

**The ecology and conservation of *Presbytis rubicunda***

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for the degree of Doctor of Philosophy on the Basis of Published Work

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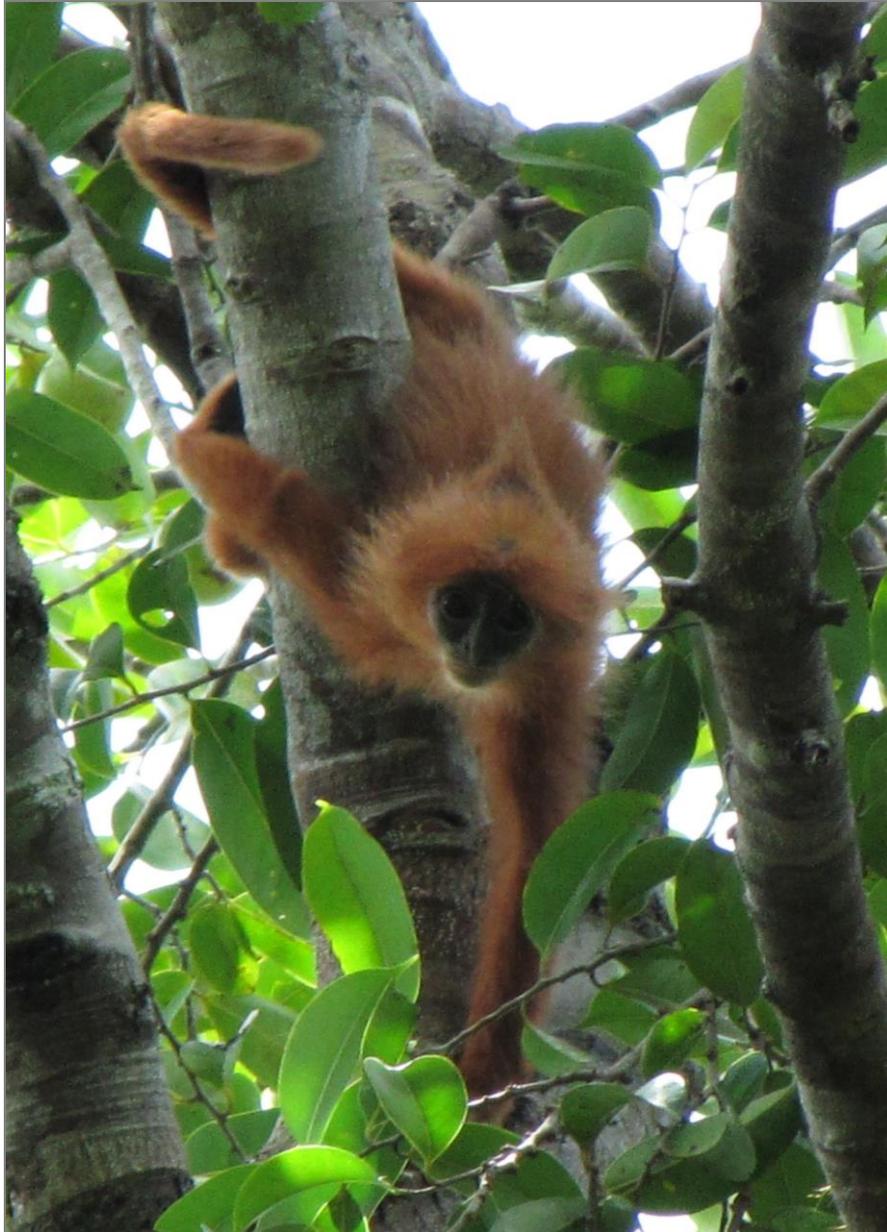
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**For Yvie, Supian, Francis and Ann**



Juvenile male *Presbytis rubicunda*

## Abstract

From 2009 to 2014 I conducted research that contributes toward a synthesis of techniques to best inform conservation management schemes for the protection of the endemic *Presbytis* monkeys on the Southeast Asian island of Borneo, using the red langur (*Presbytis rubicunda*) as a case study. To achieve this, I conducted ecological niche modelling of distributional patterns for *Presbytis* species; assessed land-use policies affecting their persistence likelihood, and reviewed the location and efficacy of the Protected Area Network (PAN) throughout distributions; conducted population density surveys within an under-studied habitat (tropical peat-swamp forests) and a small but highly productive mast-fruiting habitat, and founded a monitoring programme of *Presbytis rubicunda* concerned with establishing the ecological parameters (including behavioural, feeding and ranging ecology) required to advise conservation programmes.

The ecological niche modelling of *Presbytis* distributions demonstrated that the PAN does not provide effective protection, and land-use policies throughout distributions may continue causing population declines. Data from 27 months of fieldwork provided convincing evidence that the non-mast fruiting characteristics of tropical peat-swamp forests on Borneo had a profound effect on the ecology of *Presbytis rubicunda*. Specifically, a low variation in fruit availability appeared to facilitate the highest case of frugivory in a primate with an adaptation for folivory,

resulting in the largest home range recorded in the genus and the longest day-range length of any “folivorous” primate. I highlight the importance of conducting population surveys throughout vegetation class sub-divisions, as differing vegetation characteristics have strong limiting effects on the presence and density of primates, which consequently has implications for conservation management. Additionally, selective logging of the largest trees may negatively impact the species’ success in achieving sleeping and nutritional requirements. This synthesis of conservation biology techniques has improved our understanding of colobine ecology, and our ability to effectively conserve these threatened primates in this biodiversity hotspot.

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**List of Abbreviations**

Metres – m

Kilometres – km

Protected Area – PA

Above sea level – asl

Protected Area Network – PAN

Diameter at breast height – DBH

Kernel Density Estimates – KDE

Tropical peat-swamp forest – TPSF

Minimum Convex Polygons – MCP

Akaike’s Information Criterion – AIC

Geographic Information Systems – GIS

International Union for the Conservation of Nature – IUCN

# Chapter 1 – Introduction

## 1.1 Primate distribution and extinction risk

Non-human primates (hereafter “primates”) are one of the least anatomically specialised and most ancient orders of mammal, with the molecular clock estimating an evolutionary origin during the Cretaceous epoch some 70–80 million years ago (mya; Rowe and Myers 2010). However, currently the first documented fossils sharing the anatomical features of the primate order appear simultaneously in Europe, North America and Asia at the boundary of the Palaeocene and Eocene, ~56 million years ago (Rowe and Myers 2010; Fleagle 1999). After the Oligocene “fossil gap” some 30 mya, primate fossils were only found around the equatorial region of Eurasia, and they have remained largely tropical animals up to the present era; few species (e.g. lemurs, *Avahi meridionalis*, *Lepilemur fleuretae*; macaques, *Macaca fuscata* and *M. sylvanus*; snub-nosed monkeys, *Rhinopithecus bieti*, *R. brelichi*, *R. roxellana* and *R. strykeri*; some *Semnopithecus* langurs) have a geographic distribution entirely out of the tropics (Kirkpatrick 2011; Thierry 2011). Their distribution occurs widely across the tropical continents (Africa and Asia – the Old World; North, Central and Southern America – the New World), Madagascar, and the larger islands across the Sundaic Shelf (Borneo, Sulawesi, Sumatra and Java). Primates of the New World are of a

distinct infraorder, Platyrrhini, to those in the Old World, Catarrhini (the monkeys, apes and tarsiids, and Strepsirrhini, the lemurids and lorisids; Campbell *et al.* 2011).

Primate distribution is determined by three key factors: the ability to disperse from one area to another; the availability of food in that new area, and the ability to compete with other species for those food resources (Cowlshaw and Dunbar 2000). The rarity of a primate species may be defined by its population size, habitat and niche specificity, and geographic range (Rabinowitz 1981). Thus, species endemic to a single geographic isolation, such as an island, are often also rare. Conversely, the ‘insularity syndrome’ of endemics may result in a broader niche, wider distribution and in higher population densities (Blondel 1986).

Some species naturally occur in small populations due to geographic, competitive or nutritional constraints. However, species extinctions occur when populations decline in size, and then suffer certain processes that cause their eradication, including disruption of social structure; loss of genetic diversity leading to inbreeding depression and inability to adapt to environmental change, and demographic and environmental stochasticity (Cowlshaw and Dunbar 2000; Frankham *et al.* 2010). Additionally, life-history variables among small populations can further increase species’ extinction risks, such as those with short generational gaps (accelerating the effects of genetic drift and inbreeding;

Pope 1996); small bodies (meaning high metabolic rate and low fat stores) or large bodies (slower reproduction rate and ability to recover from stochastic events; Cowlshaw and Dunbar 2000). Dietary specialisation (e.g. Kamilar and Paciulli 2008) and social structure, specifically populations with polygynous mating systems are also more vulnerable to extinction through stochastic events (Chesser 1991). While extinction is a natural process as a result of the interactions between these intrinsic factors, and “background extinctions” occur as part of the evolutionary process (Jablonski 1995), extrinsic anthropogenic actions are greatly accelerating population declines (Purvis *et al.* 2000). Within the primate order, only extrinsic factors, including fragmentation, degradation and destruction of habitat, and extraction and hunting practises, appear to be of current threat to primate diversity and persistence, although highly fragmented populations are more vulnerable to inbreeding depression caused by a change in the relatedness of individuals within and between populations (Cowlshaw and Dunbar 2000).

## **1.2 The primates of Borneo and the conservation threats they face**

### **1.2.1 Asian primate taxonomy in flux**

Reaching a consensus of Asian primate taxonomy has long been the subject of contention; since 1996 there have been numerous attempts to resolve the

issue (c.f. Brandon-Jones 1996a 1996b, 2004, 2006; Groves 2001; Meijaard and Groves 2004; Munds *et al.* 2013; Mittermeier *et al.* 2013) that highlight the purported differences in species' pelage, morphology, genetics, and a combination of these factors. In 2014, Roos and colleagues produced a publication that attempted to ratify these differing opinions from a multi-author synthesis (Roos *et al.* 2014). The overall trend as a result of this publication was an elevation to species level of many previously-considered subspecies, and a corresponding increase in the number of endemic species.

Given the time period of my research (2009-2014) and my focus on the Borneo-endemic *Presbytis* monkey species, there are recent taxonomic changes to species treated in my publications (*Presbytis hosei* is split into three species: *P. hosei*, *P. canicrus* and *P. sabana*). While it is beyond the scope of my specific research to assess the efficacy of the taxonomic changes proposed in Roos *et al.* (2014), its multi-authored approach represents a consensus in opinion that may be necessary to take Asian primate taxonomy forward. As such, I have adopted their taxonomic system for the purpose of this thesis and have indicated throughout where these changes are apparent.

### **1.2.2 The primates of Borneo**

The island of Borneo is globally recognised as one of the world's most biodiverse regions (Myers *et al.* 2000). This is particularly true for primates

(Meijaard and Nijman 2003; Supriatna and Gurskey-Doyen 2010): across the island, some five families are represented, including Lorisidae; Tarsiidae; Cercopithicidae; Hylobatidae, and Hominidae, under which, eight genera, 20 species and 23 subspecies exist (Roos *et al.* 2014; Table 1.2.1). Of these 20 species, 75% (N = 15) are endemic (Table 1.2.1). They face significant conservation challenges, however. Of these species, three are Not Evaluated on the IUCN Red List of Threatened Species because of their recent description (c.f. Roos *et al.* 2014); two are Least Concern, and the other 15 are listed as Data Deficient (N = 1); Near-Threatened (N = 1); Vulnerable (N = 4), Endangered (N = 8) and Critically Endangered (N = 1; Roos *et al.* 2014). Thus, of the endemic species evaluated, ~83% (N = 10) are threatened with extinction.

**Table 1.2.1** The recognised primate species of Borneo (Roos *et al.* 2014)

<b>Common name (E = endemic)</b>	<b>Scientific name</b>	<b>Subspecies</b>	<b>Authority</b>	<b>Conservation status</b>
East Bornean slow loris (E)*	<i>Nycticebus menagensis</i>	0	Lydekker, 1893	VU
Bangka slow loris	<i>Nycticebus bancanus</i>	0	Lyon, 1906	NE
Schwaner Mountains slow loris (E)	<i>Nycticebus borneanus</i>	0	Lyon, 1906	NE
Kayan slow loris (E)	<i>Nycticebus kayan</i>	0	Munds <i>et al.</i> , 2013	NE
Western tarsier	<i>Cephalopachus bancanus</i>	4	Horsfield, 1821	VU
Sunda pig-tailed macaque	<i>Macaca nemestrina</i>	0	Linnaeus, 1766	VU
Long-tailed macaque	<i>Macaca fascicularis</i>	10	Raffles, 1821	LC
Cross-marked langur (E)	<i>Presbytis chrysomelas</i>	2	Müller, 1838	CR
Maroon langur (E)*	<i>Presbytis rubicunda</i>	5	Müller, 1838	LC
Hose's langur (E)	<i>Presbytis hosei</i>	0	Thomas, 1889	DD
Miller's grizzled langur (E)	<i>Presbytis canicrus</i>	0	Miller, 1934	EN

Sabah grizzled langur (E)	<i>Presbytis sabana</i>	0	Thomas, 1893	EN
White-fronted langur (E)	<i>Presbytis frontata</i>	0	Müller, 1838	VU
Silvered langur	<i>Trachypithecus cristatus</i>	2	Raffles, 1821	NT
Proboscis monkey (E)*	<i>Nasalis larvatus</i>	0	van Wurmb, 1787	EN
Bornean white-bearded gibbon (E)	<i>Hylobates albibarbis</i>	0	Lyon, 1911	EN
Müller's gibbon (E)	<i>Hylobates muelleri</i>	0	Martin, 1841	EN
Abbott's grey gibbon (E)	<i>Hylobates abbotti</i>	0	Kloss, 1929	EN
East Bornean grey gibbon (E)	<i>Hylobates funereus</i>	0	I. Geoffroy Saint-Hilaire, 1850	EN
Bornean orang-utan (E)	<i>Pongo pygmaeus</i>	3	Linnaeus, 1760	EN

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DD = Data Deficient; NE = Not Evaluated; LC = Least Concern; NT = Near-Threatened;  
VU = Vulnerable; EN = Endangered; CR = Critically Endangered

(E)\*: Endemic to Borneo and some small off-lying islands

One of the largest contributing factors to the decline of primate species on Borneo is the removal or conversion of their forested habitats for timber extraction and/or agricultural development, especially for the purpose of creating oil palm plantations, although mining and damming operations also pose considerable threats (Curran *et al.* 2004; Langner *et al.* 2007; Nellemann *et al.* 2007; Carlson *et al.* 2012; Wich *et al.* 2012). Over 56% of the island's original forest has now been converted, as a result of resource extraction, establishment of agricultural lands, illegal logging and fires (Curran *et al.* 2004; Geist and Lambin 2002; Langner *et al.* 2007; Miettinen *et al.* 2011). Of that which remains, ~80% of the forests of Kalimantan alone (Indonesia's Bornean territory that occupies the southern two-thirds of the island) have been allocated as industrial timber-logging concessions since the 1980s (Curran *et al.* 2004); similarly, in the Malaysian states of Sabah and Sarawak, nearly 80% of the land surface was impacted by high-impact logging or clearing operations from 1990 to 2009 (Bryan *et al.* 2013). By contrast, ~55% of the Sultanate of Brunei's surface contains primary forest (Bryan *et al.* 2013).

Between 2000 and 2012, the rate of forest clearance for oil-palm production increased by 212% to account for 31,640 km<sup>2</sup> of the total area of Kalimantan (Carlson *et al.* 2012), while in Sarawak and Sabah, the area of coverage of active plantations in 2010 was estimated at ~4,700 km<sup>2</sup> (48%) and 7,100 km<sup>2</sup> (62%) in the swamp forests alone (Gunarso *et al.* 2013). Oil palm plantations in Kalimantan and Sumatra are now responsible for half of

the world's palm oil production (FAO 2012), and by 2020 the Indonesian government plans to double this output by expanding plantations in both these regions, and Indonesian Papua (USDA 2010). From 1990 to 2010, 90% of land conversions for oil palm plantations occurred in forested areas (47% intact, 22% logged, 21% agroforests; Carlson *et al.* 2012), and recent estimates suggest that ~10% of Borneo is now under oil palm plantation (Gaveau *et al.* 2014).

Fire also plays a role in accelerating the degradation of Borneo's forests. In the early- to mid-2000s, 98% of all forest fires occurred in the 5 km deforestation buffer zone most commonly found along forest edges (Langner *et al.* 2007). Ancillary to being vital primate habitat (Meijaard and Nijman 2000; Morrogh-Bernard *et al.* 2003; Cheyne *et al.* 2007; Wich *et al.* 2009; Ehlers Smith and Ehlers Smith 2013), tropical peat-swamp forests (TPSFs) are particularly vulnerable to burning (Miettinen and Liew 2010; Turetsky *et al.* 2014); indeed, during the worst fires of 2002 and 2005, some 73% and 55% of all burning occurred in peat-swamp forests, respectively (Langner *et al.* 2007).

In addition to the threats posed by habitat degradation and loss, the hunting of wildlife from the natural environment negatively affects populations by altering species demography, distribution and density, and affecting reproductive rates and fitness (Cowlshaw and Dunbar 2000; Meijaard *et al.* 2005). Fewer offspring alters the competition to survive, reducing selection pressure in a less diverse gene pool and ultimately

reducing adaptability (Meijaard *et al.* 2005). Such an imbalance creates a causal sequence within forest communities, as seed dispersal, competition and predation are subsequently effected (Meijaard *et al.* 2005). With increased timber extraction and access to remote forests comes an increase in hunting pressures into previously unaffected areas (Bennett *et al.* 1999; Robinson and Bennett 2000). Consequently, wildlife in fragmented and degraded forests is particularly vulnerable to hunting pressures (Meijaard *et al.* 2005).

Large Bornean mammals, including the primates, exhibit irregular distributional patterns with expansive gaps in apparently suitable habitats, as a result of mutual exclusion through competition, and hunting pressures (Meijaard *et al.* 2005). Across Borneo, *Presbytis* monkeys (the langurs), are targeted for both consumptive use and the Traditional Asian Medicine (TAM) trade (Bennett *et al.* 1987; Bennett and Dahaban 1995; Puri 2001; Nijman 2004, 2005). Primate hunting on Borneo is typically associated with inland settlements, the timber industry, and the demand for bezoar stones in the gut of *Presbytis* monkeys for TAMs (Nijman 2004). Bezoar stones, visceral excretions from the gall bladder as a response to a foreign body in the digestive tract, are believed to have medicinal properties, and even small stones can command up to six times the official provincial monthly wage (Nijman 2005). In the Kayan Mentarang region, Nijman (2004, 2005) reported a 50-80% drop in the population density of *Presbytis hosei* over a seven year period, after a merchant paid a visit to settlements guaranteeing

the purchase of any bezoar stones. In this time period it became economically viable to indiscriminately hunt any *Presbytis* monkey with the hope that it carried a bezoar stone (although the incidence of carrying stones was low, at 1-10%). Within two years, the population had been decimated to the point where only specialised hunters that could recognise monkeys carrying the stones remained.

It was estimated that in the mid-1980s, some 1% of all wild animals hunted in Sarawak, Malaysian Borneo were *Presbytis* species, accounting for some 20,000 animals annually (Bennett *et al.* 1987). Since this time, deforestation rates, and access to remote forests, have increased > 200% across Borneo (Carlson 2012); while the precise number of *Presbytis* monkeys harvested is not known, it is likely to be elevated from this initial estimate. A recent study from Malaysian Borneo showed that hunting pressures are associated with ~30% decline in species richness, and that hunting persists even in areas where richness has been reduced to very low levels (Brodie *et al.* 2014). Declines in species richness and abundance were particularly severe for seed dispersers, such as some primate species (Brodie *et al.* 2014).

Indeed, in the Kayan Mentarang region there was a negative relationship between the distance between villages where hunters lived and *P. hosei* density (Nijman 2004). In East Kalimantan, *P. frontata* populations were similarly heavily effected by bezoar hunting in the Apo Kayan and Upper Mahakam regions (Nijman 2005). These cases indicate that habitat

protection alone is not enough to conserve forest species, and that increased access to remote forests and easier communications for transport and market-trading are exacerbating the problem (Nijman 2005).

The hunting and extraction of primates from their habitat, however, is not just for consumptive use. Asia has the highest percentage of endangered primate species, in part because of the global and local trade in wildlife (IUCN 2014; Nekaris *et al.* 2010). Trade for ornamental, consumptive or medicinal purposes is of particular concern in Southeast Asia, where a combination of cultural traditions, ease of access to exceptional numbers of species in expansive, organised markets with poor policing and law-enforcement, and a sprawling and active online market with similarly poor regulation has created a conservation crisis on an unprecedented scale (Oldfield 2003; Davies 2005; Grieser-Johns and Thomson 2005; Corlett 2007; Nijman and Shepherd 2007; Nijman 2010a).

### **1.3 The aims and objectives of this research programme and thesis outline**

The principle aim of this programme of research is to present a synthesis of techniques that may best inform conservation management schemes in a single region, the island of Borneo. I aimed to achieve this using a combination of land-use mapping and species' distributional modelling to assess primate conservation threats and status, and by collecting the

ecological data on the ground that may provide the basis of such models. To this end, using the Borneo-endemic red langur (*Presbytis rubicunda*) as a case study, I sought to obtain their ecological parameters in the field (including feeding, sleeping and home-range requirements); to provide detailed descriptions of *Presbytis* monkey distribution and ecology; to investigate threats to their habitat, populations and persistence, and to provide recommendations based on the whole body of research on how best to safeguard their persistence, through informed land-management strategies and mitigating human interactions and conflicts.

To achieve these aims, I established a long-term ecological monitoring programme of the red langur and described many aspects of its ecology never before documented, which I then put into the context of conservation management recommendations. I further investigated the conservation threats facing the endemic *Presbytis* monkeys of Borneo, through ecological niche modelling of their distributions, and analysis of land-use policies throughout these distributions and their likely conservation consequences. This research programme makes both broad and specific recommendations for safeguarding the species' persistence, based on the body of research conducted.

