *P. h. canicrus* was observed at the large sepan on 3 of 6 observation days and at the small sepan on 2 of 3 observation days with up to 11 individuals observed in a single day at a single site. Camera traps recorded a per day capture rate of 0.72 at the small sepan and 0.25 at the large sepan and a per photo capture rate of 0.50 and 0.005 respectively. These data suggest relatively frequent occurrence of *P. h. canicrus* at the sepans, but the langurs are rarely encountered elsewhere in the Wehea Forest. The discovery of *P. h. canicrus* in the Wehea Forest

confirms the continued existence of this endangered primate and is the first solid evidence demonstrating that its geographic range extends further inland than previously thought. It is not known whether the population of *P. h. canicrus* within Wehea Forest is large and stable enough to be considered viable but it is likely part of a larger population that may possibly occur across surrounding protected forests and logging concessions. Surveying this potentially large population, and securing its protection, should be a priority measure for ensuring the continued existence of *P. h. canicrus*.

Introduction

Miller's Grizzled Langur (*Presbytis hosei canicrus*), also known as Miller's Grizzled Surili, is one of the rarest primates in Borneo. Until recently, it was known only from two areas along the central coast of East Kalimantan province, Indonesia: Sangkulirang Peninsula (Mt. Talisayang and Karangan River) and Kutai National Park (Payne et al., 1985). Rodman (1978) calculated the population density of *P. h. canicrus* in the Mentoko study area of Kutai National Park as 20.4 individuals/km^2, which is relatively high for a *Presbytis* langur species in Borneo. To our knowledge, this has been the only attempt to estimate the population density for *P. h. canicrus*. In 1982-83 a prolonged El Niño and resulting drought prompted catastrophic forest fires that burned most of Kutai National Park, including Mentoko. The langur was observed in Kutai after the fire (Suzuki, 1984) but the park experienced several additional fires, human encroachment and continued forest degradation in following years. By the end of 1998, only about 5% of the primary forest in Kutai National Park remained, and much of the secondary forest has been converted into agriculture, mining, industry and degraded land (Dennis & Colfer, 2006). No comparable data on the status of *P. h. canicrus* in the Sangkulirang Peninsula was available at that time but forest degradation and land conversion were also widespread in this area, in addition to hunting pressure (Setiawan et al., 2009).

Brandon-Jones et al. (2004) were among the first to express concerns that *P. h. canicrus* might have gone extinct. In 2006, the subspecies was listed as one of the 25 most threatened primates (Brandon-Jones, 2006), which significantly increased interest in this primate. In 2008, Arif Setiawan and his colleagues conducted the first focused survey across the known geographical range of *P. h. canicrus*, including both Kutai National Park and Sangkulirang Peninsula (Setiawan et al., 2009). The team did not find evidence for the continued existence of the langur in Kutai National Park. The only solid evidence of the survival of *P. h. canicrus* was a single group of five individuals found in a patch of mangrove forest, surrounded by palm oil plantations, on the banks of the Baai River, Sangkulirang Peninsula. Local people recently confirmed this single group no longer exists in the area (Setiawan, pers. Comm., August 2011). In 2010, *P. h. canicrus* individuals were sighted, and regularly heard, by Anne Russon and her colleagues in Kutai National Park, near the original Mentoko research site. In 2011, these langurs were not seen or heard despite ongoing research activities at the field station (Russon, pers. comm., August 2011).

P. h. canicrus may still survive both in Kutai National Park and Sangkulirang Peninsula but populations are likely to be small and fragmented, decreasing its long-term viability. *P. h. canicrus* is currently classified as Endangered according to IUCN Red List criteria, however Nijman et al. (2008) noted the subspecies may be reclassified once more data on its distribution becomes available.

In this paper, we present evidence that *P. h. canicrus* does indeed occur in the forests of central East Kalimantan, west of its previously known geographic range. We recorded the presence of *P. h. canicrus* at two mineral springs (sepans) in the Wehea Forest, East Kutai district, East Kalimantan. We provide preliminary observations on these two langur groups and argue for more research on the status, ecology and distribution of this endangered primate.

Methods

Study site

This research was conducted in the Wehea Forest (01°32’46”N, 116°46’43”E) in East Kutai District, East Kalimantan, Indonesia. Wehea contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests classified as logging concessions. Approximately 30% of Wehea has been selectively logged, with the last activity taking place in approximately 1996. Wehea is classified as a logging concession but paperwork has been submitted to change Wehea's status to a Protection Forest (Hutan Lindung). The site has varied topography, containing multiple ridges, ravines, and runoff streams with elevations varying from 250 m in the east to 1750 m in the west. Wehea Forest is characterized by lowland dipterocarp and montane forests with average rainfall amounting to 3000 mm per annum and temperatures ranging from 24 to 35 °C. A dry season typically runs from June to September and the rainy season is from November to February. At least nine species of nonhuman primates have been previously reported from the site: the Bornean orangutan (*Pongo pygmaeus*), Bornean gibbon (*Hylobates muelleri*), maroon langur (*Presbytis rubicunda*), white-fronted langur (*Presbytis frontata*), silvered langur (*Trachypithecus cristatus*), short-tailed macaque (*Macaca nemestrina*), long-tailed macaque (*Macaca fasicularis*), slow loris (*Nycticebus coucang*), and the Western tarsier (*Tarsius banancus*).

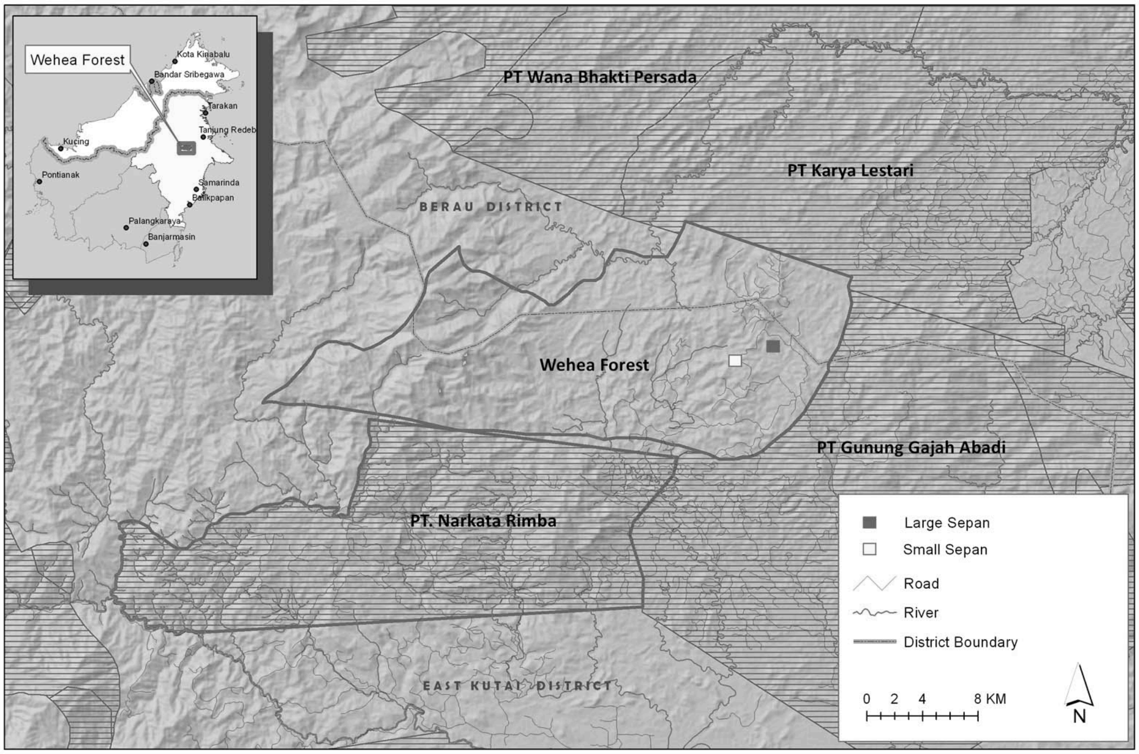

Figure 2.1 Location of sepans in Wehea Forest where Miller's Grizzled Langur (*P.h. canicrus*) was observed from June 6-August 2, 2011. Inset shows location of Wehea Forest on the island of Borneo.

Data Collection

P. h. canicrus groups were observed at two sepans in Wehea Forest (Fig. 2.1) located a distance of 4.2 km apart, during June-July 2011. In both cases, the data were collected in two ways: 1) direct observation and photographing and 2) camera trapping. Direct observations and photographs were collected by observers concealed in blinds. On days where direct observations were conducted, observers spent 8 - 10 hours in the blind watching the sepan. When the langur arrived at the sepan the observer noted the size and composition of the group and photographed all individuals for the purposes of identification. Camera trap data were acquired by battery-powered motion-triggered cameras that had been positioned strategically around the sepans.

The larger sepan (approx. 1000 m^2) consists of mixed terrain (grass, rock, gravel, mud, and water pools) with only a few small trees occurring within its borders and a small stream flowing through the site. Direct observations at the larger sepan were done using a small (2.5 x 1.2 x 1.5m) wooden blind with 12 cm tall window slits for observation. The blind was constructed several years ago so animals are habituated to the structure. Data was collected from July 3-10, 2011; direct observations were conducted during 6 days of this study period and camera trapping was done for all 8 days of this study period. Camera trapping data was obtained by two Bushnell Trophy Cam camera traps, which were positioned on two trees along the perimeter of the sepan at a height of approximately 80cm. Both camera traps were set to take 3 photos per trigger.

The smaller sepan (approx. $250m^2$) is situated beside a small river, on rocky terrain and contains a small amount of low vegetation. Direct observations of *P. h. canicrus* were conducted at this site for 3 days between June 25-29, 2011, and were done from small temporary blinds. The first blind was constructed a few days before observation data was collected but was later moved to a more convenient location. There was no habituation period but the single observer was virtually invisible to the animals, although the animals may have noted his presence by subtle auditory cues. Camera trapping was done for 58 days between June 6-August 2, 2011 using two Reconyx HC 500 camera traps. Camera traps were placed on two trees, located along the perimeter of the smaller sepan, at a height of 40-60 cm. Both traps were set to take 3 photos per trigger, with the trigger delay varying from 0 to 1 second. Camera trapping and direct observations were conducted during the same study period and largely overlapped.

Camera traps in both sepans recorded only animals observed on the ground in the proximity of the spring itself, while direct observations recorded animals observed on the ground as well as those that could be viewed in trees from the blinds. For that reason, group counts are based primarily on observational data when available. However, observations of group counts and composition were validated by inspections of the camera trap photographs as well as photographs taken during the observations by the observers at both sepans. From photographs, we closely inspected the morphology of genitalia, nipples, and individual differences in coloration to confirm the age/sex categories of the individual animals and to minimize the risk of double counting the same individuals. The maximum group counts from the camera trap photographs were also taken in consideration.

All research conducted was in compliance with American Journal of Primatology guidelines for the ethical treatment of nonhuman primates, was approved by the Ethical Commission of the Faculty of Science of University of South Bohemia for Treatment of Laboratory Animals, and adhered to Indonesian legislation. Research permits were approved by the Indonesian Ministry of Research and Technology (RISTEK).

Analysis

We analyzed our observational and camera trap data in order to determine how often *P. h. canicrus* visited each of the sepans, and how frequently they visited the sepans relative to other animals. The per day capture rate was calculated as the total number of days the langur was captured by camera trap in each sepan divided by the total number of camera trapping days at each location. The frequency of visits to the sepan by the langur was calculated as the per photo capture rate: the number of *P. h. canicrus* camera trap photos divided by the total camera trap photos. The average number of individuals per photo was calculated by counting *P. h. canicrus* individuals in each capture event (3 pictures/trigger) divided by the total number of capture events. Presence rate was used to add some behavioral information and to standardize differences in length of observation days, and was calculated by dividing the total time when *P. h. canicrus* was present at the sepan by the total time when the observer was present. The number of individuals present at the sepan was calculated from the direct observation data for each observation day. These counts may be but need not be identical to the size of the entire group.

Results

Tables 2.1 and 2.2 provide the respective summary data on the direct observations and camera trapping of *P. h. canicrus* and other primates at both sepans. At the large sepan, *P. h. canicrus* was observed on 3 out of 6 days. On July 3rd, 3 individuals were counted, including 2 adult females and 1 adult or subadult langur of unknown sex. On July 9th, 11 individuals were counted, including 1 adult male, 3 adult females with infants, 1 adult female without infant, 2 adults of unknown sex, and 1 large juvenile or subadult of unknown sex. On July 10th, only 2 individuals were observed, 1 subadult of unknown sex and 1 large juvenile or subadult of unknown sex. Both of these langurs were observed alone, as the second langur appeared at the sepan 52 minutes after the first individual went out of sight.

The camera trapping data from the large sepan occurred simultaneously to and is largely redundant with respect to the observational data. However on July 4th, one langur was photo-captured but not observed and on July 10th, two individuals were observed at the sepan but none was photocaptured. Both data sets are included for comparison and methodological consideration.

A total of 1279 photographs were taken from the large sepan during 8 camera trapping days. The per photo capture rate was very low, 0.005, which is much less than for some other mammals at this sepan, notably the sambar deer. During the 8 day study, *P. h. canicrus* was photo-captured only on July 3rd and July 4th and only one langur was captured in each photograph. The per day capture rate is relatively high, 0.25, showing that the langurs visited the sepan frequently but did not spend much time in its immediate proximity.

Table 2.1 Direct observation of Miller's Grizzled Langurs (*P.h. canicrus*) and other primates at sepans in Wehea Forest in June – July 2011.

Location	Days *P. h. canicrus* observed (total days spent at sepan)	Hours *P. h. canicrus* present (total observation hours)	Avg # indiv observed (min, max)	*P. h. canicrus* presence rate	*P. h. canicrus* per day capture rate	Other primates (per day capture rate)
Small Sepan	2 (3)	5.83 (28)	3.5 (3, 4)	0.21	0.67	*M. nemestrina* (0.33)
Large Sepan	3 (6)	1.6 (56)	5.3 (2, 11)	0.03	0.50	*P. pygmaeus* (0.50) *P. rubicunda* (1.00)

Table 2.2 Camera trapping results for Miller's Grizzled Langur (*P.h. canicrus*) and other primates at sepans in Wehea Forest from June 6 – Aug 2, 2011.

Location	Total # *P. h. canicrus* photos (total # camera trap photos)	Days *P. h. canicrus* visited sepan (total camera trap days)	Avg # indiv/photo (min, max)	*P. h. canicrus* per photo capture rate	*P. h. canicrus* per day capture rate	Other primates (per day capture rate)
Small Sepan	4124 (8184)	42 (58)	2.30 (1, 7)	0.50	0.72	*P. pygmaeus* (0.05) *P. rubicunda* (0.29) *M. nemestrina* (0.02)
Large Sepan	6 (1279)	2 (8)	1.0 (1, 1)	0.005	0.25	*P. pygmaeus* (0.25) *P. rubicunda* (0.50)

At the small sepan, *P. h. canicrus* was observed on 2 out of 3 observation days. On June 27th, we observed 4 animals, including 1 adult male, 1 adult female with infant, and 1 subadult animal of unknown sex. On June 29th, 3 animals were observed, including 1 adult male, 1 adult female and 1 subadult animal of unknown sex. Inspection of photographs indicates the group observed on the 29th was most likely the same individuals observed on June 27th, although the infant was not seen on the 29th.

A total of 8184 photographs were taken from the small sepan during 58 camera trapping days. With a per photo capture rate of 0.50 and a per day capture rate of 0.72, *P. h. canicrus* was the most frequently photo-captured mammal at the smaller sepan. The average number of individuals per photo was 2.30; the maximum number of 7 individuals from camera trap photos was more than the maximum number of langurs directly observed at the small sepan.

Other primates directly observed or photographed by camera traps at both sepans include the Bornean orangutan (*Pongo pygmaeus*), maroon langur (*Presbytis rubicunda*) and short-tailed macaque (*Macaca nemestrina*). The per day capture rate for other primates at the small sepan was less than *P. h. canicrus*, although at the large sepan the per day capture rate for other primates was equal to or greater than *P. h. canicrus*.

Discussion

Discovery of Miller’s Grizzled Langur (*Presbytis hosei canicrus*) in the Wehea Forest confirms the continued existence of this endangered primate and is the first solid evidence demonstrating that its geographic range extends further inland than previously thought. As this subspecies (which should perhaps be elevated to the species level (Meijaard & Groves, 2004) appears to be on the brink of extinction within its previously known geographic range, finding new populations and expanding the known distribution of *P. h. canicrus* is of utmost importance for determining the conservation status and securing the future of this endangered primate.

As is likely true for remnant popoulations in Kutai National Park and Sangkulirang Peninsula, our study suggests the population density of *P. h. canicrus* in Wehea Forest is very low. The high frequency of sightings at the sepans does not necessarily suggest a high abundance of the langurs. The sepans appear to be key resources for primates and other wildlife within the forest, and may be used disproportionally compared to other habitat. Unpublished observations at the large sepan suggest it has been used regularly by *P. h. canicrus* for many years. Rustam (in press) camera trapped the langurs at the large sepan in 2008, and Gabriella Fredriksson (pers. comm.) observed, photographed and video recorded one group at the large sepan in August 2010. No long-term data yet exist for the small sepan, which was discovered only recently.

At present, the two sepans in Wehea Forest are the only locations where *P. h. canicrus* is known to be observed regularly. Sepans should therefore be considered priority spots for further survey of these langurs in Wehea and other forests within their potential geographical range. Furthermore, the tendency of the langurs to remain in the trees surrounding both sepans for extended periods of time and high frequency of visits makes it possible to collect data on the behavior and ecology of this cryptic primate. Preliminary results from this study indicate possible differences in the use of the two sepans by *P. h. canicrus*, including not only the frequency and length of visits but also the number of group members that descend to the ground and approach the sepan, as indicated by differences in the presence rate, per photo capture rate and the average number of individuals per photo. However, this may also be partially explained by the large difference in camera trapping effort between the two sepans and the placement of camera traps. Results also indicate possible differences in the frequency of use of the two sepans by *P. h. canicrus* and other primates. Futher investigation on the potential differences in the use of the two sepans by *P. h. canicrus* and frequency of use by other primates, may shed light on the ecology and behavior of this little known primate and make future surveys more efficient.

No other sepans have been located in Wehea Forest so far and only one other sighting of *P. h. canicrus* outside the two sepans has been confirmed since 2004. This sighting, by Larissa Salaki (pers. comm.) in 2011, was of at least 2 adults and one infant. The langurs have not been sighted on any other occasions despite an intensive study on the ecology and behavior of sympatric Maroon Langurs that began in 2009 and is still ongoing. Ex-hunters have indicated numerous sepans exist in Wehea, making search for additional sepans in Wehea a priority.

Although our study has extended the current geographical range for *P. h. canicrus*, we emphasize this does not ensure the survival of this subspecies. Loss of habitat and hunting pressure are the two greatest challenges facing the survival of *P. h. canicrus*. However, efforts to protect the Wehea Forest have substantial buy-in from the local community. In 2004, the Wehea Dayak declared the Wehea Forest, 'protected land' under customary 'adat' law, prohibiting the cutting of trees, starting of fires and harvesting of plants and animals from the forest. The site is currently co-managed by the local Wehea Dayak community and the Wehea Management Body, a multi-stakeholder governing body consisting of the regional East Kutai government, NGO's, private companies and universities and the forest is patrolled by a team of Wehea Dayak rangers.

It is not known whether the population of *P. h. canicrus* within Wehea Forest is large and stable enough to be considered viable. But Wehea Forest is still contiguous with other large forested areas along its borders. Some of these forests have protected status, but others are exploited as logging concessions for selective timber extraction. Together with the Wehea Forest, they represent a continuous area of at least 180,000 ha of suitable primate habitat, and very likely accommodate a viable population of *P. h. canicrus* (as well as other threatened primate and wildlife species). If logging is sustainably managed, hunting kept under control, and further expansion of palm oil plantations into the abandoned logging concessions halted, this forest block could provide hope for the long-term survival of *P. h. canicrus*. These forests should be considered a priority area for future surveys for the subspecies.

Discovery of a potentially viable population of *P. h. canicrus* in and around Wehea Forest should not undermine efforts to protect the subspecies in its formerly known geographic range. Although very rare, *P. h. canicrus* still appears to persist in its former stronghold of Kutai National Park, the only area where this langur was reported to occur at relatively high densities (Rodman, 1978). Although these populations no longer exist at these densities, primarily due to the great fires of 1982-3 and 1997-8, the carrying capacity of burned forest in Kutai National Park may increase if forests are allowed or encouraged to regenerate. The possible recovery of *P. h. canicrus* in Kutai National Park should therefore be monitored and the status of the remaining population in the Sangkulirang Peninsula should be validated through thorough surveys before abandoning these potentially viable conservation causes.

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Chapter 3.

Terrestriality in Bornean Orangutan (*Pongo pygmaeus morio)* and implications for their ecology and conservation

This chapter was previously published in the article "Terrestriality in Bornean orangutan (Pongo pygmaeus morio) and implications for their ecology and conservation", co-authored by Loken, B., Spehar, S., Rayadin, Y. in the American Journal of Primatology and has been reprinted with permission from © 2013 Wiley Periodicals, Inc. I authored and completed the majority of the text and data analysis and exclusively authored the tables and figures. I conducted the fieldwork for this research.

Abstract

Aside from anecdotal evidence, terrestriality in orangutans (*Pongo* spp.) has not been quantified or subject to careful study and important questions remain about the extent and contexts of terrestrial behavior. Understanding the factors that influence orangutan terrestriality also has significant implications for their conservation. Here we report on a camera trapping study of terrestrial behavior in the northeastern Bornean orangutan, *Pongo pygmaeus morio*, in Wehea Forest, East Kalimantan, Indonesia. We used 78 non-baited camera traps set in 43 stations along roads, trails and at mineral licks (sepans) to document the frequency of orangutan terrestriality. Habitat assessments were used to determine how terrestrial behavior was influenced by canopy connectivity. We compared camera trapping results for *P. p. morio* to those for a known terrestrial primate (*Macaca nemestrina*), and another largely arboreal species (*Presbytis rubicunda)* to assess the relative frequency of terrestrial behavior by *P. p. morio*. A combined sampling effort of 14,446 trap days resulted in photographs of at least 15 individual orangutans, with females being the most frequently recorded age sex class (N = 32) followed by flanged males (N = 26). *P. p. morio* represented the second most

recorded primate (N = 110 total records) of seven primate species recorded. Capture scores for *M. nemestrina* (0.270) and *P. p. morio* (0.237) were similar and almost 7 times higher than for the next most recorded primate, *P. rubicunda* (0.035). In addition, our results indicate that for orangutans, there was no clear relationship between canopy connectivity and terrestriality. Overall, our data suggest that terrestriality is relatively common for the orangutans in Wehea Forest and represents a regular strategy employed by individuals of all age-sex classes. As Borneo and Sumatra increasingly become characterized by mixed-use habitats, understanding the ecological requirements and resilience in orangutans is necessary for designing optimal conservation strategies.

Introduction

Orangutans are only found on the islands of Borneo and Sumatra and exhibit considerable geographic variation in their biology and behavior (Wich et al., 2009). Orangutans are divided into two closely related species, the Bornean orangutan (*Pongo pygmaeus*) and Sumatran orangutan (*Pongo abelli*) (Groves, 2001). Bornean orangutans are further divided into three subspecies (the northwestern Bornean orangutan, *Pongo pygmaeus pygmaeus*; the central Bornean orangutan, *Pongo pygmaeus wurmbi*, and the northeastern Bornean orangutan, *Pongo pygmaeus morio*) (Groves, 2001). This geographic variation is thought to reflect adaptations to different ecological conditions across Borneo and Sumatra (e.g., Marshall et al., 2009; Taylor & van Schaik, 2007; van Schaik et al., 2009; Wich et al., 2012), with the forests of eastern Borneo generally recognized as the most resource-scarce and of the lowest quality in the region. The northeastern Bornean orangutan subspecies, *P. p. morio*, seems to have developed adaptations to these conditions of extreme scarcity (e.g., smaller brain size, a shorter interbirth interval, more robust jaws) (Singleton et al., 2009; Taylor, 2006; 2009; Taylor & van Schaik, 2007; van Schaik et al., 2009), and some have suggested these adaptations may even increase the resilience of *P. p. morio* to anthropogenic habitat disturbance (Husson et al., 2009; Marshall et al., 2009).

Both species of orangutan are described as predominantly arboreal (e.g., Thorpe & Crompton, 2009). However, one significant behavioral difference that has been noted between the species is in the amount of terrestriality exhibited. Terrestriality appears to be rare among Sumatran orangutans, possibly due to the presence of a large ground predator, the Sumatran tiger (*Panthera tigris sumatrae*) (Cant, 1987; Sugardjito & van Hooff, 1986; Manduell, pers. comm., April 2013). In contrast, terrestriality has been reported from several well-studied Bornean orangutan populations. This behavior seems to be most common in flanged adult males (Delgado & van Schaik, 2000; Galdikas, 1979; MacKinnon, 1974; Rodman, 1979; Tuttle, 1986; ME. Harrison, pers. comm., April 2013; Manduell, pers. comm., April 2013; AJ. Marshall, pers. comm., April 2013; Oram, pers. comm., April 2013). The contexts of terrestrial behavior appear to be obtaining food resources (e.g., fallen fruit, shoots, soil; MacKinnon, 1974) or traveling. In oil palm concessions, orangutans have been seen coming to the ground to eat young oil palm fruit and in mining concessions and oil palm and Acacia plantations, orangutans have been observed moving on the ground between fragmented forest patches (Rayadin, unpublished data). Some researchers report that flanged males spend a substantial amount of time traveling on the ground (MacKinnon, 1974; ME. Harrison, pers. comm., April 2013; Manduell, pers. comm., April 2013; AJ. Marshall, pers. comm., April 2013), possibly because their large body size makes it more energetically efficient for them to travel long distances on the ground rather than in the trees (Cant, 1987).

Unflanged males and females, particularly females with infants, are generally reported as being reluctant to come to the ground and thus exhibit terrestrial behavior far less often. However, this pattern may not be universal. Females have been seen coming to the ground to utilize resources, such as water sources and termites (Manduell, pers. comm., April 2013; Oram, pers. comm., April 2013). MacKinnon (1974) noted that females and juvenile *P. p. morio* sometimes traveled briefly on the ground at Ulu Segama in northeastern Borneo, and Manduell et al. (2011) noted that at Sabangau in southern Borneo (*P. p. wurmbii*), “sub-adult males and adolescent females have also been observed occasionally to travel substantial distances over the ground” (p. 349).

Despite these anecdotal observations, the degree of terrestriality in Bornean orangutans has not been systematically studied and important questions about the contexts and determinants of orangutan terrestriality remain. Is this behavior confined to large-bodied flanged males, or are smaller-bodied individuals (e.g., unflanged males and females) also frequently terrestrial (cf Manduell et al., 2011)? Across age-sex classes, is terrestriality generally confined to short trips to the ground to acquire resources or do individuals frequently travel on the ground? Do individuals mainly employ terrestrial behavior in areas with poor canopy connectivity (Oram, pers. comm., April 2013; Rayadin, unpublished data) or is this behavior employed in a variety of habitat types? An important factor influencing terrestriality is likely energetics; terrestrial locomotion could be more energy efficient, particularly for large individuals traveling over long distances, and thus increase foraging efficiency (Cant, 1987). However, the determinants of terrestriality in orangutans are difficult to elucidate without quantitative information about the ecological contexts in which this behavior is employed. Locomotion and habitat use are critical components of a species' ecology, and understanding terrestriality in orangutans has important implications for understanding their behavioral adaptations and strategies under different environmental conditions. This information can be integrated into comparative studies that will allow us to understand how differences in habitat quality and other environmental factors have shaped the morphology and behavior of orangutans across their geographic range (van Schaik et al., 2009).

One reason there are few quantitative data on orangutan terrestriality may be that the presence of observers (required for long-term behavioral study) inhibits terrestrial behavior (Cant, pers. comm., March 2013; Oram, pers. comm., April 2013). Camera traps offer a possible alternative for studying at least some aspects of the behavior of these elusive apes. This technology has been used extensively to study population density and abundance of elusive mammals (e.g., Kawanishi & Sunquist, 2004; Kays & Slauson, 2008; Treves et al., 2010; O'Connell et al., 2011; Wilting et al., 2012). If deployed properly they can also provide information about habitat use and behavior without requiring behavioral follows of study animals, as has been demonstrated by a number of recent studies with primates (e.g., Head et al., 2012; Olson et al., 2012; Pebsworth et al., 2012; Tan et al., 2013).

Here we report on a camera trapping study of terrestrial behavior in the northeastern Bornean orangutan, *P. p. morio*, in Wehea Forest in East Kalimantan, Indonesia. The aim of this study was to shed light on the causes and possible determinants of terrestrial behavior in *P. p. morio* by collecting quantitative data on the frequency of terrestriality by different age-sex classes and on the behavioral and ecological contexts in which terrestriality occurs. Clarifying the degree and contexts of orangutan terrestriality and the capacity for ecological flexibility is also crucial for designating priority habitat and designing optimal conservation management plans.

Methods

Study site

Wehea Forest (01°32’46”N, 116°46’43”E), located in East Kutai District, East Kalimantan, Indonesia, contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests currently classified as logging concessions. Wehea Forest is within a logging concession, but this concession is currently inactive and all logging ceased in the mid-1990s. Old logging roads, which have not been maintained since logging stopped in the forest, are very overgrown but still exist and were utilized for this study. Wehea Forest is currently protected by an agreement between a local community and the local government, and paperwork has been submitted to change its status to a Protection Forest (Hutan Lindung).

The site has a varied topography, characterized by steep ravines, multiple ridges and runoff streams. Elevations vary from 250 m in the east, where the main logging activity took place, to 1750 m in the west, where the primary forest occurs. Wehea Forest is characterized by lowland Dipterocarp, sub-montane and montane forests with mean total annual rainfall amounting to 3000 mm and a mean 24 h temperature of 27 °C. A dry season typically runs from June to September and the rainy season is from November to February. Wehea Forest lies within a center of richness for primate species (Meijaard & Nijman, 2003) and ten species of nonhuman primates have been previously reported from the site: the northeastern Bornean orangutan (*Pongo pygmaeus morio*), Bornean gibbon (*Hylobates funereus*), red langur (*Presbytis rubicunda*), Miller’s grizzled langur (*Presbytis hosei canicrus*), white-fronted langur (*Presbytis frontata*), silvered langur (*Trachypithecus cristatus*), pig-tailed macaque (*Macaca nemestrina*), long-tailed macaque (*Macaca fasicularis*), slow loris (*Nycticebus coucang*), and the Western tarsier (*Tarsius banancus*). Research is currently underway in Wehea Forest to estimate population densities for *P. p morio*, *H. funereus*, *P. rubicunda* and *P.h. canicrus*.

Camera traps

In March 2012, 68 non-baited cameras were set in pairs, or stations, along old logging roads, trails, and at one mineral lick (sepan). This station array covered an approximate area of 80 km^2 (Fig. 3.1). The cameras used were Bushnell Trophy Cams (N = 60) and Reconyx HC500 (N = 8) cameras. An additional 10 Bushnell Trophy Cams were added in May, seven set along roads and three at a second sepan, bringing the total number to 78 cameras set across 43 camera trap stations and resulting in a sampling effort of 14,446 trap days. All cameras remained at the same locations until this study concluded in October 2012.