When the field research project of red langur ecology and conservation began in 2009, the species appeared to follow fairly typical Asian colobine ecology, including a foli-frugivore feeding strategy (typically comprising 30-60% fruit consumption and 30-60% leaf

consumption in the overall diet), and use of a small home range and core range, with short daily travel lengths. With the establishment of my project in the TPSFs of Central Kalimantan, however, it has become clear that their ecology differs within this habitat type: their feeding ecology is distinct from any other Asian colobine monkey, as the proportion of fruit in the diet is the highest ever recorded (Ehlers Smith *et al.* 2013a); their population density is similarly one of the highest recorded for the species (Ehlers Smith and Ehlers Smith 2013), and their home range and day ranging lengths are the largest for the genus, and for all folivorous primates on any continent, respectively (Ehlers Smith *et al.* 2013b). Through this research programme I have also provided preliminary evidence for indirect mate defence and the hired guns hypothesis of group socio-ecology, and have offered insights into the motivation behind inter-group aggression (Ehlers Smith 2014b). Additionally, I sought to assess the population status and persistence of *P. rubicunda* elsewhere on Borneo by investigating their population density in Sungai Wain, East Kalimantan in a dipterocarp forest, the major habitat type of Borneo (Bersacola *et al.* 2014).

My work describing the distribution and conservation status of the endemic *Presbytis* monkeys of Borneo (Ehlers Smith 2014a) is consistent with the literature that uses ecological niche modelling to assess conservation threats throughout known and predicted distributions (e.g. Margules *et al.* 2002; Anderson and Martinez-Meyer 2004; Hernandez *et al.* 2006; Wich *et al.* 2012). Prior to my research, investigations had taken place

into the distribution and sympatricism of Bornean primates using Geographic Information Systems (GIS) as selection criteria for protected area placement (Nijman and Meijaard 2001; Meijaard and Nijman 2003) and the IUCN Red List assessments of *Presbytis* monkeys (Nijman and Meijaard 2008a, b; Nijman *et al.* 2008a, b). Analysing the conservation threats to Bornean *Presbytis* monkeys also followed on from the work of Wich and colleagues (2012), who provided an analysis of land-use policies on Borneo and the inherent conflicts within the predicted distribution of the Bornean orang-utan (*Pongo pygmaeus*). Using the same data-set of land-use policies, I analysed the conflicts within the modelled distributions of the *Presbytis* monkeys, which had never before been assessed. I also provided detailed distributional data and broad-scale analysis of the threats currently facing these species, making both predictions for future trends and conservation recommendations for safeguarding their persistence.

#### **1.4 The history of this PhD by Published Research**

Upon completing an MSc in Primate Conservation in 2007, I began conducting various analyses of land-use policies on Borneo, mapping the distribution of the endemic colobine monkeys on the island using GIS. These data were used to assess the conservation status of *Presbytis* monkeys on Borneo and inform conservation strategies and forest management initiatives (Ehlers Smith 2014a). During 2008, I conducted research on the

ecology and conservation of the Southern Bornean gibbon (*Hylobates albibarbis*) at the Southern Bornean Gibbon Behavioural Project at the Orangutan Tropical Peatland Project (OuTrop) in Sabangau TPSF, Central Kalimantan, Indonesian Borneo. Research was concerned with ranging, feeding and behavioural data collection on multiple groups of wild gibbons by following their movements and taking instantaneous behavioural samples of focal individuals. Further ecological research included population density through quadrangulation of groups singing and monitoring of phenological plots to establish food abundance.

In September 2009 I established the Sabangau Red Langur Research Project (SRLRP) at OuTrop, and trained two Indonesian field assistants and several foreign research assistants to assist me in data collection towards achieving the various project goals, which included establishing group sizes and population density, and the habituation of wild groups to collect ranging, feeding and behavioural data. The project also included extensive line-transect surveys to establish population density using the programme DISTANCE, and the monitoring of phenological plots.

I co-supervised an MSc student from Oxford Brookes University (Elena Bersacola) in her collection of line-transect survey data for population density estimation of red langurs in Sungai Wain, East Kalimantan, and co-supervised in the interpretation of her results, thesis preparation and subsequent publication (Bersacola *et al.* 2014).

## 1.5 A list of the publications of this research programme

**Ehlers Smith, D. A.**, & Ehlers Smith, Y. C. (2013). Population density of red langurs in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia. *American Journal of Primatology*, 75, 837–847.

**Ehlers Smith, D. A.**, Husson, S. J., Ehlers Smith, Y. C., & Harrison, M. E. (2013a). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of Primatology*, 75, 848–859.

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## Chapter 2 – The study region and study species

### 2.1 The ecology of Borneo

The island of Borneo is the third largest in the world, some 752,000 km<sup>2</sup> straddling the equatorial belt (Figure 2.1.1). It comprises three nations: the Malaysian states of Sarawak and Sabah (124,450 km<sup>2</sup> and 73,620 km<sup>2</sup>, respectively) and the sovereign nation of the Brunei Sultanate (5,770 km<sup>2</sup>) in the north, and the Indonesian provinces of West (146,750 km<sup>2</sup>), Central (152,600 km<sup>2</sup>), East (210,990 km<sup>2</sup>), South (37,660 km<sup>2</sup>) and the newly-designated province of North Kalimantan (71,180 km<sup>2</sup>) in the southern two-thirds of the island. It is sparsely populated by humans, with a total population of 19,800,000 in 2010, at a density of 26 individuals km<sup>-2</sup>.

At the turn of the millennium, the island was considered one of the world's top 25 biodiversity hotspots under threat (Myers *et al.* 2000). Its flora and fauna are some of the most diverse found anywhere on Earth, including some 10-15,000 flowering plants, 44 species of endemic mammal (50 following Roos *et al.* 2014) and over 430 species of resident birds (MacKinnon *et al.* 1997; Myers *et al.* 2000; Myers 2009). There are five floristic altitudinal zones, namely the lowland dipterocarp zone (< 300 m above sea level, asl); the hill dipterocarp zone (300-800 m asl); the upper

dipterocarp zone (800-1200 m asl), the oak-chestnut zone (1200-1500 m asl) and the montane ericaceous zone (> 1500 m asl). There are also five major vegetation classifications found across Borneo, including mangrove forest, along the shoreline boundary zone between the land and the sea, which has the highest level of productivity among natural ecosystems and performs a variety of vital ecosystem services; heath forests, or *kerangas* in the local Iban language to signify that rice does not grow on the sandy soils of its sandstone plateau (MacKinnon *et al.* 1997). Heath forests are found in the lowlands and around coastal areas, and the soils contain high levels of acidity and toxic phenols, which are thought to inhibit nutrient uptake, resulting in forests of lower species diversity than that in dipterocarp forests, with a shorter canopy of typically small, leathery leaves (Whitmore 1990). From Borneo's four mountain ranges (Crocker, Muller, Meratus and Schwaner) montane forests emerge > 800 m asl and comprise an extensive part of the island's vegetation classification, growing up to elevations of > 3,300 m asl. Canopy heights reduce as elevation increases, and the dipterocarp floristic zone, predominant in lowland forests, is replaced by the oak-chestnut, and later montane ericaceous zones. Species diversity is amongst the highest of any montane forests on Earth (Rautner *et al.* 2005), although at lower population density than found in the lowlands of Borneo (Marshall 2010; Nijman 2010b).

The remaining two vegetation classifications are the most extensive on Borneo, and are found in the lowlands. They are the dipterocarp forests and TPSFs, which are the major study sites for this research programme.



**Figure 2.1.1** The island of Borneo and its major vegetation classifications, derived from the GLC2000 project. Note that the province of North Kalimantan did not exist at the time that this map was produced, but now exists in the northern portion of East Kalimantan

### 2.1.1 Dipterocarp forests

Inland from the coastal swamp plains in the low to midlands of the island lie the ‘dipterocarp’ forests, named for the Dipterocarpaceae tree family, which dominates in this habitat class. They are ancient, dating back to over 30 mya (Muller 1970), and occur throughout Southeast Asia, occupying some 85% of all forested areas. Borneo, however, is the centre of dipterocarp distribution, with 267 species, 60% of which are endemic (Ashton 1982). In some forests in East Kalimantan, 10% of all trees, 50% of total basal area and 80% of all emergents belong to the Dipterocarpaceae (Fatawi and Mori 2000), and a study site in East Kalimantan contained more than 100 mammal species of the ~220 species known to exist (Fatawi and Mori 2000).

A major defining feature of dipterocarp forest ecology is that of ‘mast-fruiting’, which describes the synchronised, community-wide flowering and subsequent fruiting events by the majority of dipterocarp forest species, followed by long periods of little to no fruit availability (Knott 2005; van Schaik and Pfannes 2005; Cannon *et al.* 2007a, b). This strategy is assumed to be in response to seed predation, by lowering predator numbers during periods where no fruit is produced, and then fruiting irregularly and *en masse*, when predators are likely to be satiated (Janzen 1974). There is uncertainty if masting is triggered by an El Niño Southern Oscillation event (Ashton *et al.* 1988, Curran *et al.* 1999), the band

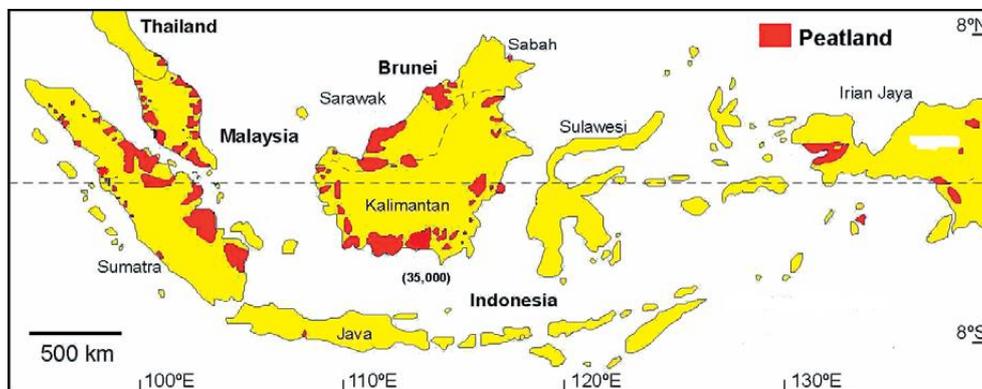
of high ocean temperatures that periodically occurs off the coast of South America, or by a prolonged drought or drop in minimum night-time temperatures (Numata *et al.* 2003, Sakai *et al.* 2006, Brearley *et al.* 2007).

### **2.1.2 Tropical peat-swamp forests**

Tropical peat-swamp forests occur in regions where sufficient rainfall and poor drainage result in permanent water-logging (Page *et al.* 1999). The accumulation of partially decayed organic matter leads to substrate acidification, and the formation of peat layers as the organic matter exceeds decomposition rates (Rieley *et al.* 1992; Page *et al.* 1999). Lowland TPSFs form domed deposits in areas of poor drainage such as valleys or between river basins, and may accumulate layers of peat up to 20 m deep, with an interconnected chain of forest types that slowly replace each other from the outside of the forest dome to the centre (Anderson 1983; Brady 1997; Stoneman 1997; Page *et al.* 1999). Because of the thickness of the peat layer, TPSFs achieve their entire external nutrient influx (with the exception of shallow plains flooded by river or tidal events) from aerial deposits (i.e. rainwater, aerosols and dust), and to a lesser extent, nitrogen fixation by micro-organisms (Jordan 1985) and the faecal deposits of their fauna (Sturges *et al.* 1974). As a result, the nutrient availability in the soil of this ‘ombrogenous’ ecosystem is poor; thus, the primary productivity is also relatively low in comparison to other tropical forest formations (Bruenig

and Droste 1995; Posa *et al.* 2011). Peatlands perform vital ecosystem functions in the form of hydrology regulation and carbon sequestration, in both the trees and the peat, although the majority of the carbon stored within these ecosystems is in the saturated peat soil, rather than the above-ground forests. (Rieley *et al.* 2005).

Tropical peat-swamp forests are found in Central and Southern America, the Caribbean and Asia, and are most extensive in Indonesia (Rieley 2001). Indeed, 70% of all TPSFs, some 260,000 km<sup>2</sup>, are located in Southeast Asia, and 50% in Indonesia and Malaysia particularly (Rieley *et al.* 2005). The Indonesian territory of Kalimantan alone contains 60,000 km<sup>2</sup> of peatland, half of which occurs in Central Kalimantan (Page *et al.* 1999, 2006; Figure 2.1.2).



**Figure 2.1.2** Tropical peat-swamp forests of Indonesia and Malaysia. Adapted from Page *et al.* 2006

Kalimantan contains two types of peatlands – shallow, fertile plains formed 4-5,000 years ago along the coastal regions, and deep peatlands of up to 20 m in thickness, which formed > 25,000 years ago between the rivers of the interior in areas of poor drainage (Anderson 1983; Page *et al.* 1999, 2004). The deep TPSFs of Kalimantan are ombrogenous with a soil pH of 2.8, and are may flooded from up to eight months of the year or permanently. All nutrients are contained within the first few metres of peat, resulting in the evolution of trees that produce either ‘breathing’ or stilted shallow roots (Page *et al.* 1999). The distribution of nutrients across the peat dome is affected by the water table, meaning that the forest type has developed into distinct sub-classes (Page *et al.* 1999). Unlike the majority of forest types elsewhere on Borneo, TPSFs are not rich in mast-fruiting tree species; thus, supra-annual mast-fruiting and flowering events are not a characteristic feature of TPSFs (van Schaik 1986; Cannon *et al.* 2007a, b).

Once considered poor in biodiversity, TPSFs are now known to contain both large and crucial remnant populations of many rare, endangered and specialised taxa, including the Bornean orangutan (*Pongo pygmaeus*; Husson *et al.* 2009); Bornean southern gibbon (*Hylobates albibarbis*, Cheyne *et al.* 2007); red langur (Ehlers Smith and Ehlers Smith 2013); Sunda clouded leopard (*Neofelis diardi*; Cheyne *et al.* 2013); Malaysian sunbear (*Helarctos malayanus*; pers. obs.); Storm’s stork (*Ciconia stormi*; Cheyne *et al.* 2014); white-winged duck (*Asarcornis scutulata*; Page *et al.* 2006); hook-billed bulbul (*Setornis criniger*) and grey-

breasted babbler (*Malacocincla albogulare*; pers. obs.). The largest remaining contiguous lowland forest block is Sabangau TPSF, Central Kalimantan.

## **2.2 Colobine monkeys**

The ‘Old World monkeys’ of Africa and Asia are regarded as belonging to a single family, the Cercopithecidae, comprising two subfamilies, the Cercopithecinae and the Colobinae, that diverged ~19 mya (Meyer *et al.* 2011). The colobines represent a highly diverse subfamily containing 10 genera. Africa, where there is a more contiguous geography and lower overall diversity of forest types (Oates 1994; Fashing 2011), is home to just three genera (*Colobus*, *Piliocolobus* and *Procolobus*), while Asia has the other seven (*Semnopithecus*, *Trachypithecus*, *Presbytis*, *Pygathrix*, *Rhinopithecus*, *Nasalis* and *Simias*). Recent mitochondrial genome analysis indicates that Asian colobine monkeys diverged from their African counterparts ~15 mya (Meyer *et al.* 2011).

### **2.2.1 Colobine feeding morphology**

The major defining feature of colobine monkeys is their specialised stomach morphology, which in turn has a profound effect on their feeding ecology (Davies and Oates 1994). The subfamily evolved these gastro-intestinal

adaptations to exploit the abundant resource of leaves (Bauchop 1978; Chivers 1994). A multi-chambered stomach containing a microbe suspension in the foregut, plus a capacious stomach chamber and elongated caecum simultaneously neutralise toxins and effectively break down plant wall cellulose, facilitating digestion of the high quantities of fibre, protein and vitamins generally contained within leaves (Kay *et al.* 1976; Bauchop 1978; Chivers 1994; Kay and Davies 1994). This adaptation is distinct from monogastric primates, including the cercopithecines, for whom the digestive morphology favours protein-poor but highly-digestible and nutrient-rich fleshy fruits (Kay and Davies 1994).

Specifically, the morphological adaptation for folivory in colobines is thought to preclude selection of ripe, fleshy fruits high in organic acids, as the forestomach fermentation process facilitated by the gut microbe community requires a constant pH of 5.5-7, and the overabundance of fatty acids from ripe, fleshy fruit pulp can cause hyperacidity and consequent morbidity (Lambert 1998; Kay and Davies 1994). Compared to the small intestine, the colobine forestomach also permits more complete digestion of the especially nutritious storage carbohydrates found in seeds (Kay and Davies 1994). Indeed, granivory (seed-eating) is a common characteristic in cases of colobine frugivory (e.g. Harrison and Hladik 1986; Maisels *et al.* 1994; McKey *et al.* 1981), and has been hypothesised as a precursor to leaf-eating in the evolution of the colobine gut (Chivers 1994; Kay and Davies 1994).

Colobines display inter-generic dietary plasticity dependent on the overall body size and resultant size and length of the digestive tract (Chivers 1994). For example, genus *Trachypithecus* has a longer digestive tract and consumes more foliage (Hladik 1977; Stanford 1991; Kool 1992, 1993) than do *Presbytis* and *Nasalis*, which have the smallest forestomachs and largest small intestines of the Colobinae, and in turn consume a higher percentage of unripe seeds and fruits (Bennett 1983; Bennett and Davies 1994; Chivers 1994; Gurmaya 1986; Supriatna *et al.* 1986; Megantara 1989; Davies 1991; Marshall *et al.* 2009a; Hanya and Bernard 2012; Ehlers Smith *et al.* 2013a). Highly selective feeding behaviour has been reported for some colobine species, however (e.g. *Rhinopithecus beiti*, Grueter *et al.* 2009), and given the ability to exploit both leaves and seeds as permitted by their feeding morphology, dietary plasticity at the inter-population level may occur. For example, *Trachypithecus vetulus nestor* frequently selected predominantly ripe domesticated fruits (monthly mean > 50% of overall diet) in an area of high anthropogenic disturbance (Dela 2007). Similarly, in a forest-plantation mosaic in Bohorok, Sumatra, the number of plant species in the diet of *Presbytis thomasi* was fewer than in the more undisturbed forest of Ketambe; additionally, the majority of the species consumed were agricultural (Gurmaya 1986, Wich and Sterck 2010).

The potential ability for dietary plasticity in colobines, therefore, implies adaptability in the face of environmental change and habitat conversion, as inflexibility in diet, and ecological specialisation and

inability to persist in multiple habitat types is highlighted as a significant extinction risk (Harcourt *et al.* 2002; Kamilar and Paciulli 2008). Thus, inhabiting modified landscapes and multiple habitat types as permitted by dietary flexibility may improve the conservation status of colobines; on the other hand, the ability to consistently exploit mature leaves may have an equally important adaptive advantage. For example, the more folivorous *Trachypithecus* species inhabit a wider range of habitats over a greater geographic range than do the more frugivorous *Presbytis* (Oates *et al.* 1994). Colobine monkeys, therefore, represent an interesting subfamily on which to test theories of extinction risk (Kamilar and Paciulli 2008).

### **2.2.2 Colobine ecology**

With the exception of the Hanuman langur (*Semnopithecus entellus*), which occupies dry, semi-terrestrial terrain (Bennett and Davies 1994; Sterck 2012), and to a lesser degree the Yunnan snub-nosed monkey (*Rhinopithecus bieti*), which also displays considerable terrestriality (Kirkpatrick and Long 1994; Kirkpatrick *et al.* 1998; Sterck 2012), colobine monkeys are an arboreal, forest-dwelling subfamily. Females typically give birth to a single offspring at a time, and the mean inter-birth interval is approximately two years (Wich *et al.* 2007; Sterck 2012). In Thomas langurs (*Presbytis thomasi*) mean age at first reproduction is 5.4 years, and life-span varies from 13 years in males to 20 years in females (Wich *et al.*

2007). Social organisation ranges from pair living in some populations of the Mentawai Island colobines (*Presbytis potenziani* and *Simias concolor*) and some populations of *P. frontata* (Nijman and Nekaris 2012), multi-male, multi-female groups in *Procolobus*, *Nasalis*, *Rhinopithecus* monkeys and some Hanuman langurs and Thomas langurs, to the single-male, multi-female society that is typical of the majority of colobine species (Gurmaya 1986; Fashing 2011; Kirkpatrick 2011; Sterck 2012). In multi-male groups, as with their cercopithecoid counterparts, alpha males compete for preferential mating access to females, although a monopoly is not always possible (e.g. Borries and Koenig 2000; Harris and Montfort 2003). However, males can emigrate more than once and reside in different groups, potentially increasing their chances for mating (Borries and Koenig 2000; Korstjens and Schippers 2003). On the other hand, males may reside in all-male bands, and are under pressure to monopolise a group of females to gain mating access as they appear to have a short period of time to do so; thus, their best chance is when they are in their reproductive prime as young adults (Sterck *et al.* 2005). Extra-group males are therefore treated aggressively as reproductive competitors (Wich *et al.* 2002; Kitchen and Beehner 2007; Ehlers Smith 2014b).

Colobine digestive physiology has a strong influence over their behavioural ecology, as for many species, their ability to exploit a ubiquitous food source results in small home ranges and short day-range lengths, less time spent travelling and feeding, and an increase in time spent

resting to aid digestion (Clutton-Brock and Harvey 1977; Dasilva 1992). However, there is evidence to suggest that not all folivores' food resources are abundant, evenly spread and of low quality; for example, the age of the leaf and the varying level of chemical compounds may influence digestibility and selectivity of certain leaves (Koenig *et al.* 1998; Koenig 2000; Grueter *et al.* 2009). Despite this, those with a higher percentage of fruits in their diets tend to have longer day-range lengths and larger total home-range sizes, presumably as a result of searching for these more patchily-distributed food resources (Bennett and Sebastian 1988; Ehlers Smith *et al.* 2013b), and in some species, day-range length has been linked to seasonal availability of foods (Davies 1984; Bennett 1986; Newton 1992). From the phylogenetic perspective, colobine digestive physiology appears to have a profound effect on social behaviour, as the abundance of food resources is thought to preclude intragroup aggression and food contest, and the subsequent need for dominance interactions and appeasements (Yeager and Kool 2000), even in the most frugivorous of colobine populations (Ehlers Smith *et al.* 2013b). Thus, group dynamics follow 'non-female bonded' patterns, and group size is limited by social factors, such as aggression by extra-group males towards bisexual groups for the purpose of infanticide, rather than food contest (the 'folivore paradox'; Dunbar 1988, 1992; Janson 1992; Treves and Chapman 1996; Steenbeek and van Schaik 2001).