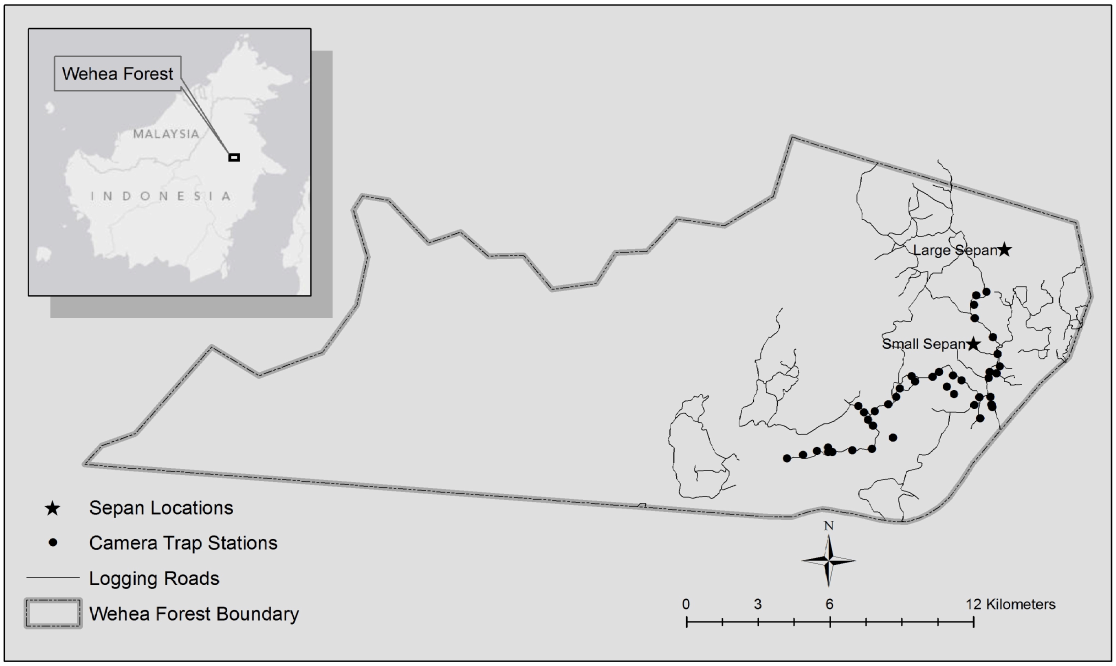

Figure 3.1 Location of camera-trap stations in Wehea Forest. Insert shows the location of Wehea Forest on the island of Borneo.

Of the 43 camera trap stations used from May onwards, five were located along trails, two at sepans, and the remaining 36 along old logging roads. All cameras were placed on trees ~50 cm from the ground and fitted with a plastic cover above and a bed of leaves below to protect against rain and mud. Each camera was set to take three pictures per trigger, with a reset time of one second. Cameras were checked a total of three times, in the middle of May, the beginning of July and again in October, at the conclusion of the study. At each visit, non-functioning cameras were replaced with new cameras, batteries were changed and the SD card storing the photos was removed from the camera and replaced by a new card.

Camera trap analysis

All photos of primates taken from March-October 2012 were first categorized by species. We then analyzed these photographic records to determine how often *P. p. morio* were photographed relative to other primates on 1) trails and old logging roads 2) at sepans and 3) in both areas. We examined the use of trails and roads separately from use of sepans (mineral licks) because sepans are areas largely devoid of trees and primates must descend to the ground to use these areas. Furthermore, primates are known to use sepans to supplement minerals in their diet by drinking the mineral rich water (Blake et al., 2010; Lhota et al., 2012, Matsubayashi et al., 2007; 2011).

The number of records of each species was calculated as the number of photos taken with >1 hr. interval between photos at each station. If an individual/species was seen at a station multiple times within an hour, this was treated as 1 record. The percent of primate records represented by each species was calculated from the total records (road + sepan) and from all stations (N = 43). A capture score for each primate was computed from the percent of total stations (e.g. 28 of 43 total stations recorded *M. nemestrina*) that recorded a given primate multiplied by the percent of total records represented by that primate (e.g. 113 *M. nemestrina* records out of 302 total primate records). A relative encounter score was based on the relative encounter rate for each species. Encouter rates were calculated by asking a set of well-trained field assistants and researchers (N = 6) to rank each primate species with a number that reflected how often they perceived encountering each species in Wehea Forest. Each field assistant and researcher spent at least 500 hours in Wehea Forest conducting primate behavior and survey research between 2010-2012 and were not affiliated with this camera trapping study. The final rank of each species was then calculated as the mean of scores for that primate given by all participants. This is meant only as a rough estimation of the relative abundance of primate species in Wehea Forest.

The number of different *P. p. morio* individuals captured was determined by carefully studying and comparing all photographs of *P. p. morio* (N = 658). These determinations were completed by an observer experienced in identifying wild primate individuals based on variation in physical appearance (Spehar). Records (sets of photographs from the same capture) were first divided into age-sex class categories (flanged male, unflanged male, female with juvenile, female without juvenile, juvenile, adult of indeterminate sex) based on external genitalia if visible, secondary sexual characteristics (cheek flanges, throat pouch, cape of hair on back, elongated nipples), and body size and shape. Photographs were then examined for cues to individual identity, noting characteristics for each of the following categories: body size; hair color and quality (e.g., thick, thin, any bald patches); facial features (prominance of brow ridges; prognathism; angle and size of nostrils and mouth; overall shape of face; etc.), shape of hair on head, and any other identifying featres (e.g., elongated nipples, marks or scars, distinctive body posture). If the individual's face and/or some other clearly identifying mark (e.g., a distinctive injury) was not visible in a photograph, we did not attempt to identify that individual. After this initial assessment was performed, photographs were placed side-by-side for comparison to determine if the same individual had been captured at multiple stations and to ensure that no individual was counted more than once. This process was completed in its entirety from the beginning two separate times by Spehar to maximize confidence in the assessment.

Habitat assessment and analysis of terrestriality

In order to determine how terrestrial behavior was influenced by canopy gaps we measured and rated canopy connectivity for each camera trap station. For this and other analyses related to orangutan terrestriality, we compared our results for orangutans to those for two other primate species: *M. nemestrina*, a species that is known to be largely terrestrial (Caldecott, 1986) and *P. rubicunda*, a species that is primarily arboreal but is ocassionally seen on the ground (Spehar, unpublished data). These two species were incorporated into our analysis because they allow us to assess how frequently orangutans use the ground relative to other known terrestrial and arboreal primates, and thus draw conclusions about the extent of *P. p. morio* terrestriality in Wehea Forest.

Canopy connectivity was assessed in the area 5 m on either side of each camera trap and directly between each paired camera trap at each station by a single observer (Loken). Habitat characteristics such as the presence of boughs, branches or lianas of sufficient size to be used by primates for crossing gaps were recorded and a canopy connectivity rating was created based on visual estimates of the minimum distance measured between these support attributes (Manduell et al., 2011; 2012; Thorpe & Crompton, 2006; Thorpe et al., 2007). Pictures were taken of the canopy from various angles at each camera trap station and cross referenced with notes to determine a final connectivity rating of low, medium or high for each station (Table 3.3).

Canopy connectivity ratings of low (gap size 5-9 m), medium (gap size 3-5 m), and high (gap size 0-3 m), were based on the observed ability and frequency of *H. muelleri*, *P. pygmaeus* and *M. fascicularis* to cross openings in the canopy of various sizes (Cannon & Leighton, 1994; Manduell et al., 2012). Our canopy connectivity rating of low was based on Cannon & Leighton's (1994) observation of a maximum gap crossing of 9 m by *H. muelleri* and that gaps of 5-9 meters were crossed in each layer of the canopy. Based on extensive behavioral observations of *P. rubicunda* and *P. h. canicrus* in Wehea Forest (Spehar, unpublished data) we believe that *P. rubicunda*, *P. h. canicrus* and *P. cristata* would be able to cross similar distances to *H. funereus*. Connectivity ratings of medium and high were based on Cannon & Leighton's (1994) maximum gap crossing widths for *M. fascicularis* (3.5 m) and Manduell et al.'s (2012) mean observed gap crossing sizes (0.96 – 2.59 m) for various *P. pygmaeus* age/sex classes respectively. All stations were located along old logging roads and trails and had canopy support attributes of sufficient size for primate gap crossing and a gap width less than 9 m.

We then calculated a "ground use" score as a measure of how often *P. p. morio*, *P. rubicunda*, and *M. nemestrina*, were terrestrial at camera trap stations located along old logging roads and trails with different canopy cover and connectivity. Ground use scores were computed for each of our three canopy connectivity ratings using the variables "station success", "record success", and "station proportion." Station success was computed from the percent of stations that recorded the species for a given connectivity rating, while record success was computed as the percent of total species records for a given connectivity rating. The multiplied result was then divided by station proportion, the percentage of total stations in a connectivity category, to obtain the ground use score. This score reflects the chance of recording the species at an individual camera trap in a particular canopy connectivity category, as well as the capture rate of species at camera traps located in a particular connectivity category. We should note that our ground use score may reflect not only the relative ground use by each species but also the relative abundance of each species within that particular canopy connectivity category. Therefore, comparison across species should be treated with some caution.

Results

A total of 2149 primate photos were taken on old logging roads, trails and at sepans in Wehea Forest between March and October 2012 (Table 3.1). A total of 302 independent records of primate species were recorded on both roads/trails and at sepans, and 218 records were recorded on roads/trails only. *M. nemestrina* was the most frequently photographed primate in Wehea Forest (N = 113 records) and was recorded at 31 of 43 stations while *P. p. morio* was the second most photographed primate (N = 110 records) and was recorded at 28 of 43 stations. When considering only records from roads/trails, *M. nemestrina* accounted for 49.5% of primate records (N = 108 records) and *P. p. morio* accounted for 34.9% of primate records (N = 76 records). However when considering records from roads/trails and sepans, the number of records for *M. nemestrina* (N = 113 records, 37.4%) and *P. p. morio* (N = 110 records, 36.4%) were similar and by far the most frequently captured primate (Table 3.1, Fig. 3.2). Capture scores for *M. nemestrina* (0.270) and *P. p. morio* (0.237) were also similar and almost 7 times higher than the primate with the next highest capture score, *P. rubicunda* (0.035) (Table 3.1). The two primates with the highest relative encounter scores were *P. rubicunda* (1.33 ± 0.19) and *H. funereus* (1.67 ± 0.19) while *M. nemestrina* (5.33 ± 0.47) had the second lowest relative encounter score. There was not a significant correlation between our capture and relative encounter scores (Spearman rank correlation, n = 7, rs = 0.14, p > 0.05).

Table 3.1 **Camera trapping results for all primates recorded along roads and at sepans in Wehea Forest from April to October 2012.**

Species	Scientific name	Total photos	Road only records	Total records (road + sepan)	% of total records	Capture score	Relative encounter score
Pig-tailed macaque	*Macaca nemestrina*	1054	108	113	37.4	0.270	5.33 ± 0.47
Orangutan	*Pongo pygmaeus morio*	658	76	110	36.4	0.237	4.33 ± 0.56
Red langur	*Presbytis rubicunda*	171	19	38	12.6	0.035	1.33 ± 0.19
Miller's grizzled langur	*Presbytis hosei canicrus*	168	0	26	8.6	0.004	5.75 ± 0.57
Long-tailed macaque	*Macaca fascicularis*	84	8	8	2.6	0.002	5.00 ± 0.42
Bornean gibbon	*Hylobates funereus*	13	6	6	2.0	0.0009	1.67 ± 0.19
White-fronted langur	*Presbytis cristata*	1	1	1	0.3	0.0001	4.58 ± 0.61

Table 3.2 **Individual *P.p. morio* records for each age/sex class and numbers of confirmed individuals along roads and at sepans.**

Age/Sex Class	No. of confirmed individuals	Total records (road + sepan)	Road only records	% of road only records
Flanged male	5	46	26	34.2
Unflanged male	4	25	11	14.5
Female without juvenile	2	10	10	13.2
Female with juvenile	4	22	22	29.0
Juvenile of indeterminate sex	-	5	5	6.6
Adult of indeterminate sex	-	2	2	2.6

Table 3.2 provides the summary data of individual orangutan records for this study. Flanged males were recorded on old logging roads and trails the most frequently of all individual age sex classes (N = 26 records); however, when all females are considered together (females with juveniles and females without juveniles), they were recorded on old logging roads and trails more than flanged males (N = 32 records). Flanged males represented the most frequently recorded age/sex class at the sepans (N = 20 records) with young males representing the second and only other age/sex class photographed at sepans. The minimum number of separate individuals recorded (that could be identified with 100% confidence) was 15. However, individuals could be identified for only 75 out of 112 or 67% of records.

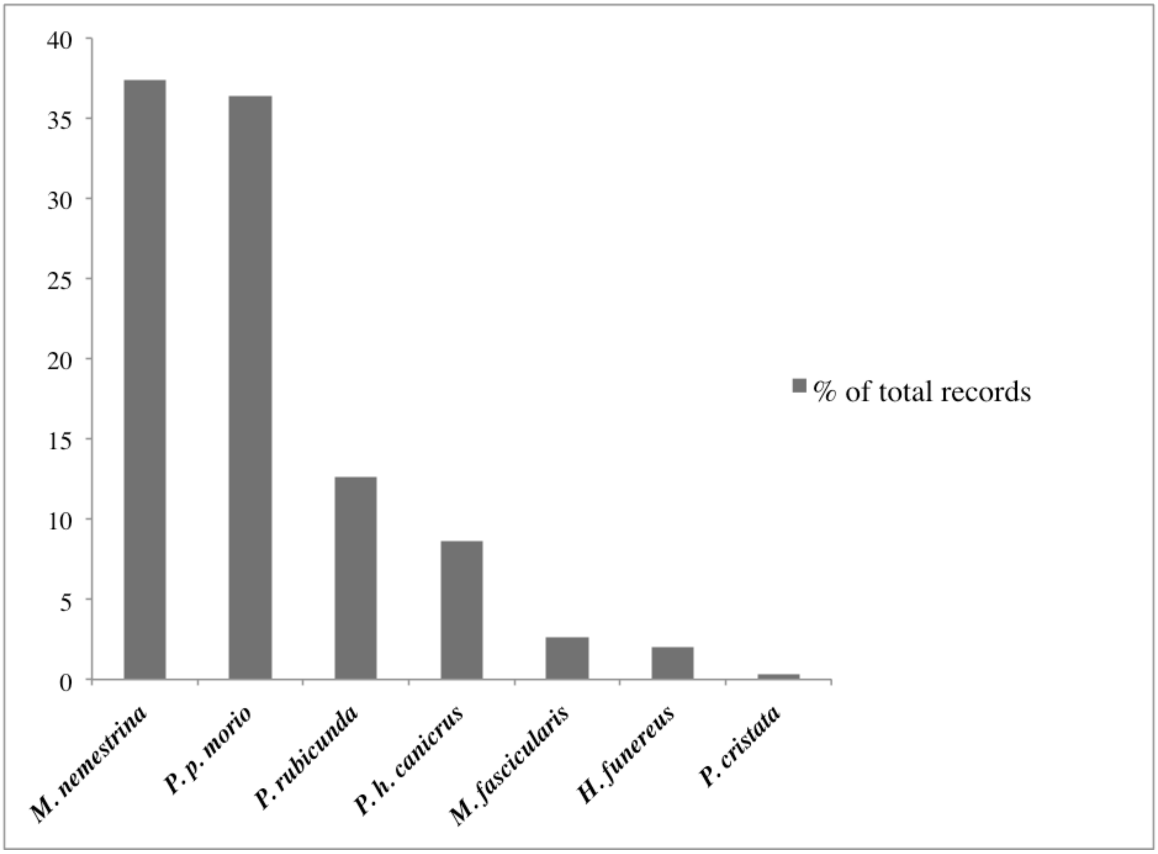

Figure 3.2 **Percent of total records for each primate species recorded along roads/trails and at sepans in Wehea Forest from March to October 2012**

For all species examined (*P. p. morio, P. rubicunda, M. nemestrina*), ground use scores across the different canopy connectivity categories (low, medium, and high) did not differ significantly (Fig. 3.3, $X^2 = 0.27$, df = 4, p = 0.99), suggesting that we were not significantly more likely to capture a species in one canopy connectivity category than another. However, some differences in patterns between species can be detected; *M. nemestrina* were more likely to be captured in areas with a canopy connectivity rating of high (N = 12 stations), while *P. p. morio* and *P. rubicunda* were more likely to be captured in areas with a canopy connectivity rating of medium (N = 11 stations). In addition, we recorded a large difference in the ground use score between *P. p. morio* (0.472) and *M. nemestrina* (0.973) in areas with a canopy connectivity rating of high (Table 3.4, Fig. 3.3).

Discussion

A possible critique of our results is that the differences in capture scores between species (Table 3.1) do not reflect more or less frequent use of the ground but simply differences in abundance between species in Wehea Forest. Although abundance certainly influences how frequently species are captured on camera traps, we believe it cannot explain all of the differences in capture scores between species in this study. We do not have absolute abundance and density estimates for the primate species in Wehea Forest, but after over three years of intensive work with the primate community at the site (Spehar, unpublished data) we are able to make broad statements regarding the relative encounter rates of the different species (quantified in our relative encounter score for each species). We found that the relative encounter score and the capture score of species are not correlated (Table 3.1), indicating that capture rates were not determined solely by relative abundance at the site. Some of the species that have the highest relative encounter scores and appear to be most abundant in Wehea Forest (i.e., red langurs and gibbons) had the lowest capture scores, while species that had much lower relative encouter scores (notably, pig-tailed macaques and orangutans) had the highest capture scores. It is possible that the elusiveness of species influenced relative encounter scores (e.g., encounter rates might be exceptionally low for Miller's grizzled langurs because this species is very cryptic and difficult to spot in a dense forest environment).

Table 3.3 **Description of canopy connectivity ratings used for analysis of forest structure and terrestriality for *P.p. morio, M. nemestrina,* and *P. rubicunda* in Wehea Forest.**

Canopy connectivity rating	Description
Low	Low connectivitiy (gap size 5-9 m), *P. rubicunda* very likely able to cross and *P. p. morio* and *M. nemestrina* very likely not able to cross
Medium	Medium connectivity (gap size 3-5 m), *P. rubicunda* able to cross, *P. p. morio* possibly able to cross, and *M. nemestrina* very likely not able to cross
High	High connectivity (gap size 0 to 3 m), *P. rubicunda, P. p. morio*, and *M. nemestrina* very likely able to cross

Categories were created using locomotor data provided by Cannon & Leighton's [1994] maximum and preferred gap crossing widths for *H. muelleri* (9 m) and *M. fascicularis* (3.5 m) and Manduell et al.'s [2012] mean observed gap crossing sizes (0.96 – 2.59 m) for various *P. pygmaeus* age/sex classes.

Table 3.4 **Ground Use scores for *P. p. morio*, M. *nemestrina*, and *P. rubicunda* recorded at camera trap stations with various canopy connectivity ratings along old logging roads and trails in Wehea Forest.**

Species	Canopy connectivity rating	Total records	Stations with records	Station Success % stations with records	Record Success % of total records	Ground Use score
Pongo pygmaeus morio	Low	31	13	0.722	0.408	0.671
	Medium	27	6	0.545	0.355	0.722
	High	18	7	0.583	0.237	0.472
Macaca nemestrina	Low	40	11	0.611	0.370	0.516
	Medium	27	9	0.818	0.250	0.762
	High	41	9	0.750	0.380	0.973
Presbytis rubicunda	Low	7	4	0.222	0.368	0.186
	Medium	7	3	0.273	0.368	0.375
	High	5	3	0.250	0.263	0.225

However, the fact that the two most commonly encountered primates at the site (red langurs and gibbons) were almost never captured on camera traps indicates that capture rate does not reflect only abundance but also how frequently that species uses the ground. It is for this reason that, although we are aware of the inherent limitations of this study, we feel comfortable making preliminary inferences about orangutan terrestriality using these data.

Previously, terrestrial behavior in Bornean orangutans was assumed to be uncommon and generally employed primarily as a means of acquiring resources on the ground (e.g., MacKinnon, 1974; Manduell, pers. comm., April 2013; AJ. Harrison, pers. comm., April 2013), although some researchers have described flanged males regularly traveling on the ground, in some cases for long distances (Galdikas, 1979; AJ. Harrison, pers. comm., April 2013; Manduell, pers. comm., April 2013; ME. Marshall, pers. comm., April 2013; Oram, pers. comm., April 2013). Terrestrial behavior also seemed to be confined largely to flanged males (Galdikas, 1979; MacKinnon, 1974), although a handful of anecdotal observations suggested that other age-sex classes also occasionally travel on the ground (Manduell et al., 2011). The results of our camera trapping study, which represent the first published attempt to quantify orangutan terrestriality, show that Bornean orangutans in Wehea Forest are captured via camera trap on the ground almost as often as the only primarily terrestrial primate found at the site, the pig-tailed macaque (*M. nemestrina*), and far more often than other primates in Wehea Forest that are of equal or greater abundance and known to be largely arboreal (Table 3.1, Fig. 3.2). Furthermore, our data suggest that terrestrial behavior is not confined primarily to flanged males whose large body size may cause them to have trouble finding adequate support in the trees, and who may be less concerned about predators on the ground, as had been previously suggested (Galdikas, 1979; MacKinnon, 1974; Rodman, 1979; Tuttle, 1986). Smaller-bodied individuals (e.g., females and unflanged males) are also frequently terrestrial (Table 3.2). Interestingly, our data show that females are terrestrial almost as often as flanged males. The fact that adult females with young were captured twice as often as females without young is likely because adult female orangutans will typically always be accompanied by an infant, rather than any actual differences in ground use between females with and without infants. Finally, the fact that multiple individuals (at least 15 total) of all age-sex classes could be identified from our orangutan camera trap photos demonstrates that these records do not represent a handful of “rogue” individuals but repeated behavior by multiple individuals. Overall, our data suggest that terrestriality in the orangutans in Wehea Forest is not an occasional behavior employed only by certain classes of individual, but instead represents a regular strategy employed by individuals of all age-sex classes.

Orangutans are typically arboreal and exhibit many morphological adaptations to arboreal locomotion (Cant, 1987; Thorpe & Crompton, 2006), which raises questions about the determinants of the frequent terrestrial behavior in these animals. In areas where canopy connectivity is poor, orangutans may have no choice but to travel on the ground, and one might expect that we would see terrestrial behavior far more frequently in these areas than in others. However, we did not find evidence for a strong relationship between canopy connectivity and how frequently orangutans were captured on the ground. Orangutans were captured on the ground most frequently at stations with medium canopy connectivity rating, followed closely by stations with low canopy connectivity rating, and least frequently at stations that had a high canopy connectivity rating (Table 3.4, Fig. 3.3). In addition, there was no significant relationship between canopy connectivity and how often orangutans were captured on the ground in an area. This suggests that orangutans are not only terrestrial in areas where they may be forced to come to the ground due to large gaps in the canopy, but employ terrestrial travel as a strategy even in areas where it may be possible for them to find pathways for arboreal travel.

There are likely several interrelated factors influencing these patterns, in particular the energetic costs and benefits of arboreal vs. terrestrial travel. Orangutans are the largest arboreal mammal, which presents special challenges to efficient travel in a complex arboreal environment (Cant, 1987; Thorpe & Crompton, 2006). Orangutans are also subject to intense energetic constraints; most orangutans live in forests that are subject to unpredictable and extended periods during which their preferred food, fruit, is extremely scarce (Marshall et al., 2009). Recent studies have suggested that orangutans are “low-energy specialists,” (Harrison et al., 2010; Knott, 1998; Pontzer et al., 2010), exhibiting physiological and likely behavioral adaptations that allow them to conserve energy and survive these long periods of scarcity. In many cases, traveling on the ground may be the most energy-efficient choice for orangutans, even in areas with relatively continuous canopy. According to Cant (1987), who studied locomotor behavior of *P. p. morio* in East Kalimantan, “the ground is certainly continuous, and terrestrial travel per se is probably less laborious than arboreal travel because of the locomotor zigs and zags imposed by canopy structure. But a pattern of traveling on the ground and climbing up and down feeding trees may be costly in locomotor energy expenditure. The actual costs and benefits of such an alternative are likely to depend on the spatial distribution of the food patches that an animal uses” (p. 85). It may be that orangutans travel on the ground frequently in Wehea Forest because it is the most energetically efficient option, given the distribution of support structures and food resources at the site.

Our results have several important implications. First, they provide a challenge to our current understanding of the ecology of Bornean orangutans, suggesting they may not be as arboreal as has been suggested by previous studies. While we do not suggest that orangutans do not rely heavily on trees, our results support previous anecdotal observations that orangutans do travel on the ground and that travel on the ground is not limited to large flanged males but extends to all age-sex classes. However, we acknowledge that this study only includes the behavior of orangutans from one study site and that results may be influenced by uneven age-sex class ratios. Furthermore, our study subspecies, the northeastern Bornean orangutan (*P. p. morio*), lives in what is often regarded as the harshest orangutan habitat (van Schaik et al., 2009). Thus, the energetic cost-benefits of arboreal vs. terrestrial travel may be different for these orangutans than for orangutans living in habitats where resources are generally more abundant. Understanding the extent of terrestriality within the different orangutan species and subspecies is necessary in order to fully understand how ecology and phylogeny influence their foraging strategies. Only a broader cross-site comparison of orangutan terrestriality across their geographic range can resolve these issues.

Second, these results also have possible implications for orangutan conservation. They suggest that orangutans may be more capable than previously thought of using landscapes that may necessitate terrestriality (e.g., disturbed habitat that include substantial canopy gaps and roads). The islands of Borneo and Sumatra, which encompass the remaining range of wild orangutans, are becoming increasingly chartacterized by mixed-use habitats: a matrix of timber plantations, agro-forestry areas, mines, and remaining patches of natural forest separated by varying distances of non-forested habitat (e.g., Meijaard et al., 2011; Wich et al., 2008; 2012). It has long been assumed that orangutans lack the resiliency to cope with widespread forest degradation, however, some recent studies (Meijaard et al., 2010) have found unexpectedly high orangutan densities in landscapes dominated by human activity (e.g., forestry and palm oil plantations), and have even observed orangutans moving extensively on the ground in these areas (Rayadin & Ancrenaz, unpublished data). This suggests that, providing sufficient availability of food exists, orangutans may be able to use mixed-use landscapes that consist of natural and human altered habitats, at least in some cases.

We emphasize that we are not suggesting natural forests are not necessary for orangutan survival. The behavior of orangutans in highly modified landscapes and the long-term viability of orangutan populations living in these landscapes remains unknown and requires further study. However, our study, demonstrating extensive terrestriality by the orangutans of Wehea Forest, suggests that Bornean orangutans may be capable of greater ecological flexibility than previously thought.

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Fraser University's Office of Research Ethics and Animal Care Committee and UW Oshkosh's Institutional Animal Care and Use Committee, and adhered to Indonesian legislation. Research permits were approved by the Indonesian Ministry of Research and Technology (RISTEK).

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Chapter 4.

Opportunistic behavior or desperate measure? Logging impacts may only partially explain terrestriality in the the Bornean orang-utan (*Pongo pygmaeus morio*)

This chapter was previously published in the article "Opportunistic behavior or desperate measures: Logging may only partially explain terrestriality in the Bornean orang-utan (Pongo pygmaeus)", co-authored by Loken, B., Boer, C., Kasyanto, N. in Oryx and has been reprinted with permission from © 2015 Cambridge University Press. I was primary author of all the text, tables and figures and exclusively completed the data analysis and fieldwork for this research.

Abstract

There is a lack of information on how the Endangered Bornean orangutan *Pongo pygmaeus morio* moves through its environment. Here we report on a camera-trapping study carried out over 2.5 years to investigate the orangutan's terrestrial behaviour in Wehea Forest, East Kalimantan, Indonesia. We set 41 camera trap stations in an area of secondary forest, 36 in recently logged forest immediately adjacent to Wehea Forest, and 20 in an area of primary forest in the heart of Wehea Forest. A combined sampling effort of 28,485 trap nights yielded 296 independent captures of orangutans. Of the three study sites, orangutans were most terrestrial in recently logged forest, which may be only partially explained by breaks in the canopy as a result of logging activity. However, orangutans were also terrestrial in primary forest, where there was a closed canopy and ample opportunity for moving through the trees. Our results indicate that orangutans may be more terrestrial than previously thought and demonstrate opportunistic behaviour when moving through their environment, including using newly constructed logging roads for locomotion, possibly indicating some degree of resilience to human

disturbance. This finding is important because of the potential role of sustainably logged forests for orangutan conservation.

Introduction

The Bornean orangutan *Pongo pygmaeus* is one of the most iconic species, yet formal studies of its terrestriality have been conducted only recently (Loken et al., 2013; Ancrenaz et al., 2014). Understanding the factors that influence orangutan terrestriality has important implications for the conservation of this Endangered great ape (Loken et al., 2013; Ancrenaz et al., 2014) but the extent and context of orangutan terrestriality remain poorly understood (Ancrenaz et al., 2008).

Camera trapping has revolutionized the study of wildlife (Hance, 2012) and provided a method for studying cryptic behaviour such as terrestriality in orangutans. Loken et al. (2013) reported that orangutans in Wehea Forest, East Kalimantan, Indonesia, were almost as terrestrial as the pig-tailed macaque *Macaca nemestrina* (Caldecott, 1986) and that there was no clear relationship between canopy connectivity and terrestriality. Ancrenaz et al. (2014) conducted a large-scale analysis of camera trap data from across Borneo and Sumatra and concluded that human disturbance does not appear to be the main driver of terrestriality. These studies indicate that orangutan terrestriality may be more common than previously thought, and that orangutans may be capable of using landscapes that necessitate terrestriality.

We report a 2.5-year camera-trapping study of terrestriality in the north-east Bornean orangutan *P. pygmaeus morio* in three forest types (secondary, recently logged and primary) in and near Wehea Forest (38,000 ha), which comprises mostly undisturbed forest bordered by active logging concessions (Fig. 3.1). A number of studies have investigated the impact of logging on orangutans (see Hardus et al., 2012). Most of these studies have focused on how populations react to logging (e.g. density) but there remains a gap in our understanding of how individuals and various (sub)species (e.g. *P.p. morio*, *P.p. wurmbii*, *P.p. pygmaeus*) react to logging.

Methods

In 2012 we established 41 camera trap stations, covering c. 80 km^2, along old logging roads in the area of secondary forest (Fig. 4.1), which was last logged in 1996. Results from this study were initially reported in Loken et al. (2013) and the methods of analysis used in the original study have been modified slightly for this study to standardize comparisons across the three forest types (secondary, recently logged and primary). Data collected at two mineral licks (sepans) and which were reported in Loken et al. (2013) were not included in the analysis for this study.