### 2.2.3 Genus *Presbytis*

The genus *Presbytis* (Eschscholtz 1821) is a monophyletic taxon confined to Sundaland, i.e. the Malaysian peninsular (and southern Thailand) and the Sundaic shelf islands of the Indo-Malay archipelago (Java and Bali; Sumatra and the Mentawi Islands, and Borneo and the Natuna Islands; Oates *et al.* 1994; Meijaard and Groves 2004; Figure 2.2.3). The marked geological and climatic variance experienced by Sundaland during the last million years has driven extensive radiation in the genus (Meijaard and Groves 2004); as such, there are ~50 recorded colour morphs across what was until recently recognised as 10 (Brandon-Jones *et al.* 2004) or 11 species (Groves 2001), meaning that *Presbytis* is one of the most diverse of the Old World monkey genera (Meyer *et al.* 2011).

Indeed, the taxonomic arrangement of the genus has been the subject of frequent revisions since the seminal description of Napier and Napier (1967). Historically, groupings were largely based on morphological, pelage and behavioural similarities (e.g. Napier and Napier 1967; Wilson and Wilson 1977; Brandon-Jones 1978, 1996a, b; Groves 1989, 2001; Brandon-Jones *et al.* 2004). The split between *Semnopithecus/Rhinopithecus/Nasalis* and *Trachypithecus/Presbytis* took place ~12 mya, and *Presbytis* split from *Trachypithecus* ~11 mya (Meyer *et al.* 2011). The emergence of 4 major lineages of *Presbytis* occurred within ~1.5 my of this date, including: 1) *P. thomasi*; 2) *P. frontata*, *P. chrysomelas* and what were until recently

considered the subspecies of *P. hosei* (now *P. hosei*, *P. sabana* and *P. canicrus*); 3) *P. femoralis*, and 4) the remaining species and their respective subspecies (Meyer *et al.* 2011). Following a revision and the inclusion of the latest research and data on morphology, behaviour, acoustics, and genetics, there are now 17 recognised species of *Presbytis* (Table 2.2.3; Mittermeier *et al.* 2013; Roos *et al.* 2014).

Genus *Presbytis* may be identified by a number of craniodental features: a short face with weakly developed brow ridges and a convex nasal profile; a deep underbite with thick dental enamel and relatively broad homomorphic incisors, and a reduced or absent hypoconulid (distal cusp) on the lower third molar (Brandon-Jones 1984; Napier 1985; Groves 1989). In comparison to ‘simple-stomached’ cercopithecine monkeys, this morphology allows for more efficient folding and slicing of leafy foods as a precursor to efficient digestion of leaf parts, providing an adaptational advantage (Oates and Davies 1994). However, the teeth of *Presbytis* may not be considered as well adapted for folivory relative to other colobine monkeys, which may contribute to their less folivorous diet and allow them further niche flexibility (Lucas and Teaford 1994; Bennett and Davies 1994). Compared to *Trachypithecus*, *Presbytis* are less dimorphic, have relatively smaller stomachs and longer hindlimbs, and leap more and use quadrupedalism less (Fleagle 1976; Strasser 1992; Chivers 1994; Oates *et al.* 1994). Body sizes are relatively gracile and range from 5.6 to 8.2 kg (Rowe and Myers 2010), and offspring display an infantile colour morph –

typically of a whitish colour – that darkens to that of the adult as it reaches independence from the mother (Pocock 1928).

In comparison to other colobine monkeys, *Presbytis* group sizes are relatively small, ranging from 3 (*P. potenziani*; Watanabe 1981) to 16 individuals (*P. siamensis*, Curtin 1980). The majority of species' population densities range from 11 to 26 individuals per km<sup>2</sup> (Kirkpatrick 2011). There is, however, marked variation (1 ind km<sup>-2</sup> to > 100 ind km<sup>-2</sup>; Davies 1994; Marshall 2010), and densities appear to be habitat-specific, based on the quality and availability of both preferred food types (Marshall 2010; Ehlers Smith and Ehlers Smith 2013), and mature foliage (Davies *et al.* 1988). *Presbytis* monkeys are among the most frugivorous and granivorous colobines, and typically consume between 25 and 65% fruit parts (Davies *et al.* 1988; Marshall 2010; Nijman 2010b). The genus is almost entirely arboreal, and, with the exception of *P. potenziani* and some populations of *P. frontata* and *P. thomasi*, maintains groups of single-adult males and multiple-adult females and their offspring. Extra-group males form all-male bands or range alone (Gurmaya 1986; Davies and Oates 1994; Nijman and Nekaris 2012).

**Table 2.2.3** The recognised species and subspecies of genus *Presbytis* (Roos *et al.* 2014)

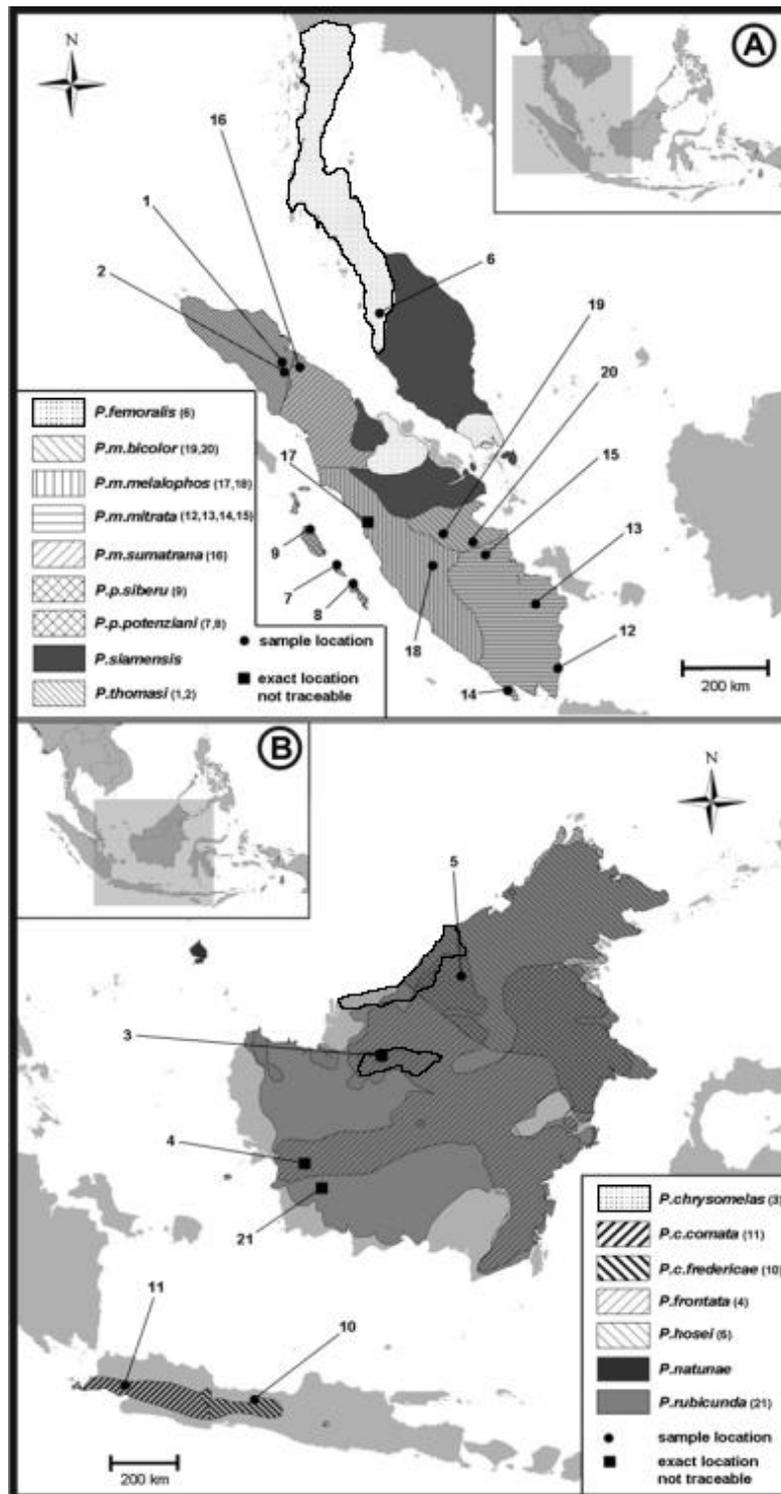
Common name	Scientific name	Recognised subspecies	Authority	IUCN Conservation Status
Thomas langur	<i>P. thomasi</i>	None	Collett, 1893	VU
Black-crested Sumatran langur	<i>P. melalophos</i>	None	Raffles, 1821	NT
Black Sumatran langur	<i>P. sumatranus</i>	None	Müller and Schlegel, 1841	EN
Black-and-white langur	<i>P. bicolor</i>	None	Aimi and Bakar 1992	DD
Mitred langur	<i>P. mitrata</i>	None	Eschscholtz, 1821	EN
Javan langur	<i>P. comata</i>	<i>P. c. comata</i>	Desmarest, 1822	EN
		<i>P. c. fredericae</i>	Sody, 1930	EN
Pagai langur	<i>P. potenziani</i>	None	Bonaparte, 1856	CR
Siberut langur	<i>P. siberu</i>	None	Chasen and Kloss, 1928	EN
Banded langur	<i>P. femoralis</i>	<i>P. f. femoralis</i>	Martin, 1838	VU
		<i>P. f. percura</i>	Lyon, 1908	DD

		<i>P. f. robinsoni</i>	Thomas, 1910	NT
		<i>P. s. siamensis</i>	Müller and Schlegel, 1841	NT
Pale-thighed langur	<i>P. siamensis</i>	<i>P. s. cana</i>	Miller, 1906	NT
		<i>P. s. paenulata</i>	Chasen, 1940	NT
		<i>P. s. rhionis</i>	Miller, 1903	DD
Natuna Islands langur	<i>P. natunae</i>	None	Thomas and Hartert, 1894	VU
Cross-marked langur	<i>P. chrysomelas</i>	<i>P. c. chrysomelas</i>	Müller, 1838	CR
		<i>P. c. cruciger</i>	Thomas, 1892	CR
		<i>P. r. rubicunda</i>	Müller, 1838	LC
		<i>P. r. carinatae</i>	Miller, 1906	DD
Maroon langur	<i>P. rubicunda</i>	<i>P. r. chrysea</i>	Davis, 1962	LC
		<i>P. r. ignita</i>	Dollman, 1909	LC
		<i>P. r. rubida</i>	Lyon, 1911	LC
Hose's langur	<i>P. hosei</i>	None	Thomas, 1889	DD

Miller's grizzled langur	<i>P. canicrus</i>	None	Miller, 1934	EN
Sabah grizzled langur	<i>P. sabana</i>	None	Thomas, 1893	EN
White-fronted langur	<i>P. frontata</i>	None	Müller, 1838	VU

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DD = Data Deficient; NE = Not Evaluated; LC = Least Concern; NT = Near-Threatened;  
VU = Vulnerable; EN = Endangered; CR = Critically Endangered



**Figure 2.2.3** Known extent of occurrence for genus *Presbytis*.  
Adapted from Meyer *et al.* 2011

#### 2.2.4 The endemic *Presbytis* monkeys of Borneo

Hose's langur complex: *Presbytis hosei*, *P. canicrus* and *P. sabana*

The taxonomy of the *Presbytis hosei* complex is an area of uncertainty, and until recently contained a single species with four subspecies (*P. h. hosei*, *P. h. canicrus*, *P. h. everetti* and *P. h. sabana*; Groves 2001). However, it has now been proposed that *P. h. hosei* and *P. h. everetti* are synonymous under the species designation *P. hosei*, the Hose's langur, while *P. h. sabana* and *P. h. canicrus* have been elevated to species level, the Sabah grizzled langur (*P. sabana*) and Miller's grizzled langur (*P. canicrus*), respectively (Roos et al. 2014; c.f. Nijman and Meijaard 2008a; Nijman 2010b; Table 2.2.3). *Presbytis (hosei) canicrus* is noteworthy as its status and distribution is currently under review. Lhota *et al.* (2012) confirmed the species' persistence in the Wehea Forest of the West Kutai district, and Brandon-Jones (1997) established that its range extends west beyond this region. Setiawan *et al.* (2009) suggested that the species may be absent in the Kutai National Park, its former population stronghold in the south of its range. The Hose's langur complex occurs in tropical wet evergreen forests on mineral soils up to 1,700 m asl in the north and east of Borneo. Above this altitude, densities become much lower (Nijman 2010b). Average group sizes range from seven to 10 individuals, at variable densities from 1-4 groups km<sup>-2</sup>. They are particularly threatened by habitat loss and hunting for bezoar stones; Nijman 2004, 2005; Nijman *et al.* 2008b).

#### 2.2.4.1 Bornean banded langur, *Presbytis chrysomelas*

*Presbytis chrysomelas* was recently elevated from a subspecies of *P. femoralis* (Groves 2001), and now comprises two of its own subspecies, *P. c. chrysomelas* and *P. c. cruciger* (Roos *et al.* 2014; Table 2.2.3). It has the most restricted distribution of the *Presbytis* monkeys and inhabits lowland tropical wet evergreen and swamp forests below 500 m asl in groups of 3–13 individuals (Ampeng and Zain 2012; Boitani *et al.* 2006; Nijman *et al.* 2008a). *Presbytis chrysomelas* is considered Critically Endangered due to its low population size, restricted distribution and the high conversion rate of its habitat (Nijman *et al.* 2008b).

#### 2.2.4.2 White-fronted langur, *Presbytis frontata*

*Presbytis frontata* is monotypic (Groves 2001; Table 2.2.3) and inhabits tropical wet evergreen forests on mineral soils in a broad distribution across the centre of the island at relatively low densities up to an elevation of 2,000 m asl (Meijaard and Nijman 2008). It lives in relatively small groups of ~6 individuals (Nijman 2001) or as male-female pairs (Nijman and Nekaris 2012) and is classified as Vulnerable due to hunting and habitat loss (Nijman 2005; Meijaard and Nijman 2008). *Presbytis frontata* is particularly cryptic and freezes upon contact with humans, making it challenging to study (Nijman and Nekaris 2012).

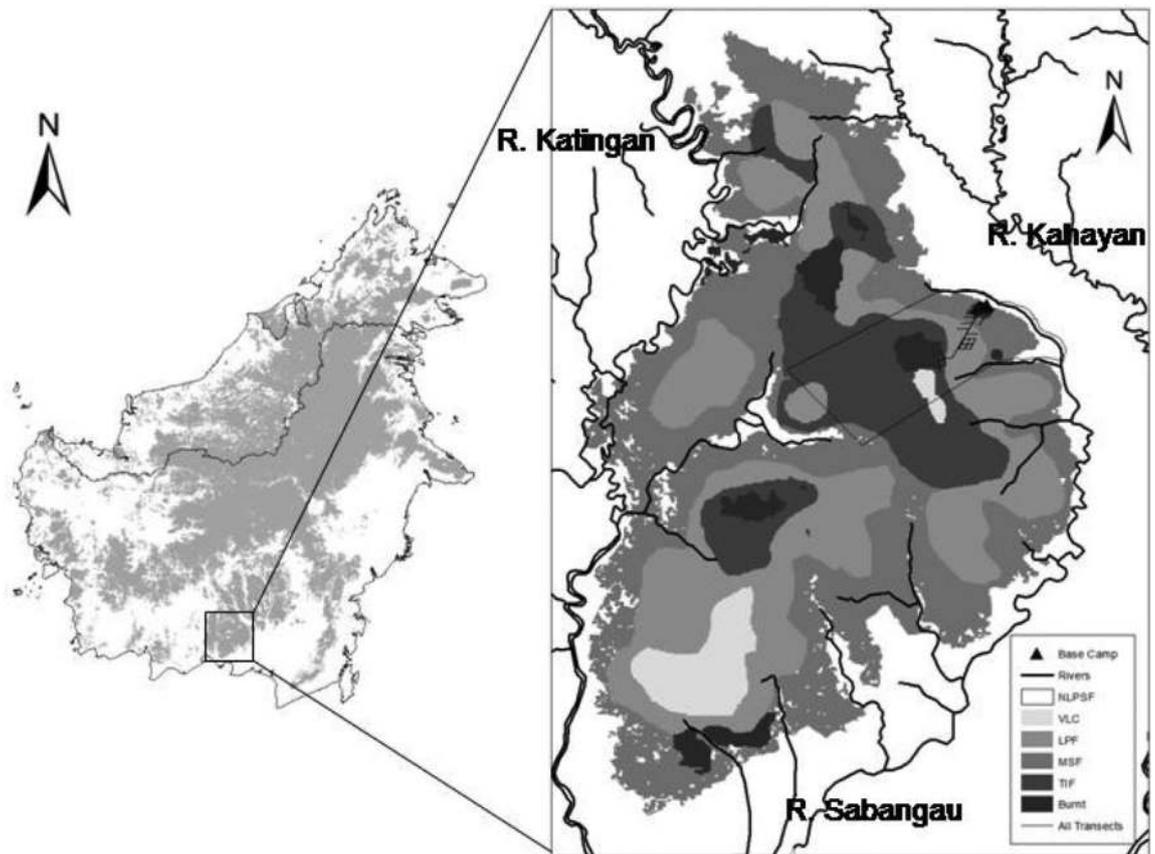
#### 2.2.4.3 Red langur, *Presbytis rubicunda*

*Presbytis rubicunda* represents the most comprehensively-studied of the endemic Bornean *Presbytis* monkeys (c.f. Supriatna *et al.* 1986; Davies *et al.* 1988; Davies 1991; Marshall 2010; Hanya and Bernard 2012; Ehlers Smith and Ehlers Smith 2013; Ehlers Smith *et al.* 2013a, b; Ehlers Smith 2014a, b; Bersacola *et al.* 2014), contains five subspecies, and is considered Least Concern due to its broad distribution (Nijman and Meijaard 2008b; Table 2.2.3). It occurs at a range of densities, dependent on the availability of high-quality foods (Marshall 2010; Ehlers Smith and Ehlers Smith 2013), and groups typically comprise 3–10 individuals. *Presbytis rubicunda* occupies TPSF and wet evergreen forests on mineral soils up to 2,000 m asl, although it is likely populations above 700–800 m asl are at such low densities that they are non-viable (Marshall 2010).

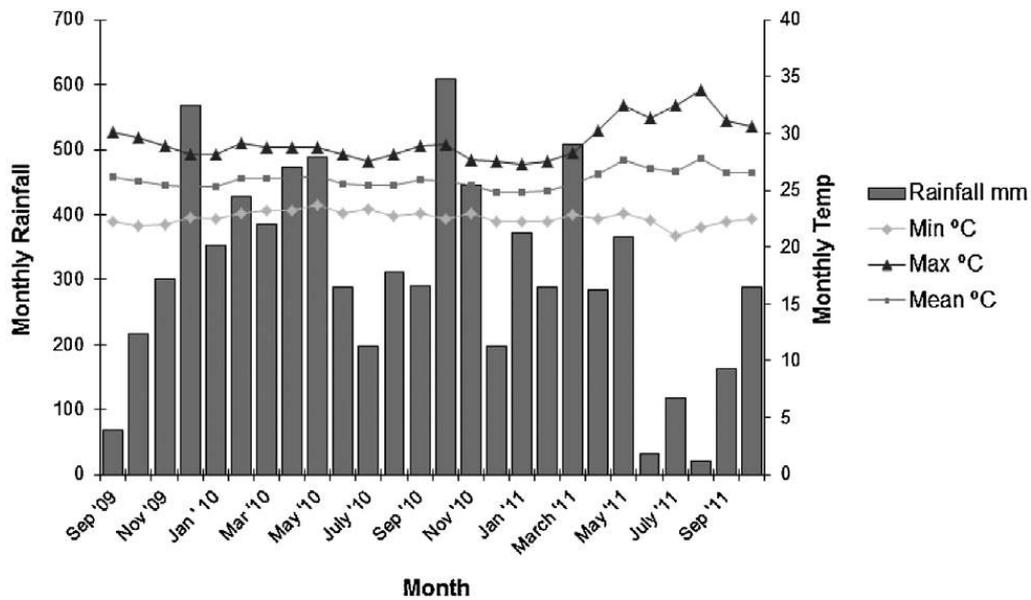
## Chapter 3 – Methods

### 3.1 Study sites

The main red langur ecological research was carried out as part of the Orangutan Tropical Peatland Project (OuTrop)—Center for the International Cooperation in Sustainable Use of Tropical Peatlands (CIMTROP) multidisciplinary research project within the 500 km<sup>2</sup> Natural Laboratory for the Study of Peat-swamp Forests in the northern Sabangau Forest, Central Kalimantan, Indonesia (2°19'S and 113°54'E; Figure 3.1.1), located 20 km south-west of the provincial capital, Palangka Raya. The research site forms part of a larger TPSF landscape (~8,750 km<sup>2</sup>) between the Kahayan River to the east and Katingan River to the west and is the largest contiguous lowland rainforest-block remaining on Borneo (Figure 3.1.1). Rainfall floods the site for eight months of the year and the wet season typically spans November-May (Figure 3.1.2).



**Figure 3.1.1** Location of the Natural Laboratory for the Study of Peat-swamp Forest (NLPSF) within Sabangau and Borneo. MSF = mixed-swamp forest; LPF = low-pole forest; TIF = Tall-interior forest; VLC = very low-canopy forest. Grey shade = forest cover, white = non-forest. Derived from Miettinen *et al.* (2011).



**Figure 3.1.2** Monthly rainfall and minimum, maximum, and mean temperatures per 24 h, averaged per month in Sabangau September 2009–October 2011 (Ehlers Smith *et al.* 2013a).

Sabangau is a true ombrogenous TPSF as, with the exception of the practically-extinct riverine forest, the nutrient influx is obtained exclusively from aerial precipitation; that is, rain, aerosol, and dust (Page *et al.* 1999). Four principle vegetation subclasses have been identified: mixed-swamp forest; low-pole forest; tall-interior forest; and very low-canopy forest (Table 3.1.1, Fig. 3.1.2; Page *et al.* 1999; Morrogh-Bernard *et al.* 2003). Further, large areas of the tall-interior forest (~50%) and areas around the edge of the mixed-swamp forest in Sabangau have burned in the last 10 years because of both accidental ignition, and deliberate ignition for land clearance.