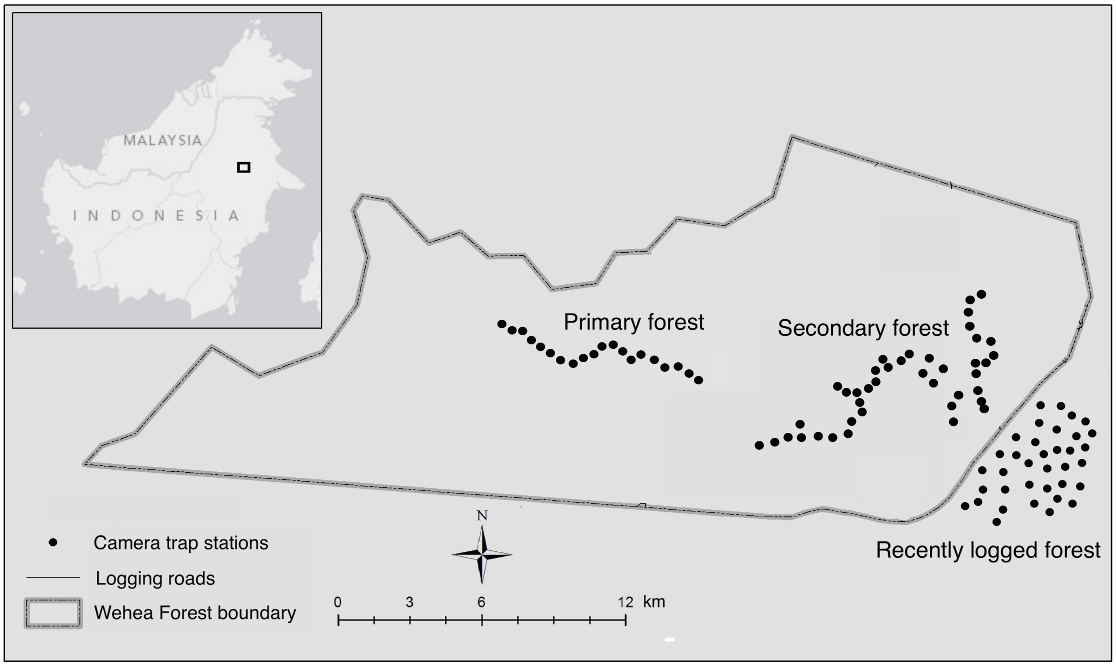

Figure 4.1 **Locations of camera trap stations in areas of secondary, recently logged and primary forest in and near Wehea Forest, East Kalimantan, Indonesia. The rectangle on the inset shows the location of the main map on the island of Borneo.**

In October 2012 we set camera traps in an active logging concession adjacent to Wehea Forest. Twenty-two 100-ha compartments were logged, but not intensively, during April 2012–April 2014. Previously this logging block had contained primary forest and had no logging roads except for an access road used to enter Wehea Forest. We set 36 camera trap stations along newly constructed secondary logging roads in 13 compartments, immediately following the cessation of logging activities there. All stations remained in place until April 2014. In July 2013 we set 20 camera trap stations in primary forest in the heart of Wehea Forest (Fig. 4.1). All stations were set along ridgelines that were part of a middle transect developed in Wehea Forest for research purposes. These stations remained in place until June 2014. In each area we used Bushnell Trophy Cam camera traps (Bushnell, Cody, USA), which were fixed to trees, c. 50 cm from the ground, and fitted with a plastic cover above and a bed of leaves below to protect against rain and mud. Each camera was set to take three pictures per trigger, with a reset time of 1 s.

We used two parameters as estimates of orangutan terrestriality across study sites. The first parameter, relative abundance index, was used to compare orangutan-trapping success (Ancrenaz et al., 2012) and is a good indicator of the amount of effort (total captures per trap night) required to obtain photographs of orangutans. The second parameter was ground-use score, which was calculated as the ratio of independent photographs of orangutans to the total number of independent photographs of all species at each study site, multiplied by the percentage of stations that recorded orangutans. Together, these parameters are a good indicator of the level of orangutan terrestriality at each of our study sites (Table 4.1).

Results

Our study comprised 7,661 traps nights in secondary forest, 15,775 trap nights in recently logged forest and 5,049 trap nights in primary forest. Photographs from each area were sorted by species, and the time and date of each independent capture (photographs taken > 1 hour apart) were recorded. Amongst c. 300,000 photographs we recorded 63 of orangutans in secondary forest, 189 in recently logged forest and 44 in primary forest.

Orangutans were more terrestrial in the recently logged forest (relative abundance index 1.20, ground-use score 1.87), which is consistent with Ancrenaz et al. (2014) and indicates that anthropogenic canopy disturbances may increase orangutan terrestriality (Rijksen & Meijaard, 1999). However, our results also indicate a high level of terrestriality in both primary (relative abundance index 0.87, ground-use score 0.87) and secondary forest areas (relative abundance index 0.82, ground-use score 0.79), indicating that anthropogenic canopy disturbances are not the only driver of terrestriality. Loken et al. (2013) demonstrated that orangutans were also terrestrial in areas with high canopy connectivity. This is consistent with our findings: orangutans also demonstrated terrestrial behaviour in the primary forest, which had a closed canopy and ample opportunity for moving through trees.

Table 4.1 Capture history and level of terrestriality of orangutans *Pongo pygmaeus morio* in and near Wehea Forest, East Kalimantan, Indonesia (Fig. 3.1), with forest type, number of trap nights, total number of captures, percentage of camera trap stations with captures, relative abundance index and ground-use score.

Forest type	Trap nights	Total captures	% of stations with captures	Relative abundance index	Ground-use score
Secondary forest*	7661	63	58.54	0.82	0.79
Recently logged forest	15,775	189	91.67	1.20	1.87
Primary forest	5049	44	75.00	0.87	0.87

* Data from secondary forest were originally reported in Loken et al. (2013)

Discussion

Possible explanations for the varying levels of terrestriality are differences in abundance and visibility of orangutans across the study sites. However, we believe these are not the primary causes of differences between our estimates. Firstly, encounter rates with orangutans were highest in the secondary forest and lowest in the recently logged forest. If used as a naive estimate of relative abundance (Loken et al., 2013), we would expect encounter rates to be highest in the recently logged forest. Secondly, visibility was the same in each forest type, as cameras were set along similar types of features (e.g. roads, ridge lines, trails).

Previously, terrestrial behaviour in orangutans was considered uncommon and used only as a means of acquiring resources (MacKinnon, 1974). Our results indicate that terrestriality may be a regular strategy, employed almost equally by males and females as a means of locomotion (Table 4.2). In the recently logged forest, where orangutans demonstrated the highest degree of terrestriality, most photographs of orangutans appeared to show the primates walking along the road rather than across it, which would be the case if they were forced to the ground by a break in the canopy. This is consistent with photographs from the other forest types, and indicates that orangutans may be taking advantage of both anthropogenic (e.g. roads) and natural (e.g. ridgelines) features in their environment, thus demonstrating opportunistic and resilient behaviour.

Table 4.2 Number of records of orangutans in each age/sex class, from secondary, recently logged and primary forest in and near Wehea Forest (Fig. 3.1).

Age/sex class	Secondary forest	Recently logged forest	Primary forest
Flanged male	23	44	16
Unflanged male	8	31	2
Female without juvenile	10	16	5
Female with juvenile	16	61	13
Juvenile of indeterminate sex	3	16	0
Adult of indeterminate sex	3	21	8

Orangutans may be using newly created roads opportunistically but the level of disturbance they can tolerate is still unknown. Orangutan populations can be maintained in sustainably logged forests (Knop et al., 2004; Husson et al., 2009; Ancrenaz et al., 2010) and these forests should be incorporated into orangutan conservation strategies (Meijaard et al., 2010; Wich et al., 2012; Wilson et al., 2014). We must be careful, however, not to reinforce the notion that orangutans can survive in any human-altered landscape. Orangutans still need trees, and lots of them, and protection of Borneo's remaining forests should continue to be of highest priority for both Indonesia and the global community.

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Chapter 5.

Comparing spatial capture-recapture modeling and nest count methods to estimate orangutan densities in the Wehea Forest, East Kalimantan, Indonesia

This chapter was previously published in the article "Comparing spatial-capture-recapture modeling and nest count methods to estimate orangutan densities in the Wehea Forest, East Kalimantan, Indonesia", co-authored by Spehar, S., Loken, B., Rayadin, Y., Royle, J.A. in Biological Conservation and reprinted with permission from © 2015 Elsevier. I contributed as an author of significant portions of the text, tables and figures and I exclusively conducted the fieldwork for the spatial-capture-recapture modeling.

Abstract

Accurate information on the density and abundance of animal populations is essential for understanding species' ecology and for conservation planning, but is difficult to obtain. The endangered orangutan (*Pongo* spp.) is an example; due to its elusive behavior and low densities, researchers have relied on methods that convert nest counts to orangutan densities and require substantial effort for reliable results. Camera trapping and spatial capture-recapture (SCR) models could provide an alternative but have not been used for primates. We compared density estimates calculated using the two methods for orangutans in the Wehea Forest, East Kalimantan, Indonesia. Camera trapping/SCR modeling produced a density estimate of 0.16±0.09-0.29 indiv/km^2, and nest counts produced a density estimate of 1.05±0.18-6.01 indiv/km^2. The large confidence interval of the nest count estimate is probably due to high variance in nest encounter rates, indicating the need for larger sample size and the substantial effort required to produce reliable results using this method. The SCR estimate produced a very low density estimate and had a narrower but still fairly wide confidence interval. This was likely due to unmodeled heterogeneity and small sample

size, specifically a low number of individual captures and recaptures. We propose methodological fixes that could address these issues and improve precision. A comparison of the overall costs and benefits of the two methods suggests that camera trapping/SCR modeling can potentially be a useful tool for assessing the densities of orangutans and other elusive primates, and warrant further investigation to determine broad applicability and methodological adjustments needed.

Introduction

Accurate information on the density and abundance of animal populations is essential to answering central questions in ecology and conservation biology. Such information allows us to test hypotheses about the relationship between environmental variables and abundance, expanding our understanding of the ecological factors that limit populations. It is also crucial for effective conservation planning, as such information can be used to assess threats to populations and species, set conservation priorities, and monitor populations (Seber, 1982; Williams et al., 2002; Borchers et al., 2003). However, obtaining accurate density and abundance estimates is challenging, especially for animals that are elusive, range widely, and live at low densities (Garshelis, 1992; Karanth, 1995; Thompson, 2004).

This is clearly illustrated in the case of the orangutan. Orangutans, the only Asian great ape, exhibit considerable geographic variation in ecology, behavior, and morphology (Wich et al., 2009). Their population densities also vary widely across their range, with Sumatran orangutans (*Pongo abelii*) generally exhibiting higher densities than Bornean orangutans (represented by the Northwest subspecies, *Pongo pygmaeus pygmaeus*; Central subspecies, *P.p.wurmbii*; and Northeast subspecies, *P.p.morio*) (Husson et al., 2009; Marshall et al., 2009a). Accurate information on orangutan densities across their geographic range, especially for the little-known Northeast Bornean orangutan (*P.p.morio*), is necessary if we are to fully understand the ecological factors that limit orangutan populations (Marshall et al., 2009a; 2009b; Wich et al., 2011a). Information on orangutan abundance and density is also crucial for orangutan conservation. Both orangutan species are classified by the IUCN as Endangered; the population of the Bornean orangutan has declined over 50% in the last 60 years and the

Sumatran orangutan population has declined an estimated 80% over the last 75 years (Ancrenaz et al., 2008; Singleton et al., 2008). The causes of this decline are extensive habitat loss and fragmentation due to logging, mining, the expansion of oil palm and acacia plantations, and fire (Marshall et al., 2006; Wich et al., 2011b; Meijaard et al., 2012), and forest conversion continues at a rapid rate on both Borneo and Sumatra (Sodhi et al., 2004; Margono et al., 2014). Hunting, and, increasingly, human-orangutan conflict are also major contributors to this decline (Meijaard et al., 2011; Davis et al., 2013). Conservation action is urgently needed to prevent further population declines, and knowledge of densities and abundance are important for implementing effective conservation policy.

However, it is notoriously difficult to obtain accurate abundance or density estimates for orangutans. They are cryptic, solitary, and generally live at low densities, making direct counts impractical for most studies. Because of these difficulties, researchers generally rely on counts of indirect sign to census their populations (Kühl et al., 2008). To-date the most popular survey method for orangutans are nest count methods, in which the sleeping platforms (nests) that orangutans build each night are used to calculate a density of individuals in an area. In the most popular version of these methods, all nests visible from a line transect or in a plot are counted; nest counts are then converted into nest densities by dividing the number of nests counted by the area surveyed, which is either known (plot surveys; van Schaik et al., 2005) or estimated using a detection function (line transects surveyed using distance sampling methods; Buckland et al., 2001; Thomas et al., 2010). Nest densities are then converted into orangutan density estimates using the following formula:

$$D_{ind} = D_{nest} / p * r * t$$

In which D_{ind} = density of individuals, D_{nest} = density of nests, p = proportion of nest builders in the population, r = number of nests built per individual per day, and t = nest decay time (Hashimoto, 1995; van Schaik et al., 1995).

Nest count methods have been used extensively to assess or monitor orangutan populations (Husson et al., 2009). However, these methods have limitations (Mathewson et al., 2008; Marshall & Meijaard, 2009; Spehar et al., 2010). First, these methods rely on the assumption of perfect detection (in the case of line transects, that all nests above the line are counted; in the case of plot surveys, that all nests in the plot are counted) although studies demonstrate that even teams of experienced observers miss nests (van Schaik et al., 1995; 2005; Johnson et al., 2005). Another major issue lies in the parameters used to convert nest density into orangutan density (*p*, *r*, and *t*). The proportion of nest builders in the population (*p*) and the rate at which nests are produced (*r*) must be based on observed values from known populations, and nest decay rate (*t*) must also be based on observations of nest longevity in an area, although mathematical modeling (Markov chain analysis) can be used to calculate nest decay from shorter-term observations (Buij et al., 2003; Johnson et al., 2005; Mathewson et al., 2008). Obtaining accurate information for these parameters requires substantial time and effort, so values calculated from a few long-term study sites are often applied in studies across the orangutan range. This can be a concern as some parameters (in particular nest decay, *t*) exhibit very high variability between sites (Mathewson et al., 2008). As any changes in parameters produce directly proportional changes in the resulting orangutan density estimate, this means that density estimates that do not use precise or locally calculated parameters could be unreliable (Mathewson et al., 2008). Such issues clearly have major implications for our understanding of orangutan ecology and for conservation planning, and finding an alternative to nest surveys should be a high priority. However most studies still calculate densities based on nest surveys, and many of these continue to employ non-local parameters due to limited time and money (Spehar et al., 2010; Meijaard et al., 2012).

A possible alternative for estimating abundance and density are camera trap methods. Camera trapping is becoming a preferred method for studying rare and elusive species (e.g., O'Connell et al., 2010). Recent advances in statistical techniques, namely spatial capture-recapture modeling or SCR (Borchers & Efford, 2008; Royle & Young, 2008; Efford, 2011; Royle et al., 2013; 2015), allow the calculation of population density from 'captures' of individual animals obtained using camera traps. SCR models have an advantage over conventional capture-recapture (CR) models in that they allow for flexible trap arrangement (e.g., grid vs. linear arrangements that do not require even spacing across the study area; Efford & Fewster, 2013; Tobler & Powell, 2013) and can incorporate both individual-level covariates (e.g., sex or age class) as well as station level covariates (e.g., road vs. trail or habitat; Sollmann et al., 2011). This type of flexibility is especially important in Borneo and Sumatra, where field conditions like difficult terrain can make research design a challenge.

SCR modeling relates the encounter history of individuals (when and where they are captured) to activity centers of individuals during the trapping period (calculated as the spatial relationship between individuals and camera traps). Density is estimated as number of individuals occurring within some delineated area (the "state-space"), usually defined by the camera trapping array plus a buffer area (Royle & Gardner, 2011). SCR modeling has now been used to estimate densities for many mammals that are elusive, occur at low densities, and occupy large home ranges (Royle et al., 2009a; 2009b; 2011; Gardner et al., 2010a; 2010b). These methods count the animals themselves and thus do not present problems related to converting indirect sign into animal densities. In addition, if deployed properly camera traps can also provide additional information about habitat use, behavior, and even demography (e.g., Galvis et al., 2014).

Despite its promise and wide application in wildlife studies, camera trapping has only recently been embraced by primatologists (Head et al., 2012; Olson et al., 2012; Tan et al., 2013; Loken et al., 2013; 2015; Galvis et al., 2014; Gregory et al., 2014). Most notably, a recent study simultaneously used nest surveys and camera trapping to estimate the relative abundance and distribution of chimpanzees (*Pan troglodytes troglodytes)* and gorillas (*Gorilla gorilla gorilla*) across different habitat types in West Africa, and found that the two methods produced roughly comparable results (Nakashima et al., 2013). However, this study was only able to use mean camera trap capture rate to calculate a relative abundance index for each species. The "next step" that would allow the calculation of absolute abundance and density is the use of new statistical techniques like SCR modeling, which have not yet been applied to primate populations. For camera traps to be used to estimate abundance and population density using SCR modeling or similar techniques, animals must be individually identifiable from photographs and individuals need to be captured and recaptured by camera traps, which are most easily placed on the ground. These criteria may be difficult to meet for some primates, but recent research suggests that this method may be appropriate for use with orangutans. Orangutans do not have unique stripe patterns or markings, but individuals are identifiable based on facial characteristics and other features that can be recognized from photographs. Secondly, recent studies indicate that Bornean orangutans may move on the ground more than previously thought, although Sumatran orangutans seem to engage in terrestrial behavior less often, perhaps because of the presence of a potential terrestrial predator, the tiger (Loken et al., 2013; 2015; Ancrenaz et al., 2014). This increases the likelihood of capture by camera traps for at least Bornean orangutans.

Given their extensive use to estimate densities for other elusive animals, we were interested in examining the applicability of camera trapping and SCR modeling to orangutan populations. The purpose of this study was three-fold: 1) to evaluate the feasibility of using of camera traps and SCR modeling to estimate orangutan densities, using a population of Northeast Bornean orangutans (*P.p. morio*) as a case study; 2) to compare results obtained using camera trapping and SCR modeling to those obtained using an established method (nest surveys); and 3) to assess the advantages and disadvantages of both methods to make general recommendations for researchers wishing to estimate population parameters for orangutans and other elusive animals.

Methods

Study site

This study was carried out in the Wehea Forest in East Kutai District, East Kalimantan, Indonesia. Wehea (01°32’46”N, 116°46’43”E) contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests currently classified as logging concessions. Logging ceased in the mid-1990s and Wehea has been protected by an agreement between a local community and the local government since 2004. Wehea Forest contains lowland Dipterocarp, sub-montane and montane forests, with mean annual rainfall of 3000 mm and a mean temperature of 27 C. The site’s topography is characterized by steep ravines, ridges and runoff streams and elevations range from 250-1750m asl. Ten species of nonhuman primate have been reported from the site (Meijaard & Nijman, 2003; Loken et al., 2013). The eastern part of Wehea contains a network of old logging roads that have not been used since logging ceased and are now heavily overgrown and more like trails. These roads were utilized for camera trapping and nest surveys.

Camera trapping: data collection and analysis

In March 2012, 68 non-baited cameras were set in pairs at ~500 m intervals along old logging roads and trails and one camera trap was set at a natural salt lick (small sepan). This design was used to maximize capture rates (Tobler & Powell, 2013) and the station array covered an approximate area of 80 km^2 (Fig. 5.1). The cameras used were Bushnell Trophy Cams (n = 61) and Reconyx HC500 (n = 8) cameras. In May, an additional Bushnell Trophy Cam was added at a second natural salt lick (large sepan), bringing the total number to 70 cameras set and resulting in a sampling effort of 7320 trap days. All cameras remained at the same locations until this study concluded in October 2012. We chose a 6-month study length in order to obtain the greatest number of orangutan photos while still assuming population closure. Each camera was placed ~50 cm from the ground and set to take three pictures per trigger, with a reset time of one second. Cameras were checked a total of three times, in the middle of May, the beginning of July and again in October at the conclusion of the camera trapping study. At each visit, non-functioning cameras were replaced with new cameras, batteries were changed and the SD card storing the photos was removed from the camera and replaced by a new card.

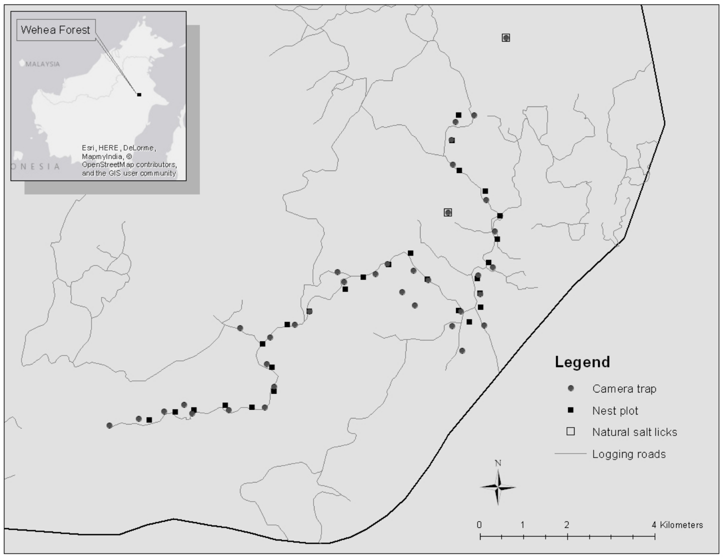

Figure 5.1 **Map of study area, indicating placement of camera traps and nest plots.**

A total of 658 photographs of orangutans were collected during this study, many of which were repeat photos of the same individual or group of individuals due to the fact that cameras were set to take 3 photos per trigger, with a reset time of 1 second. All photographs were visually examined to determine 1) the number of individuals represented, and 2) the number of times each individual was recorded at different camera trap stations, using the following process: Photos were first divided by camera trap station and then into age-sex class categories (flanged adult male, unflanged adult male, adult female, adult of indeterminate sex, juvenile) based on external genitalia if visible, secondary sexual characteristics (cheek flanges, throat pouch, cape of hair on back, elongated nipples), and body size and shape. Photographs were then examined for cues to individual identity, noting characteristics for each of the following categories: body size; hair color and quality (e.g., thick, thin, any bald patches); facial features (prominence of brow ridges; prognathism; angle and size of nostrils and mouth; overall shape of face; etc.), shape of hair on head, and any other identifying features (e.g., elongated nipples, marks or scars, distinctive body posture). If the individual's face and/or some other clear identifying mark (e.g., a distinctive injury) was not visible in a photograph, we did not attempt to identify that individual. After this initial assessment was performed, photographs were placed side-by-side for comparison to determine if the same individual had been captured at multiple stations and to ensure that no individual was counted more than once. This process was completed in its entirety from the beginning two separate times to maximize confidence in the assessment. After this process was completed, only series of photos taken with >1 hr. interval between photos of different individuals at each station were categorized as separate records (n=112 series of photos that constituted separate records). Of these records, n=67 contained images of sufficient quality or appropriate composition to allow for the successful identification of individuals in subsequent photographs (Fig. 5.2).

These n=67 individually identifiable records were then converted into individual encounter histories appropriate for SCR modeling by first discarding any records of the same individual taken at the same trap on the same day, leaving us with 64 individually identifiable captures. Using the date and location of captures of each individual we produced a record of when and where each individual was captured ("individual encounter histories") $y_{i,j,k}$ for individual i=1, 2, . . ., n; traps j=1, 2, . . ., J; and sample periods k=1, 2, . . ., K.

Figure 5.2 **Examples of series of high-quality photographs (records) used for individual identification.**

Spatial capture-recapture model

Spatial capture-recapture (SCR) models describe the spatial pattern of individual encounters using a parametric model for detection probability in which the probability (Pr) of encounter at a location *x* is a function of distance between *x* and an individual's home range center *s*. In SCR models, the home range centers are regarded as unknown random effects (Borchers & Efford, 2008; Royle & Young, 2008). In our analysis we used the half-normal model:

$$\text{Pr (encounter at location } x\text{)} = p_0 \exp\left(-dist(x,s)^2/2\sigma^2\right)$$

where p_0 is the baseline encounter probability (the probability of an individual being encountered at its home range center) and σ is a scale parameter of the encounter probability model which determines the relative change in encounter probability as distance from the sample location to home range center increases. Since male and female orangutans are known to have different ranging patterns (Singleton et al., 2009), we employed models that allowed for population substructuring, specifically sex structuring, to take into account the possibility of differences in space use and encounter rate for males and females (Royle et al., 2015). We considered sex specificity of the parameters σ and p_0, fitting a set of four models which included: null (no sex effects), p(sex) (sex-specific effects on p_0, which represents the baseline encounter probability), σ(sex) (sex-specific effects on σ, which represents the extent of space use by individuals), and both (sex-specific effects on p_0 and σ). Because our assessment of captures suggested that sepans may have a significant effect on baseline encounter probability (p_0), especially for males, we also assessed the sex-specific effects of the sepans on p_0, resulting in two models that had an additive effect on p_0: sep (sepan effect with no sex-specific effects) and sep(sex) (sex-specific sepan effects). As a result a total of 12 models were fitted. For all models, the parameter N represents the number of individuals in the state-space S, parameter D represents the density of individuals in the state-space S, the parameter ψsex represents the probability that an individual in the population is male, and sepfemale and sepmale represent the additive influence of sepan captures on baseline encounter probability (p_0) for males and females.

We estimated SCR model parameters using Maximum Likelihood Estimation (MLE). To obtain the MLEs of the SCR model parameters it is necessary to prescribe a 2-dimensional region within which individual home range centers may exist. This region is called the state-space (*S*), and the population size parameter N corresponds to the number of individuals having home range centers within this region. While the population size is sensitive to the size and configuration of the state-space, the density of individuals, D, defined as N divided by the area of the state-space *S*, is invariant to the size of the state-space under standard SCR models (Royle et al., 2014; p. 132). For our analysis we defined the state-space by buffering the minimum area rectangle containing the sample locations by 7.5 km. The total area of this state-space is 568.8 km^2. This buffer around the sample locations is at least 4 times the estimated value of σ.

We carried out all modeling using the program R as described in Royle et al. (2015). All code and scripts used are available as supplemental material to that paper at *Ecological Archives*, http://dx.doi.org/10.1890/ES14-00148.1.sm.

Nest surveys: data collection and analysis

Nest surveys were carried out in June-August 2013. We used the plot method, developed by van Schaik et al. (2005), to survey for orangutan nests. The plot method is more effective than line transects in extremely difficult terrain like that at Wehea. We established 50 x 50 m plots at ~500 m intervals (following van Schaik et al., 2005) along the same routes on which camera traps were placed in order to survey the same area (Fig. 5.1). Plots were placed at least 100 m from roads to ensure that edge effects did not influence nest counts. Each nest plot was surveyed by a team of 4-5 trained observers. Observers “swept” the plot by spacing themselves out at ~10 m intervals along one of the plot boundaries and then walking slowly, searching the trees for orangutan nests. This was done once in each direction for all plots to ensure no nests were missed. When orangutan nests were spotted on the first sweep, the location of the nest was marked so the same nest would not be counted again on the return sweep.

Individual densities were then calculated using the following formula (van Schaik et al., 2005):

$$D_{\mathrm{ind}} = N_{count} / s * p * r * t$$

Where N_{count} = the total number of nests counted, s = the total survey area, p = proportion of nest builders in the population, r = number of nests built per individual per day, and t = nest decay time. No significant variation in the proportion of nest builders has been found between Bornean populations (Ancrenaz et al., 2004a; Johnson et al., 2005; van Schaik et al., 2005; Husson et al., 2009), so we used the commonly cited p value of 0.89. The rate at which nests are produced does seem to differ between populations, with Bornean nest building rates ranging from 1.00 in Kinabatangan in Sabah (Ancrenaz et al., 2004a) to 1.15-1.17 at other Bornean sites (Johnson et al., 2005; van Schaik et al., 2005; Husson et al., 2009). As the orangutans at Kinabatangan live in highly disturbed forest, which may influence their nest building and reuse rates, we chose to use an average Borneo-specific r value of 1.16. As nest decay varies substantially between sites, even within Borneo (Mathewson et al., 2008; Husson et al., 2009), we used a t value from a neighboring site (<40 km), Lesan, of 604 days (Mathewson et al., 2008). This site was close enough to Wehea, and the forest structure and climatic conditions so similar, that we believe this can be considered a local decay time. We employed the Delta Method (following Buckland et al., 2001; Mathewson et al., 2008; Ancrenaz et al., 2004b), which incorporates error from all parameters and values used to obtain a density estimate, to obtain a confidence interval for our final orangutan density estimate.

Results

Camera trapping and SCR analysis

From March 21 to October 18, 2012, we obtained a total of 112 distinct camera trap records of orangutans. Photos were high-quality enough to allow us to clearly identify individuals in 67 of these 112 records (60%) (Fig. 5.2); the remaining records in which photos were not of sufficient quality or composition to facilitate identification of an individual (n=45) were discarded. Adult males accounted for n=23 or 51% of discarded records; adult females for n=9 or 20% of discarded records; and individuals of unknown age/sex for n=13 or 29% of discarded records. Of these 67 individually identifiable records, 3 cases consisted of an individual captured at the same trap in the same day, so these were discarded, leaving us with 64 individual captures that could be used to create individual encounter histories for the SCR analysis. These 64 captures consisted of 16 unique orangutan individuals: 8 adult males, 6 adult females and 2 individuals of unknown sex. Adult males (flanged and unflanged) represented 56% of all captures, compared to 38% for females (Table 5.1) and also had the highest number of individual captures during the study (Table 5.2). Further investigation revealed that the reason for this difference was largely due to captures obtained from the two sepans (natural salt licks), which were entirely of males (n=19 captures, or 30% of male captures). We modeled this heterogeneity in capture probability by including parameters that accounted for sex-specific effects of the sepans on baseline encounter probability, as described in the Methods.

Table 5.1 Individually identifiable records across age-sex classes for orangutans in the Wehea Forest from Mar-Oct 2012.

	# indiv	# records	% total records
Flanged adult males	5	22	34%
Unflanged adult males	3	14	22%
Adult females	6	24	38%
Unknown	2	4	6%

Table 5.2 Individual frequencies of capture for orangutans in the Wehea forest from Mar-Oct 2012. Rows represent unique trap frequencies and columns represent total number of captures (e.g., we captured 2 males 1 time, by default in only 1 trap; we captured 1 female 4 times in 3 different traps, etc.)

Adult males (flanged and unflanged)

	# captures					
# traps	1	2	3	7	8	11
1	2	0	0	0	1	1
2	0	1	1	0	0	0
3	0	0	1	0	0	0
4	0	0	0	1	0	0

Adult females

	# captures		
# traps	3	4	8
1	2	0	0
2	1	0	0
3	1	1	0
4	0	0	1

Unknown

	# captures	
# traps	1	3
1	1	0
2	0	1

The 12 models fitted consisted of different combinations of the four basic models: *p(sex)* (sex-specific effects on p_0, or encounter probability), *σ(sex)* (sex-specific effects on σ, or the extent of space use by individuals), Both (sex-specific effects on *p* and σ), and Null (no sex-specific effects); plus the two sepan effect models: *sep(sex)* (sex-specific effects of sepans on p_0) and *sep* (non-sex-specific effects of sepans on p_0) (Table 5.3). The top three models all include the sex-specific sepan effect indicating that sepans had an important sex-specific effect on encounter probability. Indeed, the results indicate that near sepans, encounter probability for males (sep_{male}) was nearly 1 but for females ($\text{sep}_{\text{female}}$) was near 0 (the effects are modeled on the logit p_0 scale and so large negative values indicate p_0 near 0 whereas large positive values indicate p_0 near 1). However, the sepan effect did not appear to influence overall population (N) and density (D) estimates (for example, compare results of models Both and Both+*sep(sex)*). The favored model was Both+*sep(sex)*, indicating that there is a difference in baseline (p_0) and sepan encounter probability for males and females, and that males have larger home ranges than females (σ), consistent with what was observed in our data and what is known about orangutan ranging patterns (Singleton et al., 2009). Under this model the probability that an individual in the population is male (ψ_{sex}) is 0.315 (CI: 0.128-0.590), and orangutan density is estimated at 0.16 indiv/km^2 (95% CI: 0.0912-0.2909 indiv/km^2) within the state-space (568.8 km^2).

Nest surveys

A total of 27 plots were surveyed during this study. We counted 44 nests total in all plots, with a mean of 1.63±0.32 nests per plot and a nest encounter rate of 6.52±1.28 nests/ha. The calculated density of individuals from this survey, using the parameters outlined in Table 5.4, is 1.05 indiv/km^2 (95% CI 0.18-6.01 indiv/km^2).

Table 5.3 **Results of fitting sex-specific and null models to orangutan data set. # parm refers to the number of parameters used for each model. All values are real values except for the sep_{female} and sep_{male} parameters, where effects are modeled on the logit(p_0) scale and large negative values indicate p_0 near 0 and large positive values indicate p_0 near 1. Please see text for further explanation of model parameters.**

Model	# parm	p_{female}	p_{male}	σ_{female}	σ_{male}	N	D	ψ_{sex}	sep_{female}	sep_{male}	AIC
Both+*sep(sex)*	7	0.0055	0.0027	0.9259	1.6636	89.186	0.1568	0.3150	-12.041	18.853	375.876
σ(sex)+sep(sex)	6	0.0037	0.0037	1.0523	1.6586	87.450	0.1537	0.3053	-12.128	18.842	375.917
p(sex)+sep(sex)	6	0.0034	0.0028	1.4903	1.4903	72.149	0.1268	0.4287	-11.23	18.749	379.527
Both+*sep*	6	0.0076	0.0027	0.7741	1.660	78.803	0.1385	0.3631	18.324	18.324	386.486
σ(sex)+sep	5	0.0050	0.0050	0.8253	1.6736	76.099	0.1338	0.3466	18.131	18.131	389.478
p(sex)+sep	5	0.0070	0.0029	1.3539	1.3539	62.479	0.1098	0.6061	18.423	18.423	400.945
Null+*sep*	4	0.0044	0.0044	1.3165	1.3165	64.521	0.1134	0.5715	18.455	18.455	401.714
Null+*sep(sex)*	5	0.0041	0.0041	1.3485	1.3485	65.501	0.1152	0.5941	18.455	5.078	403.095
σ(sex)	4	0.0057	0.0057	0.9130	1.7914	90.889	0.1598	0.3766	N/A	N/A	446.146
Both	5	0.0055	0.0060	0.9222	1.7878	90.739	0.1595	0.3745	N/A	N/A	448.127
p(sex)	4	0.0035	0.0070	1.4638	1.4638	79.498	0.1398	0.5038	N/A	N/A	452.357
Null	3	0.0053	0.0053	1.4814	1.4814	76.643	0.1347	0.5715	N/A	N/A	452.533

Table 5.4 Parameters used to calculate orangutan densities from nest counts.

Parameters	Values
N_{count} (nest number) for all 27 plots	44 (mean 1.63±0.32)
s (survey area, in km^2)	0.0675
p (proportion of nest builders in population)*	0.89
r (number of nests built per day)*	1.16
t (nest decay time, in days)†	604

*Borneo-specific values (Buij et al., 2002; Johnson et al., 2005)
† Decay time from nearby site (Lesan) (Mathewson et al., 2008)

Discussion

This study is the first to use camera traps and SCR modeling to estimate the densities of orangutans, or indeed, any primate. Below, we compare camera trapping and SCR modeling to nest counts and discuss the implications for decision making when choosing a method to assess the populations of orangutans or other elusive primates.

Comparing results obtained using the two methods

The two methods produced density estimates that differ considerably (Table 5.5). A possible explanation for this difference that must be considered up-front is that there was an actual change in orangutan density in the Wehea Forest between October 2012 (when camera trapping ended) and June 2013 (when nest surveys commenced). Orangutans may engage in large-scale movements between areas in response to changes in resource availability (MacKinnon, 1974; Singleton & van Schaik, 2001; Buij et al., 2002), which presents a challenge for any survey method that is deployed over a relatively short time frame. However, we believe this is not the primary cause of differences between our estimates because we used all visible nests (the standing crop method), rather than only newly built nests (the marked nest count method), to calculate density estimates using the nest count method. The standing crop method incorporates nests built in the past and thus provides an estimate of the average orangutan population in an area over a wider timeframe (Spehar et al., 2010). Given the longevity of nests in this part of East Kalimantan (Mathewson et al., 2008), our nest surveys almost certainly incorporated nests built during the camera trapping period and provide an average density for orangutans in the area during the timeframe covered by this study.

Table 5.5 Comparisons of orangutan density estimates and extrapolated population size of orangutans in the 38,000 ha^2 Wehea Forest, assuming sampled area is similar to extrapolated area, using camera trapping/SCR modeling and nest surveys. Density and population size are presented not to suggest that these numbers represent true population abundance in the Wehea Forest, but as a means of contrasting the results provided by the two methods.

	indiv/km^2	95% CI	# indiv	95% CI
Camera traps/SCR	0.16	0.09-0.29	60.80	34.66-110.542
Nest count	1.05	0.18-6.01	397.24	69.20-2283.04

Assuming that a substantial change in actual densities did not occur between survey periods allows us to focus on the possible methodological reasons for the difference in density estimates. The 95% confidence interval for the nest count method is very wide, indicating the imprecision and therefore high uncertainty of the density estimate calculated using this method. This wide confidence interval is likely due to high variance in nest encounter rates between plots (mean: 6.52 nest/ha, 95% CI 3.95-9.09; range: 0-7 nests per 0.25 ha plot). This highlights the need for sufficient sample sizes (in the form of a sufficient number of plots or transects to address the issue of high variation in nest encounter rate; van Schaik et al. 2005) when calculating density estimates from nest surveys. This can take a long period of time and a great deal of effort to achieve in areas with low orangutan densities like the Wehea Forest. Thus, rather than being a relatively quick and easy method, nest surveys can require a substantial investment of time and effort if they are to produce reasonably reliable density results, even when locally derived parameters are available (Plumptre, 2000; Mathewson et al., 2008; Marshall & Meijaard, 2009; Spehar et al., 2010).

The density estimate provided by camera trapping/SCR modeling (0.16 indiv/km^2) is much lower than most densities reported for other relatively undisturbed sites in Borneo (Husson et al., 2009). Although a comparison of the precision of two estimates calculated using different methods and parameters should be done with caution, both estimates reference orangutan density and it is worth noting that the narrower 95% confidence interval for the camera trapping/SCR density estimate indicates that this estimate is somewhat more precise than the nest survey density estimate. However, the CI of the camera trapping estimate is still fairly wide. We can identify three issues that may have influenced these results. First, this method may have underestimated density due to unmodeled heterogeneity in the camera trap data. We did model sex-specificity of model parameters and trap effects (specifically, sepan effects), both of which seemed to be important sources of variation in encounter probability. However, other sources of detection heterogeneity, including age class, behavior (e.g., some individuals may stay in the trees) and social structure, are potentially present which, because of limited data (n=16 individuals) and limited precision of estimates we did not feel warranted further model development.

Second, small sample size (low number of captures and recaptures of individuals) likely influenced the precision of our results. SCR models require that sufficient individuals are captured and that at least some individuals have spatial recaptures (captures at multiple camera trap locations). For some species, this could be accomplished by having an extensive and dense trapping array (Tobler & Powell, 2013; Sollmann et al., 2014). However, we believe that for a wide ranging and mainly arboreal species such as orangutans this design is infeasible, given the logistics and the high costs associated with such an array. We chose instead to pursue a design that covered a larger area and located traps along likely paths of movement. We believe a more important factor contributing to our low sample size was our positioning of camera traps for this study. Given that camera trapping combined with SCR modeling had never been previously attempted for orangutans or any primate, we employed camera trap placement that has been used extensively for capturing the flanks of felids for identification (two camera traps per station set perpendicular to and on opposite sides of the road or trail). The fact that only 67 of 112 orangutan records resulted in individually identifiable photos indicates that this is probably not the most appropriate placement for primates, for whom facial features are much more important for individual identification. Based on our experience studying and identifying wild orangutans, we believe that the low number of individually identifiable photos of orangutans was due to these issues with trap placement, and not because some orangutans are simply not identifiable (meaning that with good photos, all orangutans are in theory identifiable). If a trap arrangement better suited for orangutans had been used, more individuals would have been identified and our sample size (and thus the precision of our estimate) increased. One simple adjustment to increase sample size, while allowing for camera trapping array design similar to the one used in this study, is setting 3-4 camera traps per station and/or adjusting their placement so that more angles are covered to maximize the likelihood that the facial features of each orangutan are captured.

There are also other possible changes to study design that could increase sample size. Setting cameras in the trees is one possibility. Recent studies demonstrate that it is possible to obtain captures of primates with arboreal camera traps (Gregory et al., 2014) and cameras placed in carefully selected arboreal locations could supplement records on the ground. This might be especially useful in areas where there is a sex difference in use of the ground, as may be the case at certain locations in Wehea (e.g., sepans) and has been found at other orangutan study sites (e.g., Manduell et al., 2011). This technique, however, presents many hurdles (e.g., determining placement of cameras, the requirement of specialized expertise and equipment) and may also not be cost-effective in many areas. Sample size could also be increased by setting clusters of camera traps throughout the study area in places where orangutans are more likely to be terrestrial (e.g. canopy gaps, ridges, trails and roads). The flexibility in SCR modeling allows for this type of clustered survey design, which would result in more area covered and fewer cameras used (Efford & Fewster, 2013). Baiting camera traps could increase the likelihood of captures across age-sex classes (Royle et al., 2011b; Olson et al., 2012). Lastly, sample sizes could be increased by combining SCR data to estimate shared model parameters from multiple independent camera trapping studies (see Sollmann et al., 2014). Depending on resources, studies could be conducted simultaneously or in successive years and focused in various geographic areas (e.g., within the range of *P.p. morio*). This type of combined information study would yield a large enough data set for more precise and possibly accurate density estimates and also important information how orangutan densities vary across their geographic ranges.

Third, the spacing of camera traps in this study was too close relative to the typical amount of space used by orangutans in this study. Trap spacing of roughly $2 \times \sigma$ has been shown to be nearly optimal from a statistical standpoint based on simulation work (Royle et al., 2014, section 10.3). In the present study the average trap spacing was about $0.5 \times \sigma$ or less. A wider spacing would have potentially allowed the capture of more individuals, increasing sample size and potentially improving our estimates. However, the likely success of this and other camera placement strategies should be evaluated using simulations before such designs are employed in the field.

Implications for orangutan survey methods

Our results suggest that with methodological adjustments, camera trapping and SCR modeling could be successfully used to estimate the densities of orangutans and, potentially, other elusive primates. Without applying these methods to a population of known density, it is impossible to determine which method is more accurate, but our results suggest that in at least some settings, camera trapping/SCR modeling may offer more precise results than traditional nest surveys. However, the balance of costs and benefits must be considered carefully before researchers make the decision to use this, or any other, method. We have summarized comparisons of the costs, in both money and effort (Table 5.6) and overall advantages and disadvantages (Table 5.7) of the two methods below, acknowledging that this is a simplification and that whether the outcome of the comparison is in favor of one method or another will likely be specific to the study.

Camera trapping does have much higher initial costs than traditional methods like nest surveys. For our camera trapping study, we estimate equipment costs were around $15,000, and for a study utilizing more stations and more camera traps per station, the estimated cost rose to almost $38,000 (Table 5.6) even when using a relatively inexpensive camera trap model (Bushnell TrophyCam HD, $180/unit, plus costs of batteries and SD card). Because our site was remote, we did not need to use devices for preventing camera trap theft, but at sites closer to human habitation this is often an issue. Such devices are $20-$50 per camera, and with this factored in the cost of a study like ours would increase by $1440-$3600. This is a substantial investment of resources and not all researchers will have access to this kind of money. However, camera traps can be used for multiple seasons, at many study sites and even shared between researchers, all of which would reduce costs. Camera trapping requires slightly higher effort in the field than nest surveys alone as each trap must be placed and then checked regularly over the course of the study, but when the effort required to calculate a local nest decay time is considered, camera traps actually require about the same or less effort in the field than nest surveys (Table 5.6).

Table 5.6 Cost comparison for camera trapping and nest surveys. Costs are calculated for this study, and for a hypothetical study designed to increase sample size and/or reliability of results.

This study	**Camera trapping***	**Nest survey$^{\beta}$**	**Nest survey + Nest decay$^{\gamma}$**
Equipment ($)	15120	900	2000
Field time (hours)	324	135	335
Person hours (field time x personnel)	648	540	940
Hypothetical study			
Equipment ($)	37800	900	2000
Field time (hours)	450	200	400
Person hours (field time x personnel)	900	800	1200

*This study: 36 stations, 70 total cameras; 6 month study, cameras checked twice; 2 observers needed. Hypothetical study: 45 stations, 4 cameras each; 6 month study, cameras checked twice; 2 observers needed

$^{\beta}$This study: 27 plots, checked once; 4 observers needed. Hypothetical study: 40 plots, checked once; 4 observers needed.

$^{\gamma}$Nest decay for both studies: surveying a set of 40 nests; 1 initial visit and 2 revisits; 2 observers needed

Camera traps offer additional benefits that nest surveys do not (Table 5.7). First and foremost, camera trapping counts the animals themselves and does not require the application of parameters to obtain density estimates, removing a major potential source of error and providing estimates that may be more reliable in many settings. Camera trapping also provides additional data beyond population abundance or density that can allow researchers to develop a more well-rounded understanding of elusive and difficult-to-study populations. This includes information about population structure, demography, activity and ranging patterns, social interactions, and body condition (Head et al., 2012; Nakashima et al., 2013; Galvis et al., 2014; Gregory et al., 2014). For example, once encounter history data is obtained using camera trapping, more general SCR models for open populations or accommodating non-IDed detections can be developed, allowing researchers to obtain a more detailed understanding of population demographics. Camera traps do not just collect data on the target species but on all animals that pass by, potentially allowing the calculation of general abundance indices for other species and information on the general biodiversity found in a study area. Finally, camera trapping studies provide compelling images that can be used for educational or conservation purposes. The value of these images for raising public awareness and support for conservation should not be underestimated (Hance, 2012).

Table 5.7 Comparison of camera trapping (CT) and nest survey (NS) methods as used to calculate animal density, with the overall "winner" in each comparison indicated in the "Outcome" column.

Camera trapping	Nest surveys	Outcome
High equipment cost (Table 5.6), but camera traps can be reused, reducing average cost across surveys	Low equipment cost (Table 5.6)	NS
Relatively high effort (field time and person hours) required to obtain sufficient captures and recaptures and maximize ability to ID individuals from photos (Table 5.6)	Relatively low effort (field time and person hours) required for single surveys, but high effort required to obtain sufficient nest encounter rates and local parameters (Table 5.6)	Draw
Only appropriate where animals use ground regularly	Appropriate regardless of substrate use by animals	NS
Possible detection heterogeneity (e.g., due to age-sex class, behavior) could influence results	Probability of detection same for all subsets of population	NS
Potential for equipment failure, or theft in areas with high human use	Equipment failure and theft are nonissues	NS
Parameters not needed to obtain density estimates	Must calculate local values for some parameters to obtain reliable density estimates, at additional effort and cost	CT
SCR and other modeling approaches allow flexibility in study design	Little flexibility in study design possible (line transects or plots)	CT
Provide additional info about target population: e.g., demography, movement and activity patterns, behavior, body condition	Provide little additional info about target population	CT
Provides additional info about animal community and biodiversity in study area	Provides no additional info about animal community or biodiversity in study area	CT
Images have multiple uses: education, advocating for conservation	Pictures of nests don't get people excited about conservation	CT

We believe that nest surveys still have a place in the survey methodology toolbox. Obtaining accurate and precise density estimates from nest counts require a substantial investment of time and effort, but rapid assessments of an area can be done using nest encounter rates or nest densities, which do not require the application of troublesome parameters. Such measures can be used to compare between sites and to get a general sense if the orangutan density in an area is likely to be low or high. If the site seems potentially important, and if camera trapping seems feasible, researchers can conduct a more detailed assessment and study of the population using camera traps or other methods. Nest surveys are also useful for monitoring populations, in which case changes in nest encounter rate or nest density over time can be used. If resources and time permit, a combination of methods (camera trapping and nest counts) to estimate density or abundance could provide even greater confidence in density estimates and a more well-rounded understanding of populations (Nakashima et al., 2013). Finally, there are situations in which camera trapping is not feasible (e.g., when working with study animals for which obtaining a sufficient number of captures and recaptures is very difficult), and in these settings nest surveys may be the best option.

Conclusions

Overall, we believe that camera trapping and SCR modeling are promising methods that, with some methodological adjustments, could potentially be useful tools for assessing the densities of orangutans as well as other elusive primates. We believe this method warrants further investigation to determine when and where it is most applicable and what methodological adjustments are needed. In general, we encourage researchers to think carefully about survey goals and to consider the wide range of options available to them before making a decision about methodology. Choosing to employ alternative methods may allow conservationists to allocate more of their limited resources toward the ultimate goal of reducing threats to species survival.

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Chapter 6.

Assessing the precision and uncertainty of density estimates for the Sunda clouded leopard *Neofelis diardi* using spatial capture-recapture modeling

Abstract

The Sunda clouded leopard (*Neofelis diardi*) is one of the most challenging felids to study. With the advent of camera trap technology and spatial-capture recapture (SCR) models, researchers have begun to estimate densities for this felid. However, the appropriateness and limitations of using camera traps and SCR models to study the Sunda clouded leopard have not been critically assessed. The purpose of this study was to use various study length configurations (53 days, 106 days and 212 days) to evaluate the precision and uncertainty of clouded leopard density estimates in Wehea Forest, Borneo. We collected data over 212 days and, for analysis, we divided the study into 3 sample configurations consisting of (1) four 53-day windows, (2) two 106-day windows and (3) one 212-day window. For each window, we estimated density using both a sex specific SCR model and a simplified sex-generic model, which assumed equal parameter values for both sexes. Density estimates varied both between windows and sample configurations and using longer windows did not improve precision. The high uncertainty in our estimates was likely due to a small sample size, while the difference in estimates between the two 106 day windows may have been due to ecological differences between the sampling seasons. The high uncertainty that we found in our estimates is shared among all clouded leopard studies and makes it difficult to accurately assess the conservation status of this enigmatic cat. Action is needed to improve both methods and estimates before habitat loss and hunting quietly force the Sunda clouded leopard below a critical population threshold and inexorably put it on same path of extinction as the Formosan clouded leopard.

Introduction

Estimates of abundance (total number of individuals in a particular ecosystem) and density (number of individuals per unit area) are some of the most basic requirements for managing large carnivores (Lebreton et al., 1992; Reed et al., 2002; Udevitz & Gould, 2013). To obtain accurate estimates, all individuals need to be recorded at a given time and location. However, this is only possible if animals are easily detectable. For rare carnivores, this is rarely feasible because they very often have large home ranges, occur at low densities, exhibit heterogeneous capture probabilities, and are often extremely elusive (Garshelis, 1992; Karanth, 1995; Thompson, 2004).

The Sunda clouded leopard (*Neofelis diardi*), found on the islands of Borneo and Sumatra, is one of these extremely rare and difficult-to-study carnivores. It is the largest carnivore on Borneo and 2nd largest on Sumatra but is still one of the least known cat species in the world. This may possibly be due to the particularly challenging environment in which they live and exacerbated by the fact that they are the most arboreal of all large cats (Grassman et al., 2005; Holden, 2001; Sanderson et al., 2008). What is currently known about clouded leopard ecology is mainly derived from observation of captive animals (Selous & Banks, 1935), anecdotal reports (Rabinowitz et al., 1987; Santiapillai & Ashby, 1988), and chance observations. The only recently published study on clouded leopard ecology was Hearn et al. (2013), which discussed aspects of the species spatial and temporal ecology.

There is even less known about the population ecology of the Sunda clouded leopard. Prior to 2012 only two studies attempted to estimate the density of Sunda clouded leopards. These studies used track and observation surveys and most likely overestimated population size with estimates ranging from 25 individuals/100 km² (Davies & Payne, 1982) to 8 individuals/100 km² (Wilting et al., 2006). Since then there have been a number of published (n = 8) and unpublished (n = 7) studies that have estimated clouded leopard densities on Borneo (n = 11) and Sumatra (n = 4). These studies have produced much lower estimates ranging between 0.767 individuals/100 km² (Sollmann et al., 2014) to 4.41 individuals/100 km² (Cheyne et al., 2013; Table 6.1).

Table 6.1 Summary of results for Sunda clouded leopard *Neofelis diardi* studies published since 2012.

Study	Protected area (total area)	Total days (study area)	Analysis (placement)	Total ind. (# for each sex)	Photos	indiv/100 km^2 (95% CI)	Extrapolated population size
Brodie & Giordano (2012)	Malinau Basin, Sabah, Malaysia (588 km^2)	81 (75 km^2)	SCR (Trail/road)	4 (4 unknown)	59	1.9 – w/mask (0.7 – 5.4) 0.8 – w/o mask (0.2 – 2.6)	11.17 (4.12 – 31.75) 4.70 (1.18 – 15.29)
Wilting et al. (2012)	Tangkulap-Pinangah, Sabah, Malaysia (500 km^2)	126 (122 km^2)	SCR (Grid)	5 (3 male; 2 female)	29	0.837 (0.246 – 1.830)	4.19 (1.23 – 9.15)
Wilting et al. (2012)	Segaliud Lokan, Sabah, Malaysia (572 km^2)	96 (114 km^2)	SCR (Grid)	5 (3male; 1 female; 1 unknown)	15	1.038 (0.288 – 2.552)	5.94 (1.65 – 14.60)
Cheyne et al. (2013)	Sabangau, Kalimantan, Indonesia (5600 km^2)	90 (50 km^2)	CR (Trail)	4 (3 male; 1 female)	23	(0.72 - 4.41)	(40.32 – 246.96)
Sollmann et al. (2014)	Renah Kayu Embun, Sumatra, Indonesia (13,300 km^2)	130 (121 km^2)	SCR (Trail)	7 (6 male; 1 female)	16	1.570 (0.578 – 3.273)	168.91 ** (57.06 – 365.35)
Sollmann et al. (2014)	Sipurak, Sumatra, Indonesia (13,300 km^2)	91 (94 km^2)	SCR (Trail)	2 (2 male)	6	0.767 (0.145 – 2.101)	
Sollmann et al. (2014)	Bungo*, Sumatra, Indonesia (13,300 km^2)	238 (322 km^2)	SCR (Trail)	6 (5 male; 1 female)	8	1.618 (0.576 – 3.375)	
Sollmann et al. (2014)	Ipuh*, Sumatra, Indonesia (13,300 km^2)	222 (706 km^2)	SCR (Trail)	7 (4 male; 2 female; 1 unknown)	17	1.110 (0.417 – 2.239)	

* for analysis the study length was divided into two time periods to ensure closure

** average density of 1.27 (0.429 – 2.747) across all 4 study sites was used to estimate extrapolated population

These lower estimates are likely a result of the recent use of camera traps and spatial-capture recapture (SCR) models (Hance, 2012; Macallum, 2012). SCR models have emerged as a preferred method for estimating density using photographic data from camera traps (Foster & Harmsen, 2011; Royle et al., 2011). These models have an advantage in that they accommodate various types of detector arrangements including traditional grids (e.g. Wilting et al., 2012), evenly spaced cameras along roads and trails (e.g. this study; Spehar et al., 2015) and unequally spaced cameras set throughout the study area (Sollmann et al., 2014). In addition they can incorporate both individual-level covariates (e.g. sex or age class) as well as station level covariates (e.g. road vs. trail or habitat; Sollmann et al., 2011). Conventional capture-recapture (C-R) models are less flexible and require that the entire population be exposed to cameras with no 'holes' in the survey area (Efford & Fewster, 2013). The flexibility of SCR models is especially important in Borneo and Sumatra, where field conditions can make research design a challenge.

Here we report on a camera trapping study of the Sunda clouded leopard (*Neofelis diardi*) in Wehea Forest, East Kalimantan, Indonesia. The purpose of this study was to examine the effects of different study design and analytical approaches on the conclusions to be drawn from camera-trap-based SCR studies of clouded leopards. Specifically, I use various study length configurations (53 days, 106 days and 212 days) to evaluate the precision and uncertainty of clouded leopard density estimates in Wehea Forest, Borneo. Current studies of Sunda clouded leopards have restricted their study length to between 81 to 130 days to ensure population closure (Karanth & Nichols, 1998; Silver et al., 2004; Karanth et al., 2006). However, given the extremely elusive nature of clouded leopards and the difficulty of conducting research on Borneo and Sumatra, we wanted to explore whether shorter or longer study lengths would impact the precision and uncertainty of our estimates. Based on our results, we then make specific recommendations for future research.

Methods

Study Area

Wehea Forest (01°32’46”N, 116°46’43”E) located in East Kutai District, East Kalimantan, Indonesia, contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests currently classified as logging concessions (Fig. 6.1). Wehea Forest lies within an old logging concession, a portion of which was last selectively logged in the mid-1990s. Old logging roads, which have not been maintained since logging ceased, are overgrown but are still used as animal trails and were therefore utilized for this study. Wehea Forest is currently protected by an agreement between a local community and the local government, and its status was recently changed to a Protection Forest (Hutan Lindung).

The site has a varied topography, characterized by steep ravines, multiple ridges and runoff streams. Elevations vary from 250 m in the east, where the main logging activity took place, to 1750 m in the west, where the primary and montane forests occur. Wehea Forest is characterized by lowland Dipterocarp, sub-montane and montane forests with mean total annual rainfall amounting to 3000 mm and a mean 24 h temperature of 27 °C. A dry season typically runs from June to September and the rainy season is from November to February.

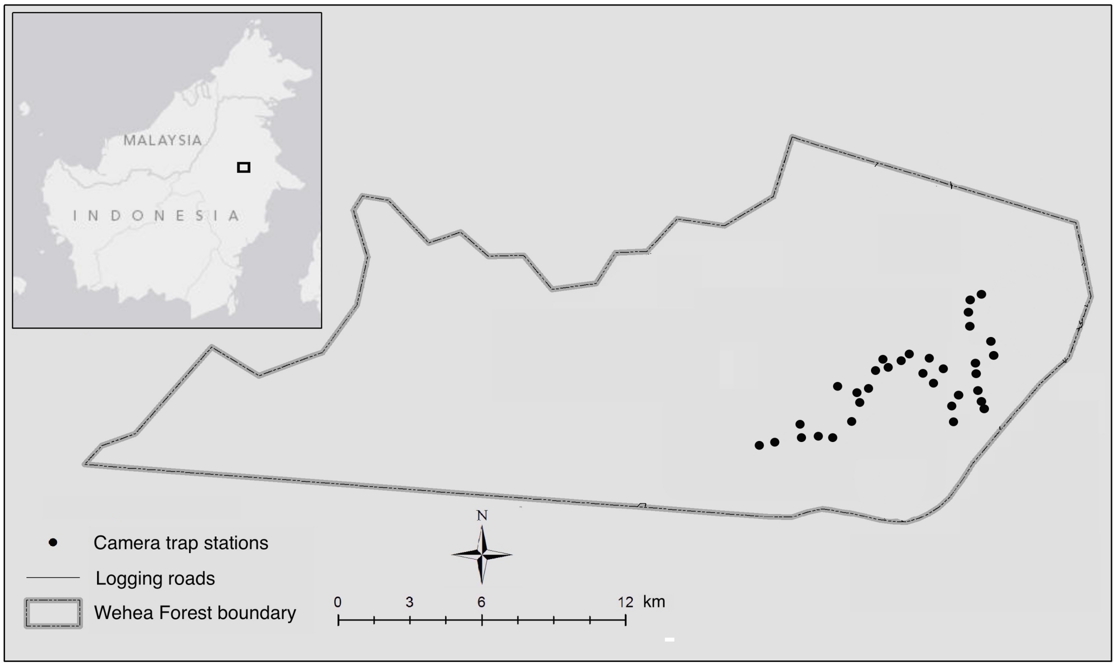

Figure 6.1 **Location of camera-trap stations in Wehea Forest. Insert shows the location of Wehea Forest on the island of Borneo.**

Camera trapping and data preparation

In March 2012, 68 non-baited cameras were set in pairs, or stations, along old logging roads and trails in order to maximize capture rates (Tobler & Powell, 2013; Spehar et al., 2015). This station array covered an approximate area of 80 km^2 (Fig. 6.1). The cameras used were Bushnell Trophy Cams (n = 60) and Reconyx HC500 (n = 8) cameras. An additional 9 Bushnell Trophy Cams were added in May, all set along roads and at two mineral licks (sepans), however data from these cameras were used only to help identify clouded leopards and not for analysis. The 68 cameras were set across 34 camera trap stations and resulted in a sampling effort of 6,951 trap nights for a total of 212 nights. All cameras remained at the same locations until this study concluded in October 2012.

All cameras used in this study were placed on trees ~50 cm from the ground and fitted with a plastic cover above and a bed of leaves below to protect against rain and mud. Each camera was set to take three pictures per trigger, with a reset time of one second. Cameras were checked a total of three times, in the middle of May, the beginning of July and again in October, at the conclusion of the study. At each visit, non-functioning cameras were replaced with new cameras, batteries were changed and the SD card storing the photos was removed from the camera and replaced by a new card.

We identified clouded leopard individuals in photographs based on their unique spot patterns and identified gender by size and primary sexual characteristics, mainly the presence of external genitalia. If the individual's unique spot pattern was not visible in a photograph, we did not attempt to identify that individual. All photographs were reviewed two separate times to maximize confidence in the assessment.

Study design

We divided our entire 212-day study length into 3 sample configurations consisting of (1) four 53-day consecutive windows, (2) two 106-day consecutive windows and (3) one 212-day window. For each window, we noted how often an individual was photographed at each station along with the date and time. The 53-day sample-configuration was chosen as the lower end of survey length used in other felid studies (e.g. Gray & Prum, 2012; Harihar et al., 2009; Silver et al., 2004) and to simulate a rapid assessment survey (Alonso et al., 2011). These surveys are especially useful in difficult research environments such as Borneo and Sumatra and are a good way to assess large areas in a shorter time. The 106-day sample-configuration was chosen as the traditional survey length for closed population studies (e.g. Karnath & Nichols, 1998; Karnath & Nichols, 2000; Wilting et al., 2012) and because this falls within the same survey length used by other clouded leopard studies (see Table 6.1). The 212-day sample-configuration was chosen because extended survey lengths can increase capture probabilities for extremely elusive animals, and in many situations the data gained by extending the survey length outweighs the risk of violating closure (Tobler & Powell, 2013).

Spatial capture-recapture model

We used SCR models to estimate densities for each of our 7 windows so we could compare how densities varied both between windows and sample-configurations. SCR models assume that each individual has an independent activity center, which is located within a defined state-space S. Abundance (N) is estimated by the number of activity centers within the state space. We defined our state space by adding a 20 km buffer to our Eastern, Western, Southern and Northernmost camera traps. This resulted in a state space of 2303 km^2, which we believe was large enough to include all individuals that were exposed to the trapping array.