**Table 3.1.1** Vegetation sub-classes of Sabangau, with descriptions of its plants and animals relative to tropical forests on mineral soils (based on Page *et al.* 1999).

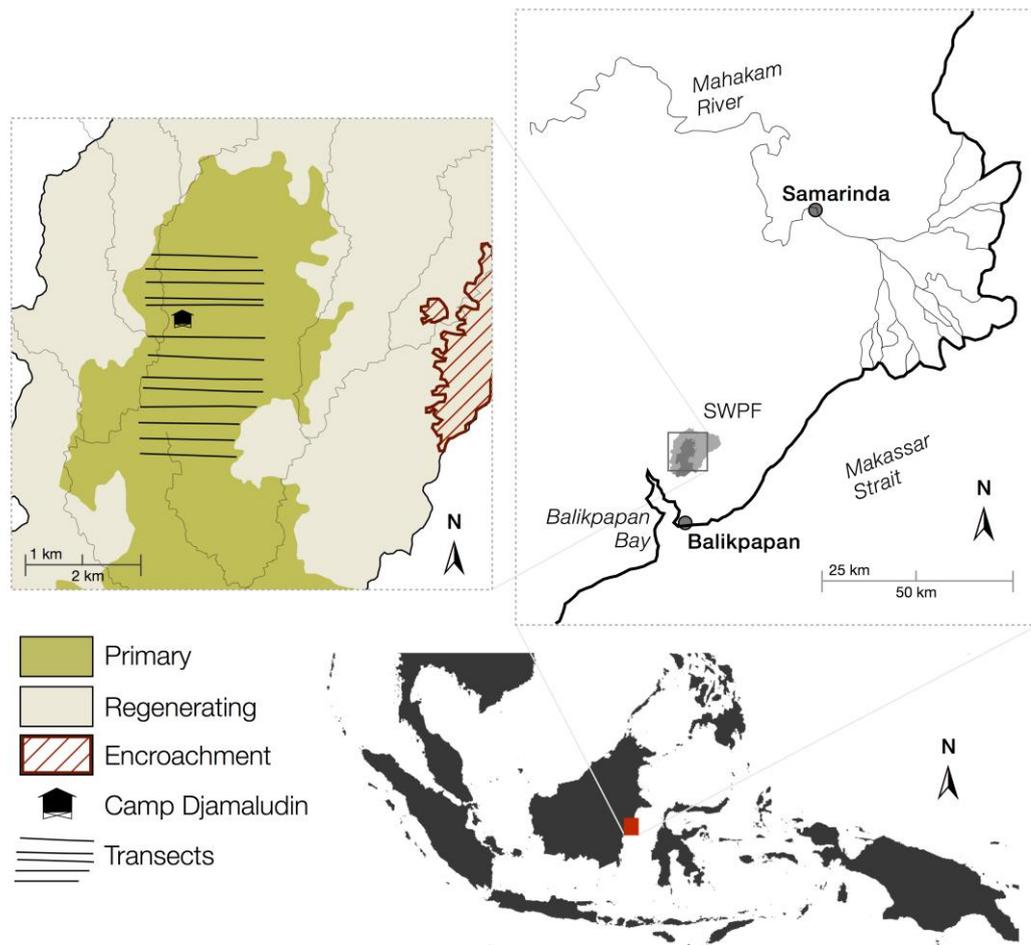
Vegetation Class ID	Characteristics	Total area (km <sup>2</sup> )
Mixed-swamp forest (MSF)	Located beyond the limit of riverine forest on peat thickness of 2–6m. Seasonally flooded. Mixed mean canopy height (15–25m), intermediate biodiversity and density of flora and fauna. Predominant tree genera <i>Mesua</i> , <i>Horsfeldia</i> , <i>Neoscortechinia</i> , <i>Palaquium</i> , <i>Calophyllum</i>	2,745
Low-pole forest (LPF)	Located beyond the limit of the MSF on peat thickness of 7–10m. Water table permanently high; trees grow on hummocks. Low mean canopy height (< 15m), very low biodiversity and density of flora and fauna. Predominant tree genera <i>Syzygium</i> , <i>Palaquium</i> , <i>Shorea</i> , <i>Combretocarpus</i> , <i>Camptosperma</i>	1,850

Tall-interior forest (TIF)	Located beyond the limit of the LPF in the interior, on the thickest peat. Peat-water table permanently below the surface. Tall emergent trees and mean canopy height (30–40m), high biodiversity of flora and fauna. Predominant tree genera <i>Palaquium</i> , <i>Neoscortechinia</i> , <i>Stemonorus</i> , <i>Mezzetia</i>	930
Very low-canopy forest (VLC)	Permanently high water table, large pools of water. Very open, low mean canopy height (< 2m), few faunal species. Predominant tree genera <i>Calophyllum</i> , <i>Comretocarpus</i> , <i>Cratoxylum</i> , <i>Dactylocladus</i> , <i>Litsea</i>	280
Burned	Discontinuous vegetation and canopy, large open areas, very few faunal species	255

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In addition to the ecological monitoring programme established in Sabangau TPSF, population density estimates of red langurs were conducted in Sungai Wain Protection Forest (SWPF; 1°16' E 116°54') which occupies an area of approximately 100 km<sup>2</sup> (Figure 3.1.3), and is located within the administrative area of Balikpapan, Kalimantan's second largest city and the second major oil production and commerce centre in Indonesia. The SWPF is categorised as Hutan Lindung (Protected Forest), and was established to be managed as a water catchment area for the oil company 'Pertamina' in Balikpapan. The SWPF is part of the Balikpapan Bay ecosystem, which consists of a network of freshwater rivers, marine waters, mangroves, dipterocarp forests and other non-mangrove forests (Stark *et al.* 2012). Characterised by a high biological diversity, taxa present in Balikpapan Bay include proboscis monkeys *Nasalis larvatus* (van Wurmb 1787), Sunda clouded leopards *Neofelis diardi* (G. Cuvier 1823), and a Critically Endangered population of Irrawaddy dolphins *Orcaella brevirostris* (Gray 1866). Road construction, logging and the increase in magnitude of fires due to deforestation, are a major conservation threat in Balikpapan Bay, as animal populations and habitats are becoming increasingly fragmented. At present, the SWPF's core area is the largest lowland primary forest left in the south-eastern part of East Kalimantan (Fredriksson 2002). The study site (20 km<sup>2</sup>) is the northern part of the primary forest within the 40 km<sup>2</sup> core area. The forest at the study site is a mixture of humid and dry hilly

dipterocarp forest, with occasional small swamp forest patches. The average annual rainfall in the SWPF is 2,790 mm (Simbolon *et al.* 2012).



**Figure 3.1.3** Map and location of Sungai Wain Protection Forest study site (Bersacola *et al.* 2014)

### **3.2 Distribution mapping, home-range and GIS analysis**

Basic knowledge of a species' occurrence and distribution is an essential starting point for predicting extinctions as a result of habitat loss, and to subsequently devise strategies to focus conservation efforts (Margules and Pressey 2000; Groves 2003). Three types of species occurrence data exist: point localities, at which a species has been observed; extent of occurrences, as broad geographic ranges within which are all the localities that a species is recorded; and predicted distributions, in which the suitability of environmental conditions within a known extent of occurrence are assessed for the likelihood of species' occupancy (Corsi *et al.* 1999; Guisan and Zimmermann 2000; Rondinini *et al.* 2006). If environmental (e.g. climatic variables) and habitat (e.g. vegetation characteristics) requirements are known, ecological niche models as applied in Geographic Information Systems (GIS; mapping programmes capable of analysing spatial data layers grouped by themes, e.g. altitude, vegetation, etc.) can refine extent of occurrence data by omitting areas that are unsuitable (Rondinini *et al.* 2005, 2006), as these data representations often overestimate species' distributions (commission errors).

For the prediction of *Presbytis* distributions, I accessed GIS data layers of primate species' extent of occurrence from "All The World's Primates" (Rowe and Myers 2010), land cover layers of Insular Southeast Asia from 2000 to 2010 produced by the CRISP project (Miettinen *et al.*

2011), and elevation data from the World Database on Protected Areas Consortium (WDPA 2006). I extracted by attribute the appropriate forest cover classes from the land cover maps of 2000 and 2010 for each subspecies according to its habitat requirements, as listed in the Southeast Asian Mammal Databank (Boitani *et al.* 2006) which represents a consensus of the literature. For each subspecies I merged all habitat classes as appropriate, and then clipped the resultant layer by its recorded altitudinal limit. I then clipped each extent of occurrence layer by its species-specific habitat layer to produce a distribution layer, from which I then erased all rivers that bisected habitats as natural geographic barriers.

Geographic Information Systems have further applications for ecological research including the analysis of spatial data to create calculations of animal home-range sizes and attributes. Kernel density estimates (KDE; Worton 1987, 1989) have largely become the standard in home range analyses, replacing earlier techniques such as Minimum Convex Polygons (MCP), although a comparison of methods is recommended when evaluating the validity of a predicted model (Boyle *et al.* 2009). The method places a point (kernel) over each GPS location within an animal's home range, and applies objective algorithms (bandwidths) to determine both the distance between the kernel and an evaluation point in the environment, and the contribution of the kernel to the overall density estimate at a location (Silverman 1986; Seaman *et al.* 1999). KDE is subject to less unpredictable bias in comparison to MCP (Borger *et al.* 2006; Gitzen and Millsaugh

2003; Worton 1995), and more importantly, provides insight into area usage within home ranges by providing a probability density function (Silverman 1986) that corresponds to an animal's utilisation distribution (van Winkle 1975; Worton 1987; Kernohan *et al.* 2001). Percentage volume contours of the probability density can be set to highlight core (typically 50%) and total ranges (90-95%; Horner and Powell 1990; Powell 2000). KDE is, however, highly sensitive to the various bandwidth values (Silverman 1986; Seaman *et al.* 1999). Over-smoothing occurs when the bandwidth is set too high and can overestimate by degrees the size of an utilisation density; under-smoothing when the bandwidth is set too low will fragment the density and produce underestimates (Kernohan *et al.* 2001). Of the numerous bandwidth methods available, the reference method is known to perform poorly except in the case of unimodal distributions (Seaman *et al.* 1999), while the Least-Squares Cross-Validation method is sensitive to sample size (Gitzen and Millspaugh 2003; Gitzen *et al.* 2006; Kie *et al.* 2010). Second generation methods, including the Plug-in and Smooth Cross-Validation algorithms, which control for these known issues, have since improved performance (Beyer 2012).

To obtain home-range data of red langurs in the field for subsequent GIS and KDE analysis, I obtained an initial geographic location upon encountering a group using hand-held Garmin 60C Sx Global Positioning System (GPS) units, and thereafter took points of the group's location every five minutes to coincide with the collection of behavioural scans of a chosen

focal langur individual (Altmann, 1974; see section 3.4) until the follow concluded, either by the monkeys' entering an evening sleeping-tree or no longer being able to locate the group (Ehlers Smith *et al.* 2013b). I then converted the GPS locations to kernels in GIS and performed KDE using four bandwidths: the Least-Squares Cross-Validation, Plug-in, Smooth Cross-Validation and the Biased Cross-Validation methods. I chose one model, the Smooth Cross-Validation method as the model that provided the mean home-range size estimate as a compromise between under- and over-smoothing (Ehlers Smith *et al.* 2013b).

### **3.3 Transect surveys**

Effective strategies for conservation planning are required to ensure species long-term survival. Obtaining accurate population density and precise distribution estimates of threatened taxa across a range of habitats are vital prerequisites for informing such strategies and subsequent on-the-ground actions (Margules *et al.* 2002; Lammertink *et al.* 2003; Morrogh-Bernard *et al.* 2003; Quinten *et al.* 2009; Rainey *et al.* 2009). To estimate primate population density, Distance sampling techniques of line-transect surveys (Buckland *et al.* 2001, 2010) are now widely employed in the forests of the Neotropics (e.g., Ingberman *et al.* 2009; Norris *et al.* 2011); Africa (e.g., Fashing *et al.* 2012; Rainey *et al.* 2009) and Madagascar (e.g. Meyler *et al.* 2012), and Asia (e.g., Palacios *et al.* 2011; Quinten *et al.* 2009).

The programme DISTANCE predicts population density by determining a detection probability function of observing an animal at increasing perpendicular distances from the transect line, as it assumes that all animals on the transect line will be observed, but some may be undetected at increasing distances from the transect (Buckland *et al.* 2001). The programme corrects for observations missed by testing the distribution of the distance of sightings against several best-fit models, to establish the most likely effective strip width (Buckland *et al.* 2001). The model functions providing the lowest Akaike's Information Criterion value (AIC; a quantitative method for model selection seeking to best fit a detection function with the data-set) and highest chi-squared goodness of fit value are chosen as an objective, statistically robust selection method (Buckland *et al.* 2001). Truncation of 5-10% of the data-set to remove bias from outlying results further improves the prediction accuracy (Buckland *et al.* 2001). Assuming that certain sampling conditions are consistently met (e.g. all animals are detected with certainty on the transect line; distances to animals are measured accurately; distances are recorded from the animal's original location and not as a reaction to the observer), the Distance programme provides a robust estimate of population density even in challenging survey environments, given its objective model selection (Buckland *et al.* 2001).

The DISTANCE programme provides a tool for setting the location and number of transects suited to obtaining the minimum sample size and spatial distribution of sightings facilitating a robust population density

calculation within a specific habitat patch to be surveyed (Buckland *et al.* 2001). However, due to time and financial constraints, in both Sabangau TPSF and Sungai Wain Protection Forest, we employed the basis of these principles across a series of existing 12 x 1 km transects and 13 x ~2 km transects in Sabangau and Sungai Wain, respectively, to obtain estimates of red langur population density (Ehlers Smith and Ehlers Smith 2013; Bersacola *et al.* 2014).

### **3.4 Behavioural data collection**

Collection of behavioural data provides the basis for a deeper understanding of an animal's interaction with its environment and ecological requirements. Instantaneous behavioural sampling of a group of individuals or a focal individual at set time intervals is a standard method of unbiased behavioural sampling that is not subject to under- or over- representing natural behaviours as they are presented in a wild setting (Altmann 1974). Such data can only be collected on animals habituated to human presence, however; thus, before I recorded any behavioural data I habituated each group of red langurs for a period of 3-6 months, until all fleeing and defensive behaviours disappeared and travel and feeding behaviours took place in a relaxed manner, and I was able to approach each group without them retreating.

Given the dense nature and consequent poor visibility in the tropical peat-swamp forest environment in which my study took place, I recorded focal-animal data (Altmann 1974) on a single adult female member of the group every five minutes in conjunction with a GPS location. The selection of females as focal individuals had a practical application: females were more visible than males and were less likely to lead us away from the group and then freeze or retreat. I selected an individual adult female as the focal target before the beginning of the follow on the basis of ensuring an even balance between focal individuals and minimising observer bias. I recorded seven classes of data, including 1) the primary activity, which was divided into five categories: feeding; resting; traveling; social behaviours; and unknown (for when the focal individual was not visible); 2) the secondary activity, which explained how the primary activity was achieved; 3) height of the focal individual in tree/substrate by 5 m categories; 4) height of the tree/substrate by the same 5 m categories; 5) distance of the focal individual to other adults in group by 10 m categories; 6) assessment of forest condition by mean height of canopy and canopy percentage, and 7) a unique GPS location tag, specific to each follow (Ehlers Smith *et al.* 2013b). I simultaneously recorded continuous feeding data on the focal individual, for which I documented the species, food type, and food item during all feeding bouts  $\geq 30$  s. I obtained GPS locations of all feeding stems; however, only stems  $> 6$  cm DBH were tagged (Ehlers Smith *et al.* 2013a).

### 3.5 Vegetation sampling and phenological monitoring

Many aspects of primate ecology are determined by vegetation species composition, the quality of habitat (e.g. pristine vs. degraded forests) and the nutritional content and availability of food, and standardised measures of forest structure and productivity are required to provide insight into these determinants (Marshall *et al.* 2009b; Dillis *et al.* 2014). To investigate the influence of forest composition and food availability on the population density and behavioural ecology of red langurs in Sabangau TPSF, I used vegetation plots established by Morrogh-Bernard *et al.* (2003) within the two vegetation sub-classes where population density surveys were conducted (mixed-swamp and low-pole forest; Ehlers Smith and Ehlers Smith 2013), and the single vegetation sub-class (mixed-swamp forest) where behavioural ecology data were collected (Ehlers Smith *et al.* 2013a, b). These standardised vegetation plots have been used for the purposes of forest comparisons in other studies across Indonesia (c.f. Marshall *et al.* 2009b).

For establishing the determining factors of population density in Sabangau, we quantified vegetation characteristics using two plots of 300 m x 5 m per vegetation sub-class in the mixed-swamp forest and low-pole forest, in which all trees  $\geq 10$  cm DBH, and all lianas  $\geq 3$  cm DBH were identified, measured and enumerated (Harrison *et al.* 2010; Morrogh-Bernard *et al.* 2009). In Sungai Wain Protection Forest, we established 73

plots measuring 10 m x 10 m, which were systematically located on both sides of transect lines at a minimum distance of 30 m from each other to aid sampling independence, although across small spatial scales it is possible that autocorrelation occurred, given the small nature of the forest at the study site (20 km<sup>2</sup>). To assess vegetation structure we recorded DBH of all the  $\geq 10$  cm DBH trees, height of all  $\geq 10$  DBH trees (measured on an ordinal scale: 1-5 m, 6-10 m, etc.) and total number of trees (Ganzhorn 2003; Hamard *et al.* 2010).

We measured food availability in Sabangau TPSF through the monthly monitoring of six permanent, randomly located plots (total area = 2.4 ha) all located in the same vegetation sub-class (mixed-swamp forest) throughout a 4 km<sup>2</sup> total area of forest, within and adjacent to the ca. 1 km<sup>2</sup> home range of the focal group (centre of home range = 2°19'03"S, E113°53'98"E). In these plots, all trees  $\geq 6$  cm DBH, and all lianas and figs  $\geq 3$  cm DBH were identified, measured, tagged and enumerated as part of previous research (Harrison *et al.* 2010; Morrogh-Bernard *et al.* 2009). We monitored each tagged stem  $\geq 10$  cm DBH for the presence of ripe and unripe fruits, open flowers and flower buds and each stem  $\geq 6$  cm DBH for the presence of new leaf shoots (Harrison *et al.* 2010; Marshall *et al.* 2009b; Morrogh-Bernard *et al.* 2009; Vogel *et al.* 2008; Wich *et al.* 2011).

### 3.6 Statistical analysis and modelling

Statistical analysis is a standard practise in scientific research methods for providing objective, robust and unbiased interpretations of a data-set. For the majority of statistical analyses a significance value is provided, which provides an effective method for assessing whether the results of analyses are due to chance or some deliberate process (Gravetter and Wallnau 2008). Statistical analysis falls into two categories, dependent on whether the data to be interpreted have an even or normal distribution (parametric statistics) or are skewed in some way (non-parametric statistics).

To establish the distribution of my data-sets, I used a Kolmogorov-Smirnov test, which determined if subsequent analyses would involve parametric or non-parametric tests. I tested for statistically significant relationships ( $P < 0.05$ , where the probability of relationships being due to chance is  $< 5\%$ ) between the behavioural data (including the activity budget, home and day-ranging patterns) and feeding data recorded, and the langurs' environment, including seasonality (wet and dry season) and food availability (by food type, e.g. fruit, young leaves and flowers; Ehlers Smith *et al.* 2013b). This allowed me to assess hypotheses that inferred environmental influence on behavioural ecology (Ehlers Smith *et al.* 2013a, b).

For analysis of the continuous feeding data-set, to establish if there was a relationship between characteristics of dietary selection and the

availability of certain food types, I tested for significant negative correlations ( $P < 0.05$ ) using a Pearson Product Moment correlational test where data were normally distributed, and a Spearman Rank-Order Correlation where data were not. Correlational analyses test for strengths in relationships between two variables (correlation coefficients) within the limits -1 to +1, indicating a negative correlation, or positive correlation, respectively. Correlation tests do not, however, determine that within the relationship of coefficients, one causes the other (Fowler *et al.* 1998). To establish the importance of tree diameter at breast-height (DBH) in feeding tree selection, I also used a Spearman Rank-Order Correlation between feeding tree DBH and feeding bout length, after determining that the data sets were not normally distributed via a Kolmogorov-Smirnov test (Ehlers Smith *et al.* 2013a). I tested potential relationships between the availability of the preferred food items (as potential drivers of ranging behaviours) and ranging behaviour variables, including day-range length, activity period, and behaviours pertaining to foraging (i.e., feeding, traveling), through Pearson's Product-Moment correlational tests after determining that the data sets were normally distributed via a Kolmogorov-Smirnov test (Ehlers Smith *et al.* 2013b).

I tested for significant differences in the mean monthly activity budget scores and monthly day-range lengths across the two seasons using a *t*-test (which determines if two sets of data are different from each other by looking for significant differences in the distribution of their means), after a

Kolmogorov-Smirnov test determined data were normally distributed. For ensuring that the survey data collected were comparable between researchers and thus able to be pooled, we performed a one-way analysis of variance (ANOVA) test, which operates in a similar way to a *t*-test, but allows for more than two variables to be tested against each other (Fowler *et al.* 1998; Ehlers Smith and Ehlers Smith 2013; Bersacola *et al.* 2014).

I sought to identify preferred food items using a Chesson's Selectivity Index (Chesson 1978), which ranks dietary items from 0-1, based on the frequency of selection of a food type versus its overall availability in the environment. This method allows for meaningful comparisons between differing abundances of food types as it offers a standardised index that is unaffected by changes in those relative abundances (Lechowicz 1982); rather, it represents the red langur (the forager)'s perceptions of the value of the food item, in relation to both its own abundance and the abundance of other food types.

For estimating the population density of langurs, we used the programme DISTANCE, which produces a series of best-fit models testing for model robustness, to determine the detection probability function and to establish the likely effective strip width (see Section 3.3). The four models tested, the uniform, half-normal, negative exponential, and the hazard rate, assess the shape criterion, a visual representation of the histogram of the distances of langur sightings from the transect. Each model may then be subject to series expansions (the cosine, simple polynomials and hermite

polynomials) to further test histogram shape. After analysis, the model function that provides the highest chi-squared goodness of fit value is proposed as the model candidate; however, as the power of such a test may be low in the case of determining differences in histogram shape near the transect line, an additional model selection method, the AIC, is employed, and selects for the model providing the lowest AIC value. The programme then suggests the best-fit model candidate based on these criteria (Buckland *et al.* 2001).

## Chapter 4 – Discussion

The overall aim of this body of research and the PhD thesis was to investigate the ecological parameters for some of the most under-studied of the endemic Bornean primates, the *Presbytis* monkeys, and to use these data to assess their threat statuses and inform conservation management schemes. To achieve this, I used an ecological niche modelling technique to provide an assessment of the study species' distributions and the conservation threats therein, and investigated their ecological requirements on the ground through an intensive population and behavioural case study of the red langur.

The research programme has addressed several gaps in the literature by:

- Providing population density estimates of *Presbytis rubicunda* in a non-masting habitat, namely tropical peat-swamp forest.
- Providing feeding, ranging and behavioural ecology, including the first ever activity budget, of *P. rubicunda* in a non-masting habitat, namely tropical peat-swamp forest.
- Showing how a constant provision of high quality foods (i.e. fruit) in a non-masting habitat may influence the distribution, population

density, feeding, ranging and behavioural ecology of primate species with morphological adaptations for folivory.

- Providing preliminary evidence for both the ‘hired guns’ and the ‘indirect-mate-defence via female-resource-defence’ hypotheses in *P. rubicunda*.
- Providing the first detailed assessments of habitat loss between 2000–2010 and the current conservation threats throughout the entire distributions of the endemic Bornean *Presbytis* monkeys.

#### **4.1 Primate ecology**

The distributional patterns and recorded population density estimates of Asian colobines and the species of the genus *Presbytis* display wide variation depending upon habitat characteristics, including floral composition, food availability and elevation (Marshall 2010; Kirkpatrick 2011). I have shown that the presence and density of fruit-bearing trees with a high DBH (> 20 cm) determined the presence or absence of red langurs across narrow landscape scales (Ehlers Smith and Ehlers Smith 2013), which is supported in the wider literature where seasonality of food abundance is known to affect biomass in other primate species (Hanya *et al.* 2011). Furthermore, I have shown that despite poor nutrient availability in TSPFs, population density of *P. rubicunda* was in the upper quartile of

recorded densities in this vegetation class (Ehlers Smith and Ehlers Smith 2013). This relatively high population density was most likely facilitated by the low variation and consistency in fruit availability found in the non-masting TPSF habitat, which is supported by the absence of the species in an adjacent habitat sub-class whose principle difference was the low mean DBH; consequently, availability of preferred fruit was exceptionally low (Ehlers Smith and Ehlers Smith 2013).

The importance of fruit availability in the ecology of *P. rubicunda* in TPSF was exemplified by the highest recorded level of frugivory (and granivory, given the high percentage of seeds in the diet) in any colobine monkey species recorded to date: 83.7% of the annual diet of *P. rubicunda* in Sabangau TPSF comprised fruit parts, of which 76.4% were seeds (Ehlers Smith *et al.* 2013a). This result is particularly striking for two reasons: 1) the morphological adaptation for folivory that *P. rubicunda* possesses, and 2) the availability of young leaf shoots (which were more frequently consumed) in the environment was ~92% of all foods assessed across the study period, versus the ~4% availability of fruits in the environment during the same period, indicating that when available, fruits are highly preferred by red langurs.

Fruit consumption was consistently high in Sabangau across study months and fluctuations in fruit availability were fairly low; as such, fruit consumption was not dependent on fruit availability, thus neither young nor mature leaves (nor any other food type) were not used as fallback foods

(Ehlers Smith *et al.* 2013a). This result is contrary to that found for the same species in masting forests, where fruit availability is low and inconsistent (Hanya and Bernard 2012). Elsewhere, fruit availability constrains the feeding behaviour of orang-utans (*Pongo* sp.) in mast-fruiting forests on Borneo (Knott 1998), but not on Sumatra where orang-utans are able to maintain a high percentage of fruit in their diet year-round (Wich *et al.* 2006), and where there is higher overall forest fruit production (Wich *et al.* 2011).

As may be expected, this extreme shift from the ‘average’ recorded feeding ecology of colobines (1-64% and 11-62% frugivory for African and Asian colobines, respectively; Fashing 2011; Kirkpatrick 2011) had a profound effect on other aspects of the behavioural ecology of red langurs. The home range in the study group was also the largest recorded in genus *Presbytis*, and one of the largest ever recorded in colobine monkeys in general, and the day-range length was the longest recorded in any primate with adaptations for folivory on any continent (Ehlers Smith *et al.* 2013b). This result is consistent with the wider literature, which indicates that home-range sizes and day-range lengths increase with increasing proportions of fruit in the diet, and that species have larger range requirements when high quality food resources are available (Bennett 1986; Davies 1991; Stanford 1991; Newton 1992; Fimbel *et al.* 2001; Fashing *et al.* 2007). Given the large home-range sizes and relatively high population density, it is

reasonable to assume a high degree of home range overlap, although home range data for neighbouring groups was lacking.

The activity budget was also less subject to seasonal variation than that of the average Asian colobine, presumably as a result of the low variation in fruit availability and consistency of frugivory (Huang *et al.* 2003; Matsuda *et al.* 2007, Kirkpatrick 2011; Ehlers Smith *et al.* 2013b).

Phylogenetic inertia, however, appeared to have a strong influence on social behaviour in the study group. The abundance of food resources for traditional folivorous primates is thought to preclude intragroup aggression and food contest competition, and the subsequent need for dominance interactions and appeasements (Yeager and Kool 2000). The almost complete absence of social activities recorded between adults in the focal group is noteworthy, even in this highly frugivorous population, and consistent with that recorded in other, more folivorous Asian colobines (Poirier 1970; Bennett 1983; Kirkpatrick 2011). Given the abundance of food resources for colobines, it is unclear if this effect, rather than food contest, may also influence group size, which is thought to be limited by social factors such as infanticide risk (Dunbar 1988, 1992; Janson 1992; Treves and Chapman 1996; Steenbeek and van Schaik 2001). In the study population, mean group size was consistent with the species average, which may reflect contest over fruit, or may be determined by infanticide risk and social aggression (Ehlers Smith and Ehlers Smith 2013; Ehlers Smith

2014b), although no direct evidence for infanticide was recorded during the study period.

Indeed, the reliance of the study group on fruit provided the basis to test theories of inter-group aggression and the various strategies employed by primate groups and individuals to protect their resources, as high-quality food resources can be considered particularly defensible (Trivers 1972; Wrangham 1980). The majority of aggressive encounters between the study group, and other groups or extra-group males, occurred in the ‘core-range’ of both feeding and sleeping tree resources, indicating that the females of the group benefited from indirect resource defence as a result of the aggressive protection provided by the resident male as a ‘hired gun’ (Wrangham 1980; Ehlers Smith 2014b). Additionally, after the takeover of the study group by an invading male, the post-takeover home and core ranges overlapped their pre-takeover ranges by 75% and 43% respectively, and post-takeover, the group reused ~50% of sleeping trees, suggesting that the invading male established himself in the territory of the resident females, who then continued to use those valuable resources within their original home range. This is the first preliminary evidence for indirect mate defence via resource defence in red langurs (Ehlers Smith 2014b), and is consistent the results of playback experiments in Thomas langurs, which were shown to react more vigorously to playback calls of intruding males in the centre, as opposed to the periphery, of their home ranges (Wich *et al.* 2002).

## 4.2 Primate distribution

The methods used for the construction of distributional maps in this research programme, and the conclusions drawn from both the field surveys and the modelled distributions, are multi-faceted and represent both the challenges and innovation that this particular aspect of primate conservation research requires. The results of the population surveys of red langurs in Sabangau between two sub-classes of one major vegetation class, TPSF, and their absence in one sub-class and abundance in another, demonstrate the importance of both ground-truthing remotely-sensed vegetation maps, and the need for accurate and detailed population surveys across an entire landscape gradient (Ehlers Smith and Ehlers Smith 2013). They also highlight the inherent dangers of generalising presence data to broad vegetation attributes (Ehlers Smith and Ehlers Smith 2013).

Where conservation threats are extreme and population declines are severe, predicting primate distributions based on their ecological requirements and known localities can provide crucial platforms upon which to investigate conservation threats and make management recommendations. My threat assessment of the endemic Bornean *Presbytis* monkeys highlights habitat loss over a 10 year period, and the conservation issues within the predicted distributions as a result of anthropogenic disturbance and land-use policies (Ehlers Smith 2014a). This is the only

comprehensive study to investigate both current threats to these species across their entire ranges and the extent of forest loss since the turn of the millennium, and the results are stark. Despite the modelling caveats, as both omission and commission errors may have occurred given the broad scale of the distributional mapping, their understudied nature and the rapid habitat destruction occurring throughout species' ranges means that the model still has useful applications for conservation planning, despite potential errors in the modelling process (Ehlers Smith 2014a).

### **4.3 The significance and impact of my research for primate conservation**

#### **4.3.1 Ecological research**

My field research has demonstrated that TPSF is of vital importance for the persistence of red langurs; this vegetation class also contains the largest remaining populations of both Bornean orang-utans and Southern Bornean gibbons (Morrogh-Bernard *et al.* 2003; Cheyne *et al.* 2007; Husson *et al.* 2009; Ehlers Smith and Ehlers Smith 2013). This is because of 1) the high population density; 2) the extensive, contiguous nature of the forest, and 3) its low elevation. Much of the lowland forests on Borneo have either been cleared or are now comprehensively fragmented and degraded (Curran *et al.* 2004; Miettinen *et al.* 2011), and although much forest at elevation remains, densities of *Presbytis* monkeys in these habitats (> 750 m asl) are so low

they may be unable to support viable populations (Marshall 2010; Nijman 2010b). The implications of the findings of my field research in TPSF, therefore, is that owing to their extensive range requirements, the identification and protection of larger and more contiguous tracts of lowland rainforests than may have been indicated previously by other studies of colobine ecology are crucial considerations in any future conservation strategies for red langurs.

However, small, undisturbed forest patches in masting forests, where ranging requirements may be smaller given the scarcity of fruit availability, may be critical for population refugia. This is exemplified by our work in Sungai Wain Protection Forest where a large population at high density was identified. These smaller populations may be of particular importance as anthropogenic disturbance and encroachment in the region continues (Bersacola *et al.* 2014).

Selective logging practises, whereby the most commercially viable trees are removed from otherwise intact forests, are likely to be of particular concern to the conservation of Bornean *Presbytis* species, as those most valuable trees tend to be the largest with the highest DBH (Meijaard *et al.* 2005). The limiting factor to presence and population density in Sabangau appeared to be the availability of large (> 20 cm DBH) preferred fruit/seed-bearing stems, as red langurs were present in high densities in the vegetation sub-class where large trees with preferred fruits were at the highest density, but absent from the adjacent vegetation sub-class in which large, preferred

fruit-bearing stems were present at very low densities (Ehlers Smith and Ehlers Smith 2013). Additionally, feeding bout length of the study group was positively correlated with feeding tree DBH, indicating that achieving their nutritional requirements is dependent upon the presence of large trees > 20 cm DBH (Ehlers Smith *et al.* 2013a), which provide > 150% more fruit than those below this threshold (Morrogh-Bernard *et al.* 2009). Furthermore, the largest tree species in Sabangau (mean ~55 cm DBH) were consistently selected for use as sleeping sites, presumably as these are the largest and most robust structures that may ensure safety during the vulnerability of sleeping (Chapman 1989; Spironello 2001; Ehlers Smith 2014b). Some of these species are Dipterocarpaceae, which is frequently targeted for commercial logging (Cannon *et al.* 1998).

#### **4.3.2 Distributional mapping research**

My distribution modelling study highlights the importance of accurate and comprehensive maps that show primate occupancy, as they form the basis of threat assessments and conservation management plans. This was illustrated by the presence of red langurs in high density in the mixed-swamp forest vegetation sub-class, and their absence in the adjacent low-pole forest sub-class of the broader classification of Sabangau TPSF. For the genus *Presbytis* I have highlighted that which has been previously documented for both natural habitats and other primate species therein (e.g. Miettinen *et al.*

2011; Wich *et al.* 2012): that anthropogenic disturbance, degradation and destruction of forests are rapidly causing habitat reduction and population declines across the island of Borneo (Ehlers Smith 2014a). Current land-use policies, including the continuation of forest conversions for agriculture, and management under logging concessions will almost certainly result in further habitat losses and population declines. Furthermore, current PAs are degraded and under threat, and also poorly located for maximal efficiency of primate species conservation (Nellemann *et al.* 2007; Thorn *et al.* 2009; Ehlers Smith 2014a). However, research shows that natural timber concessions in Kalimantan display a similar ability to maintain forest cover as the PAN (Gaveau *et al.* 2013); effective safeguarding of species may therefore rely on a combination of land-use policies as anthropogenic pressures increase on natural habitats, if the effects of selective logging practices on *Presbytis* persistence can be ascertained. Given the reliance of red langurs on the largest trees in TPSFs, however, the result may be that logging concessions cannot sustain *Presbytis* populations even though they maintain canopy cover.

## **4.4 Recommendations for future ecological research and conservation management**

### **4.4.1 Ecological research**

The frugivorous population of red langurs in Sabangau TPSF offers the potential to investigate the influence of phylogenetic inertia and the effect that environment has on the behavioural and socioecology of a species, by investigating how a low fluctuation in availability fruit may change the behavioural ecology of a primate species adapted for folivory. There is the potential to examine whether frugivory in a ‘folivorous’ primate species alters behavioural and socioecology, or if phylogenetic inertia means that ‘folivorous’ behavioural traits are retained.

There is potential to investigate the impact of seed predation by a supposed folivore on seed dispersal and forest ecosystems, as *Presbytis* digestive morphology permits the consumption of unripe seeds in great number. To understand the impact of frugivorous *Presbytis* populations on forest ecology, it may be advisable to analyse stem density and fruit phenology of the most important fruit species in the diet, in conjunction with ingestion rates by individual langurs, and the known population density, home-range size and day-range length of *Presbytis* populations. As red langurs eat unripe seeds, there is potential to quantify the impact of competitive exclusion and the degree to which they may determine the diet of sympatric, frugivorous primates that eat the ripe fruits of the same species. Analysing the degree of dietary overlap with sympatric Bornean

orang-utans (Morrogh-Bernard *et al.* 2009) and Southern Bornean gibbons (Cheyne 2010) may improve our knowledge of tropical forest ecology, species' interactions and potential pressures on other primate species' feeding ecology as determined by frugivorous "folivores".

Investigation into the nature of 'non-female bonded' group behaviour may be conducted (Wrangham 1980), as social interactions among group members in the Sabangau study group were virtually absent (Ehlers Smith *et al.* 2013b). However, food resources that are patchily distributed and defensible (such as fruit) are thought to determine intragroup aggression and food contest competition, and the subsequent need for dominance interactions and appeasements (Yeager and Kool 2000). Additionally, there is potential to study how the preference for a nutritionally valuable food source may influence and select for 'female-biased distributed leadership', whereby the female members of the group collectively make the lead decisions on the ranging behaviours of the group as a whole (Leca *et al.* 2003), as reproductive success in females is limited by access to high quality food resources (Trivers 1972). This would corroborate the preliminary evidence for the indirect-mate-defence via female-resource-defence observed in Sabangau, as a group of females that had been taken over by an invading male remained in their original home range and continued to use the resources therein post-takeover (Ehlers Smith 2014b).

Lastly, there is potential to study the effects of high frugivory and social phenomena on determining the optimum group size of red langurs to further investigate the ‘folivore paradox’ and the possible limiting factors to the number of individuals in a colobine group, including inter- and intra-group food contest, aggression and infanticide risk avoidance (Treves and Chapman 1996; Steenbeek and van Schaik 2001).

#### **4.4.2 Conservation research and management**

The use of ecological research to inform management decisions has been shown to have some success in influencing decision-makers’ policies (Walsh *et al.* 2014). Determining distribution and population density across a wide range of vegetation sub-classes should be considered a priority for all species, as surveys to determine distributional boundaries across the remote interior of Borneo are lacking. This is crucial for the Critically Endangered and Data Deficient species and subspecies, including both subspecies of *P. chrysomelas*; *P. rubicunda carimatae*, and *P. r. chrysea* (Ehlers Smith 2014a; Roos *et al.* 2014). To this end, delineating vegetation sub-classes across Borneo to identify population boundaries within forested areas, as illustrated by the distribution of red langurs across sub-classes of Sabangau TPSF (Ehlers Smith and Ehlers Smith 2013), would facilitate accurate ecological niche modelling and the subsequent projection of any available

population density estimates into remnant forest patches to quantify population sizes.

Given the degraded nature of much of the remnant forest on Borneo, assessing the population status and viability of *Presbytis* monkeys in degraded habitats is also a priority. Furthermore, the response of *Presbytis* monkeys to habitat disturbance appears unclear (Meijaard *et al.* 2005), although selective logging of large trees is likely to have detrimental effects on the ecology of red langurs as they are dependent on them for achieving feeding and sleeping requirements (Ehlers Smith and Ehlers Smith 2013; Ehlers Smith *et al.* 2013a; Ehlers Smith 2014b). Given the high percentage of land-use policies attributed to logging concessions in particular and disturbance activities in general (Ehlers Smith 2014a), quantifying their response in terms of population status and behavioural and socioecological changes should be of precedence. Furthermore, quantifying population densities of threatened primate taxa within logging concessions may be considered a priority, as concession managements are apparently as effective as the PAN at maintaining forest cover (Gaveau *et al.* 2013); however, whether primate species persist within concessions is currently poorly documented. This will allow for informed consideration of the impacts of future land-use changes and management schemes, such as logging concessions (Gaveau *et al.* 2013), on the persistence of *Presbytis* monkeys (Ehlers Smith 2014a).

Finally, the degraded nature of the majority of PAN is of particular concern, with many further under threat from mining and logging activities (Nellemann *et al.* 2007). I therefore recommend an extension of adjacent PAs for connectivity (Thorn *et al.* 2009), and the priority gazetting of unallocated lands to PAs within the distribution of Critically Endangered *P. chrysomelas* and *P. sabana*, which have experienced an exceptional rate of forest loss in the last 10 years (22-50 %; Ehlers Smith 2014a).

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**Appendices: The published work of the  
PhD research programme**

## **Appendix 1**

**Ehlers Smith DA, Ehlers Smith YC (2013).** Population density of red langurs in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia. *American Journal of Primatology* 75: 837-847.

Concept and design: DA Ehlers Smith; Fieldwork: DA Ehlers Smith, YC Ehlers Smith;  
Data analysis: DA Ehlers Smith; Manuscript preparation: DA Ehlers Smith, YC Ehlers Smith

## Co-Author Statement

**Ehlers Smith DA**, Ehlers Smith YC (2013). Population density of red langurs in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia. *American Journal of Primatology* 75: 837-847.

Concept and design: DA Ehlers Smith; Data collection: DA Ehlers Smith, YC Ehlers Smith  
Data analysis: DA Ehlers Smith; Manuscript preparation: DA Ehlers Smith, YC Ehlers Smith

I, co-author Yvette C. Ehlers Smith, confirm that David Ehlers Smith made the stated contributions to this publication.



Signature \_\_\_\_\_

Date: 23/10/2014

## RESEARCH ARTICLE

## Population Density of Red Langurs in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesia

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Because of the large-scale destruction of Borneo's rainforests on mineral soils, tropical peat-swamp forests (TPSFs) are increasingly essential for conserving remnant biodiversity, particularly in the lowlands where the majority of habitat conversion has occurred. Consequently, effective strategies for biodiversity conservation are required, which rely on accurate population density and distribution estimates as a baseline. We sought to establish the first population density estimates of the endemic red langur (*Presbytis rubicunda*) in Sabangau TPSF, the largest remaining contiguous lowland forest-block on Borneo. Using Distance sampling principles, we conducted line transect surveys in two of Sabangau's three principle habitat sub-classes and calculated group density at 2.52 groups km<sup>-2</sup> (95% CI 1.56–4.08) in the mixed-swamp forest sub-class. Based on an average recorded group size of 6.95 individuals, population density was 17.51 ind km<sup>-2</sup>, the second highest density recorded in this species. The accessible area of the tall-interior forest, however, was too disturbed to yield density estimates representative of the entire sub-class, and *P. rubicunda* was absent from the low-pole forest, likely as a result of the low availability of the species' preferred foods. This absence in 30% of Sabangau's total area indicates the importance of in situ population surveys at the habitat-specific level for accurately informing conservation strategies. We highlight the conservation value of TPSFs for *P. rubicunda* given the high population density and large areas remaining, and recommend 1) quantifying the response of *P. rubicunda* to the logging and burning of its habitats; 2) surveying degraded TPSFs for viable populations, and 3) effectively delineating TPSF sub-class boundaries from remote imagery to facilitate population estimates across the wider peat landscape, given the stark contrast in densities found across the habitat sub-classes of Sabangau. Am. J. Primatol. 75:837–847, 2013. © 2013 Wiley Periodicals, Inc.

**Key words:** Borneo; colobinae; distance sampling; folivore; habitat quality

## INTRODUCTION

Tropical rainforests cover some 19.6 million km<sup>2</sup> of the Earth's surface [Asner et al., 2009] and represent some of the most biodiverse biomes on the planet [Pimm & Sugden, 1994]. Approximately 13 million hectares, however, are currently deforested annually [FAO, 2010]. As an order largely confined to tropical rainforests, 53% of all primate species are now classified as threatened with extinction by the IUCN Red List of Threatened Species [Mittermeier et al., 2012]. Consequently, effective strategies for conservation planning are urgently required to ensure species' long-term survival. Obtaining accurate population density, abundance, and distribution estimates of threatened taxa across a range of habitats are vital prerequisites for informing such strategies and subsequent on-the-ground actions [Lammertink et al., 2003; Margules et al., 2002; Morrogh-Bernard et al., 2003; Quinten et al., 2009; Rainey et al., 2009].