We estimated N for each sampling window separately using a Bayesian analysis by data augmentation and Markov chain Monte Carlo (MCMC) to obtain Bayesian estimates of all parameters: abundance, movement, capture probability, and sex-ratio (N, σ, λ_0 and Ψ), respectively (Royle & Dorazio, 2012; Royle et al., 2007). Data augmentation assumes a uniform (0, M) prior for N for some large M. We let M be a number that is larger than the largest possible population size N in S, which in our case was 200 individuals. We induced the uniform prior by adding to the detection histories of n, which were the number of clouded leopard individuals detected during the study, a large number (M – n) individuals that were never detected and thus have encounter histories that are all zero. For all M potential individuals we introduced an auxiliary variable, z, which was 1 if the clouded leopard was part of the population and 0 if it was not. N was then estimated by the sum over all z's and density D was derived by dividing N by the area of S (Kéry et al., 2010; Royle et al., 2014; Sollman et al., 2011; Sollmann et al., 2013)

We ran two models, the first of which allowed for sex-specific baseline encounter rates (λ_0) and a sex-specific movement parameter (σ). λ_0 (photos occasion^{-1}) is the expected encounter rate of an individual with a trap if that trap center were located precisely at the individual's activity center. The parameter σ (km) is the scale parameter of the Gaussian kernel and is related to animal home range radius (Reppucci et al., 2011). We set a uniform prior of (0 – 50 km) for both σ_{male} and σ_{female}, and a uniform prior between 0 and 1 for the sex-ratio Ψ. This sex-specific model gave us a total abundance estimate (N_{total}), which was based on unequal encounter rates and movement parameters for males and females, along with an estimate of the sex-ratio. Sex-specific abundance and density estimates were derived by multiplying the total abundance or density by the estimated sex ratio. We also ran a second, more simplified model (N_{simple}), which assumed equal encounter rates and movement parameters for each sex and used the same prior distributions as above.

Models were implemented in the software JAGS (v. 3.1.0, Plummer, 2011) accessed through the rjags package (Plummer, 2013) and analyzed using the coda package (Plummer et al., 2006) in R (v. 3.0.3 R Development Core Team, 2014). For each model, we ran 3 parallel Markov chains with 1 million iterations each, a burn-in of 20,000 iterations and a thinning rate of 200. For all parameters we report posterior means and standard errors, as well as 90% Bayesian Credible Intervals (BCI) (Sollman et al., 2013).

Results

From March 21 to October 18, 2012, we obtained a total of 87 clouded leopard records consisting of 5 males and 7 females. Both males and females were recorded in each of our windows. Males represented 87% (n = 76) of all records (n = 87) with one male accounting for 54% (n = 47) of all photographs. The fact that one male was photographed a disproportionate number of times within the study area is consistent with other clouded leopard studies (Brodie & Giordana, 2012; Cheyne et al., 2013; Wilting et al., 2012). All 5 males were recaptured more than one time and at more than one station (Table 6.2). Of the 7 females recorded during the 212-day study, only 4 were recaptured a second time and only 1 of these recaptures was photographed at more than one station. Three males and one female were also photographed during a pilot study in 2011 leading us to believe that these were resident individuals.

The lowest and highest abundance estimates for males were both found within the 53 day sample-configuration and ranged from the lowest N_{male} = 7.98 in window 53(3) to highest N_{male} = 29.91 in window 53(2) (Table 6.3). The lowest abundance estimate for males (N_{male} = 7.98) also corresponded with the lowest baseline encounter rate for males (λ_{0male} = 0.01) and highest movement parameter (σ_{male} = 17.21). Males were recorded the same number of times (*n* = 3) in window 53(2) and window 53(3), however window 53(2) produced more total recaptures (Table 6.2).

Males had far higher baseline encounter rates (λ_{0male}) than females, with the lowest male baseline encounter rate close to 100 times greater than the lowest baseline encounter rate for females and almost 5 times greater than the highest female baseline encounter rate found in the 212-day sample-configuration. The highest movement parameter for males (σ_{male} = 17.21) was less than half the largest movement parameter for females (σ_{female} = 27.01) in windows 53(3) and window 106(1) respectively and almost 3 times higher than the smallest female movement parameter (σ_{female} = 6.23) found in the 212 day sample-configuration (Table 6.4).

In our 53 and 106-day sample-configurations, density estimates varied between windows and sample-configurations, with the 106-day sample-configuration showing the greatest inter-window variation (Table 6.3). Both 106-day windows captured the same number of males (*n* = 5), however males were seen less often and recaptured less often in window 106(2), resulting in a 63.9% decrease in our estimate of males. Females were also captured the same number of times in each 106-day window (*n* = 4), however one additional recapture in 106(2) appeared to drive the baseline encounter rate up by a factor of 3 and reduced the female density estimate by almost half.

Table 6.2 Clouded leopard capture history from each of the three configurations and seven windows.

Sex	Parameter	Configuration 1				Configuration 2		Configuration 3
		53 days (1)	53 days (2)	53 days (3)	53 days (4)	106 days (1)	106 days (2)	212 days
Males	*n* seen	4	3	3	3	4	4	5
	Total times seen	24	21	14	17	45	31	76
	Total stations	15	19	13	10	22	18	25
	Total days	12	13	10	13	25	23	48
Females	*n* seen	2	3	4	2	5	5	7
	Total times seen	2	3	4	2	5	6	11
	Total stations	2	3	4	2	4	4	7
	Total days	2	3	4	2	5	6	11

Table 6.3 Summary of posterior distributions for both sex-specific (male, female, total) and sex-generic (simple) abundance (*N*) and density (*D* – individuals per 100 km^2) estimates of clouded leopards.

	Configuration 1				Configuration 2		Configuration 3
	53 days (1)	53 days (2)	53 days (3)	53 days (4)	106 days (1)	106 days (2)	212 days
Parameter	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)
N_{male}	22.67 ± 14.89 (5.05-54.03)	29.91 ± 20.28 (5.23-71.95)	7.98 ± 7.45 (1.68-26.19)	9.25 ± 6.37 (2.32-23.27)	25.12 ± 14.84 (6.45-55.29)	9.07 ± 5.62 (2.83-21.33)	15.95 ± 8.91 (4.96-34.28)
N_{female}	59.40 ± 46.91 (4.81-159.15)	65.23 ± 46.18 (7.49-159.42)	68.58 ± 50.91 (8.37-175.86)	54.68 ± 48.77 (3.75-164.21)	77.13 ± 47.09 (13.26-168.18)	48.73 ± 45.17 (7.21-155.81)	110.27 ± 55.05 (10.82-191.94)
N_{total}	82.08 ± 51.37 (16.00-185.00)	95.14 ± 50.46 (23.00-189.00)	76.56 ± 52.28 (13.00-185.00)	63.92 ± 50.76 (9.00-176.00)	102.26 ± 50.15 (30.00-195.00)	57.79 ± 46.20 (14.00-166.00)	126.22 ± 55.62 (23.00-206.00)
N_{simple}	45.30 ± 24.92 (13.00-95.00)	74.01 ± 38.30 (22.00-148.00)	37.93 ± 27.36 (9.00-99.00)	18.52 ± 11.85 (6.00-45.00)	69.24 ± 28.57 (30.00-124.00)	28.34 ± 14.29 (12.00-59.00)	54.02 ± 21.28 (25.00-95.00)
D_{male}	0.98 ± 0.65 (0.22-2.35)	1.30 ± 0.88 (0.23-3.12)	0.35 ± 0.33 (0.07-1.14)	0.40 ± 0.28 (0.10-1.01)	1.09 ± 0.64 (0.28-2.40)	0.39 ± 0.25 (0.12-0.93)	0.69 ± 0.39 (0.22-1.49)
D_{female}	2.58 ± 2.04 (0.21-6.91)	2.83 ± 2.00 (0.33-6.92)	2.98 ± 2.21 (0.36-7.64)	2.37 ± 2.12 (0.16-7.13)	3.35 ± 2.04 (0.58-7.30)	2.12 ± 1.96 (0.31-6.77)	4.78 ± 2.39 (0.47-8.33)
D_{total}	3.56 ± 2.23 (0.69-8.03)	4.13 ± 2.19 (1.00-8.21)	3.32 ± 2.27 (0.56-8.03)	2.78 ± 2.20 (0.39-7.64)	4.44 ± 2.18 (1.30-8.47)	2.51 ± 2.01 (0.61-7.21)	5.48 ± 2.41 (1.00-8.94)
D_{simple}	1.97 ± 1.09 (0.56-4.13)	3.21 ± 1.66 (0.96-6.43)	1.65 ± 1.19 (0.39-4.30)	0.80 ± 0.51 (0.26-1.95)	3.01 ± 1.24 (1.30-5.38)	1.23 ± 0.62 (0.52-2.56)	2.35 ± 0.92 (1.09-4.13)

Table 6.4 Posterior distributions of the σ - movement parameters (km), λ_0 - baseline encounter rates (photos occasion^{-1}), and Ψ – proportion of females in the population.

	Configuration 1				Configuration 2		Configuration 3
	53 days (1)	**53 days (2)**	**53 days (3)**	**53 days (4)**	**106 days (1)**	**106 days (2)**	**212 days**
Parameter	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)	Mean ± SE (90% BCI)
σ_{male}	3.93 ± 1.46 (2.25-7.06)	2.87 ± 1.01 (1.64-4.97)	17.21 ± 12.39 (3.79-44.55)	6.36 ± 2.02 (3.60-10.24)	2.97 ± 0.69 (2.09-4.37)	7.20 ± 2.09 (4.20-11.08)	4.30 ± 0.91 (3.04-6.05)
σ_{female}	24.34 ± 13.62 (2.60-47.40)	26.47 ± 12.98 (5.01-47.72)	27.00 ± 12.66 (6.08-47.74)	25.54 ± 13.27 (3.85-47.52)	27.01 ± 12.61 (6.11-47.59)	23.68 ± 13.44 (2.87-47.09)	6.23 ± 10.75 (0.83-36.21)
σ_{simple}	3.29 ± 0.96 (2.12-5.28)	2.54 ± 0.76 (1.63-4.14)	6.49 ± 2.70 (2.96-11.84)	5.62 ± 1.66 (3.31-8.76)	2.71 ± 0.50 (2.03-3.68)	5.68 ± 1.41 (3.57-8.22)	3.57 ± 0.60 (2.73-4.71)
λ_{0male}	0.16 ± 0.69 (0.01-0.70)	0.15 ± 0.24 (0.01-0.81)	0.01 ± 0.01 (0.002-0.02)	0.06 ± 0.06 (0.01-0.19)	0.38 ± 0.63 (0.02-2.08)	0.02 ± 0.01 (0.01-0.05)	0.17 ± 0.21 (0.01-0.71)
$\lambda_{0female}$	0.0008 ± 0.0009 (5.58E-06 - 0.27E-02)	0.0002 ± 0.0002 (8.44E-06 - 0.08E-02)	0.0002 ± 0.0002 (1.16E-05 - 0.06E-02)	0.0004 ± 0.0003 (5.20E-06 - 0.01E-01)	0.0001 ± 0.00009 (7.98E-06 - 0.03E-02)	0.0003 ± 0.0003 (1.75E-05 - 0.01E-01)	0.002 ± 0.002 (1.19E-04 - 0.06E-01)
$\lambda_{0simple}$	0.09 ± 0.09 (0.01-0.30)	0.04 ± 0.02 (0.01-0.09)	0.005 ± 0.008 (0.002-0.010)	0.03 ± 0.02 (0.01-0.07)	0.05 ± 0.04 (0.01-0.14)	0.01 ± 0.003 (0.01-0.02)	0.03 ± 0.02 (0.01-0.09)
Ψ_{female}	0.64 ± 0.23 (0.19-0.94)	0.63 ± 0.22 (0.21-0.93)	8.85 ± 0.14 (0.51-0.98)	0.75 ± 0.20 (0.31-0.97)	0.71 ± 0.18 (0.34-0.94)	0.76 ± 0.17 (0.41-0.96)	0.82 ± 0.17 (0.41-0.97)

Increasing the size of the sample-configuration from 53 to 106 days did not result in a materially larger number of male clouded leopards being photographed. The 4 windows in our 53-day sample-configuration captured an average of 3.25 males whereas this increased to only 4 males per window when the size of the sample-configuration was doubled to 106 days. Doubling the size of the sample-configuration did nearly double the number of female clouded leopards captured from an average of 2.75 females in our 53-day sample-configuration to 5 females in our 106-day sample-configuration and increased the number of recaptures for both males and females. However these increases were not enough to decrease the uncertainty of our estimates.

The highest male or female abundance estimate was found in the 212-day window (N_{total} = 126.22) and is almost 8 times higher than the male estimate of N_{male} = 15.95 in the same window. This window also corresponded with the most total female clouded leopards seen (n = 7) and the largest female baseline encounter rate ($\lambda_{0female}$ = .002) and smallest female movement parameter (σ_{female} = 6.23; Table 6.4). Our sex-specific abundance estimates (N_{total}) averaged 79.63 individuals across our 53 and 106-day sample-configurations and increased to our highest total abundance estimate of 126.22 individuals in our 212-day sample-configuration.

Our simplified model, which assumed equal λ_0 and σ for each sex, showed similar variation in abundance estimates (N_{simple}) between windows and sample configurations and were consistently lower when compared to our sex-specific model (N_{total}). Abundance was lowest (N_{simple} = 18.52) in 53(4) and highest (N_{simple} = 74.01) in 53(2). Abundance (N_{simple}) in 106(1) was 2.44 times higher than in 106(2) and our 212-day window estimate (N_{simple} = 54.02) was 2.34 times lower than our sex specific abundance (N_{total}) estimate in our 212-day window (Table 6.3).

Discussion

The use of camera traps has emerged as a powerful research tool over the past two decades, with 73% of camera trap studies being published after 2005 (McCallum, 2012). Of all camera trap studies published since 1994, the two most common taxa represented were *Panthera tigris* (22%) and *Panthera pardus* (16%) with the most common objective of the study type being estimating population density (McCallum, 2012). Of population density studies involving camera traps, non-spatial C-R (capture recapture) and more recently SCR (spatial capture-recapture) models have become the common methods for estimating population density of elusive terrestrial mammals (Foster & Harmsen, 2011) – representing 38 of 47 published studies focusing on felids. Recently, these methods have been used to estimate densities for clouded leopards with 5 of 6 studies published since 2012 (see Table 6.1) and a number of other studies being planned or currently underway. Despite the popularity of these methods, our study demonstrates that given the low precision and high uncertainty in our results (and results from past studies) that continuing to use these same methods to study clouded leopards will not further improve our understanding of their total population size.

Impact of study length on density estimates

When studying elusive animals such as Sunda clouded leopards, it is important to consider the appropriate length of time in which to leave cameras in the field in order to detect as many animals as possible while still maintaining both geographic and demographic closure (Williams et al., 2002). In the absence of suitable closure tests, a survey period of approximately 100 days has been suggested for big cats (Karanth & Nichols, 1998; Silver et al., 2004). However, other researchers have chosen to extend sampling periods so sufficient captures are obtained for analysis including several studies, which sampled for 6–14 months (Karanth, 1995; Kawanishi & Sunquist, 2004; Haines et al., 2006; Simcharoen et al., 2007; Mazzolli, 2010). While violating the population closure assumption is a concern for long survey periods, currently there are insufficient data from clouded leopard studies (see Table 6.1) to suggest the appropriate survey length while still assuming population closure.

It could be assumed that our estimates in the four windows of our 53-day sample-configuration would show the lowest precision and highest uncertainty due to a smaller time period and therefore reduced number of captures and recaptures. However, our study showed that neither the precision, as demonstrated by the lack of agreement in estimates within windows, nor uncertainty of our estimates, as demonstrated by the wide credibility intervals (CIs), improved by extending the sample-configuration to 106-days (Table 6.3) even though the total number of recaptures for both males and females increased (Table 6.2). To improve estimates, it has been suggested that for extremely elusive animals the data gained by extending the survey period could outweigh the risk of violating closure (Tobler & Powell, 2013). Our data suggests, however, that for clouded leopards extending the sample-configuration to 212 days did not yield estimates with any less uncertainty (Table 6.1).

In addition to extending the sampling window, using the most simplified model that is consistent with the data should, a priori, be used for small sample sizes. Our simplified model that assumed equal home range sizes and capture probabilities did marginally decrease the uncertainty in our estimates as reflected in the slightly narrower CIs. However, given that behavioral differences do exist between the sexes of most large felids (Conde et al., 2010), estimates from our simplified model should also be treated with caution.

Factors influencing the high uncertainty in estimates

A potential concern with the results from past studies of clouded leopards (Table 6.1) and this study (Table 6.3) is the consistently wide CIs. We believe the main factor driving this uncertainty are the small sample sizes used to estimate densities (see Table 6.1 and 6.2). Given such small sample sizes, adding or removing only a few individuals from a data set can have a significant impact on estimates. Simulations with SCR models showed they worked well and produced unbiased results for adequate sample sizes (n = 200) but bias increased with low capture probabilities (Marques et al., 2011; Royle & Young, 2008). Given that the largest sample size for clouded leopards from past studies is n = 22 (Sollmann et al., 2014) and only n = 12 individuals from this study, we should be very cautious in making any conservation related management recommendations based on our current knowledge of this felid.

In addition to small samples sizes, only 30 percent of total records from past studies are female. In this study, 58 percent of our records were female (7 of 12), although these records were mainly from a single station, thus making it impossible to calculate σ separately for males and females (Sollmann et al., 2014). Given that SCR models are sensitive to un-modeled heterogeneity in detection probability, leading to estimates that are biased low, current clouded leopard estimates may be underestimating actual densities. One possible explanation for the low female encounter rates is that they occur at lower densities than male clouded leopards. However, our understanding of the population dynamics of other felids indicates that female clouded leopards may out-number males (Schaller & Crawshaw, 1980; Sollmann et al., 2011; Sunquist, 1981). This difficulty in photographing females may arise from a higher level of arboreality, a smaller home range (Sandell, 1989, Sharma et al., 2009; Sollmann et al., 2011), a trap shy response, as has been shown by tigers (Wegge et al., 2004) or an avoidance of roads, as has been shown by panthers, amur tigers and jaguars (Conde et al., 2010; Kerley et al., 2002; Maehr, 1997).

Another potential factor that may be impacting the precision and uncertainty in our density estimates is our lack of understanding of the temporal ecology of clouded leopards. Hearn et al. (2013) characterized clouded leopard activity as mainly nocturnal, however the temporal ecology of clouded leopards over weeks and months is unknown. The present study indicates that temporal variation in density estimates may exist for studies using the recommended survey length of approximately 100 days (Karanth & Nichols, 1998; Silver et al., 2004). In the simple model, density estimates were significantly different in windows 106 days (1) (D_{simple} = 3.01) and 106 days (2) (D_{simple} = 1.23; Table 6.3). We consider parameters significantly different from each other if the 90% BCI of one does not include the mean of the other (Sollmann et al., 2014). In addition, the movement parameter (σ) was more than twice as large in 106 days (2) indicating a significant change in spatial behavior by the clouded leopards. This could be driven by a number of factors including changes in distribution of a particular prey species (e.g. primates; Matsuda et al., 2008) due to resource availability or in response to mating. If sampling season does significantly impact density estimates for clouded leopards, as it did in our study, then we cannot be certain if the estimates from Table 6.1 are a true reflection of density or only of the season in which the study was carried out.

One critique of the differences in density between models 106 days (1) and 106 days (2) is that animals may have immigrated or emigrated (i.e. transients) into or out of the study area between time periods, thereby violating population closure. However we have two reasons to believe this is not the primary cause in the differences between our estimates. First, in each time period, four individual males were seen, three of which were photographed repeatedly in each time period and on a regular basis between 2011 and 2013 and therefore are most likely resident males. Secondly, of the five females recorded in each time period, three were captured during both study periods and all five individuals were recorded at only one station.

The difficulty in assessing the conservation status of the Sunda clouded leopard

The high uncertainty in current density estimates makes it extremely difficult to accurately assess the conservation status of Sunda clouded leopards. However, we believe there is still heuristic value in exploring the impacts that this uncertainy has on our ability to determine the overall population size of Sunda clouded leopards. To do this, we use the concept of minimum viable population (MVP) since it is well known there is a strong relationship between extinction risk and population size (Shaffer, 1981; Reed et al., 2003; Brook et al., 2006; Traill et al., 2007). The concept of MVP is a core component of the IUCN Red List of Threatened Species rules (Criterion C and D; IUCN, 2012) and has a good deal of empirical development behind it (Frankham, 1995; Franklin & Frankham, 1998; Brook et al., 2002; Reed et al., 2003; Brook et al., 2006; Traill et al., 2007; Traill et al., 2010). Although the use of MVP in conservation biology has been criticized (Flather et al., 2011), we believe there is value in using it to explore whether clouded leopards may or may not be near critical population thresholds. In addition, given the high uncertainty in our current estimates and until better methods can be developed, the use of MVP may provide a scientifically defensible generalization concerning managing viable sub-populations within protected areas and meta-populations on Borneo and Sumatra.

For sub-populations if we assume that 50 individuals (Franklin, 1980; Wilting et al., 2006; Traill et al., 2010) is the absolute minimum threshold for simply maintaining short-term fitness (to avoid inbreeding), then Sabangau (N = 40 - 247), and the Kerinci landscape (N = 169) are the only surveyed areas that may contain short-term viable populations of clouded leopards. However, the estimates from Sabangau (Cheyne et al., 2013) may be high since a closed population capture-recapture (C-R) model was used that is known to over-estimate density (Tobler & Powell, 2013). If we consider a genetically effective population size (N_e) of 500 individuals than none of the areas surveyed approach this threshold and Sabangau and the Kerinci landscape have only a

50% probability of supporting a genetically viable population of clouded leopards over a 30 year time-scale (Trail et al., 2010).

For meta-populations, a significant body of research estimates that both the evolutionary and demographic constraints on populations require sizes to be at least 5000 adult individuals (Frankham, 1995; Reed et al., 2003; Thomas, 1990; Traill et al., 2007; Traill et al., 2010). This adult population size of 5000 individuals represents a threshold or a key moment where a declining population becomes a small population with increased vulnerability to extinction (Traill et al., 2010). We recognize that generalizing too broadly among species can be problematic, however we believe this is a fair starting point from which to begin a discussion about the number of clouded leopards needed to maintain long-term viability. When extrapolating across the predicted Sunda clouded leopard range (~ 491,317 km^2; Hearn et al., 2008) we estimate an overall population size of as few as 2324 to as many as 14,474 individuals with the average mean population size being approximately 6196 individuals.

For the Sunda clouded leopard to meet the population threshold of 5000 adult individuals would require an overall density of 1.02 individuals/100 km^2 across its predicted range. Since the average mean density from all studies, including this one, is 1.26 individuals/100 km^2, it may be possible that the Sunda clouded leopard population meets this threshold. However we believe for a number of reasons that caution should be used before inferring this to be the case. First, the estimated geographic range for Sunda clouded leopards is based not on observation data of the cat but on its probability of occurring in 16 types of habitat found on Borneo and Sumatra (Struebig et al., 2015). Second, given that published clouded leopard studies have only surveyed at most 5 types of habitat, mainly in Sabah, Malaysia, the actual geographic range may be much smaller than currently estimated. If the known geographic range were to shrink by only 20%, then the estimated overall population would fall below the 5000 individual threshold. Third, the studies used to estimate sex ratios in felids (e.g. Schaller & Crawshaw, 1980; Sollmann et al., 2011; Sunquist, 1981) do not necessarily capture the role of dispersers and transients within their estimates of sex-ratios. In a long-term dynamics study, Karanth et al. (2006) show a large presence of transients among male tigers (18%), which produces a sex ratio closer to 1:1. If a 1:1 sex ratio is also true of

Sunda clouded leopards then the densities listed in Table 6.1, which all used a simplified sex-generic model, may be closer to actual densities and not underestimates.

Recommendations for improving density estimates

The most obvious consideration when designing future studies is on developing methods, which yield larger sample sizes. This could potentially be accomplished by increasing both the size of the trapping array and the density of camera stations (Sollmann et al., 2014; Tobler & Powell, 2013). Although theoretically possible, we believe this may be logistically infeasible for clouded leopards given the difficulty of setting cameras in most study areas and the high costs that would be associated with obtaining enough cameras to conduct studies across the clouded leopard's range. Research so far has been conducted in what could be considered 'optimal' clouded leopard study sites (e.g. protected areas, lowland forest, research sites with pre-existing trails, areas with low hunting rates) and even under these 'optimal' conditions sample sizes were small and CI's wide. In addition, we believe that due to the high level of clouded leopard arborality, that cameras should mainly be set along roads and trails, especially since increasing the sample size is a priority (Tobler & Powell, 2013). This idea is reinforced by the fact that the clouded leopard studies with the greatest number of independent photos also had cameras set along roads and trails (Table 6.1). Given that most research sites may not have an adequate network of trails and roads, it may be difficult to find study sites that would yield significantly larger sample sizes. For these reasons, we believe that focusing on larger study areas with a denser network of cameras is not the most effective method for improving the accuracy of estimates.

Another possible way to obtain larger sample sizes would be to extend the study length. During our study, when only considering independent photos, extending our sampling season to 212 days yielded 87 photos of clouded leopards, which was more than double the number taken during the 2nd sampling season (n = 37 photos). However, when considering total number of individuals, extending the sampling season only increased the number of individuals from $n = 9$ to $n = 12$ individuals (Table 6.2), which was still not large enough to improve the precision and decrease the uncertainty of our estimates. In addition, extending the study length could be problematic because population closure may be violated.

We believe the most promising idea for increasing sample size is to combine SCR data from similarly designed surveys to estimate shared model parameters (e.g. Wilting et al., 2012; Sollmann et al., 2014). Depending on resources, surveys similar to the one used in this study could be conducted simultaneously or in successive years and focused in various geographic areas. Given that our results indicate that shorter surveys (e.g. 53 days) yield similar results to longer surveys (e.g. 106 days), a rapid assessment of multiple study sites should be considered. This type of combined information study would yield a large enough data set for more accurate density estimates and also important information how clouded leopard densities vary throughout their geographic range. If resources and expertise are shared among clouded leopard researchers, we believe this type of large-scale assessment would be cost effective and could be completed within 4 to 5 years, especially if a rapid assessment approach is used.

One additional survey design that should be considered for increasing sample size is the use of clusters of camera traps set throughout the study area (Efford & Fewster, 2013). This type of camera layout can be used with SCR models and would allow for more area to be covered and less cameras to be used. We originally considered this type of trap arrangement for our study in Wehea Forest. However limited availability of roads and trails did not allow for this type of design. We did find, however, that with some of our mini-clusters of cameras that were set < 200 m apart, clouded leopards were still only recorded at single stations, possibly indicating they only travel along roads and trails for small stretches at a time. In addition, our most frequently photographed clouded leopard was recorded in only two sections of our study area (see Fig. 6.2) and more frequently at certain stations than others, possibly providing support for this type of clustered trap arrangement.

In addition to the previous recommendations for increasing sample sizes, we also suggest longer, multi-year studies be carried out. These multi-year studies would allow researchers to rigorously investigate the population dynamics (Karanth et al., 2006) of clouded leopards and depending on study location, they could provide valuable insights into the resilience of this species to anthropogenic disturbances. Lastly, telemetry studies on clouded leopards would also provide much needed information on the spatial and temporal ecology of this species.

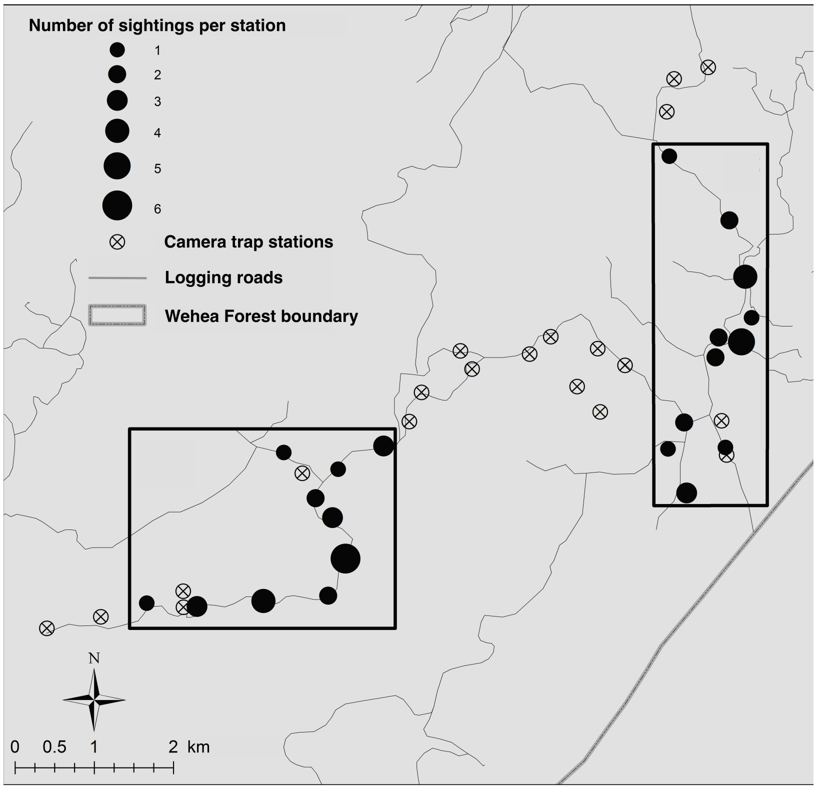

Figure 6.2 **The only two sections within our trapping array where our most frequently photographed clouded leopard was recorded and the number of sightings per station.**

Conclusion

If we are serious about the long-term survival of the Sunda clouded leopard, we must aim for an overall population of thousands of individuals (Frankham, 1995; Reed et al., 2003; Thomas, 1990; Traill et al., 2007). This may be difficult in Borneo and Sumatra, where preserving adequate contiguous habitat for Sunda clouded leopards is becoming increasingly challenging and impractical given that rapid economic growth and development are fueling an unprecedented transformation of the landscape (Hansen et al., 2013; Hearn et al., 2008). In reality, most Sunda clouded leopard populations may be forced to exist as fragmented sub-populations and therefore identifying key sub-populations will be important when deciding where to invest time and effort in protection or research activities (Traill et al., 2010).

Alongside climate change, eliminating large carnivores from ecosystems is one of the most significant anthropogenic impacts on nature (Estes et al., 2011; Ripple et al., 2014). Despite their importance, 80% of large cats continue to face dramatic population declines worldwide (IFAW et al., 2010). The Sunda clouded leopard is no exception, however what makes this cat unique is that on top of possibly lying precariously close to a critical population threshold, it is also experiencing a rapid loss of habitat and an increase in illegal trade in its body parts (Brodie et al., 2014; Nijman & Shepherd, 2015). Given this reality, we can't waste any more time or money expecting that current methods will someday yield estimates that are more precise and less uncertain. Doing so may quietly and inexorably put the Sunda clouded leopard on the same path toward extinction as the now extinct Formosan clouded leopard.

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Chapter 7.

Evaluating the utility of common-pool resource theory for understanding forest governance and outcomes in Indonesia between 1965 and 2012

This chapter was previously published in the article "Evaluating the utility of Common-pool resource theories for understanding large scale patterns of deforestation in Indonesia between 1965 and 2012", co-authored by Fleischman, F.D., Loken, B., Garcia-Lopez, G.A., Villamayor-Tomas, S. in the open access International Journal of the Commons © 2014 The Authors. I helped in authoring significant portions of the text, tables and figures and making changes to the manuscript throughout the review process.