Indonesian rainforests represent crucial biodiversity hotspots and habitats of major conservation value, particularly for primates [Meijaard & Nijman, 2003; Supriatna & Gursky-Doyen, 2010], but are subject to some of the highest global rates of destruction [Curran et al., 2004; Matthews, 2002; Nellemann et al., 2007]. Southeast Asia is also home

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to most (~60%) of the world's tropical peat-swamp forests (TPSFs), 80% of which are found in Indonesia [Page, 2006; Rieley et al., 1997]. Studies indicate that TPSFs contain lower population densities and species richness—particularly in the case of plant species—than tropical forests on mineral soils because of extreme chemical and hydrological conditions creating a paucity of available nutrients and high pH [Paoli et al., 2010; Posa et al., 2011; Yule, 2010]. They represent a unique and diverse ecosystem, however, providing refuge for many specialist wetland species of plants and animals [Posa et al., 2011; Yule, 2010]. Because of the large-scale destruction of tropical rainforests on mineral soils, TPSFs are becoming increasingly essential for conserving remnant biodiversity in addition to specialist taxa, particularly in the lowlands where the majority of habitat conversion has occurred [Curran et al., 2004; Erb et al., 2012; Miettinen et al., 2011a; Posa et al., 2011].

The island of Borneo is at the forefront of deforestation, degradation, and habitat conversion [Kronstedt et al., 2012; Langner et al., 2007; Rautner et al., 2005], and TPSFs comprise a significant portion of remnant lowland forest on Borneo (~24,000 km<sup>2</sup> [Miettinen et al., 2011a]). Indeed, Bornean TPSFs are particularly important for endemic primate populations, including the proboscis monkey (*Nasalis larvatus*) [Meijaard & Nijman, 2000]; Bornean orangutan (*Pongo pygmaeus*) [Husson et al., 2009; Morrogh-Bernard et al., 2003], and Bornean southern gibbon (*Hylobates albibarbis*) [Cheyne et al., 2007]. At over 6,000 km<sup>2</sup>, the Sabangau peat-swamp ecosystem in Central Kalimantan represents the largest remaining contiguous lowland forest-block on Borneo [Page et al., 1999; Wich et al., 2008]. It also contains the largest populations of *P. pygmaeus* [Wich et al., 2008] and *H. albibarbis* [Cheyne et al., 2007], and is home to six other primate species. Six of these eight species are endemic, including the red langur (*P. rubicunda*), an Asian colobine monkey.

Colobines represent a diverse subfamily of leaf-eating monkeys from Africa and Asia [Davies & Oates, 1994]. Population densities in natural habitats range from as few as 3 individuals km<sup>-2</sup> (*Colobus angolensis*) [Bocian, 1997] up to 315 ind km<sup>-2</sup> (*Colobus guereza*) [Davies, 1994] in Africa, and 1 ind km<sup>-2</sup> (*P. rubicunda*) [Marshall, 2010] up to 220 ind km<sup>-2</sup> (*Simias concolor*) [Watanabe, 1981] in Asia. The population density of the genus *Presbytis*, restricted to Peninsular Southeast Asia and the Greater Sunda Islands, has been reported to exceed 100 ind km<sup>-2</sup> in the lowland forests of Peninsular Malaysia (*P. siamensis*) [Davies, 1994], but the majority of species' densities range between 11 and 26 ind km<sup>-2</sup> [Davies, 1994; Kirkpatrick, 2011]. Within its genus, previous surveys indicate *P. rubicunda* occurs at a relatively high density in the pristine lowland dipterocarp forests of Lanjak Entimau, Sarawak [Blouch, 1997] and at intermediate levels in those at Sepilok, Sabah [Davies & Payne, 1982], but at lower levels in Barito Ulu, Central Kalimantan [McConkey & Chivers, 2004], and the Gunung Palung ecosystem in West Kalimantan [Marshall, 2010] (Table I). Swamp forests and montane forests above 750 m support the lowest densities in Gunung Palung [Marshall, 2010], and populations of *P. rubicunda* may not be viable in the large tracts of montane forests remaining (Table I) [Marshall, 2010].

This habitat-specific range of densities is positively correlated with the quality and availability of the monkeys' preferred food types (foods disproportionately selected relative to their availability) [Marshall & Wrangham, 2007] in Gunung Palung [Marshall, 2010], and the quality of mature foliage in Sepilok [Davies et al., 1988]. Food resources are generally preferred because of their high nutritional quality, but are costly for plants to produce and are therefore rare in the environment [Marshall & Wrangham, 2007; Stephens & Krebs, 1986]. The availability of preferred foods in particular is thus considered to limit population density [Balcomb et al., 2000; Marshall, 2010]. However, in some

**TABLE I. Recorded Population Densities of *Presbytis rubicunda* on Borneo**

Site	Habitat	Population density (ind km <sup>-2</sup> , 95% CI where stated)	Source
Sepilok	Lowland dipterocarp	16.2	Davies [1984]
Barito Ulu	Lowland dipterocarp	8	McConkey & Chivers [2004]
Gunung Palung	Peat Swamp	2.52 (1.13–5.62)	Marshall [2004, 2010]
Gunung Palung	Freshwater Swamp	7.79 (4.53–13.39)	Marshall [2004, 2010]
Gunung Palung	Alluvial Bench	10.53 (6.26–17.71)	Marshall [2004, 2010]
Gunung Palung	Lowland Sandstone	5.85 (3.27–10.47)	Marshall [2004, 2010]
Gunung Palung	Lowland Granite	7.26 (4.40–12.02)	Marshall [2004, 2010]
Gungung Palung	Upland Granite	6.89 (4.19–11.32)	Marshall [2004, 2010]
Gunung Palung	Montane	1.24 (0.48–3.22)	Marshall [2004, 2010]
Lanjak Entimau	Primary dipterocarp	21.56 (16.53–26.61)	Blouch [1997]
Lanjak Entimau	Disturbed dipterocarp	5.37 (1.57–9.17)	Blouch [1997]

populations, the availability of fallback foods (selected increasingly as preferred foods become less available) [Marshall & Wrangham, 2007] are also hypothesized to limit population density as they are more abundant in the environment, yet compared to preferred foods are energetically inferior as they are difficult to process [Davies et al., 1988; Marshall et al., 2009; Marshall & Wrangham, 2007]. In Sabangau TPSF, fruit is nutritionally superior compared to other food resources [Harrison, 2009], and is preferred by *P. rubicunda* [Ehlers Smith et al., 2013]. No other food types are preferred or used as fallback foods [Ehlers Smith et al., 2013].

To investigate the population density of *P. rubicunda* in TPSFs and its possible limiting factors, we conducted line-transect surveys using the sampling principles of Distance [Buckland et al., 2001, 2010] in three habitat sub-classes of the largest remaining ombrogenous TPSF habitat on Borneo, the Sabangau Forest. In particular, we aimed to test the hypotheses that 1) because of a paucity of available nutrients in the peat-swamp environment, population density would be lower in Sabangau than reported in forests on mineral soils, and 2) that the availability of preferred food types would be a limiting influence on the population density of *P. rubicunda* in the nutrient-poor TPSF environment [Marshall, 2010].

## METHODS

We obtained permission for the study from the Indonesian Institute for Research and Technology and all research adhered to Indonesian legislation. Our research was purely observational and is in strict compliance with the Ethical Treatment of Non-Human Primates as described by the American Society of Primatologists.

### Study Site and Study Species

This research was carried out as part of the Orangutan Tropical Peatland Project (OuTrop)—Center for the International Cooperation in Sustainable Use of Tropical Peatlands (CIMTROP) multi-disciplinary research project within the 500 km<sup>2</sup> Natural Laboratory for the Study of Peat-Swamp Forests in the northern Sabangau Forest, Central Kalimantan, Indonesia (2°19'S and 113°54'E; Fig. 1), located 20 km south-west of the provincial capital, Palangka Raya. The research site forms part of a larger peat-swamp forest landscape (~8,750 km<sup>2</sup>) between the Kahayan River to the east and Katingan River to the west and is the largest contiguous lowland rainforest-block remaining on Borneo (Fig. 1). Rainfall floods the site for 8 months of the year and the wet season typically spans November–May (Fig. 2). We monitored the temperature and

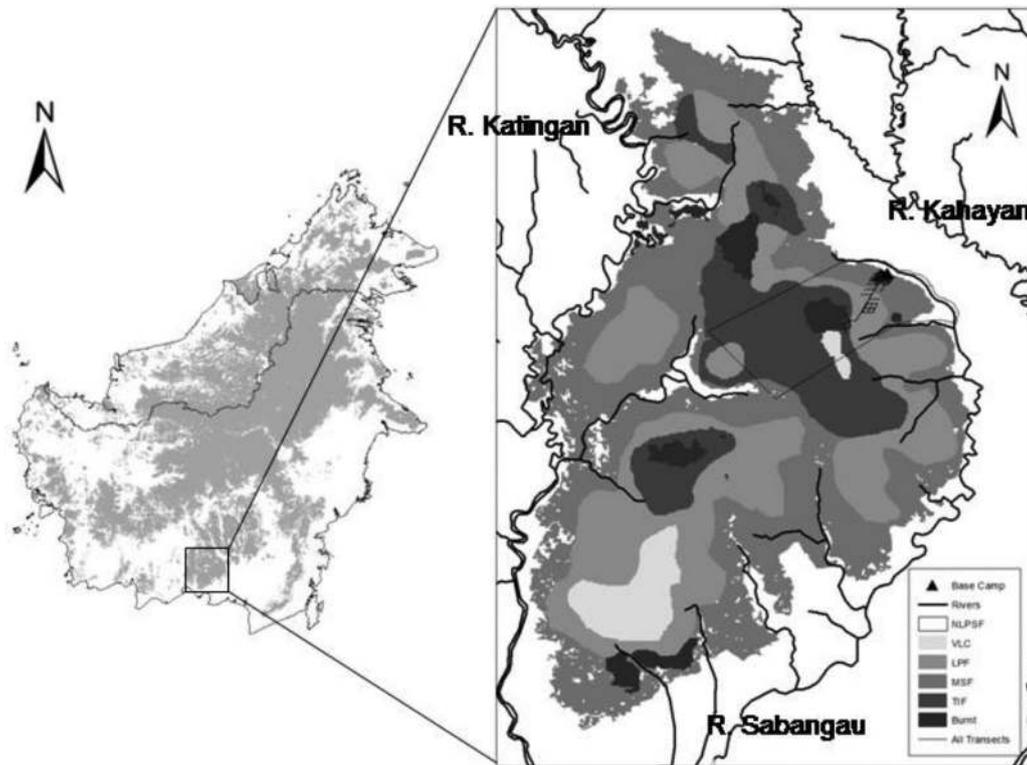


Fig. 1. Location of the Natural Laboratory for the Study of Peat-swamp Forest (NLPSF) within Sabangau and Borneo. MSF, mixed-swamp forest; LPF, low-pole forest; TIF, Tall-interior forest; VLC, very low-canopy forest. Gray shade = forest cover, white = non-forest. Derived from Miettinen et al. [2011b].

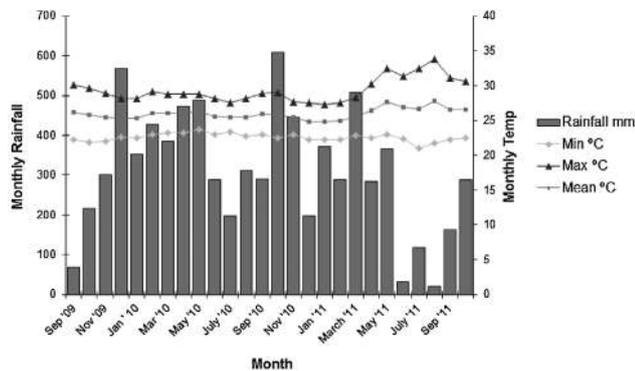


Fig. 2. Monthly rainfall and minimum, maximum, and mean temperatures per 24 h, averaged per month in Sabangau September 2009–October 2011.

rainfall each day at 06:00 and 18:00 using a minimum–maximum thermometer situated inside the forest, and a rain-gauge situated at the base camp (Fig. 2).

Sabangau is a true ombrogenous TPSF as, with the exception of the practically-extinct riverine forest, the nutrient influx is obtained exclusively from aerial precipitation, that is, rain, aerosol, and dust [Page et al., 1999]. Four principle habitat sub-classes have been identified: mixed-swamp forest; low-pole forest; tall-interior forest; and very low-canopy forest (Table II, Fig. 1) [Morrogh-Bernard et al., 2003; Page et al., 1999]. Further, large areas of the tall-interior forest (~50%) and areas around the edge of the mixed-swamp forest in Sabangau have burned in the last 10 years because of deliberately ignited fires.

*Presbytis rubicunda*, an Asian colobine monkey endemic to Borneo and the adjacent island of Karimata [Medway, 1970], has a broad distribution across the island and occupies most habitat types. *P. rubicunda rubida* occurs in the south-western portion of Borneo, south of the Mahakam River, and west of the Barito River [Groves, 2001]. It is sexually

monomorphic and is physiologically adapted for folivory [Bauchop & Martucci, 1968] although a significant proportion of its diet comprises unripe seeds (30–76%) [Davies, 1991; Ehlers Smith et al., 2013; Marshall, 2010; Supriatna et al., 1986]. Groups include from three to ten individuals and typically comprise a single adult male, and up to three adult females and their offspring [Davies, 1984; Supriatna et al., 1986].

## Data Collection

### Line transect surveys

To estimate primate population density, Distance sampling techniques of line-transect surveys [Buckland et al., 2001, 2010] are now widely employed in the forests of the Neotropics [e.g., Ingberman et al., 2009; Norris et al., 2011]; Africa [e.g., Fashing et al., 2012; Rainey et al., 2009] and Madagascar [e.g. Meyler et al., 2012], and Asia [e.g., Palacios et al., 2011; Quinten et al., 2009]. Distance predicts population density by determining a detection probability function of observing an animal at increasing perpendicular distances from the transect line, and correcting for observations missed by testing data against several models to establish effective strip width [Buckland et al., 2001].

We conducted surveys for population density estimates of *P. rubicunda* in the mixed-swamp forest and the low-pole forest (Fig. 1), two of the three principle habitat sub-classes that support primate populations [Cheyne et al., 2007; Morrogh-Bernard et al., 2003]. We conducted an exploratory survey in February 2011 to the third principle habitat sub-class, the tall-interior forest, during the wet season but we conducted no subsequent population surveys, as up to 50% of this sub-class had been cleared by burning in the last 10 years, and more recently by selective logging. The accessible location in this habitat sub-class was a narrow corridor between the low-pole forest and the burn scar (Fig. 1), which

**TABLE II. Habitat Sub-Classes of Sabangau, With Descriptions of Its Plants and Animals Relative to Tropical Forests on Mineral Soils (Based on Page et al., 1999).**

Habitat ID	Characteristics	Total area (km <sup>2</sup> )
Mixed-swamp forest	Mixed mean canopy height, intermediate biodiversity and density of flora and fauna. Predominant tree genera <i>Mesua</i> , <i>Horsfeldia</i> , <i>Neoscortechinia</i> , <i>Palaquium</i> , <i>Calophyllum</i>	2,745
Low-pole forest	Low mean canopy height (<15m), very low biodiversity and density of flora and fauna. Predominant tree genera <i>Syzygium</i> , <i>Palaquium</i> , <i>Shorea</i> , <i>Combretocarpus</i> , <i>Camptosperma</i>	1,850
Tall-interior forest	Tall emergent trees and mean canopy height (30–40m), high biodiversity of flora and fauna. Predominant tree genera <i>Palaquium</i> , <i>Neoscortechinia</i> , <i>Stemonorus</i> , <i>Mezzetia</i>	930
Very low-canopy forest	Very open, low mean canopy height (<2m), lacking in fauna. Predominant tree genera <i>Calophyllum</i> , <i>Combretocarpus</i> , <i>Cratoxylum</i> , <i>Dactylocladus</i> , <i>Litsea</i>	280
Burned	Discontinuous vegetation and canopy, large open areas, lacking in fauna	255

suggested a compression of the *P. rubicunda* population to artificial levels by the recent disturbance events [e.g., Decker, 1994; Robinson & Ramirez, 1981]. Thus, we felt that estimates of population density from this habitat type would not be representative of a stable population, and therefore not usable for total population extrapolations.

We conducted the surveys in the dry season between October and December 2009 (mixed-swamp forest) and in September 2011 (low-pole forest) when forest flood waters were absent. Surveying in the dry season was preferable as noise created by observers wading through the flood-waters impedes primate detectability and causes targets to flee their initial location. We collected the survey data following the principles of Distance [Buckland et al., 2001, 2010] using a standard line survey approach across a system of 12 transects of 1 km in length in both the mixed-swamp forest and the low-pole forest (Fig. 1). Survey design and sampling effort reflected a balance between obtaining a robust data-set of observations with the expense and logistics of surveying a relatively inaccessible terrain for sustained periods. The randomly placed transects were located in areas representative of each habitat sub-class in their entirety [Buckland et al., 2010]. We used transects systematically placed at least 1 km apart to ensure independent sighting events during simultaneous surveys.

Six researchers with extensive experience working in the research site and fully trained in survey methods carried out the surveys, which we conducted at 06:30–08:30 and 14:00–16:00 to coincide with peak foraging patterns for maximum detectability [DA Ehlers Smith, pers. obs.]. Three survey teams simultaneously walked parallel transects spaced 1 km apart on a continuous bearing. Although a 2-day interval between surveys has been recommended [National Research Council, 1981], time constraints forced us to use a minimum of 1 day between repeat surveys of each transect, which reflected a balance between achieving a large sample size for a robust density estimate and maintaining independence of sighting events. Walking at a speed of ~1 km/hr, we recorded all visual encounters with *P. rubicunda*, including: 1) time of day; 2) GPS location and location on transect; 3) angle to center of group-cluster from transect; 4) distance from observer to center of group-cluster; 5) group size and composition (if identifiable); 6) group spread; 7) reaction of group to encountering observer; and 8) detection method. We then calculated perpendicular distances of group cluster-to-transect using simple trigonometry. We recorded only visual encounters because of the difficulty of accurately measuring the distance to a non-visible group-cluster, and to eliminate possible confusion of the target species with sympatric primates if no vocalizations were heard. We devoted extensive time to training all researchers in the survey methods, and

although distance to groups clusters were estimated rather than calculated using laser range-finders, all researchers regularly calibrated estimating distances in group training sessions using tape measures to maximize accuracy and minimize researcher bias [Mitani et al., 2000].

#### *Group composition*

Group size and composition determined from transect survey data are often underestimates of the true number of individuals in a group [Hassel-Finnegan et al., 2008], as transect surveys require the observer to spend <10 min per observation event resulting in individuals missed [National Research Council, 1981]. We established an ecological study of *P. rubicunda* in the mixed-swamp forest in March 2010 after potential groups for habituation had been identified during the population survey effort. We regularly encountered (minimum bimonthly) seven out of the ten known groups in the core research area from March 2010–December 2011, and at each instance recorded the group composition and the distinguishing features of each group member. We calculated the mean number of individuals recorded for each group across all encounters during the study period, and thus calculated mean group size in the research area. We combined these records with GPS data to provide a spatially referenced map of langur groups within the research grid, and observational information on changes in group composition over time. We defined adults as reproductively active individuals of full body size, either with infants or pregnant (females) or “loud calling” (males); sub-adults as larger than three-quarters the body size of a fully grown adult but not yet displaying adult characteristics; juveniles as weaned from the mother and less than three-quarters the body size of an adult, and infants to be still nursing and dependent on their mother.

#### *Data analysis*

Using the program *Distance v.5* [Thomas et al., 2006] we calculated population density estimates after the minimum independent sighting sample size for a robust estimate ( $N = 40$ ) was obtained [Buckland et al., 2001]. We found no significant differences in the means of sighting distances between researchers (one-way ANOVA,  $N = 3$ ,  $F_{2,37} = 0.597$ ,  $P < 0.556$ ), suggesting no evidence of inter-observer bias in the sighting data collected. We conducted analysis on the data-set with three detection probability functions (half-normal; uniform, and hazard rate) and their respective cosine adjustments. The negative exponential function was not modeled as our data-set was not applicable to the parameters for its use [Buckland et al., 2001]. As per the recommendation that 5–10% of the data are truncated to avoid bias from outlying observations [Buckland et al., 2001], upon a visual inspection of the

histogram we then truncated 8% of the data at 31 m, removing conspicuous outliers where observations were far fewer. We then chose the function providing the lowest Akaike's Information Criterion value (AIC; a quantitative method for model selection seeking to best fit a detection function with the data-set) and highest chi-squared goodness of fit (chi-square) value [Buckland et al., 2001], in this case the half-normal detection function on the truncated data-set (Table III). However, the delta AIC ( $\Delta\text{AIC}$ , the difference between the minimum AIC and another key function model) was small enough ( $\Delta\text{AIC} < 2$ ) that all models may be suitable for inference [Burnham & Anderson, 2002; Table III].

### Biomass

The recorded mass of adult male langurs = 6.3 kg; adult females = 6.0 kg, and juveniles and sub-adults = 3.0 kg and average group size = 7 [Davies & Payne, 1982]. Since mixed-sex groups comprise 1 adult male +  $Z$  adult females with  $\sim Z$  infants, juveniles, and sub-adults (where  $Z$  = number of each age/sex class), biomass =  $6.3 + (4.5 \times Z)$ . Davies and Payne [1982] therefore estimated a mass of 4.5 kg for an average langur irrespective of group size, as mean group size exceeds five individuals and mean group weight = 30 kg [Davies & Payne, 1982]. Thus, we also calculated biomass as  $4.5 \text{ kg} \times \text{individuals}/\text{km}^{-2}$ .

### Vegetation characteristics and abundance of preferred food stems

To establish the abundance of foods, we quantified vegetation characteristics using two plots of  $300 \text{ m} \times 5 \text{ m}$  per habitat sub-class in the mixed-swamp forest (stems enumerated  $N = 321$ ) and low-pole forest ( $N = 442$ ), in which all trees  $\geq 10 \text{ cm}$  DBH, and all lianas  $\geq 3 \text{ cm}$  DBH were identified, measured and enumerated [Harrison et al., 2010;

Morrogh-Bernard et al., 2009]. This population of *P. rubicunda* was highly frugivorous and spent  $>80\%$  of feeding time on the seeds of unripe fruits [Ehlers Smith et al., 2013]. Fruit was selected disproportionately to its relative availability, and thus was the preferred food type [Ehlers Smith et al., 2013]. Therefore, in both habitat sub-classes, we calculated the density of preferred fruit stems (trees  $\geq 10 \text{ cm}$  DBH, and lianas  $\geq 3 \text{ cm}$  DBH). We also calculated stem density of preferred fruit stems  $\geq 20 \text{ cm}$  DBH, as these trees produce  $>150\%$  more fruit than those  $<20 \text{ cm}$  DBH [Morrogh-Bernard, 2009], and feeding bout length was significantly positively related to the DBH of food stems [Ehlers Smith et al., 2013].

## RESULTS

### Population Density of *P. rubicunda* in Sabangau TPSF

The total survey effort in the mixed-swamp forest was 355 survey walks, resulting in the minimum number of independent observations required for a robust density estimate ( $N = 40$ , Table IV) [Buckland et al., 2001]. The low encounter rate, which was spread out evenly across time (1 group/8.9 km; mean 8.8 surveys between sightings,  $N = 40$ ), and the very high day range length by the langur groups (mean day range  $>1,500 \text{ m}$ ,  $N = 63$ ; DA Ehlers Smith, unpublished preliminary data) suggests independence of the sighting events across survey days. Group density in the mixed-swamp forest was calculated to be  $2.52 \text{ groups km}^{-2}$  (Table III, Table IV). Group density as calculated by Distance corresponded exactly to the number of known groups in the  $4 \text{ km}^2$  research grid ( $N = 10$ ). Effective strip width was calculated at 21.3 m. Truncation of the data-set at 31 m provided the lowest AIC value

**TABLE III. Calculated Group Density of *P. rubicunda* in the Mixed-Swamp Forest Based on the Three Detection Functions, Tested Before and After Truncation of the Data-Set at 31 m**

Truncation	Key function	Adjustment	AIC <sup>a</sup>	$\Delta\text{AIC}^b$	Goodness of fit <sup>c</sup>			Group density <sup>e</sup>
					$\chi^2$	df	PD <sup>d</sup>	
None	Half-normal	—	285.87	0.41	0.83	22	0.49	2.57 (1.67–3.94), 20.9
	Uniform	Cosine 1	285.45	—	0.79	13	0.53	2.38 (1.62–3.49), 18.0
	Hazard Rate	—	287.11	1.66	0.73	29	0.54	2.34 (1.48–3.40), 22.7
31 m	Half-normal <sup>f</sup>	—	258.01	—	0.98	28	0.69	2.52 (1.56–4.08), 23.9
	Uniform	Cosine 1	258.23	0.22	0.96	26	0.66	2.62 (1.64–4.20), 23.2
	Hazard Rate	—	259.72	1.71	0.98	26	0.76	2.27 (1.41–3.66), 23.5

<sup>a</sup>Akaike's Information Criterion.

<sup>b</sup>Difference between key function AIC value and the selected (minimum) AIC value.

<sup>c</sup>Measured by chi-squared test [Buckland et al., 2001].

<sup>d</sup>Probability of detection.

<sup>e</sup>Group density, 95% confidence interval (in parentheses) and coefficient of variation (sensitivity for detecting percentage change in the population between survey cycles).

<sup>f</sup>Model selected for providing group density based on lowest AIC value.

TABLE IV. Survey Effort for Population Density Estimation of *P. rubicunda* in Sabangau TPSF

	Mixed-swamp forest	Low-pole forest
Season surveyed	Dry (Oct–Dec 2009)	Dry (Sep 2011)
No. of transects	12	12
Survey effort (km)	354.6	72
Number of Independent Survey Walks	355	72
Observations	40	0
Mean group size (individuals)	6.95 ( $N = 7$ groups)	
Group density $\text{km}^{-2}$ (95% CI, CV)	2.52 (1.56–4.08, 23.9)	
Population density, individuals $\text{km}^{-2}$ (range)	17.51 (10.84–28.36)	
Biomass density, $\text{kg km}^{-2}$ (range)	78.80 (48.78–127.62)	

Group density with 95% confidence intervals (CI) and coefficient of variation (CV).

and increased the chi-square value and detection probability from the original estimate (Table III).

The low-pole forest expedition yielded no encounters after a substantial survey effort (Table IV), indicating that *P. rubicunda* is absent or extremely rare in this habitat sub-class. We did not conduct transect surveys in the tall-interior forest because of anthropogenic disturbance at the research site.

#### Group Composition in Sabangau TPSF

We recorded data on group composition from seven groups of *P. rubicunda* in the mixed-swamp forest (Table V). Six of the seven were mixed-sex, single-male multi-female groups ranging from five to nine individuals. The seventh was an all-male band which ranged from four to seven individuals and displayed a transient group composition, as members typically resided in the group for a short period (<3 months). We also frequently encountered a solitary sub-adult male between October 2009 and August 2010. During the 22-month-study period, four

of the six mixed-sex groups lost members to either sub-adult male emigration (Group KB; Table V); invasion and tenure change of the adult male and subsequent disappearance of offspring (Group TN; Table V), or the disappearance and/or death of individuals (Group KB, Group G8; Table V). We identified one birth during the study period in Group GC (Table V). Across the entire study period, the grand mean group size was 6.95 individuals/group ( $N = 7$  groups), calculated from the mean number of individuals per group per encounter (Table V).

#### Abundance of Preferred Food Stems

The mean stem density across the two vegetation plots of all trees  $\geq 10$  cm DBH and lianas  $\geq 3$  cm DBH was 1476.7 stems/ha in the low-pole forest and 983.4 stems/ha in the mixed-swamp forest. Mean stem density of preferred food stems (trees  $\geq 10$  cm DBH and lianas  $\geq 3$  cm DBH) was 476.7 stems/ha in the low-pole forest and 486.7 stems/ha in the mixed-swamp forest. Mean stem density of preferred food

TABLE V. Composition of Seven Groups of *P. rubicunda* at in the Mixed-Swamp Forest Based on a Minimum of Bimonthly Encounters Between March 2010 and December 2011

Group ID	Group size range	Mean group size	Group composition	Reason for group composition change
KB	5–8	6.77 ( $N^a = 44$ )	1AM; 2–3AF; 0–1SAM; 2–3IM	SAM emigration; 1AF and 1IM death
GC	8–9	8.59 ( $N = 44$ )	1AM; 3AF; 1SAM; 2J; 1–2I	1 birth
TN	7	7.0 ( $N = 26$ )	1 AM; 2AF; 1SAF; 2I	AM tenure change in this group resulted in expulsion of resident AM and disappearance of 2I
TD	5	5.0 ( $N = 20$ )	1 AM; 2AF; 1SAF	New group created after AM tenure change in Group TN
G8	5–8	6.77 ( $N = 44$ )	1AM; 3AF; 1SAM; 0–3I	Disappearance of 3I
GZ	9	9.0 ( $N = 44$ )	1AM; 3AF; 2SA; 1J; 2I	
BB	4–7	5.54 ( $N = 44$ )	4–6AM; 0–1SAM	Composition frequently changed as members typically resided in group <3 months
Grand mean group size		6.95		

A, adult; SA, aub-adult; J, juvenile; I, infant; M, male; F, female.<sup>a</sup>Number of encounters per group.

trees  $\geq 20$  cm DBH was 26.7 stems/ha in the low-pole forest and 70.0 stems/ha in the mixed-swamp forest.

## DISCUSSION

### Population Density of *Presbytis* and Its Limiting Factors

Here, we present the first population density estimates for *Presbytis rubicunda* in Sabangau TPSF, the largest lowland forest-block remaining on Borneo. The results show that the mixed-swamp forest sub-class contained the second highest population density recorded in the species (Tables I and IV), while in the adjacent low-pole forest, populations appeared to be absent (Table IV). Density in the mixed-swamp forest was also relatively intermediate within genus *Presbytis* irrespective of habitat type; thus in this case, we reject our first hypothesis that because of a paucity of available nutrients, the population density in the TPSF would be lower than that in forests on mineral soils. Conversely, the absence of *P. rubicunda* from the low-pole forest is consistent with our first hypothesis, indicating that complex ecological relationships existed within the broad classification of a TPSF.

In supporting this relatively high population density, the mixed-swamp forest of the Sabangau ecosystem represents a crucial population stronghold for *P. rubicunda*, as it does for sympatric *Hylobates albibarbis* [Cheyne et al., 2007] and *P. pygmaeus* [Morrogh-Bernard et al., 2003]. The remnant lowland forest populations are particularly important for the persistence of the species as the population density of *P. rubicunda* decreases in forests above 700–800 m above sea level to such low densities that they may not be viable [Marshall, 2010]. Relative to other *Presbytis* monkeys that occur in TPSFs, our results also indicated a higher than average population density in the mixed-swamp forest: the Mentawai langur (*P. potenziani*) occurred at just 2.7 ind km<sup>-2</sup> in the TPSFs of the Mentawai islands, Indonesia [Quinten et al., 2009], and *P. rubicunda* occurred at 2.5 ind km<sup>-2</sup> in the TPSFs of Gunung Palung, West Kalimantan [Marshall, 2010]. Peat-swamp forests are also recognized as important refuges for threatened colobine monkeys. For example, the relatively high population densities of the critically endangered pig-tailed langur (*Simias concolor*; 65.5 ind km<sup>-2</sup>) in the TPSFs of the Mentawai Islands are comparable to those in some forests on mineral soil [Quinten et al., 2009]. Likewise, the endangered proboscis monkey (*Nasalis larvatus*) occurs at the highest densities in the swamp forests of Tanjung Puting, Central Kalimantan [Yeager, 1990].

Quinten et al. [2009] suggested that the lack of prevalent food species in the TPSF environment of Mentawai has a limiting effect on the population density of *P. potenziani*, as Marshall [2010] cited the low productivity of the peat swamps of Gunung

Palung as the limiting factor for populations of *P. rubicunda*. Indeed, habitat quality, as a function of the net energy available to support primate populations and thus limit carrying capacity, can vary markedly across habitat types on small spatial scales [Marshall, 2010]. In Sabangau, the focal group was highly frugivorous, and feeding bout lengths were significantly dependent on the increasing DBH of food stems [Ehlers Smith et al., 2013], as stems  $> 20$  cm produce 150% more fruit than those of 10–19 cm DBH [Morrogh-Bernard, 2009]. Between the two markedly different habitat sub-classes surveyed in Sabangau, the total stem density of preferred foods  $\geq 10$  cm DBH was, in fact, comparable across the mixed-swamp ( $N = 486.7$  stems/ha) and the low-pole forest ( $N = 476.7$  stems/ha). The density of preferred stems  $\geq 20$  cm DBH, however, was substantially higher in the mixed-swamp forest ( $N = 70$  stems/ha) than in the low-pole forest ( $N = 26.7$  stems/ha), suggesting that populations may also be limited by the density of large, fruit abundant trees in the environment. In Gunung Palung, the density of *P. rubicunda* was strongly correlated with the abundance of preferred foods, and the variation in fallback food availability did not explain variation in population density across habitat types [Marshall, 2010], while the study group in Sabangau was not dependent on fallback foods [Ehlers Smith et al., 2013]. The low-pole swamp forest environment of Sabangau with its paucity of available fruits, then, may be analogous to these lower quality peat-swamp habitats elsewhere. While our sample size of survey sites was too small to empirically test this relationship, the results are consistent with both the data from Gunung Palung and our second hypothesis that the availability of preferred fruits would limit population density in Sabangau Forest.

### Comparisons With Other Colobine Monkeys

Our results are consistent with documented relationships between the quality and abundance of food resources, and the population densities and group sizes in other colobine monkeys [Fashing, 2011; Kirkpatrick, 2011; Marshall, 2010; Yeager & Kirkpatrick, 1998]. In Rwanda, a population of colobus monkeys, *Colobus angolensis*, exceeded group sizes of 300 individuals at a site that provided an abundance of high quality foods [Fashing et al., 2007]. Likewise, proboscis monkey density was highest (63 ind km<sup>-2</sup>) in peat swamps where fruit was predominant in the diet (40%) [Yeager, 1989]. By contrast, colobines that maintain the lowest population densities (e.g., *Rhinopithecus*; *Colobus satanas*) also have larger than average ranges and pronounced seasonal shifts in the availability of food resources, suggesting that their densities are limited by resource availability [Fleury & Gautier-Hion, 1999; Kirkpatrick et al., 1998; Yeager & Kirkpatrick, 1998]. Although *Presbytis* monkeys

generally occur at lower population densities relative to other Asian and African colobine genera (c. f. *Colobus*; *Ptilocolobus*; *Nasalis*; *Semnopithecus*) [Davies, 1994; Kirkpatrick, 2011], a comparison of the density and diets across two populations (*P. siamensis* and *P. rubicunda*) illustrates the ecological plasticity within the genus when high-quality food resources are abundant in the habitat [Davies et al., 1988]: in the dipterocarp forests of Sepilok, *P. rubicunda* maintained relatively low group sizes and population densities (Table I), and obtained most of its food sources from species rare in the environment. Conversely, while the overall dietary composition was almost identical, *P. siamensis* obtained its food items from the most common species in its habitat, and maintained the largest group sizes and highest population density recorded within *Presbytis* [Davies et al., 1988].

### Conservation Planning and Conclusions

The absence of *P. rubicunda* in the low-pole forest, which constitutes 30% of Sabangau's remnant forested area, is a pertinent discovery for conservation planning for the species. This absence highlights the critical nature of in situ surveys of primates for predicting population sizes based on extant forested areas. Assuming homogeneity of the wider peat-swamp forest landscape of Central Kalimantan, it is likely that *P. rubicunda* populations are absent from any low-pole forest habitat within the larger area. Characterizing and analyzing habitat sub-classes such as low-pole forest remotely outside Sabangau TPSF is problematic, however, as remotely sensed data presenting forest cover are not detailed to the sub-class specific level [e.g., Langner et al., 2007; Miettinen et al., 2011b]. Thus, the differences in population density between the mixed-swamp forest and low-pole forest in Sabangau is encompassed and presented under a single TPSF umbrella when applied to the wider peat-swamp landscape. Without habitat-specific surveys quantifying the variation in habitat quality, conservation planning involving population estimates may over-estimate the abundance and viability of threatened populations in Kalimantan [Marshall, 2010].

The response of *P. rubicunda* populations to habitat disturbance appears to be unclear. Meijaard et al. [2008] predicted intolerance to logging, and Blouch [1997] reported a substantial drop in population density after the logging of a lowland dipterocarp site (Table I). In other lowland dipterocarp forests of Sarawak, however, *P. rubicunda* was reported to be neutral to the effects of logging [Bennett & Dahaban, 1995]. Across Borneo, large areas of TPSF are now damaged and degraded by logging and fires, although populations of *P. pygmaeus*, *H. albibarbis*, and *P. rubicunda* still inhabit them [Husson et al., 2009; DA Ehlers Smith, pers. obs.].

Degraded forests have been recognized as crucial for the conservation of other Bornean fauna [Edwards et al., 2010; Husson et al., 2009], but populations of *P. rubicunda* therein have not previously been quantified. Here, we have shown the importance of TPSFs for the conservation of *P. rubicunda*, both by maintaining a relatively high population density and by representing the largest remnant lowland forest-block on Borneo. We therefore recommend three actions to further quantify the population of *P. rubicunda* in TPSFs and focus conservation initiatives: 1) to quantify the response of *P. rubicunda* to the logging and burning of its habitat; 2) to conduct population density surveys in degraded TPSFs to assess viability of populations; and 3) attempt to delineate TPSF habitat sub-classes across Kalimantan to facilitate accurate quantification of population boundaries by forest area coverage.

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## **Appendix 2**

**Ehlers Smith DA**, Husson SJ, Ehlers Smith YC, Harrison ME (2013a). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of Primatology* 75: 848-859.

Concept and Design: DA Ehlers Smith, ME Harrison; Data Collection: DA Ehlers Smith, YC Ehlers Smith; Data analysis: DA Ehlers Smith, SJ Husson; ME Harrison; Manuscript preparation: DA Ehlers Smith, YC Ehlers Smith, ME Harrison

## Co-Author Statement

**Ehlers Smith DA**, Husson SJ, Ehlers Smith YC, Harrison ME (2013a). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of Primatology* 75: 848-859.

Concept and design: DA Ehlers Smith, ME Harrison; Data collection: DA Ehlers Smith, YC Ehlers Smith; Data analysis: DA Ehlers Smith, ME Harrison, SJ Husson; Manuscript preparation: DA Ehlers Smith, ME Harrison, SJ Husson, YC Ehlers Smith

I, co-author Mark E. Harrison, confirm that David Ehlers Smith made the stated contributions to this publication.

Signature \_\_\_\_\_  \_\_\_\_\_

Date \_\_\_23<sup>rd</sup> October 2014\_\_\_

## RESEARCH ARTICLE

# Feeding Ecology of Red Langurs in Sabangau Tropical Peat-Swamp Forest, Indonesian Borneo: Extreme Granivory in a Non-Masting Forest

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Southeast Asia's lowland dipterocarp forests experience supra-annual "mast" fruiting and flowering events, in which the majority of trees reproduce simultaneously at irregular intervals, with extensive intervening periods of very low primate food availability. This scarcity of food results in a negative energy balance and a reliance on "fallback foods" in some primate species. By contrast, ombrogenous tropical peat-swamp forests are non-masting, and show lower variability of food availability. We sought to test the influence of fruit availability on primate diet and preference in peat-swamp habitats and assess whether it differs from masting forests. We collected behavioral-dependent feeding data on three adult females in a group of red langurs (*Presbytis rubicunda*: Colobinae) between January and December 2011 in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia, as colobine monkeys are adapted for folivory, and are therefore generally considered less reliant on temporally variable fruits than monogastric primates. We documented the highest level of granivory recorded to date in colobine monkeys: mean annual diet comprised 76.4% seeds and 7.3% other fruit parts; 7.7% young and 2.5% mature leaves; 2.8% flowers; 2.6% piths, and <1% on other minor food items. Fruit availability was fairly constant throughout the year and fruit parts were consumed at consistently higher levels than expected based on availability, confirming that fruit is preferred. Leaves and flowers were consumed consistently less than expected and thus are not preferred. There were no significant correlations between preferred food availability and consumption of potential fallback foods, suggesting that reliance on fallback foods did not occur in Sabangau during the study period. Furthermore, consumption of fruit was not significantly correlated with its availability. Our findings suggest that the relatively constant availability of fruit in this habitat affords *P. rubicunda* regular access to a nutritionally superior food, and that reliance on fallback foods is therefore not required. *Am. J. Primatol.* 75:848–859, 2013. © 2013 Wiley Periodicals, Inc.

**Key words:** Colobinae; fallback foods; folivore; frugivore; granivore; mast fruiting

## INTRODUCTION

All primates face the challenge of ensuring adequate nutritional intake for survival, growth, and reproduction, while avoiding ingestion of intolerable levels of toxins and digestion inhibitors [Freeland & Janzen, 1974; Pyke et al., 1977; Schoener, 1971]. Primate nutritional requirements are not uniform across species, however, and an individual species' requirements reflect morphological (e.g. body size) and physiological (e.g. digestive efficiency) traits [Felton et al., 2009; Ross, 1992]. Indeed, diet, morphology and physiology are inextricably linked; the biochemistry and mechanics of food items exert selective pressures on primate anatomy and, in particular, the digestive [Chivers & Hladik, 1980] and masticatory systems [Vogel et al., 2008]. For example, leaves contain relatively high protein levels, but also have a high tannin and fiber content,

which is indigestible to most mammals [Waterman & Kool, 1994].

The sub-family Colobinae however, as predominantly leaf-eating primates [Curtin, 1980;

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Hladik, 1977; Hoang et al., 2009; Kool, 1986; Li et al., 2003; Matsuda et al., 2009; Oates et al., 1980], has evolved gastro-intestinal adaptations to exploit this abundant resource [Bauchop, 1978; Chivers, 1994]. A multi-chambered stomach containing a microbe suspension in the foregut, plus a capacious stomach chamber and elongated caecum simultaneously neutralize toxins and effectively break down plant wall cellulose, facilitating digestion of the high quantities of fiber, protein, and vitamins generally contained within leaves [Bauchop, 1978; Chivers, 1994; Kay & Davies, 1994; Kay et al., 1976]. This adaptation is distinct from monogastric primates, for whom the digestive morphology favors protein-poor but highly digestible and nutrient-rich fleshy fruits that characterize the bulk of their diet [Kay & Davies, 1994].

Specifically, the morphological adaptation for folivory in colobines is thought to preclude selection of ripe, fleshy fruits high in organic acids, as the forestomach fermentation process facilitated by the gut microbe community requires a constant pH of 5.5–7, and the overabundance of fatty acids from ripe, fleshy fruit pulp can cause hyperacidity and consequent morbidity [Kay & Davies, 1994; Lambert, 1998]. Compared to the small intestine, the colobine forestomach also permits more complete digestion of the especially nutritious storage carbohydrates found in seeds [Kay & Davies, 1994]. Indeed, granivory (seed-eating) is a common characteristic in cases of colobine frugivory [e.g. Harrison & Hladik, 1986; Maisels et al., 1994; McKey et al., 1981], and has been hypothesized as a precursor to leaf-eating in the evolution of the colobine gut [Chivers, 1994; Kay & Davies, 1994].

Colobines display inter-generic dietary plasticity dependent on the overall body size and resultant size and length of the digestive tract [Chivers, 1994]. For example, *Trachypithecus* has a longer digestive tract and consumes more foliage [Hladik, 1977; Kool, 1992, 1993; Oates et al., 1980; Stanford, 1991] than do *Presbytis* and *Nasalis*, which have the smallest forestomachs and largest small intestines of the Colobinae and in turn consume a higher percentage of unripe seeds and fruits [Bennett, 1983; Bennett & Davies, 1994; Chivers, 1994; Davies, 1991; Davies & Ballie, 1988; Gurmaya, 1986; Hanya & Bernard, 2012; Marshall et al., 2009a; Megantara, 1989; Supriatna et al., 1986]. Dietary plasticity at the inter-population level can occur, however; for example, *Trachypithecus vetulus nestor* frequently selected predominantly ripe domesticated fruits (monthly mean >50% of overall diet) in an area of high anthropogenic disturbance [Dela, 2007, 2012].