Abstract

While Common Pool Resource (CPR) theory has been widely applied to forestry, there are few examples of using the theory to study large-scale governance. In this paper we test the applicability of CPR theory to understanding forest governance and outcomes in Indonesia between 1965 and 2012. Indonesia contains one of the world's largest tropical forests, and experienced rapid deforestation during this time frame, with forest cover dropping from close to 85% to less than 50%. Using a mixture of within case comparison and process tracing methods, we identify key variables that influenced the levels of deforestation during two time periods: before 1998, when governance was dominated by the dictatorship of President Suharto, and after 1998, when democratic governance and political decentralization were initiated, and deforestation rates fell and then rose again. Our results point to the value of CPR theory in identifying important variables that influence sustainability at large scales, however they also illustrate important limitations of CPR theory for the study of forests with large spatial extent and large numbers of users. The presence and absence of key variables from CPR theory did emerge as important causes of deforestation. However, some variables, such as

strong leadership and local rule-making, appeared to work in the opposite direction as predicted by CPR theory. In addition, key variables that may have influenced deforestation rates are not well captured in CPR theory. These include the intention of the governance system, the presence of clientelistic politics, the influences of international politics & markets, and the influence of top-down governance. Given that CPR theory does not fully explain the case at hand, its applicability, as is, to large-scale commons should be treated with some caution.

Introduction

Human drivers of changes in forest ecosystems have been subject to intensive study for several decades, however none of the major traditions examining human-forest interactions have focused on understanding the influence of governance on forests at the level of the nation-state, where many decisions about forest management are made. Common-Pool Resource (CPR) theory, as applied to forestry, largely focuses on the prospect for collective action to solve commons dilemmas at the local or village level (Araral, 2014; Tucker, 2010). While Land Use and Cover Change (LUCC) scholarship focuses on large-scale drivers of forest cover change, it is largely silent on the role of policy and governance (Rudel, 2008). Finally, political ecology, while frequently engaging with national-level policies, tends to focus on the impact of national governance at the local level, rather than at the national level (Robbins, 2002). Similar problems plague studies of other types of commons, with knowledge about governance of environmental commons with large spatial extent and involving large numbers of actors particularly limited (Berkes, 2006).

One proposed solution to this problem is to apply common-pool resource theory derived from village and community-level studies to study systems in which the number of potential actors is large and the spatial extent of the commons and governance system is much greater than in community-level studies (Keohane & Ostrom, 1995; Berkes, 2006). Although CPR theory is one of the most prominent contemporary theories of environmental governance, there have not been systematic tests of its applicability to large-scale forest governance. As a result, it is not clear whether CPR theory is suitable to be applied to the study of forests with large spatial extents and large numbers of users, whether the theory requires modification to be applicable to these systems, or whether the theory is not useful for the study of these forests. Specifically, it is unclear which variables and design principles from CPR theory can be applied at these larger scales, or whether the logic of collective action underlying CPR theory can be used to study cases involving large numbers of actors. Previous scholarship on the matter (e.g. Araral, 2014; Dietz, 2003; Keohane & Ostrom, 1995; Stern, 2011) has provided conflicting answers.

In this paper we address a critical research frontier and explore the applicability of CPR theory to the governance of large-scale forest systems with the goal of generating hypotheses that can be tested in more detail with a larger number of cases in the future. Our focus is on systems in which both the commons and the governance system have a much larger spatial scale than in community-level studies, and we chose to focus at the level of a large nation-state because nation states make important decisions about forest management. To do this we apply the lens of the Social Ecological Systems Meta-Analysis Database (SESMAD; see Cox, 2014) to a case study of forest governance in Indonesia between 1965 and 2012. The primary research questions are: (1) What does this case tell us about the applicability of CPR theory to large-scale forest governance systems? and (2) how does the application of CPR theory contribute to understanding the outcomes of the last 45 years of forest management in Indonesia?

The case of Indonesian forestry management is a useful case for examining the applicability of CPR theory to large-scale systems for three reasons. First, with nearly 100 million hectares of forest remaining, Indonesian forests are an example of large-scale Common Pool Resource (i.e. a resource typified by rivalrous consumption and difficult exclusion) with global importance (Barr et al., 2006; Araral, 2014). These forests represent the world's third largest tropical forested area, contain 23 GT of carbon stocks (Van der Werf et al., 2009), and 2 of 25 global biodiversity hotspots (Myers et al., 2000). Second, changes in governance of Indonesia's forests since 1965 provide a good opportunity to explore the utility of CPR theory for explaining the effect of large-scale governance on forest outcomes. Existing literature on Indonesian forest governance emphasizes the role of corrupt state-sponsored resource extraction, government resettlement policies, and smallholder agriculture prior to 1998 (Sunderlin &

Resosudarmo, 1996), and of decentralization and democratization after 1998 (Arnold, 2008). These are important processes, which we will use in this paper to challenge CPR theory. Third, as noted above, others have used Indonesia as an example of CPR theory's inapplicability to large-scale cases. Beginning with an unlikely case provides a strong test of CPR theory – if we in fact found that CPR theory could be applied to understanding the case, it would provide strong evidence that CPR theory could be applied to other cases (George & Bennett, 2005). This paper also goes beyond a focus on broad-level institutional changes to scrutinize how governance changes altered the incentives and behavior of different actors, and how those changed behaviors interacted with the biophysical system to produce changes in deforestation rates. That said, given the large number of causal variables involved, the analysis should be seen primarily as an exploratory case study which identifies potential relationships between variables, but cannot definitively prove causal relationships (George & Bennett, 2005).

The paper is structured as follows. In the next section we explain why applying CPR theory to large-scale forest governance is likely to reveal new insights. We then present the research methods of the SESMAD project and show how they are applied to this case study. In the fourth section, we briefly review the history of forest management in Indonesia since 1965 and identify the main policies and actor configurations within it, and then analyze how key variables drawn from CPR theory are relevant to understanding the outcomes of Indonesian forest governance over the last half century.

Theory

CPR theory focuses on the ability of people to act collectively to overcome the management dilemmas inherent to common-pool resources. The theory developed in response to the work of Olson (1965) and Hardin (1968), both of whom argued that groups of people were not likely to work effectively together. Hardin, in particular, blamed resource degradation on the "tragedy of the commons," in which users are unable to cooperate to achieve mutually beneficial outcomes. Although Hardin used the term "commons" in a generic fashion, we now understand that Hardin's tragedy was the result of a confluence between two variables: a type of resource, which we call a common-pool resource (or commons for short), in which exclusion is difficult, but consumption rival, encouraging overuse, and an open-access property regime, in which there is no collective regulation of access and/or use (Hardin, 1994; McKean, 2000). Thus, CPR theory is a theory about the conditions under which open access management of common-pool resources can be avoided through collective action.

Beginning in the 1970s, a large number of scholars noted that Hardin's dour predictions were inconsistent with empirical observations. Syntheses of this growing literature were published in a series of reports from the late 1980s through the early 2000s (National Research Council, 1986; Wade, 1988; Ostrom, 1990; Ostrom et al., 1994; Baland & Platteau, 1996; Agrawal, 2001; Ostrom et al., 2002). These syntheses focused on identifying variables that contributed to collective action in the management of common-pool resources, and have received strong support in subsequent studies (see Cox et al., 2010). For the forest sector, CPR theory has been tested by the International Forestry Resources and Institutions (IFRI) research program on small-scale forest systems, with supportive results (Gibson et al., 2000; Tucker, 2010). In this paper, we use the term CPR theory to refer both to this group of variables, as well as to the theories that connect these variables with collective action and successful resource governance.

A potential problem with CPR theory is that most of the cases used to develop CPR theory were small-scale – consisting, for example, of a village or a few villages interacting with a forest area, as in the IFRI program. CPR theory developed a focus on the ability of local users of the commons to sustain collective action in traditional management systems. This focus was later extended to examine the local management of forest resources that were decentralized by central governments (Andersson & Ostrom, 2008).

Although a number of authors have attempted to apply the lessons of CPR theory at larger scales, these efforts have not been systematic. Some authors have largely confined themselves to speculations about the applicability of CPR theory, without attempting to seriously grapple with the theoretical complexities of such a process, nor systematically comparing their predictions to actual cases (e.g. Keohane & Ostrom 1995; Dietz et al., 2003; McGinnis & Ostrom, 2007). A second related literature has focused on 'cross-scale' and 'multi-level' governance, providing useful insights on the role of governance at scales above the local, including the regional, national and international (see e.g. Brondizio et al., 2009; Armitage, 2008; García López, 2012; Mwangi & Wardell, 2012; Gruby & Basurto, 2014).

Others have delved into the specific problem of large-scale commons governance, occasionally informing their theory in a haphazard fashion through case studies, and have arrived at conflicting conclusions. Stern (2011) argues that global commons are potentially governable, although the nature of collective action problems at the global scale are different from those at the local scale. Specifically, he differentiates between local and large-scale commons in terms of scale, number of users, salience of degradation, distribution of interests and power, cultural and institutional heterogeneity, feasibility of learning, resource regeneration, and knowledge about and stability of resource dynamics. Departing from this observation, Stern argues that while most of Ostrom's (1990) design principles apply, "defining boundaries for resources and appropriators is not a meaningful exercise for global commons," presumably because the global scale includes everything. Stern also argues that an additional set of principles apply at global scale, including investments in science to understand resource dynamics, integrating science with deliberation, multi-level connections for rule-making, and planning for institutional adaptation and change. However, he does not explain how he derived these principles, nor why he believes they are relevant at global, but not at local scales. A further weakness of Stern's work is that he focuses only on global commons problems such as global climate change, and thus it is not clear how his nascent theory would apply to regional or national level commons, which while much larger than those traditionally studied in CPR theory, are nonetheless much smaller than the entire globe. For example his critique of the relevance of boundaries seems to apply more to commons that are genuinely global in scale, as opposed to those that are regional or national.

By contrast with Stern's optimistic view that CPR theory can be used – with modification – at a global scale, Araral (2014) offers a pessimistic outlook on our ability to overcome collective action problems at large scales. While he argues that although the theoretical dilemmas of the local and large commons are the same (e.g. overharvesting, free riding, monitoring and enforcement), differences in scale, transaction costs, and the nature of the actor groups (individuals vs. nation-states) create wicked problems in which Hardin's tragedy may be inescapable. Although Araral differs from Stern in that he discusses specific cases of large-scale commons failures to support his theory, including forests in Indonesia, these examples appear to be chosen haphazardly and are only discussed in a cursory fashion, so again, it is not clear if his theoretical reasons are well supported or are merely speculation.

The project reported on in this special issue aims to evaluate the questions raised by Araral and Stern in a systematic fashion. Because prior authors seem to disagree about what aspects of scale are theoretically most relevant – or even whether CPR theory is applicable beyond the local scale – we follow an inductive research strategy, aiming to identify what aspects of CPR theory may be relevant or difficult to apply to the Indonesian forest case. In this regard, our case and the others in this special issue, suggest that the pessimism about applying CPR theory to understanding large-scale systems is not necessarily warranted. Although our reporting negative outcomes appears to support Araral's contention that large-scale commons problems may be particularly difficult to resolve, we also show that most of the causes of unsustainable forest management in Indonesia are not scale-dependent. Put in other words, the failures of forest management in Indonesia should probably be seen primarily as a symptom of the difficulties of resolving commons dilemmas at any scale, rather than a particular problem unique to large-scale commons. Moreover, because we follow this inductive strategy, we also engage with two additional frameworks that have been applied by scholars from other traditions to study large-scale forest commons: "Land Use and Cover Change" (LUCC) and political ecology.

The literature on LUCC grew alongside CPR theory in the 1980s and 1990s, driven in part by the easy availability of remotely sensed data on forest cover change. These studies used remotely sensed data and macro level demographic and economic variables such as population, economic growth, market prices, tenure security and the rule of law, and infrastructure projects such as roads to understand patterns of change in forest cover, often at large scales (Lambin et al., 2001; Geist & Lambin, 2002). CPR scholars have critiqued land use and cover change studies for abstracting away from the agency of local communities in conserving or destroying their local forests (Gibson et al., 2000). Furthermore, LUCC scholars have critiqued their own literature for inattention to the ways that policies and other forms of collective action influence forest management (Rudel, 2008), an area where CPR theory may be well suited to making a contribution.

Political ecology offers an alternative conceptualization, focused on the influence of macro-level historical and political-economic factors –such as governments seeking to extract rents or votes, large corporate interests, macro-economic crises, and unequal power relations between communities and the state– on local collective action. As with CPR scholars, political ecologists drew on anthropological research showing communities' ability to organize and devise local institutions to manage resources collectively. Yet whereas CPR scholars have been more interested in the local-level dynamics and characteristics that facilitated this local collective action, political ecologists' focus has tended to be on how governments, markets, corporations, or other powerful actors, oppress communities and prevent local autonomy in resource management (e.g. Peluso, 1992). An additional concern is the deleterious effect of privatization and commodification (the expansion of markets) of natural resources (Peet & Watts, 2004; Peet et al., 2001). While political ecology offers insight into the influence of large-scale factors on local level changes, which we will show here may be used to complement CPR theory, it has somewhat less to say about the influence of these factors on large-scale outcomes, and thus suffers from some of the same limitations of CPR theory for exploring large-scale governance.

Methods

As with the other papers in this special issue, this paper follows methods that were developed collaboratively as part of the Social Ecological System Meta-Analysis Database (SESMAD) project, and are described in greater detail by Cox (2014). SESMAD collects systematic information on the social and ecological attributes of large-scale social-ecological systems, the basic unit of analysis, through content analysis of published studies. For the Indonesian forest case, information was gathered through a review of secondary sources, including peer-reviewed publications and grey literature published by reputable organizations such as the Indonesia-based Centre for International Forestry Research (CIFOR) and the Food and Agriculture Organization (FAO). Controversial data and information gaps were filled with the aid of area experts.

Co-author Brent Loken was conducting field research in Indonesia at the time of writing, and thus was able to add considerable knowledge based on his own research.

Information gathered was used as the basis for entering data into the SESMAD database, a relational database hosted at Dartmouth College (see Cox, 2014). This database contains information on approximately 200 variables of relevance to the study of social-ecological systems (SESs), including variables important to CPR theory, as well as variables not emphasized in CPR theory, but important in other theories about the performance of social-ecological systems. These are stored in tables describing the SES itself, its components, and the interactions among these components. The structure of the database is based on Ostrom's SES framework (Ostrom, 2007; 2009) as modified by Cox (2014).

The case table collects general information on the SES, which is defined as a unit containing at least one environmental commons, at least one governance system, and one or more actor groups that relate to the commons within the context of the governance system. An SES in the SESMAD framework then can have these three types of components. A governance system (referred to as GS in figures) is a set of institutional arrangements (including rules, policies, norms, and other governance activities – see Ostrom, 2005) that are used by one or more actor groups to interact with and govern a commons (for a similar definition, see Lemos & Agrawal, 2006). An actor group (A in figures) can be comprised of individuals, organizations, or nations that have developed a set of institutional arrangements in order to manage human interactions with a specific environmental system. An environmental commons (EC in figures) is an environmental phenomenon that can be subjected to human use and governance – in this case, forests in Indonesia. Within the relational database, interactions between these components are stored as records in the interactions table and in tables that link the interactions to individual components, and are labeled as such. Different interactions frequently represent different "snapshots" of time within the same case. When this is the case, we have labeled the interactions to reflect these different time periods.

Figures 7.1 and 7.2, described in more detail in the results section below, show how this framework was operationalized for this case for two separate time periods: the boxes in the figure refer to the actual tables in the relational database (the case table is not represented as it is general to the entire case), while the connecting arrows represent the linking tables.

Our focus in this paper is on the analysis of key variables that CPR theory has identified as making a major contribution to the potential for collective action. We focus on 17 variables emphasized in Agrawal's (2001) synthetic review, as well as on other seminal theoretical works and syntheses (Ostrom, 1990; 1992; Poteete et al., 2010; Cox et al., 2010). These variables are all measured in the SESMAD database, along with a large number of other variables, including those emphasized in other theories such as political ecology and land use and cover change. Our aim in focusing on these variables is to identify, in the absence of specific and well-developed theories about the impact of scale on commons governance, whether those variables emphasized in CPR theory – or in political ecology and LUCC – can be applied to understanding forest management at the scale of the nation state, and if so, what their influence might be.

Inferences about the empirical relevance of the CPR variables were made in three steps. First, we examined whether the values of variables during the New Order Regime (1965-1998 – see next section) correlated with forest outcomes in the ways predicted by CPR theory (e.g. did a lack of monitoring contribute to worse forest outcomes?). Second, we explored whether changes in these variables from the New Order period to the Democratic period (1998-present) were correlated with changes in deforestation rates, allowing us to make multiple observations within a controlled environment (King et al., 1994). Third, we used process tracing to assess whether there was a potentially causal relationship between the values of a variable and changes in deforestation rates (George & Bennett, 2005; Collier, 2011). Through this process, we were also able to observe that other variables not emphasized in CPR theory were playing an important role, and we conducted the same analysis with these variables that were identified inductively. In many cases, other authors had already conducted similar process-tracing exercises, and where there appeared to be widespread agreement about the process and the underlying causality associated with it, we have reported that result.

Results

Case synopsis and timeline

Table 7.1 Major events in the history of Indonesian forests since 1965.

	Date	Event
Snapshot 1: “New Order” regime 1965 - 1997	1965	Sukarno sidelined by Suharto & placed under house arrest
	1967	Basic Forestry law asserts central govt. control over all forests. Logging permits granted by local govt. to small-scale enterprises.
	1970-1	Central government revokes local logging permits. Large-scale concessions begin to be granted to political allies of regime.
	Early 1980s	Transmigration program: Javanese moved to outlying islands. Erosion of customary (“adat”) law Ban on log exports forces concession holders to invest in plywood and pulp processing, which are subsidized
	Late 1980’s	Development of Industrial Timber Plantations
	Mid 1990s	“forestry crisis” – high levels of deforestation, overcapacity in wood processing sector, decline in timber concessions Rise of coal mining & palm oil industries
	1997	Asian monetary crisis hits Indonesia
	1997-8	Massive forest fires due to El Nino droughts & extensive logging.
Snapshot 2: Early democratic era 1998 - present	1998	Fall of Suharto’s government, democratic elections Villagers demand local control over resources Log export ban removed
	1999	Laws grant greater autonomy and revenue control to districts, districts permitted to grant small forest concessions
	2000	Constitution amended to recognize customary law
	2002	District government authority to grant concessions suspended
	2004	New laws reverse trend towards regional autonomy
	2006	National Land Reform Program begins
	2009	President commits to reducing CO2 emissions by 26% by 2020
	2010	Norway and Indonesia sign REDD+ partnership aimed at reducing emissions from deforestation and forest degradation
	2011 and 2013	2 year ban implemented (2011) and extended (2013) on new logging & forest conversion concessions
	2013	Indonesia’s Constitutional Court invalidates the Indonesian government’s claim to millions of hectares of forest land

Table 7.1 provides an overview of the major events that have affected forest management in Indonesia. The first time period we examine in depth is the period from 1965 to 1998, which coincides with the dictatorship of Suharto. The second time period, beginning in 1998, and lasting up until the present, begins with the fall of Suharto and the onset of democratic elections at the national level and decentralization.

Structure of the case

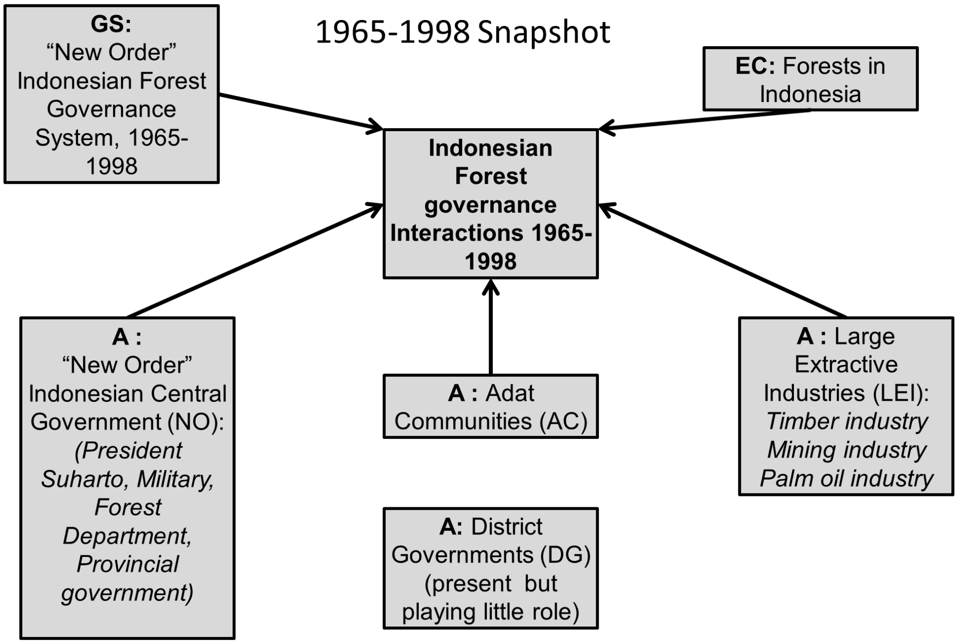

Figure 7.1 The structure of Indonesian forest governance during the "New Order" period, 1965-1998

From 1965 to 1998 the Indonesian forest governance system was dominated by a single actor, the Indonesian central government with President Suharto at its center. This was a top-down governance system that suppressed most forms of self-organization, raising doubts about whether those aspects of CPR theory which focus on self-organization will apply here. The workings of this system have been extensively documented elsewhere (Peluso, 1992; Dove, 1996; Poffenberger, 1997; Dauvergne, 1998; Brown, 1999). Suharto maintained the political support of elites, particularly military officers, through dispensing patronage, often in the form of timber, mining and plantation concessions. The taxes and royalties generated by timber extraction flowed to the government in Jakarta. Thus the establishment of large-extractive industries was closely connected with the central government and, in particular, the military, which held many concessions and was frequently called upon to defend the claims of concessionaires (Peluso, 1992; FWI/GFW, 2002). Concessionaires in turn worked their connections to influence forest and other related policies, both in terms of the regulation of concessions and in terms of trade policies for the timber sector (Ross, 2001). Groups of people ("Adat Communities") who had formerly possessed customary rights ("Adat") to use the forest continued to harvest products. The formal rights of these people to use the forests were eliminated, and people who attempted to use these rights were frequently and violently suppressed by powerful concession holders and the government. However, resistance was widespread and in some areas, particularly those that were remote or difficult for the military to access, local communities were able to enforce their own rules on community members, and even in intimidating concessionaires into following local rules (Palmer & Engel, 2007).

Economic and political tensions within the elite, and between the elite and the rest of the population, contributed to the fall of Suharto's government in 1998 (Fukuoka, 2013). A new democratic constitution dramatically altered the formal structure of the central government, decentralized substantial amounts of power to district governments, formally recognized customary rights, and opened up new spaces for local political and economic entrepreneurs, as well as media and civil society actors to play a role. The result was an entirely new governance system, with new or newly empowered actor groups. In particular, this governance system provided much greater (though still limited) opportunities for self-governance at local, regional and national scales.

Substantial responsibilities that formerly rested with the central government were moved to the 465 district governments (few responsibilities were given to the 34 intermediate provinces). The exact details of these arrangements varied over this time period, with districts briefly claiming the authority to grant small timber concessions from 1998-2002. Forest department field personnel were transferred to the district government, and district governments developed local level patronage networks between locally prominent politicians and businessmen (McCarthy, 2000; 2001; Barr et al., 2006; Wollenberg et al., 2006; Arnold, 2008). Decentralization provided new opportunities for local politicians and entrepreneurs to develop local patronage networks. Adat communities were formally recognized, and although their power remained weak, formal recognition and decreased suppression did provide them with greater means to build networks and increase their involvement in forest products trade.

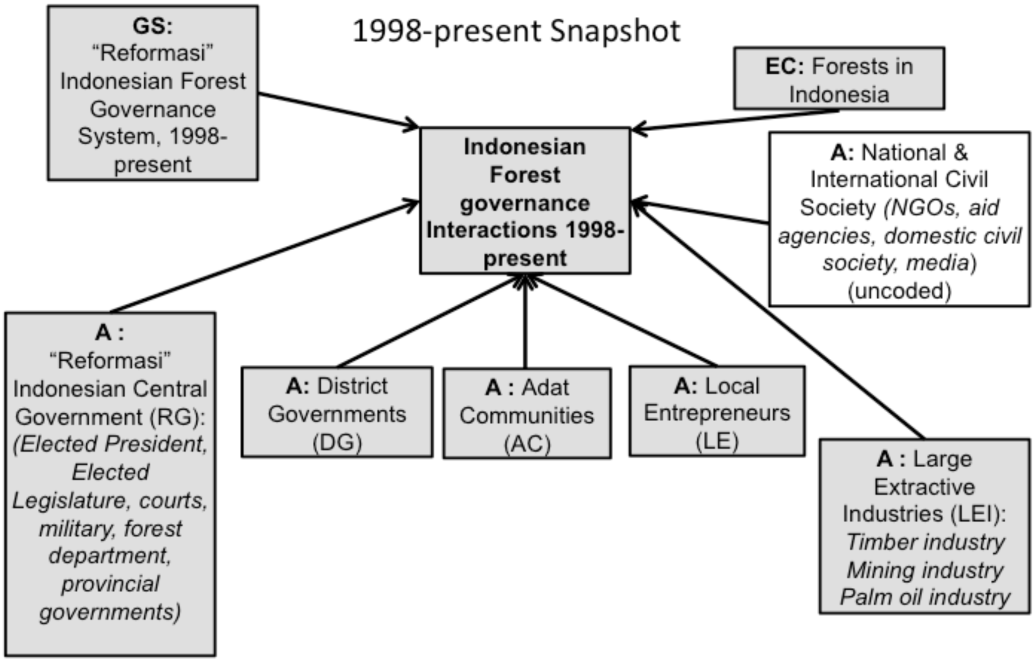

Figure 7.2 **The structure of Indonesian forest governance during the "Reformasi" period, 1998-present**

Changes after 2005 were driven by newly emergent actors, including a growing local and national civil society and media freed from restrictions under the dictatorship, as well as international civil society groups and aid agencies. Following the 13th meeting of the Conference of Parties of the Intergovernmental Panel on Climate Change hosted in Bali in 2007, Indonesia has been involved in an increasing number of agreements to prevent or sequester carbon emissions through improved forest management. Additionally, forest certification under the Forest Stewardship Council and more recently, the United Nations REDD (Reduced Emissions from Deforestation and Degradation) program have played significant roles in changing forest management in some areas (see Dauvergne, 2005; 2011 and Murdiyarso et al., 2011).

Social-ecological outcomes

We focus first on forest cover and deforestation rate as the primary measure of the effect of governance on resource conditions. While there are other measures of resource conditions, such as conditions of remaining forests, or presence of a diversity of species, data on these are not widely available, and forest cover is a decent proxy for the overall ability of the forest to provide ecosystem services. Forest cover data for Indonesia is difficult to obtain due to persistent cloud cover in the region, as well as low levels of investment in government monitoring, so we report the best available estimates, drawing on data from multiple sources. Forest Watch Indonesia and Global Forest Watch (2002) provide the oldest estimates of forest cover in Indonesia, basing their data on old government documents. According to these documents, forests in Indonesia covered 162.29 MHa in 1950 and 119.7 MHa in 1985, and 100 MHa in 1997, yielding an average annual rate of forest loss of 1.2 MHa between 1950 and 1985 and 1.64 Mha between 1985 and 1997. Since available sources imply that there was limited deforestation between 1950 and 1965, actual rates between 1965 and 1985 may have been higher. Other measurements place the deforestation rate for the decade of the 1990s slightly higher, consistent with the story that deforestation rates were at a peak during the final years of the Suharto regime (see Table 7.2).

Available data indicate a fairly dramatic drop in deforestation rates between 2000 and 2005 (see Table 7.2), followed by a rise from 2005-2012, though there is disagreement about the magnitude of the rise. FAO data indicate a modest rise to rates still substantially lower than those experienced in the 1990s, but Hansen et al.'s latest remote-sensing based estimates (2013) indicate that deforestation rates for 2011-12 have returned to 1990 levels (see also Margono et al., 2014). This large discrepancy between published estimates introduces substantial uncertainty into our analysis: while it is clear that deforestation rates dropped in the immediate aftermath of the 1998 transition, it is not clear if that drop was sustained (supported by FAO data) or whether it was a temporary slow-down that has not been sustained (supported by Hansen et al.'s data). We believe that Hansen et al.'s (2013) estimates may be more accurate, since the FAO data is based on government self-reports, while Hansen used rigorous remote sensing methods that have been subject to peer review, however further replication of Hansen et al.'s results are needed before they can be accepted as definitive. Margono et al. (2014) report that a major source of the difference between FAO and independent remote sensing estimates by Hansen et al. (2013) and Margono et al. (2014) is an overly restrictive definition of forests adopted by government reports (and thus reflected by the FAO).

Table 7.2 Estimates of deforestation rates in Indonesia from 1990-2012.

	1990 – 2000 (95 % CI)	2000 – 2005 (95 % CI)	2005 – 2012	Source
Average annual forest loss	1.78 Mha (1.40 – 2.16)	0.71 Mha (0.54 – 0.88)	1.6 Mha	Hansen et al. 2013 Hansen et al. 2009
	1.914 Mha	.310 Mha	.685 Mha	FAO (2010; 2013)

While systematic data on forest outcomes other than forest cover are not available, anecdotal evidence allows us to make some limited claims. First there has been an increase in the rights of indigenous people to manage and benefit from their forests since 1998 (Arnold, 2008), and an increased influence of local communities on the terms of logging contracts with timber companies, as well as increased benefits from logging to local people (Engel & Palmer, 2006; Engel et al., 2006). Benefits to local communities still remain limited, however a landmark ruling in May 2013 by Indonesia’s Constitutional Court invalidates the central government’s claim to millions of hectares of land. This ruling could potentially give indigenous and local communities the right to manage their customary forests (Butler, 2013a). Improving the rights and capabilities of indigenous people to manage their forests is a substantively important outcome in its own right, and it is also a factor, which may have contributed to lower deforestation rates. Data is not available on the effects of access to forest products on poverty among forest dependent people. Second, while deforestation rates remain high, there are also significant levels of damage being done to forests through intensive harvesting that does not remove crown cover (i.e. degradation), but existing data do not quantify these levels of damage, so it is difficult to determine whether degradation rates are rising or falling. Finally, while illegal logging continues to be a substantial problem, increased international and domestic scrutiny of logging operations and wood-product exports have resulted in some modest improvements (Obidzinski et al., 2007).

Influence of important CPR variables

In order to assess the utility of CPR theory for explaining forest management in Indonesia, we must answer two distinct questions. First, why were deforestation rates high during Suharto's reign? Second, why did they decline after 1998 but rise to significantly higher levels after 2005? We show how causal configurations present in each period may explain the results, while recognizing how our ability to make inferences is limited both by uncertainty in outcome data, as well as by indeterminacy in the causal configurations we observe. Furthermore, while some changes in the values of variables are correlated with the effects that would be predicted by CPR theory, process tracing indicates that these variables may not be the most important causal factors. Instead, changes in other economic and political variables not normally emphasized in CPR theory may be more important. A summary of the major variables, which may be important is presented in Table 7.3.

Table 7.3 Theoretically important variables used in this case.

Theoretical variable	Suharto "New Order" period 1965-1998	Democratization & "Reformasi" Period 1998-present
Social variables		
Social monitoring	Central govt. does little monitoring. Some adat communities also monitored their own behavior and that of timber concessionaires.	Govts. do some monitoring, as do local communities, civil society groups, and international agencies. Satellite technology makes monitoring cheaper.
Leadership	Dictator is strong, not accountable, and extraction oriented.	Leadership diffused between multiple levels of elected govt. & civil society.
Proportionality of costs & benefits	Timber revenue & taxes flow to central government & associated timber companies. Many costs passed on to future generations or local communities.	Benefits continue to flow to large companies & central actors. District govts. & adat communities bear costs, but tax revenue from forestry goes only to central govt.
Governance variables		
Nesting & Multilevel	Strong centralization. Little multilevel governance.	Complex multilevel relationships develop between central & district govts., adat communities, industries, civil society & international actors.
Group size	Small number of actors with power consolidated within Suharto's inner circle.	Large number of actors with power decentralized across Indonesia.
Sanctions	Govt. sanctions applied to rural poor but rarely to politically powerful. Adat communities have informal sanctioning systems.	Formal sanctioning authority shared btwn levels of govt. In last 5 years sanctions are increasingly applied to powerful interests.

Collective choice	Central government made most decisions, and some of the large extractive industries played an important role. Other collective choice venues were suppressed.	Numerous collective choice venues created at national and local level. Central politicians & industries play the largest role, but small industries, local politicians, media, & civil society have some access.
Rights to organize	Only central, politically powerful actors have rights to organize.	Formal rights to organize spread to districts, adat communities, civil society, and media.
Tenurial security	Tenurial security very weak for local communities, and somewhat weak for concessionaires.	Tenurial security improves for all actors, but remains weak.
Dependence on resource	All actors are heavily economically dependent on forest. Adat communities also have a high level of cultural dependence.	
Non-CPR variables		
Intl. markets	High prices for timber & exhaustion of other sources lead to large interest in Indonesian timber products.	While timber prices drop, prices for coal & palm oil encourage forest conversion. Indonesian recession in 1998 also suppresses all economic activity.
Intl. politics	No influence.	Forest Certification (FSC) & funding for Reduced Emission from Deforestation and Degradation (REDD) are influences on forest management.
Intention of governance system	The governance structure was specifically designed for large-scale and rapid extraction of timber as a strategy for economic growth and political stability.	Governance system is more balanced between path dependencies from extraction-orientation & new pressures for conservation.
Top-down state intervention	Top-down intervention is aimed at timber extraction (see Intention, above).	Since 2010, central govt. has committed to policies to conserve forests in exchange for support from developed countries wishing to offset carbon emissions.
Clientelistic relationships	Clientelistic relationships between President & military & political elites facilitated by granting of timber concessions.	Clientelism also pervades local govt, which frequently favors local industries including illegal loggers & plantations.

Significance of variables during the New Order period, 1965-1998

Although there are a number of variables that account for high deforestation rates in the New Order Regime, we find that two connected variables appear to be the primary underlying causes of deforestation: the intentions (or goals) of the governance system (to overexploit the commons), and the presence of strong leadership. These variables interact: General Suharto, a dictatorial leader, was the person who –coalescing with political and corporate interests that supported him– designed the governance system with the intention of maximizing short-term revenues at the expense of sustainability. There is a consensus among studies conducted during this period that these two variables were essential underlying causes for Indonesia's high deforestation rates (e.g. Barr, 1998; Brown, 1999; Dauvergne, 1998; Dove, 1996; Dove & Kammen, 2001; Peluso, 1992; Poffenberger, 1997). According to these authors, the high degree of centralization, lack of monitoring and sanctioning of forest extraction, and the undermining of local tenure, rights to organize, and collective choice processes were all results of the combination of a strong leader with an intention to overexploit the commons, and were thus secondary or proximate causes of deforestation. There is also some evidence that the most important direct driver of deforestation may have shifted in the 1980s. Prior to about 1985, state-assisted colonization by small-holders played a very important role in deforestation in Indonesia, but by the 1990s, large-scale enterprises (e.g. large plantations or logging concessions) were causing most of the deforestation in Indonesia (Rudel et al., 2009). We follow these authors in using these process-based accounts, which emphasize how conditions on the ground were re-shaped by the regime in Jakarta to favor deforestation.

The role of these two variables in this case presents a strong challenge to CPR theory. The intention or goal of governance systems is not generally considered in CPR theory, which tends to assume that sustainability is the governance goal. There is abundant evidence that the governance system was designed to enrich Suharto and his political allies while alleviating potential political tensions in Java by encouraging industrial development and out-migration to the outer (forested) islands. Forest destruction was an intentional byproduct of this system. The system worked through clientelism: concessions were granted to Suharto's allies, particularly members of the military, who aimed to extract as much money as possible from the country's vast forest estate, with little concern for longer-term sustainability (see e.g. Peluso, 1992; Brown, 1999; Dove & Kammen, 2001; Ross, 2001). The importance of intention has been emphasized to a much greater degree in political ecology, which documents how environmental degradation is often the intentional result of policies designed to benefit various powerful elites at the expense of other, typical poor and or indigenous users (Blaikie, 1985; Peluso, 1992; Dove, 1996). Given the abundance of timber in Indonesia, Suharto and his allies did not seem particularly concerned about exhausting the commons, but they also believed that the profits from timber extraction would lead to long-term economic development, enabling them to escape from dependence on timber.

Similarly, CPR theory has largely assumed that leaders are political entrepreneurs who assist in overcoming collective action problems that hinder sustainability (Ostrom, 1992; Poteete et al., 2010). In this case, strong leaders pushed the system away from sustainability. Suharto's leadership enabled elites to overcome collective action problems that might have previously prevented them from exploiting forest resources on the outer islands (McLeod, 2000). In addition, Bob Hasan, a timber entrepreneur and close ally of Suharto, helped organize concession holders and reinforce their political power within the broader national governance system (Barr, 1998). These leaders did help overcome collective action problems, but they did so in ways that increased the pressure for resource extraction. This finding is particularly disturbing for CPR theory, which has largely equated collective action with sustainable management.

The importance of the intention of the governance system and of strong leaders in encouraging unsustainable behavior was discovered here in a large-scale case, however there is no inherent reason why similar dynamics could not take place in the sort of small-scale village level cases traditionally investigated in CPR theory. In fact, this shortcoming of CPR theory has been noted by previous authors (Agrawal, 2001; Robbins, 2011). However our findings here reiterate the finding from political ecology scholarship that we need to look up from the local level to understand how power dynamics at the level of the nation state may affect the distribution of rights at the local level (see e.g. Peluso, 1992; Robbins, 2002).

Variables other than leadership and intent played an important role in the New Order period. These variables, which are explained below, performed largely as expected in CPR theory, but to a great extent their values were proximate causes that were themselves caused by the underlying causes of authoritarian leadership and a system designed to maximize extraction. In addition, global market forces, a variable poorly captured in CPR theory, probably also played a role in increasing deforestation by keeping international demand and prices for Indonesian timber and agricultural products high.

According to CPR theory, users with tenurial security, rights to organize, and participate in decision-making about resource management (i.e. collective choice) are more likely to contribute to long-term sustainable management (Ostrom, 1990). Tenurial security is represented in Table 7.2 by several other variables, including the existence of monitoring and sanctioning and collective choice mechanisms. In Indonesia under Suharto, tenurial security of all resource users was very limited, while rights to organize and participate in decision-making were confined to a narrow group of elites who, as noted above, wished to liquidate forest assets and convert them to financial assets. These variables were largely the result of the authoritarian, patronage based political system. According to Di Gregorio (2011), the heavily centralized administration system “filtered down to every village in the vast archipelago”, so that the Suharto regime “effectively controlled” the forest areas. Local villagers were deprived of rights to organize formally, local leaders were coopted, and local collective choice mechanisms were destroyed, leading to increasing and uncontrolled agricultural colonization in some areas (Heydir, 1999). Concessions were granted without regard to existing customary uses, and with limited monitoring or sanctioning, industrial interests often harvested timber outside of their legally granted areas, often with military support. Concessions themselves were of limited duration and could be reassigned based on political concerns.

The lack of tenurial security and rights to organize and participate contributed to deforestation in several ways. Insecurity, combined with weak monitoring and enforcement, contributed to the near open-access environment in which timber companies sought to grab as many resources as possible as quickly as possible (Ross, 2001; Colfer & Resosudarmo, 2002). Without rights to organize and participate in decision-making, disenfranchised users may have also contributed to uncontrolled deforestation. Furthermore, voices that may have promoted conservation were silenced or bought off by the central state, decreasing the opposition to unsustainable logging.

Perhaps the most strongly supported variables in the literature on the management of forest commons are those related to social monitoring and enforcement. Weak monitoring and sanctioning systems played a role in the high deforestation rates in Indonesia under Suharto, as CPR theory would predict. Local users were stripped of formal authority, and any attempts to enforce local customs ran the risk of state oppression. CPR theory has not clarified the relationship between central governments and local monitoring and enforcement. However, Indonesian forest department authorities in the outer islands had “little or no regulatory oversight” (Colfer & Resosudarmo, 2002; p. 4), and rarely enforced any sanctions against timber concessionaires who violated the rules (Ross, 2001) or against farmers who illegally expanded cultivation (Heydir, 1999). Bureaucrats in Jakarta were in a weak position to enforce regulations on powerful actors (Ross, 2001). Even if it had been willing, it is not clear how the government could have enforced its rules in vast, remote areas where it had little authority and where local users were stripped their political power. Unsustainable rates of timber extraction led companies to increasingly remote areas, which in turn increased the difficulties of monitoring and enforcement of forest management rules (Gellert, 2010).

Similarly, a lack of proportionality between benefits received from timber extraction and the costs of deforestation contributed to increased deforestation, particularly through its interaction with levels of economic dependence. Benefits from timber extraction activities flowed almost entirely to elites associated with the central state in Jakarta, yet these people bore few of the costs from deforestation and thus had few incentives to reduce their extraction, particularly given the fact that the spatial extent of the resource was sufficiently large that they could not reasonably expect to exhaust it within their lifetimes (Ross, 2001). Central state actors were dependent on the forest, in the sense that forest resource extraction formed the core of their economic activities, but their activities could be moved from one patch of forest to another, or even from one industrial sector to another, and thus the loss of any particular forest patch did not hurt them, even if it did hurt local forest-dependent communities. In a sense, these actors could be compared to the “roving bandits” described by Berkes et al. (2006) – mobile resource harvesters with high discount rates who move from place to place depleting resources – however in this case, their actions were primarily contained within Indonesia. This conception of proportionality differs somewhat from conventional CPR theory, which emphasizes proportionality between benefits derived from using a resource and the costs associated with contributing to public goods to make the resource available.

Significance of Variables in the Reformasi Period: 1998-Present

Political reforms following the fall of Suharto in 1998 transformed governance in Indonesia. These reforms correlated with a significant decline in the deforestation rate, but the deforestation rate remained high in the international context, and began to rise again after 2003 (Hansen et al., 2009; FAO, 2010; Hansen et al., 2013). Many analyses focus on the reasons for continued deforestation and the shortcomings of the decentralization and democratization processes (e.g. Colfer & Resosudarmo, 2002; Arnold, 2008), but there are few analyses which attempt to explain why deforestation rates first dropped, and then rose again, and the evidence we present here does not lead to definitive answers, particularly since the extent of the post 2003 rise in logging rates is contested.

Significant changes occurred in the governance of Indonesian forests after 1998, which we would predict would lead to decreased deforestation. In particular, the presence of strong leadership, one of the causes that we identified as contributing to high deforestation rates under Suharto, was removed. In addition, the governance system moved slowly but significantly towards a more inclusive and participatory political order that CPR theory predicts would lead to more sustainable resource governance. These trends, while still limited, appear to have strengthened over time, with the gradual consolidation of democratic rule, and with the government of Indonesia making significant public commitments to forest conservation.

At the same time, although forest clearing initially declined after 1998, it has risen significantly since 2003, with some estimates placing current forest clearing rates as high as those of the 1990s. Two possible explanations for this rise are plausible: first, the governance changes described above may have been insufficient and/or have led to the development of a new order which favors deforestation (i.e. the intention of the governance system may have remained the same), and second, other non-governance factors may be driving changes in deforestation rates. Economic factors may be particularly important: governance changes in 1998 were triggered by a severe economic crisis which crippled economic activity, and in a broad sense the decline and subsequent rise of deforestation correlates with the decline and subsequent recovery of Indonesia’s economy. Unfortunately, the existing literature on which this review is based is not very helpful in differentiating these causes. Most studies conducted on the post 1998 period have focused on using governance variables to explain continuing deforestation, but have not attempted to explain the drop and subsequent rise in deforestation rates, nor have they examined whether governance variables or economic variables were more important in these changes. Detailed remote sensing studies have focused on documenting changing deforestation rates, but have not been structured to understand the causes of change (Hansen et al., 2009; Broich et al., 2011; Margono et al., 2012; Hansen et al., 2013; Margono et al., 2014).

Governance reforms after 1998 focused on democratizing the central government, decentralizing power to elected district governments, and opening up room for greater public engagement through a freer press and civil society. These led to changes in several of the key variables emphasized by CPR theory, in directions that CPR theory would predict would favor better resource governance. In particular a more participatory leadership, decreases in centralized power, increasing monitoring and enforcement efforts, new vertical and horizontal interplays between different stakeholders, and new political opportunities in a more open political system would all be predicted by CPR theory to contribute to lower deforestation. In addition the removal of the authoritarian leader with a strong personal and political interest in encouraging forest clearance, the most important causal factors identified above, would in and of itself be predicted to encourage lower deforestation. All of these factors could have contributed to the decline in deforestation after 1998, but it is difficult to sort out their effects from the effects of the economic downturn. Furthermore, the exhaustion of easily accessible lowland forests prior to 1998 may have made it difficult to sustain high clearance rates, regardless of governance or economic changes (Hansen et al., 2009). However if exhaustion drove a decline in clearance rates in 1998, it is not clear why deforestation rates rose again after 2005.

At the same time, political reforms have opened up spaces for a broad variety of new actors. Some of these actors have used their newfound rights to organize and access to collective choice processes to push for decreased deforestation, while new, democratically elected leaders are more open to listening to the demands of rural social movements and are committed to effective conflict resolution processes for land struggles (Dermawan et al., 2006; Di Gregorio, 2011). The pressure of media, political parties, and local organizations for accountability – and for decreased deforestation – appears to be increasing over time as these groups gain experience and power in the new political system (e.g. see Lang, 2012). Although elements of the old oligarchy retain power, our finding that new actors are having a real impact on the governance process is in contrast to literature that argues that Indonesia remains stuck in a closed, oligarchical form of democracy (Fukuoka, 2013).

CPR theory would predict that these changes would consistently lead to better resource governance, but the evidence shows that even as this democratic consolidation has taken hold in Indonesia, forest clearance has increased. However the decentralized political order has also created opportunities for many more actors at local and regional levels to pursue political and economic power through overuse of resources, and these opportunities may be driving the increase in deforestation. This could, in fact, be consistent with CPR theory: decentralization and political empowerment in Indonesia may not support improved resource governance because it has failed to empower the appropriate set of actors (Agrawal & Ribot, 1999; Gruby & Basurto, 2014). Decentralization has empowered district governments but not the resource users themselves, who still face serious barriers to their exercise of power (in spite of their improved position relative to the Suharto era), and it is the empowerment of resource users, not decentralization in general, which leads to improved outcomes in CPR theory (see e.g. Chhatre & Agrawal, 2008; Persha et al., 2011).

In spite of reforms beginning in 1998, the reality of weak land tenure remains for many rural land holdings in the outer islands of Indonesia (Barr et al., 2006; Elson, 2011). Similarly, monitoring and sanctioning of timber concessions, and of the growing number of palm oil plantations and mining operations, was largely nonexistent. This seems to have changed slightly in recent years, with a few high profile cases of sanctions. These may be the result of increased civil society pressure, or improved satellite-monitoring technologies (Obidzinski et al., 2007; Lang, 2012). Despite this, Indonesia remains a center for illegal logging and land conversion activities (Tacconi, 2007; Dauvergne & Lister, 2011). This can be understood from the perspective of political ecology, particularly the study of the politics of decentralization (e.g. Ribot et al., 2006; Poteete & Ribot, 2011), which have observed a tendency to recentralize authority in powerful actors in these processes; and political ecology analyses of the politics of multi-level/cross-scale governance, which has emphasized that the definition of what decisions are taken at which scales is a power- and conflict-laden process (e.g. Gruby & Basurto, 2011; Thiel & Egerton, 2011).

The second interpretation of decentralization's potential negative effects on forest management is a greater challenge to conventional CPR theory. There is a large body of research demonstrating that local governments tend to be more oriented towards economic development than larger scale entities (Peterson, 1995), and at least some research demonstrating that in the US, state governments are less oriented towards protecting natural resources than the national government (Koontz, 2002). This is in contrast to an assumption frequently made in CPR theory that local groups will conserve resources given the opportunity (although for a cogent critique of this assumption from within CPR theory, see Agrawal & Gibson, 1999). Indonesia possesses great natural resource wealth, and there is no a priori reason for assuming that distributing power to lower levels and smaller spatial scales would not recreate the dynamic that existed in the Suharto era, in which political leaders see their fortunes tied to the development, rather than conservation, of this natural resource wealth. While it is not clear if this is occurring, there is clear evidence that forest-clearing industrial development (e.g. plantations, mining, etc.) plays a growing role in Indonesia's economy (Gellert, 2010). For example, a recent study in West Kalimantan found that in 2007–2008, 27% of deforestation was ascribed to palm oil plantations, whereas over the entire period of 1994 to 2008, only 6% of deforestation was attributable to the creation of palm oil plantations (Carlson et al., 2012). This growth could create political incentives for local elites to take advantage of decentralization to promote deforesting industries. Tax policy could provide further incentives for local governments to favor deforestation, because while the central government collects all timber revenues, district governments only receive tax revenue from agriculture and mining. Therefore, local governments have strong incentives to increase the quantity of agriculture and mining in their districts, at the expense of forest.

The political pressure coming from internal groups is joined by increasing outside pressures in various forms, which are not well captured in current CPR theory: global forces and top-down state intervention. There is a tendency to focus on fluctuations in global market prices as drivers of domestic policy changes, however, other international forces have promoted improvements in forest governance, such as growing forest certification initiatives (Cashore & Stone 2012; Bartley, 2010; Dennis et al., 2008; Tacconi, 2007) and local interventions of international NGOs (Engel et al., 2006). In May 2009, Indonesia became the first country to enact regulations for a national REDD program (Barr et al., 2009) and in 2010 the government of Norway pledged up to US$1 billion to support development of a national REDD program in Indonesia (Murdiyarso et al., 2011). The following year, the president of Indonesia announced a two-year moratorium on new logging concessions (Edwards et al., 2012; Sloan et al., 2012) and in May 2013, this moratorium was extended for two more years (Butler, 2013b). The moratorium, enforced by the central government, as well as the action by international state actors (e.g. Norway) and non-state actors (e.g. International NGOs and the Forest Stewardship Council) illustrate examples of the ways that global forces and top-down state interventions could interact to reduce deforestation at large scales in ways that are poorly theorized by CPR theory. At the same time, the apparent ineffectiveness of the ban in reducing deforestation points to the possibility that the central state either continues to lack capacity to make its intention felt in remote areas, or actually continues to see these resources as vital to future economic development, and is actively subverting its own official dictates.

Discussion and Conclusion

Our study demonstrates that CPR theory is helpful in explaining patterns and outcomes in the governance and management of Indonesian forests over the last 45 years, however the theory may need to be revisited, and supplemented with insights from the political ecology tradition, to more fully account for the observed patterns. However, even though CPR theory did not fully explain the case at hand, we cannot dismiss its applicability to large-scale commons. For example, during the Suharto regime, a small but powerful group of actors who were economically dependent on the resource contributed to high rates of deforestation. However the absence of key variables from CPR theory, such as monitoring and sanctioning, tenurial security, participation in rule-making processes and the right to organize also emerge as important causes of deforestation, and changes in these variables may help explain some of the reduction in deforestation rates immediately following the onset of democracy in 1998. Not all variables from CPR theory, however, worked in their expected direction: strong leadership is postulated to enable overcoming collective action dilemmas, and thereby encourage conservation, however we found that Suharto's strong leadership contributed to increased deforestation, and local rule-making after 1998 has played an ambiguous role.

Other important variables from CPR theory appear to have little relevance for the case: we found that social boundaries, environmental monitoring, conflict resolution mechanisms, system productivity, and group heterogeneity did not appear to play important causal roles in driving the outcomes observable in the cases. We had difficulty locating information on levels of trust, reciprocity and communication between actors, and thus could not assess their role. There were not glaring spatial mismatches between the scale of the governance system and the scale of the resource. Group size was difficult to assess in this case, since it is not clear what group is relevant to measure, but in contrast to Araral's (2014) argument that large group size makes collective action unfeasible, we did not see clear relationships between group size and outcomes. Several sources argue that not all factors from CPR theory need be present for a case to be successful (e.g. see Ostrom, 1990), so comparison with a larger number of cases will be necessary to determine whether these variables are less relevant for large-scale CPRs generally, or only for this particular case. However this list of variables provides a preliminary list of variables from small-scale CPR theory that may be less relevant at large scales, and should be investigated in future studies.

Our analysis shows that CPR theory needs to be complemented with insights from other theoretical traditions to be useful for understanding this case. A focus solely on variables drawn from CPR theory would miss important causal factors. CPR theory has largely ignored the impacts of these broader political and economic drivers. Without Suharto's political leadership, his intention to log forests, and the clientelistic system he developed, it is difficult to imagine deforestation on the scale it was observed between 1965 and 1998. These are variables emphasized in political ecology, including in landmark studies of forestry in Indonesia during this period (e.g. Peluso, 1992; Dove, 1996). Without a vibrant international market for forest products during this period, Suharto would not have had such strong motivations to encourage logging. More recently, international markets have encouraged forest conversion for oil palm plantations and coal mines, while international agreements and international NGOs have contributed to increased conservation. The negative role of leadership can also be understood through research on manipulative, corrupt and abusive or so called “dark” leaders in organizational studies, which has been applied recently to study CPR outcomes (e.g. García López, 2012; Theesfeld, 2009).

Again, comparisons with a larger number of cases is necessary to understand whether these variables are important in this case because this case focuses on a larger scale than CPR theory, or whether they may also be important in small-scale CPR cases, yet neglected in CPR theory. Recent studies of small-scale CPRs have emphasized the role of NGOs as interveners in local commons problems (e.g. Barnes & Van Laerhoven, 2013; Barsimantov, 2010), the importance of understanding local power dynamics (e.g. Clement, 2010; Perez-Cirera & Lovett, 2006; Wilshusen, 2009), and the role of international markets in influencing local commons management (e.g. Tucker, 2008), and thus it may be that these factors are equally important, but neglected, in local scale studies of CPRs. In order to examine whether these variables are scale dependent, we will need to conduct additional studies examining the importance of these variables at both small and large spatial scales.

In the introduction to this paper we highlighted a contrast between Stern’s (2011) optimistic view of the value of CPR theory at large-scales, and Araral’s (2014) pessimistic view, and critiqued both authors for giving insufficient attention to empirical cases. Our findings partially support Araral’s pessimism – it is in fact the case that forest clearing in Indonesia continues at a rapid pace. At the same time, supporting Stern, we did not find that there are fundamental differences between small-scale and large-scale systems. Since there are many cases of governance failure in small-scale CPRs, we should expect that large scale CPRs will also not always be well governed, and the existence of an example of continuing weak governance should not be taken as a sign that CPR theory is not applicable to large-scale forest governance.

Araral argued that the failure to halt deforestation in Indonesia was typical of the challenge of governing systems involving large numbers of actors, however we were unable to draw conclusions about the relevance of group size for the governance of Indonesia’s forests. While decentralization certainly increased the number of actors engaged in governing Indonesia’s forests, our analysis points to other factors- notably a continuation of a clientelistic system dependent on resource extraction to support elites and denial of rights to local people – as central to continued deforestation. This is consistent with broader arguments that democratization has not fundamentally changed the exploitative character of Indonesia's democracy (cf Arnold, 2008; Fukuoka, 2013). It also may imply that the failings of CPR governance in Indonesia are not the result of its large scale (as argued by Araral), but instead the result of other factors which could potentially be present in small as well as large-scale cases.

Findings from this study have to be taken with caution for several reasons. First, while CPR theory emphasizes collective action, the linkage between collective action and environmental sustainability is unclear. Establishing a causal connection between cooperation and sustainability may be relatively straight forward in local contexts but it is much less so in large scale-contexts. Second, the political environment in Indonesia has changed rapidly in the last three decades, which further complicates analysis. Third, inferences in this case are drawn with a limited focus on forest policy from 1965 to present. We have not focused on other potentially connected policies like trade or agriculture, nor assessed the variation within or between districts. Finally, our analysis here is based on published literature which leaves great uncertainty on several points, including the extent of recent deforestation, as well as the identity of the main drivers of change in deforestation rates in the post-Suharto era. More in-depth, field-based research needs to be done to understand the nature of these changes, particularly as the international community is investing large amounts of money in policies (such as the ban on new logging concessions) that may not be effective.

Our results point to the value of CPR theory in identifying important variables that influence sustainability at large scales, however they also illustrate important limitations of CPR theory for the study of forests with large spatial extent and large numbers of users, including the study of forests at the level of the nation state. CPR theory tends to assume that actors aim for sustainability, but under Suharto, actors specifically extracted forest resources unsustainably. While these variables are likely to be important in both large and small-scale systems, greater spatial extent may enable predatory and destructive actors to persist in single locations for longer periods of time – a predatory actor or group of actors owning a small forest is likely to degrade it quickly and be forced to move on, leaving little evidence of their actions for scholarly study. By contrast, Indonesia has witnessed decades of overexploitation, yet still has some of the world's largest forest resources.

The finding that CPR theory's most important shortcomings with regards to understanding the Indonesian case are probably not scale dependent supports the use of CPR theory to understand forest management at the level of the nation state or even larger. At the same time, it points to areas where the traditional focus of CPR theory should be complemented with other theoretical frameworks such as land use and cover change and political ecology, which offer deeper insight into some of the drivers of forest change. Assessing whether these theories offer conflicting explanations, or whether they can be usefully combined to generate a more integrative theory of forest cover change, will require investigation of a larger number of cases, as well as more carefully examination of cross-scale linkages that connect patterns observed at the local level to policy-making at the national level. Based on this study, we argue that these studies will need to pay particular attention to the role of power dynamics, governance intention, market forces, and NGO and international interventions to better conceptualize the roles of these variables, while continuing to examine variables drawn from the core of CPR theory. Such studies will also require more consistent and higher quality measures of changes in forest level outcomes across scales.

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Chapter 8.

Conclusion

Most of the earth's biodiversity is located in regions of the world that also have the highest levels of poverty (Sanderson et al., 2002; Sanderson, 2005). Given the juxtaposition of biological wealth and human poverty, many conservation organizations in recent decades have adopted an approach that attempts to simultaneously improve human well-being while protecting biodiversity. Often called community-based natural resource management (CBNRM) this "people centered" approach to conservation (see Introduction) seeks "win-win" solutions and have become highly marketable given that they claim to preserve biodiversity and improve human welfare using a single approach (McShane et al., 2011). However, despite their popularity in recent years, the record indicates that in most cases, a win-win solution is not feasible and trade-offs need to be made between biodiversity conservation and human livelihood (Sunderland et al., 2008; Sandker et al., 2009).

When I first visited Wehea Forest in 2009, there were a number of reasons that I believed this community-based conservation (CBC) initiative had the potential to be an example of just such a win-win approach. First, there seemed to be an enthusiastic and unified indigenous community (Wehea Dayak) who were led by a strong leader committed to conservation. Second, the Wehea Dayak appeared to have a long enduring history of 'self governance' (*adat*) and customary rights to their resource. Third, the forest had clearly defined boundaries and seemed large enough to maintain significant levels of biodiversity, including an estimated population of over 700 orangutans (Herutomo & Dettman, 2010). Fourth, the project was established using a multi-scale institutional arrangement between the local community, district government and private industry and external authorities recognized local rights to organize. Fifth, the forest was monitored by a group of local forest guardians called the *Petkuq Muhuey* and sanctions to rule violators could be levied by the *kepala adat* (head of *adat* or local governing body). Last, there was potential for economic development opportunities arising from protection of Wehea Forest. This initial set of ecological and social factors, which were theoretically supported by common-pool resource (CPR) theory, appeared to set the stage for a win-win CBC project where viable populations of charismatic endangered species could be maintained and the welfare of the local community improved.

However, after five years of working, living and doing research in Wehea, I now believe that given the specific ecological and social factors of this CBC project, a win-win outcome may be not possible. I suspect that either the long-term viability of clouded leopards, orangutans or Miller's Grizzled Langurs will need to be compromised for the sake of human well-being, or the current protected area will need to be maintained at the expense of economic development and poverty alleviation. Below I discuss the interplay of ecological and social factors upon which I draw this conclusion and present possible implications for the conservation of charismatic endangered animals across Borneo.

Ecological factors in charismatic endangered species conservation

Density and abundance of each species

Borneo is blessed with incredible biodiversity. Some of this biodiversity, however, (e.g. orangutans and clouded leopards) are found at relatively low densities across the island, the cause of which is mainly attributed to scarce resources and low productivity of forests. This creates a condition where some species require extremely large areas of habitat to achieve population sizes that might support long-term viability. For example, clouded leopards occur at extremely low densities throughout their known range (see Table 6.1) and in Wehea Forest specifically, I found them to occur at a density of approximately 2 individuals/100km^2 (see Table 6.3) and have large home ranges (see chapter 6). One clouded leopard that I photographed over the course of 3 years was seen regularly at camera trap stations more than 20 km apart and may have a home range greater than 100km^2. Orangutans had a higher density (~ 16 individuals/100km^2; see Table 5.5) than the clouded leopard but a lower density than in other sites across

Borneo (Husson et al., 2009). Although we were unable to calculate a density for Miller's Grizzled Langur, preliminary, unpublished data suggest that it lives in family groups of 5-7 individuals and has a much smaller home range of approximately 1 km^2.

Although accurate information on the density of animal populations is essential to answering central questions in ecology, to infer the vulnerability of the target population under investigation to various threats, estimates of abundance are also necessary (Seber, 1982; Williams et al., 2002; Borchers et al., 2003). The most common method for estimating abundance is to sample a subset of the population and extrapolate across the entire area (Güthlin et al., 2014). In Wehea Forest, due to the challenging terrain and field conditions, I was only able to sample an 80 km^2 area in the most eastern section of the forest (see Fig. 3.1). I then used these results to estimate population sizes of clouded leopards and orangutans for the entire forest (see below). In spite of being widely used, this method can be problematic, since you need to assume that species are uniformly distributed throughout the forest (WWF, 2004). Although uniform distribution is highly unlikely, I did find that orangutans and clouded leopards in the center of Wehea Forest occurred at similar relative abundances when compared to the eastern study site (see Fig. 4.1; Loken & Brodie, unpublished data). Therefore, if I assume uniform distribution in Wehea Forest and use the densities from above, clouded leopards would have a population size of N = 7.6 and orangutans N = 60.8. Given that Miller's Grizzled Langur was only photographed and heard in one section of Wehea Forest, it is difficult to know whether this primate is evenly distributed throughout Wehea Forest or has a more restricted or patchy distribution. However, we were able to identify 3 family groups in the study area and therefore Wehea Forest has at least N = 20 Miller's Grizzled Langurs.

Uncertainty in estimates

Although the densities stated above are useful, they also should be treated with caution given that they incorporate a high level of uncertainty. This uncertainty is not uncommon for animals that are elusive, range widely, and live at low densities (Garshelis, 1992; Karanth, 1995; Thompson, 2004). However, this could lead to either an under or overestimation of the actual population sizes for all three species, which in turn impacts our ability to assess their vulnerability to threats. To highlight this, if we use the largest 90% credibility interval from window 53 (2) in D_{simple} in the clouded leopard study (see Table 6.3), then the true population size may be between 3.65 to 24.43 individuals. For orangutans, the 95% confidence interval indicates the population size could be as low as 34.66 individuals to as high as 110.54 individuals (see Table 5.5), which is considerably lower than the original estimate done by The Nature Conservancy (N = 700; Herutomo & Dettman, 2010). This uncertainty is driven by a number of factors discussed in chapters 5 and 6 and improving on current estimates in Wehea Forest will be difficult if not impossible given the challenging research conditions found in the forest.

Vulnerability to threats for each species

Even after three years of intensive research, I still do not know, with certainty, the population sizes of clouded leopards, orangutans and Miller's Grizzled Langur in Wehea Forest. I can conclude, however, that given my current estimates, each species is vulnerable to local extinction even when anthropogenic threats are excluded from the calculus. Although we don't know how many animals would be necessary to maintain viable populations of each species (Flather et al., 2011), a population viability analysis (PVA) done by Marshall et al. (2009) for orangutans provides some insight into how vulnerable these three populations actually are. If we assume that Wehea Forest contains at least 100 orangutans and there are no external threats (e.g. hunting and habitat loss) to this population, after 1000 years we would have a population size of N = 17 and a 44% probability of extinction. Although we don't have PVAs for clouded leopards and langurs, they may be even more vulnerable to local extinction given that their populations in Wehea Forest are most likely well below 100 individuals.

If external threats are included in the calculus and if these threats increase the annual mortality by only 2-3%, then the orangutan would be driven to extinction in Wehea Forest in only 20 years. On Borneo, as in other tropical rainforests, the 2 main anthropogenic threats to species are habitat loss and hunting (Corlett & Primack, 2011; Brodie et al., 2014). I believe the 3 species studied in this thesis are vulnerable to hunting given that between 1950 and 3100 orangutans on Borneo are killed each year from hunting (Meijaard et al., 2011), clouded leopards are one of the most illegally traded species of big cat (Nijman & Shepherd, 2015), and Miller's Grizzled Langur have already been hunted to extinction in other parts of Borneo (Setiawan, pers. comm., August 2011). An increase in hunting is even more likely as the forests surrounding

Wehea become logged, roads are constructed and access becomes easier (Clements et al., 2014). Prior to 2013, reaching Wehea Forest was limited to one old logging road and took approximately 6 hours by truck from the Wehea village of Nehas Liah Bing (see Fig. 8.1). Beginning in 2013, the primary forest surrounding Wehea Forest was logged, roads were constructed and access time was reduced to only 1.5 hours from the village. This has led to a spike in hunting on Wehea's borders and also even within the protected area itself. I photographed a number of hunters on camera traps throughout the duration of this study and we even saw evidence of hunting deep in the interior of Wehea Forest.

The other potential threat to these three species could come from habitat loss. Although Wehea Forest is a designated protected area, there is a strong and vocal segment of the Wehea Dayak who are advocating for opening it up for small-scale logging (for more detail see discussion of social factors below). Although, this action may not result in the local extinction of clouded leopards, orangutans and Miller's Grizzled Langur, it would be prudent to understand how each species may respond to any anthropogenic changes to their habitat. Orangutans have been shown to be surprisingly resilient to habitat disturbances (Meijaard et al., 2010). This includes being able to adjust their diet and live almost solely from bark and leaves when needed (Russon et al., 2009). This is good news if logging results in a loss of fruit and other feeding trees. In addition, my insights into orangutan terrestriality reveal they may be more opportunistic than we had previously thought. Logging results in new roads, which orangutans may in turn use for getting around the forest in search of food (Loken et al., 2013; 2014). Orangutans may therefore be able to tolerate some level of logging without impacting their long-term viability.

Clouded leopards, on the other hand, seem to be less tolerant of modified landscapes. Although very little is known about this elusive cat, they seem to strongly prefer lightly disturbed forest and to avoid plantations, large roads, mining areas and grasslands and their reproductive success depends on having an abundance of prey species (Bay et al., 2013). In addition to small-scale logging, some Wehea Dayak are also advocating for allowing hunting of some species (e.g. pig and deer) within Wehea Forest. If hunting is allowed, this could deplete certain species of prey and have an immediate impact on the already small clouded leopard population (Brodie et al., 2015). The seemingly varied diet of Miller's Grizzled Langur and their high reproductive potential (Spehar et al., unpublished data) may make this primate tolerant to some level of disturbance, however too little is known about this species to draw firm conclusions.

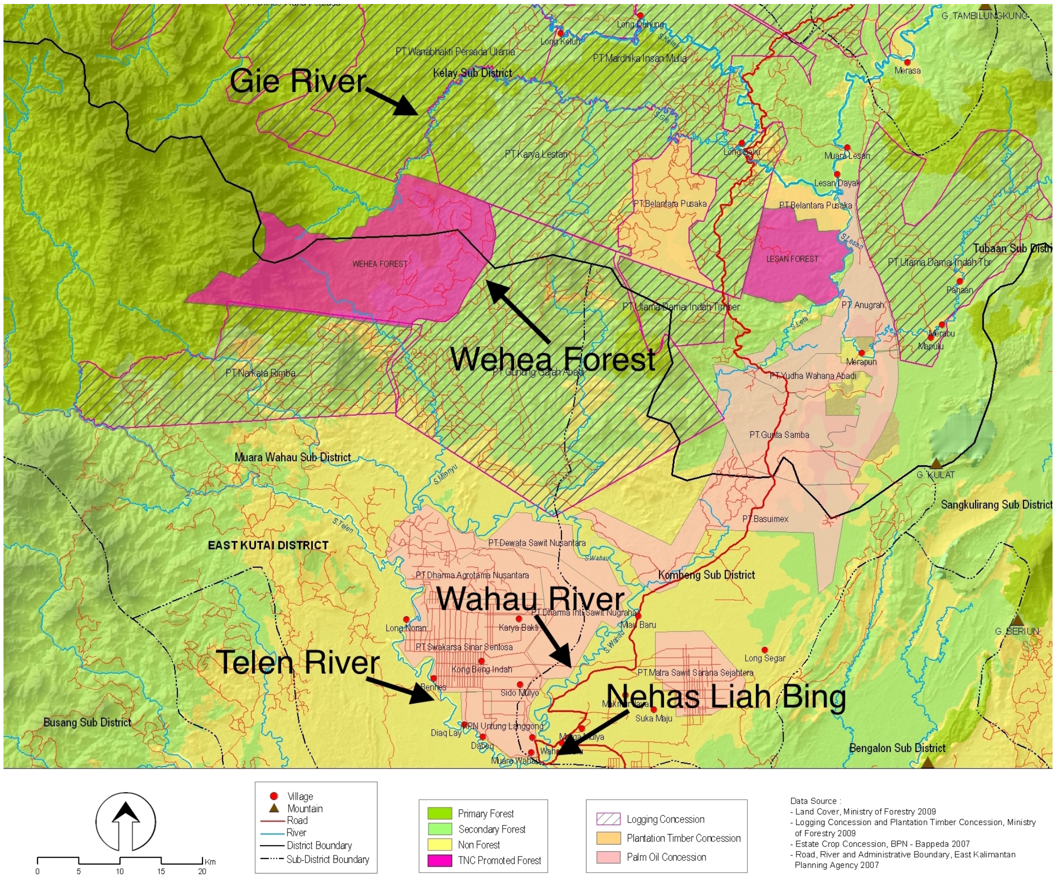
Although orangutans may tolerate the most disturbance and clouded leopards the least, it is highly likely that any resource extraction in Wehea Forest would result in smaller population sizes of each species over time, likely as a result of decreased quality of habitat (Brinkman et al., 2009). Although sustainably logged forests have been shown to retain considerable amounts of biodiversity (Meijaard & Sheil, 2007; Edwards et al., 2011; Putz et al., 2012), local abundance of some species can be negatively affected (Gibson et al., 2011). I found this to also be the case in Wehea Forest. Preliminary results from a study I did comparing species abundance and diversity in primary, secondary and recently logged forest indicates significantly reduced levels of species diversity in both secondary and recently logged forest when compared to primary forest (Loken & Brodie, unpublished data). My results also indicate higher relative abundances of clouded leopards and orangutans in primary forest in Wehea compared to the secondary forest where the majority of the research for this thesis took place.

Social factors in charismatic endangered species conservation

Background and context

In the section above I outlined some ecological factors in the conservation of charismatic endangered species in Wehea Forest arising from three years of field research of each species. In this section, I combine these ecological lessons with the insights derived from a combination of my study of CPR theory (see chapter 7) and having spent almost 4 years immersed with the Wehea Dayak, both for this research and conducting the broader activities of my NGO. During this time, I lived with the Wehea Dayak up to 6 months each year and participated in their ceremonies, shared meals with families, hosted celebrations and meetings at our house in the village, and participated in hundreds of formal and informal interviews and discussions. The topics of these were diverse and included legends about important animals, the history of the Wehea Dayak, concerns for the preservation of Wehea Dayak culture, strategies for protecting Wehea Forest, and the impacts of forest loss on the Wehea Dayak.

Originally, these interviews and discussions painted a picture of a unified people working to protect their culture and forest. However, over time, and as people began to trust me, the tone and topics of the discussions changed and the underlying complexity and challenges of this CBC project emerged as people started to share more mixed feelings about protecting Wehea Forest and the internal politics going on within the community. Therefore, the insights I discuss below are, I believe, a fair representation of some of the social factors that may influence the conservation of clouded leopards, orangutans and Miller's Grizzled Langur in Wehea Forest.



Data Source :
- Land Cover, Ministry of Forestry 2009
- Logging Concession and Plantation Timber Concession, Ministry of Forestry 2009
- Estate Crop Concession, BPN - Bappeda 2007
- Road, River and Administrative Boundary, East Kalimantan Planning Agency 2007

Figure 8.1 Map showing the entire study area including the Wehea Dayak village of Nehas Liah Bing and Wehea Forest.

CPR theory and "commons projects"

Although common pool resource (CPR) theory was developed from the study of small-scale commons, there is growing recognition that CPR theory may not be applicable to the design of some types of "commons projects" (mainly CBNRM) and may even have contributed to their poor performance (Roe & Nelson, 2009, Murphree, 2001; 2009; Nelson & Agrawal, 2008; Blaikie, 2006). In Wehea, the original CBC project, which was spearheaded by The Nature Conservancy, has many of the characteristics of commons projects implemented in other parts of the world (Saunders, 2014). I also used insights from CPR theory when initially assessing the potential of this project (see second paragraph of conclusion) and when designing our conservation initiatives. However, using CPR theory as a theoretical framework from which to design the CBC project in Wehea, may have led to overlooking several critical social factors that are not captured by CPR theory, but which may have a significant influence on the outcome of this CBC initiative.

First, CPR theory assumes users have managed the resources in question for decades, if not centuries and that natural resource institutions have evolved through social learning processes associated with the creation of trust (Ostrom, 1990). However, in Indonesia, President Suharto appropriated all forest land in 1967 (see Table 7.1) and worked to erode existing customary institutions such as *adat*. After the fall of Suharto in 1998, local communities began to demand control over their resources and slowly, as in Wehea, this control is being returned to them. However, when resource management authority is returned to a community after being under central government control for some time, it cannot be assumed that the prior customary natural resource institutions still function as they did in the past (Saunders, 2014). The entire system may have been irrevocably changed and a return to historical conditions may not be possible. This is the context in Wehea and there remains much uncertainty in the local community over how to govern Wehea Forest. This may have resulted in the poor performance of this CBC project as indicated by decreased monitoring of the forest for illegal activities, inability to levy sanctions against rule violators, inability to financially benefit from tourism and a tree nursery, increase in illegal activities within the forest, and poor working conditions for the *Petkuq Mehuey* (forest guardians). Currently, the *Petkuq Mehuey* who do chose to work in Wehea Forest have to spend up to 30 days away from the village (see Fig. 8.1; more than 70 km) with no cell-phone access or electricity, limited and poor food which mostly includes a diet of rice and ramen noodles, and a lack even basic equipment such as boots, shoes and uniforms. All of this has increased disenchantment with the CBC project among the community members who are most supportive and committed to it.

Second, CPR theory is mainly apolitical and places emphasis not on power and politics as shaping forces but on voluntary exchanges that are mutually agreed upon and beneficial (McCay, 2002). It addition, CPR theory assumes that the intention of the governance system is toward sustainability (see chapter 7 for more discussion). This assumption can mislead practitioners regarding the actual politically motivated and power driven ambitions of some community members. In Wehea, I initially assumed community homogeneity in support of conserving Wehea Forest. However, over time, I came to understand that the community was divided in their intentions about and support for the CBC project. One segment of the community supported continued protection of Wehea Forest; another segment supported its development, while a third group was ambivalent.

These differences seem to have become more divisive over time, especially since the originally promised benefits from protecting Wehea Forest were yet to be realized. Ecotourism has only generated a fraction of what was anticipated and a tree nursery project has also failed to live up to expectations. Both of these projects are not generating the levels of quick revenue they see their neighbors receiving from logging and planting oil palm. This situation created a dynamic of competing ambitions regarding Wehea Forest, some of which may pose a threat to the viability of the three species studied in this thesis. These conflicts may be difficult to resolve collectively given the erosion of the Wehea Dayak *adat* during the Suharto era, the rise of clientelistic relationships (see chapter 7 and below for more discussion), and the possibility of ‘elite capture’ of this CBC project, which is a well documented downfall of many CBC projects (Johnson, 2001; Chhotray, 2004; Mansuri & Rao, 2004; Robbins, 2004; Gibbes & Keys, 2010; Saunders et al., 2010).

Last, large scale political (e.g. biofuel policies in Europe) and economic (e.g. demand for palm oil and coal) forces are driving the conversion of forests in and around Wehea Forest. This has led to a kind of “development fever” where short-term profit is driving decision-making. Many Wehea Dayak are currently selling their rice paddies to palm oil companies and instead of planting rice, they are choosing to buy it in the local market. Only a few years ago, this would have been unthinkable given the importance of rice to the Dayak culture. In addition, with the rise of coal mining and palm oil in the region, many young people are leaving the *Petkuq Mehuey* (forest guardians) and are instead choosing to work in these industries where conditions and salaries are better. This is creating a situation where it is becoming increasingly difficult to find individuals who are willing to stay in the forest to patrol boundaries, guide tourists and maintain facilities. Lastly, clientelistic relationships appear to be developing between the large companies and the *adat*, and institutions such as the *Petkuq Mehuey* are being co-opted. The most troublesome example of this includes one palm oil company who signed a Memorandum of Understanding with the *kepala adat* to have the *Petkuq Mehuey* guard and patrol their 1000 ha (10 km^2) corporate social responsibility (CSR) forest. Although this forest is too small to support viable populations of many species, each month, there are more *Petkuq Mehuey* patrolling this small forest than the much larger 38,000 ha (380 km^2) Wehea Forest. I believe this is mainly because some members of the local community are receiving more benefits from protecting this small CSR forest than Wehea Forest and because the pay and working conditions are better.

Some of the challenges discussed above may be the result of the initial conditions under which this CBC project was established. In 2004, the Wehea Dayak were asked to manage Wehea Forest, which, administratively, was an old logging concession located more than 70 km from the nearest Wehea community of Nehas Liah Bing (see Fig. 8.1). Given its distance from the village, few Wehea Dayak had ever visited the forest, and there were competing historical and cultural ties to the forest with other Dayak communities, especially those located along the Gie river just to the north of Wehea Forest (see Fig. 8.1). Expecting then to craft natural resource management institutions that didn't evolve through a 'social learning process' may be contributing to the current poor performance of the Wehea CBC initiative (Saunders, 2014). As Li (2002) points out:

> *"there is a deep but unacknowledged tension between the assertion that sustainable resource-managing communities have existed since eternity (thus proving their effectiveness and viability), and the idea that communities or groups need to be created, their social capital developed and institutions crafted by outside stimulation and investment by the State or NGOs."*

Hard choices and trade-offs

During the past twenty years in sub-Saharan Africa, CBNRM has been adopted widely in the context of decentralization (Fabricius et al., 2004). However, despite the continuing popularity of these projects, they often generate disappointing outcomes in practice (Blaikie, 2006; Shackleton et al., 2010). Indonesia went through the process of decentralization beginning in 1998 and more recently indigenous communities have won rights to their land. This devolution of rights to local communities may be a positive step in the direction of improving human-well being for millions of individuals. However, when faced with a trade-off between wildlife conservation or development, it may be naive to assume that poor communities on Borneo would necessarily chose to protect charismatic endangered wildlife at the expense of local community development.

Given this, we should consider carefully whether it’s realistically possible to conserve charismatic endangered wildlife such as clouded leopards, orangutans and Miller’s Grizzled Langur using CBC as our main tool. To help evaluate this, let’s look at the possible choices that the Wehea Dayak may have regarding how they want to continue to use and protect Wehea Forest (see Table 8.1). They could either: 1) maintain it as a PA, patrol for illegal activity and not allow any resource extraction; 2) maintain the PA, allow for some harvesting of non-timber forest products (NTFPs) and continue to promote ecotourism; 3) adopt CBNRM and allow some timber harvesting and hunting; or 4) integrate the PA into the logging concessions bordering Wehea. Out of these four scenarios, the only option likely to be successful at conserving all three species is to integrate the PA into the surrounding logging concessions and manage this as a greater conservation area (Meijaard, 2007; Gaveau et al., 2013). This may be the only chance to protect a large enough area to ensure the long-term survival of the clouded leopard and this approach has been shown in other developing countries to conserve large areas that retain considerable amounts of biodiversity (Edwards et al., 2011; 2014; Putz et al., 2012). However, in this approach the Wehea Dayak are likely to lose financially since it would not generate any additional benefits from the protection of Wehea Forest.

Table 8.1 An overview of the various conservation approaches that could be adopted by the Wehea Dayak and the winners and losers of each approach.

Conservation Approach	Description of Approach	Winners and Losers			
		Wehea Dayak	Clouded Leopard	Orangutan	Miller's Grizzled Langur
Protect	Maintain Wehea Forest and not allow any resource extraction	Lose	Lose	Win	Win
ICDP	Maintain Wehea Forest, allow some harvesting of NTFPs and promote ecotourism	Lose	Lose	Win	Win
CBNRM	Allow some timber harvesting and hunting in Wehea Forest	Win	Lose	Lose	Lose
Integrate	Integrate Wehea Forest into surrounding logging concessions	Lose	Win	Win	Win
Expand	Expand territory and allow some timber harvesting and hunting	Win	Win	Win	Win

On the flip side, the only option considering current conditions that is a win for the Wehea Dayak is to adopt a CBNRM approach and allow some timber harvesting and hunting in Wehea Forest. If Wehea Forest was sustainably logged, this would bring in a significant amount of revenue for the foreseeable future as long as the terrain could support reduced impact logging. The trade-off of adopting such an approach could mean that all three species studied in this thesis may eventually be lost from Wehea Forest. This reflects one of the key points of NCS opponents who claim that trying to balance human-well being while protecting biodiversity dismisses the relationship between species diversity and ecosystem function and inevitably exclude keystone species (Soule, 2013). This win-lose approach might be the most tempting option for the local community, especially since the promised win-win outcome has yet to be realized and the initial optimism surrounding this conservation initiative is quickly turning into disenchantment by the original and strongest community supporters of this project.

The only option that may actually be a win-win is for the Wehea Dayak to claim rights to a large enough territory to maintain viable populations of all three species while still allowing for some resource extraction. This potential scenario may sound far-fetched but earlier this year, all six Wehea Dayak villages submitted an application to the government to claim land rights to 385,482 ha (3854.82 km^2) of forested land (Kaltim, 2015). If approved, this could make the Wehea Dayak one of the largest private landholders in Kalimantan. The details of this application and what the Wehea Dayak intend to do with this land are currently unknown. Although this could be a win-win solution for the Wehea Dayak and endangered species, given the social factors that I've discussed in this conclusion, I am skeptical that all six communities would be able to collectively work together to develop natural resource institutions to sustainably manage this large of an area.

The future of conservation on Borneo

Although in this thesis I focussed on ecological and social factors in the conservation of the Bornean clouded leopard, orangutan and Miller's Grizzled Langur from a single case study in Northeastern Borneo, these factors are likely characteristic of many CBC projects across Borneo. They include: 1) a protected or community forest that contains a number of charismatic endangered species; 2) high uncertainty in the population sizes and population ecology of the species found in the forest; 3) a small community with competing ambitions about the goals and intentions of the CBC project; 4) a small community who may have lost the social learning processes necessary for building effective natural resource institutions; 5) a CBC project embedded in an area of high resource extraction and influenced by large scale political and economic forces; and 6) a CBC project supported by an NGO who may use theoretical assumptions of CPR theory to build a conservation program. As we saw in the case study of Wehea, these conditions set the stage for win-lose conservation projects, with the most likely loser being charismatic endangered species such as the clouded leopard, orangutan and Miller's Grizzled Langur. Although data doesn't currently exist to support my claim that these are six characteristics typical of CBC projects, most conservation practitioners would agree that this is the reality of practicing the art of conservation on Borneo.

Although the Wehea Dayak may be able to pull off a win-win solution if they successfully win land rights to their entire forested area, most communities on Borneo will not have the same option to claim rights to so much territory. However, given that communities now have a legal right to claim land to any forest estate that has been "controlled and exploited" by the community for 20 consecutive years, a likely scenario for the future of Borneo is that current forest land, including protection and conservation areas, could legally be divided up and claimed by local communities. It is possible that many of these communities will want to protect their land and establish their own CBC projects. However, I believe it is highly unlikely that once these communities have legal rights to what was previously State land and given the history of marginalization and disempowerment under Suharto, that they will chose to forego development so a few charismatic endangered species can be protected. This view is supported by Feintrenie et al. (2010) who found that some communities in Indonesia were responsive to economic opportunities and quickly changed their livelihood system if it increased their income. In addition, WWF (2015) recently claimed that the largest threat to forest degradation in Sumatra came from small-scale encroachment by local communities. Meijaard (2015a) echoed these sentiments in a recent editorial to the Jakarta Post in which he wrote:

> *"[R]ealistically, what will communities or individual people do when they can get legal title to what was previously state owned land? Your guess is as good as mine, but I would think many will immediately sell their land to whoever is the highest bidder: likely industrial-scale companies investing in oil palm, pulp and paper, rubber, and mining. Surely, some local people will hang on to their land…. In my experience, in the many more loosely organized communities, those community-members with the best connections and most power will lay claim to most lands, either directly or through proxy claimants."*

As I write this, human-set forest fires are raging on Borneo and Sumatra in what is being called the biggest environmental crime of the 21st century (Meijaard, 2015b). These fires have also been called a "crime against humanity" (The Guardian, 2015a) and have severely affected more than 500,000 people with warships being readied to evacuate children and others suffering from smoke inhalation (Jakarta Globe, 2015). Fires have already destroyed large areas of peatlands and natural forest and threaten one-third of the world's remaining wild orangutans (The Guardian, 2015b). Fingers are being pointed and blame cast with the most common culprit being large oil palm plantation owners. Certainly, these large companies are partially to blame but local communities and small shareholders may be equally responsible as some studies suggest (Gaveau et al., 2014; Marlier et al., 2015) and as evidenced by recent pictures posted to facebook of the Wehea Dayak clearing large areas of forest by burning.

When I started this thesis, I believed that local communities were the main solution to solving the conservation crisis facing Borneo. However, in the end, the scientific and working knowledge gained from my time in Wehea has forced me to change my mind. I now agree with the skepticism voiced by the NCS opponents (e.g. McCauley, 2006; Soule, 2013; Doek et al., 2014) and believe that on Borneo, relying solely on conservation approaches that attempt to conserve biodiversity while improving human well-being will ultimately result in small, fragmented forest patches that are devoid of Borneo's charismatic endangered species. This is not to say, however, that local communities do not have a role to play in conserving Borneo's biodiversity. I'm sure that many CBC projects will be able to strike a balance between local community development and biodiversity conservation. However, I doubt that enough of these CBC projects will be able to successfully protect large, wide ranging and low-density species such as orangutans, clouded leopards and Miller's Grizzled Langurs to ensure their long-term viability. This is currently the case across Africa where Lion (*Panthera leo*) populations are declining rapidly except in intensively managed areas (Bauer et al., 2015).

If we are serious about conserving species such as the orangutan, clouded leopard, and Miller's Grizzled Langur, we need to begin investing in more intensively managed "nature-centered" projects such as WWF's Heart of Borneo (HoB) initiative, which aims to protect more than 220,000 km^2 of contiguous higher elevation forest in the center of Borneo (Wulffraat, 2014). This region of Borneo will become even more important in the future as climate change destroys lower elevation forests and shrinks suitable habitat by at least a third by 2080 (Struebig et al., 2015). However, projects such as this will only be made possible if we accept that given the ecological and social factors found on Borneo that CBC initiatives might not yield win-win solutions. Facing this conservation reality is not an indictment of local communities but is more a reflection of the challenges of conserving charismatic endangered species using community-based conservation in a globalized world.

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Appendix A.

Code used for SCR analysis of clouded leopards

```
 model {
  sigma[1] ~ dunif(0,50)
  sigma[2] ~dunif(0,50)
  sigma2[1] <- sigma[1]*sigma[1]
  sigma2[2] <- sigma[2]*sigma[2]

  lam[1] ~ dgamma(.1,.1)
  lam[2] ~dgamma(.1,.1)

  psi ~ dunif(0,1)
  psi.sex ~ dunif(0,1)

  for(i in 1:M){
    w[i]~dbern(psi)
    catfemale[i] ~ dbern(psi.sex)
    Male1Fem2[i] <- catfemale[i]+1
    sx[i]~dunif(Xl,Xu)
    sy[i]~dunif(Yl,Yu)

    for(j in 1:ntrap){
      dist2[i,j] <- pow(sx[i]-trap[j,1],2) +pow(sy[i]-trap[j,2],2)
      exposure0[i,j] <- lam[Male1Fem2[i]]*exp(-dist2[i,j]/(2*sigma2[Male1Fem2[i]]))
      log(pmean[i,j]) <- log(K[j])+log(exposure0[i,j])
      tmp[i,j] <- pmean[i,j]*w[i]
      y[i,j] ~ dpois(tmp[i,j])
    }
  }
  N <- sum(w[1:M])
  Nfemale <- N*psi.sex
  Nmale <- N*(1-psi.sex)
}
```

And here's the code for the simplified model:

```
model {
  sigma ~ dunif(0,50)
  sigma2 <- sigma*sigma
  lam0 ~ dgamma(.1,.1)
  psi ~ dunif(0,1)

  for(i in 1:M){
    w[i]~dbern(psi)
    sx[i]~dunif(Xl,Xu)
    sy[i]~dunif(Yl,Yu)
```

```
    for(j in 1:ntrap){
      dist2[i,j] <- pow(sx[i]-trap[j,1],2) +pow(sy[i]-trap[j,2],2)
      exposure0[i,j] <- lam0*exp(-dist2[i,j]/(2*sigma2))
      log(pmean[i,j]) <- log(K[j])+log(exposure0[i,j])
      tmp[i,j] <- pmean[i,j]*w[i]
      y[i,j] ~ dpois(tmp[i,j])
    }
  }
  N <- sum(w[1:M])
}
```

Appendix B.

Calculation of Confidence Intervals for nest plot surveys using the Delta Method

Following Mathewson et al. (2008) and Ancrenaz et al. (2004)

Note: all values rounded here, but not in initial calculations

Orangutan density estimates calculated using the following equation to convert nest counts to ape density:

$$D_{\text{ind}} = D_{\text{nest}} / (prt), \qquad \textbf{(Eq. 1)}$$

where D_{ind} = density of individuals; D_{nest} = density of nests; p = proportion of nest builders in the population; r = nests built per individual per day, and t = nest decay time (Ghiglieri 1984).

We need to account for variation in D_{nest}, p, r, and t to get the coefficient of variation for OU density:

$$CV^2(Dind)=CV^2(N) + CV^2(p) + CV^2(r) + CV^2(t) \qquad \textbf{(Eq. 2)}$$

CV for N: mean nests per km^2 was calculated based on nests encountered in each plot. Mean = 651.85, std dev = 671.01

So the CV for N=671.01/651.85 = 1.02

CV for p: four studies have estimated p values for Bornean OU (values reported: 0.89, 0.89, 0.85, 0.85). Mean = 0.8775; std. dev. = 0.019.

So the CV for p = 0.019/0.8775 = 0.022

CV for r: three studies have estimated r values for Bornean OU in undisturbed habitat (values reported: 1.16, 1.17, 1.15). Mean = 1.16; std. dev. = 0.01

So the CV for r = 0.01/1.16 = 0.0086

CV for t: t is very site-specific so we used the values calculated by Mathewson et al. 2008. They used 1000 bootstrap estimates to come up with a CV for t. The std. dev. of the 1000 estimates = 82.408. The mean of 1000 values = 603.66.

So the CV for t is 82.408/603.66 = 0.137

So, plugging the numbers into **Eq. 2**:

$CV^2(D_{ind}) = 1.02^2 + 0.022^2 + 0.0086^2 + 0.137^2 = 1.066$

So the coefficient of variation for the OU density estimate = sqrt(1.066) = 1.032

Next, we followed Ancrenaz et al. 2004 and their methods for using the delta method to calculate a 95% CI for orangutan density estimates.

The first step is to calculate the estimated variance of OU density:

$$\mathrm{var}(D_{ind}) = D_{ind}^2 * [\mathrm{CV}^2(D_{nest}) + \mathrm{CV}^2(p) + \mathrm{CV}^2(r) + \mathrm{CV}^2(t)] \qquad \textbf{(Eq. 3)}$$

Plugging in numbers: $\mathrm{var}(D_{ind}) = 1.05^2*[1.02^2 + 0.022^2+0.0086^2 +0.137^2]$

$= 1.17$

Next, the upper and lower CI limits were calculated: $(D_{ind}/C, D_{ind}*C)$, where

$$C= \exp(t_{df}(0.05)*\mathrm{sqrt}(\mathrm{var}(\ln D_{ind}))), \qquad \textbf{(Eq. 4)}$$

$$\text{where } \mathrm{var}(\ln D_{ind}) = \ln[1+(\mathrm{var}(D_{ind})/D_{ind}^2))], \qquad \textbf{(Eq. 5)}$$

and $t_{df}(0.05)$ is the two-sided 5% level t-distribution percentile.

Plugging numbers in to **Eq. 5**:

$$\mathrm{var}(\ln D_{ind}) = \ln[1+(1.17/1.05^2)] = 0.7258$$

Next, df needs to be calculated (see eq 4 on p. 378 in the Ancrenaz et al (2004)) in order to figure out the t multiplier.

Plugging numbers into the numerator:

$$[1.02^2 + 0.022^2+0.0086^2 +0.137^2]^2 = 1.14$$

Next the df for the individual parameters:

Df for D_{nest}: 27 plots were used, so assume df = 26

Df for p = 4-1 = 3

Df for r = 3-1 =2

Df for t = 88 nests were used in nest decay estimate in Mathewson et al. 2008, so df =87

So plugging numbers into the denominator:

$$[(1.02^4/26) + (0.022^4/3) + (0.0086^4/2)+(0.137^4)/87] = 0.0421$$

So df = 1.14/0.0421= 26.97

Thus the t multiplier = $t_{27}(0.05) = 2.052$

So C = exp(2.052*sqrt(0.7258)) = 5.74

The resulting 95% CI = $(D_{ind}/C, D_{ind}*C)$ = (1.05/5.74, 1.05*5.74) = (0.182, 6.008)