In addition to influencing primate physiology and morphology, food resources also affect social systems and population demography through their distribution, abundance, and phenology [Harrison & Chivers, 2007; Isbell, 1991; Koenig et al., 1997; Marshall et al., 2009a; McConkey et al., 2003; Sterck et al., 1997].

Seasonal variation in the availability of food resources places physiological and energetic stress on primate individuals and groups to meet their energetic and nutritional requirements in times of food shortage [e.g. orangutans: Harrison et al., 2010; Knott, 1998; Vogel et al., 2012], which can in turn influence dietary selection [Davies et al., 1999; Di Fiore & Rodman, 2001; Leighton, 1993; McConkey et al., 2003].

The lowland dipterocarp forests of Southeast Asia can be a particularly challenging environment for primates to live in, as these forests experience masting, in which most plant species reproduce simultaneously at irregular and widely spaced intervals, with extensive intervening periods of very low fruit and flower availability [van Schaik & Pfannes, 2005]. Tropical peat-swamp forests, by contrast, do not experience the supra-annual fruit masting that is characteristic of drier lowland forests of Southeast Asia because of the relatively low density of trees from the Dipterocarpaceae and other masting tree families [Cannon et al., 2007; van Schaik & Pfannes, 2005].

The scarcity of food resources in the masting forests of Southeast Asia leads to periods of negative energy and protein balance in some primates [Knott, 1998; Vogel et al., 2012] who frequently rely on exploitation of unpreferred “fallback foods” [Hanya & Bernard, 2012; Harrison & Marshall, 2011; Marshall & Wrangham, 2007; Marshall et al., 2009a]. Fallback foods can be operationally defined as “foods whose use is negatively correlated with the availability of preferred foods” and preferred foods as “foods that are selected disproportionately often relative to their abundance within the population’s habitat” [Marshall & Wrangham, 2007, pp. 1220–1221]. Fallback foods are generally relatively abundant in the environment, but are difficult to process with low energetic returns. Heavy reliance on fallback foods therefore challenges consumers to process food efficiently, and selects for appropriate morphological and physiological adaptations. By contrast, feeding on preferred foods, which are nutritionally of a higher quality but typically rare in the environment, challenge the consumer to locate and harvest foods efficiently, favoring behavioral adaptations [Lambert, 2007; Marshall & Wrangham, 2007].

In the masting dipterocarp forests of Borneo, the endemic red langur (*Presbytis rubicunda*) spends 13–46% of feeding time consuming leaves ( $N = 5$  studies); 30–65% on seeds and 12–19% on other fruit parts ( $N = 4$ ; fruit and seeds not distinguished for Supriatna et al. [1986], who document 52% of time feeding on all fruit parts), and 2–12% on flowers ( $N = 4$ ; no information on flower consumption provided in Salafsky [1988]) [Davies et al., 1988; Hanya & Bernard, 2012; Marshall, 2004; Salafsky, 1988; Supriatna et al., 1986]. We present here the first detailed feeding ecology data for *P. rubicunda* in a non-masting rainforest, the Sabangau tropical peat-swamp forest in Central Kalimantan, Indonesia. In light of the above

considerations, we hypothesized that: (1) fruit, especially unripe fruit and seeds, would be the preferred food class, because of its superior nutritional quality compared to other food classes in Sabangau [Harrison, 2009] and the morphological features of *Presbytis* that allow a higher degree of frugivory relative to other Asian colobines [Chivers, 1994]; (2) in the Sabangau population, fruit would form a larger proportion of the overall diet than in masting forests where red langur diet has been documented previously, as a likely consequence of smaller fluctuations in fruit availability in non-masting tropical peat-swamp forests [Harrison et al., 2010; Marshall et al., 2009b]; and consequently, (3) fallback foods would be used less than in masting forests as a result of this more stable fruit availability in Sabangau compared to masting forests.

## METHODS

We obtained permission for the study from the Indonesian State Ministry for Research and Technology (RISTEK), and all research adhered to Indonesian legislation. Our research was purely observational and was in strict compliance with the Ethical Treatment of Non-Human Primates as described by the American Society of Primatologists.

### Study Site

This research was carried out as part of the Orangutan Tropical Peatland Project (OuTrop)—Center for the International Cooperation in Sustainable Management of Tropical Peatlands (CIMTROP) multi-disciplinary research project in the Natural Laboratory for the Study of Peat-swamp Forest. This is a 500 km<sup>2</sup> area within the Sabangau tropical peat-swamp forest, located between the Sabangau and Katingan rivers in Central Kalimantan, Indonesia (2°19'S and 113°54'E). The research site is contiguous with a larger landscape covering 8,750 km<sup>2</sup> of tropical peat-swamp forest between the Kahayan River to the east and Katingan River to the west. It is a true ombrogenous tropical peat-swamp forest; that is, all nutrient influx is acquired through aerial precipitation (rainwater, aerosols, and dust), soil nutrient availability is poor and the peat soil has an average pH of 2.8 [Page et al., 1999]. Typical of peat swamps throughout Central Kalimantan, our study site was subject to concession and then illegal logging until 2004, but subsequent protection efforts have been successful and the forest retains a relatively natural peat-swamp forest flora and fauna community. Together with the adjoining Sebangau National Park, this is the largest remaining contiguous lowland forest block on Borneo, and contains the world's largest remaining populations of Bornean orangutan (*Pongo pygmaeus*) [Morrogh-Bernard et al., 2003] and Bornean southern gibbon (*Hylobates albibarbis*) [Cheyne et al., 2007]. The forest is

seasonally flooded by rainfall for ca. 8 months each year, with a marked dry season spanning June–September. From January 2011 to December 2011, mean day and night temperature was 26.2°C (±SD 1.0°C) and annual rainfall was 3,406 mm [Ehlers Smith & Ehlers Smith, 2013].

### Study Species

The red langur (*P. rubicunda*) is endemic to the rainforests of Borneo and the adjacent island of Karimata [Medway, 1970]. It occupies the majority of forest types found on Borneo, including various lowland dry-forest types [Davies, 1984; Hanya & Bernard, 2012; Marshall, 2010], swamp forest [Marshall, 2010; Supriatna et al., 1986] and lower montane forest [Marshall, 2010]. It is a gracile monkey (males 6.3 kg, females 6.0 kg) that exhibits little sexual dimorphism [Davies & Payne 1982; Fleagle, 1999]. Social groups of 3–10 members comprise a single adult male and multiple adult females and young [Davies, 1984; Ehlers Smith & Ehlers Smith, 2013; Supriatna et al., 1986].

### Feeding Data Collection

We collected feeding data between January 2011 and December 2011 on three adult females from one habituated study group of *P. rubicunda*. The group comprised seven individuals between January 2011 and July 2011 and five individuals between July 2011 and December 2011 after the death of an adult female and the subsequent disappearance of her infant. Focal females were readily identifiable by individual distinguishing characteristics of overall body sizes, nipple lengths, and shape of tails. We followed the group from morning sleeping-tree to evening sleeping-tree for 3–11 days each month ( $N = 84$  days; Mean = 7 days/month), for a total of 924.6 hours (Mean =  $77.1 \pm$  SD 25.2 follow hours/month). Limited visibility in the habitat made simultaneous scan sampling of all individuals impossible. Instead, we conducted focal samples of a single adult female selected before the beginning of the follow to ensure an even balance between focal individuals and minimize observer bias; this individual was then closely followed for the entire duration of each follow-day [Altmann, 1974; Cheyne, 2010; Harrison et al., 2009, 2010; Knott, 1998]. Using behavioral-dependent sampling, we recorded the exact start and end times of every feeding bout (defined as the harvesting with hands and mouth, and chewing or ingesting, of plant or animal material from one or more trees of the same species with interlocking branches, uninterrupted by other behaviors) that lasted longer than 30 sec (adult female (AF) 1: mean =  $9.9 \pm$  SD 2.8 feeding hr/month over 12 months; AF 2: mean =  $8.4 \pm$  SD 6.3 hr/month over 11 months; AF 3: mean =  $4.4 \pm$  SD 4.0 hr/months over 6 months). For

approximately 7% of all scan samples, and generally for periods <5 min, the focal animal was out of sight.

As we collected data during protracted focal-animal follows, each feeding bout cannot be considered independent of the next [Marshall & Wrangham, 2007]; however, continuous data collection is considered to represent an accurate account of foraging effort [Conklin-Brittain et al., 2006; Harrison et al., 2009; Knott, 1998]. For each feeding bout, we recorded plant species, “food class” (fruit/flowers/leaves/pith/fungi/invertebrates), species-specific “food item” (plant species and part eaten: fruit seed/pulp/skin/whole fruit; flower bud/mature flower; leaf shoot/whole leaf); maturation stage (ripe/unripe fruit; young/mature leaf), feeding bout duration and GPS location. We assigned a unique ID tag number to all food trees, except for very small trees used for leaf feeding. We collected, photographed, identified, and stored all food items in a herbarium at the base camp. Expert local botanists with extensive knowledge of local tree fauna and primate foods assisted our identifications of food samples [Cheyne, 2010; Harrison et al., 2010].

Consumption varied in a similar way between the three adult females across months, thus we pooled the feeding data-set ( $N = 12$  months, total hr = 250.4, mean =  $20.9 \pm SD 7.1$  hr/months). We took a mean value for the consumption of each food class in a month based upon values obtained from each female followed in that month; an average was then taken from these monthly figures across the entire study period to determine mean monthly food class consumption.

### Vegetation and Phenology

We measured red langur food availability through monthly monitoring of six permanent, randomly located plots (total area = 2.4 ha). These plots were all located in the same habitat sub-class (mixed-swamp forest) [Page et al., 1999] throughout a 4 km<sup>2</sup> total area of forest, within and adjacent to the ca. 1 km<sup>2</sup> home range of the focal group (center of home range = 2°19'03"S, E113°53'98"E). In these plots, all trees  $\geq 6$  cm DBH, and all lianas and figs  $\geq 3$  cm DBH were identified, measured, tagged and enumerated as part of previous research [Harrison et al., 2010; Morrogh-Bernard et al., 2009]. We monitored each tagged stem  $\geq 10$  cm DBH for the presence of ripe and unripe fruits, open flowers and flower buds. We monitored each stem  $> 6$  cm DBH for the presence of new leaf shoots (mean no. of stems sampled/month  $> 10$  cm =  $1,593 \pm SD 10.2$  trees; range 1,582–1,606; mean no. of stems/month  $> 6$  cm =  $1,065 \pm SD 30.7$  trees; range 1,034–1,101) [Harrison et al., 2010; Marshall et al., 2009b; Morrogh-Bernard et al., 2009; Vogel et al., 2008; Wich et al., 2011]. Given that stems  $\geq 20$  cm DBH in Sabangau produce over 150% more fruit than those  $< 20$  cm

DBH [Morrogh-Bernard et al., 2009], we sought to test the relationship between bout length and fruit tree DBH through a Spearman's rank correlation analysis, after a Kolmogorov–Smirnov test confirmed that the data were not normally distributed.

### Data Analysis

We calculated the absolute diet composition (or dietary importance [Marshall & Wrangham, 2007]) as the time spent feeding on a food class/total time spent feeding on all food classes in a given month, and then used these figures to calculate the mean monthly percentage contribution of each food class to the diet across the entire study period, thereby ensuring that means were not biased by months with more data. As it was not feasible to quantify availability of fungi, pith, or invertebrates, they were excluded from calculations of relative consumption used for assessing preference.

To establish preference, we calculated the relative consumption of a food class  $f_i$  for which availability was measurable (i.e. fruit, flowers, and leaves) within a month as the time spent feeding on that food class/total time spent feeding on all food classes for which availability was measurable. We then calculated the mean monthly percentage consumption of each food class across the study period, as described above for absolute diet composition. We calculated relative availability of a food class  $a_i$  each month as the total number of stems of food class  $i$  producing food/the total number of stems of all food classes producing food that could be measured (i.e. fruit stems + young leaf producing-stems + flowering stems) in the phenology plots. We then established preferred food classes as those for which the monthly percentage relative consumption across the study period was consistently greater than that of its relative availability across months.

We also identified individual preference values for each species-specific item (e.g. seed of *Neoscortechinia kingii*) based on its relative consumption and relative availability, using Chesson's  $\alpha$  Selectivity Index [Chesson, 1978], which varies from zero (complete avoidance) to one (maximal preference):

$$\alpha_i = \frac{f_i/a_i}{\sum_i f_i/a_i}$$

We then ranked species-specific items according to the preference values to assess correspondence between important and preferred foods in the diet. Finally, we established fallback food classes through the presence of significant negative correlations between the monthly relative availability of the preferred food classes identified through the above procedure and the monthly absolute consumption of all other food classes identified in the diet (Pearson product-moment test where relative availability and

relative consumption of each food class were normally distributed, as established by a Kolmogorov–Smirnov test, and Spearman rank-order correlation where data were not normally distributed) [Harrison & Marshall, 2011; Marshall et al., 2009a].

## RESULTS

### Overall Diet

The langurs fed on 105 separate food items from six food classes: fruit, leaves, flowers, pith, fungi, and invertebrates (Table I). They were also observed drinking water from tree holes and canals. Species-specific plant food items came from 65 species in 32 families, of which there were 54 tree species, 7 lianas, 3 climbers, and 1 epiphyte. We also identified seven fungi species and two invertebrate food items, including ants from an unidentified epiphyte bulb and ant larvae within rotten fruits of *Diospyros bantamensis*.

In an average month, subjects spent 76.4% ( $\pm$ SD 13.5; range 49.2–92.8) of overall feeding time feeding on seeds and 7.3% ( $\pm$ SD 8.6; range 0–23.0) on other fruit parts (pulp 5.6  $\pm$  SD 8.0%; pulp and seed 0.4  $\pm$  SD 1.2%; pulp and skin 1.1  $\pm$  SD 16.4%; whole fruit 0.3  $\pm$  SD 0.6%). They spent 7.7% ( $\pm$ SD 8.0; range 0.4–26.9) of feeding time on young leaves and 2.5% ( $\pm$ SD 4.5; range 0–15.2) on mature leaves; 2.0% ( $\pm$ SD 1.5, range 0.1–4.1) on flower buds and 0.8% ( $\pm$ SD 2.6; range 0–9.1) on mature flowers; 2.6% ( $\pm$ SD 3.7; range 0–12.7) on pith; 0.4% ( $\pm$ SD 0.9 range 0–2.7) on invertebrates; 0.3% ( $\pm$ SD 0.9 range 0–3.0) on fungi, and 0.1% ( $\pm$ SD 0.3; range 0–0.7) drinking water (Fig. 1).

Twenty-five individual species-specific food items contributed  $\geq 1\%$  of the annual diet, which when pooled accounted for 87.7% of total feeding time (Table II). The majority of these food items vary widely in their importance across months (e.g. *Palaquium cochlearifolium*, range 0–44.7%), but are a dominant item in at least 1 month of the study (Table II). The group visited a total of 995 individual trees and lianas to feed during the 12-month period, and 16.6% ( $N = 165$ ) were visited more than once for feeding. There was a significant positive correlation between feeding bout length and fruit-tree DBH (Spearman rank correlation:  $N = 832$ ,  $r_s = 0.253$ ,  $P < 0.001$ ).

### Preferred Foods

Relative fruit consumption (mean 86.5  $\pm$  SD 10.8%, range 67.3–99.3) exceeded relative fruit availability (mean 3.7  $\pm$  SD 1.2%, range 1.9–5.6) in all 12 months of the study by a minimum factor of 15.6 (i.e. relative fruit consumption/relative fruit availability  $\geq 15.6$  in each month), so fruit is thus considered a preferred food class. Relative young leaf consumption (mean 8.0  $\pm$  SD 8.5%, range

0.4–28.3) was lower than relative young leaf availability (mean 91.6  $\pm$  SD 1.2%, range 89.1–93.0) in all 12 months by a minimum factor of 0.3, and is thus considered not preferred. Similarly, relative flower consumption (mean 2.9  $\pm$  SD 3.4%, range 0.1–12.4) was lower than relative flower availability (mean 4.7  $\pm$  SD 1.1%, range 3.1–6.6) in 11 out of 12 months, and is also considered not preferred.

Overall, seeds were the preferred food (Table II and Fig. 1), although there was a marked increase in consumption of young *Xanthophyllum cf. ellipticum* leaves and mature *D. bantamensis* leaves at the end of the dry season and the onset of the wet season (October–November; Table II and Fig. 1). The majority of the most preferred species-specific items were also among the 25 most important items comprising  $\geq 1\%$  of the overall diet (Table II), with the exception of *Calophyllum sclerophyllum* seeds, *Myristica lowiana* seeds, *Fragria* sp. pulp, *Xerospermum laevigatum* seeds, and *Zyzyphus angustifolius* seeds, which were highly preferred in the rare periods when they were available. Conversely, two species that were important in the overall diet (*Mezzetia leptopoda* pulp, *Horsfieldia crassifolia* seeds; Table II) were abundant but less preferred.

### Food Availability and Fallback Foods

We discovered no significant correlation between preferred food (i.e. fruit) availability and overall leaf consumption (Pearson correlation:  $N = 12$ ,  $r = -0.091$ ,  $P = 0.779$ ), young leaf consumption (Pearson:  $r = -0.239$ ,  $P = 0.455$ ) or mature leaf consumption (Pearson:  $r = 0.215$ ,  $P = 0.502$ ), nor between fruit availability and flower consumption (Pearson:  $r = 0.138$ ,  $P = 0.669$ ), pith consumption (Pearson:  $r = -0.262$ ,  $P = 0.411$ ), fungi consumption (Spearman rank correlation:  $r_s = 0.125$ ,  $P = 0.699$ ), or invertebrate consumption (Spearman:  $r_s = -0.290$ ,  $P = 0.360$ ) Further, we found no significant correlation between fruit availability and fruit consumption (Pearson:  $r = 0.144$ ,  $P = 0.656$ ).

## DISCUSSION

### Dietary Composition, Preferred, and Fallback Foods of the Sabangau Population

Here, we provide the first detailed feeding ecology data for *P. rubicunda* in a non-masting tropical peat-swamp forest. The focal group's diet contained the highest mean monthly fruit consumption recorded in any colobine monkey [Fashing, 2011; Kirkpatrick, 2011]. This was predominantly in the form of unripe seeds, which dominated the diet (76.4%), while other fruit parts made a lesser contribution (total 7.3%). The unripe seeds of 3 tree species (*N. kingii*; *P. cochlearifolium*; *Blumeodendron tokbrai*), and in particular *N. kingii*, were extremely important, comprising 39.6% of the annual diet

TABLE I. Food Items Consumed by *P. rubicunda* in Sabangau From January 2011 to December 2011

Family	Species <sup>1</sup>	Plant type <sup>2</sup>	Fruit part <sup>2</sup>	Leaf <sup>2</sup>	Flower <sup>2</sup>	Pith <sup>2</sup>
Anacardiaceae	<i>Camptosperma squamatum</i>	T	Sd			
Anisophyllaceae	<i>Combretocarpus rotundatus</i>	T	Sd	YL		
Annonaceae	<i>Artobotrys cf. roseus</i>	L	Sd	YL	F	
	<i>Polyalthia glauca</i>	T		YL		
	<i>Mezzetia leptopoda</i>	T	Pu			
	<i>Xylopia cf. malayana</i>	T	Sd			
Apocynaceae	<i>Dyera lowii</i>	T		YL	FB	P
	<i>Willughbeia</i> sp.	L	Sd, Pu			
Burseraeae	<i>Santiria cf. laevigata</i>	T	Sd			
Chrysobalanaceae	<i>Licania splendens</i>	T	Wh	YL		
Clusiaceae	<i>Garcinia</i> sp.	Cl		YL		
	<i>Garcinia cf. parvifolia</i>	T		YL		
	<i>Calophyllum hosei</i>	T		YL		
	<i>Calophyllum sclerophyllum</i>	T	Sd			
	<i>Calophyllum cf. fragrans</i>	T	Sd			P
	<i>Calophyllum</i> sp.	T		YL		
	<i>Garcinia bancana</i>	T		YL		
	<i>Mesua</i> sp.	T	Sd			P
Crypteroniaceae	<i>Dactylocladus stenostachys</i>	T		YL		
Dipterocarpaceae	<i>Shorea teysmanniana</i>	T		YL		
Ebenaceae	<i>Diospyros confertiflora</i>	T		YL		
	<i>Diospyros bantamensis</i>	T		ML		
Elaeocarpaceae	<i>Elaeocarpus mastersii</i>	T	Pu, Sk	YL		
Euphorbiaceae	<i>Blumeodendron tokbrai</i>	T	Sd			
	<i>Neoscortechinia kingii</i>	T	Sd			
Fabaceae ( <i>Leguminosae</i> )	<i>Archidendron borneensis</i>	T	Sd			
	<i>Koompassia malaccensis</i>	T	Sd			
	<i>Dialium patens</i>	T		YL		
	<i>Adenanthera pavonina</i>	T	Sd	YL		
Flagellariaceae	<i>Flagellaria</i> sp.	Cl				P
Icacinaceae	<i>Stemonorus cf. scorpiodes</i>	T	Sd	YL	F	
Lauraceae	<i>Litsea cf. resinosa</i>	T	Sd			P
	<i>Litsea cf. elliptica</i>	T	Sd			P
	<i>Litsea cf. rufo-fusca</i>	T	Wh	YL		
Loganiaceae	<i>Fragraea</i> sp.	L	Sd		FB	
Magnoliaceae	<i>Magnolia bintulensis</i>	T		YL		
Meliaceae	<i>Aglaia</i> sp.	T	Sd			
Menispermaceae	<i>Fibraurea tinctoria</i>	L	Sd	YL	FB/F	P
Moraceae	<i>Parartocarpus venenosus</i>	T	Sd			
Myristicaceae	<i>Myristica lowiana</i>	T	Sd			
	<i>Horsfieldia crassifolia</i>	T	Sd			
Myrtaceae	<i>Syzygium cf. lineatum</i>	T	Sd	YL		
	<i>Syzygium cf. valevenosum</i>	T		YL		
	<i>Syzygium</i> sp.	T		YL		
	<i>Syzygium</i> sp.	T		YL		
	<i>Syzygium havilandii</i>	T		YL	FB	
Pandanaceae	<i>Freycinetia</i> sp.	Cl				P
Polygalaceae	<i>Xanthophyllum cf. ellipticum</i>	T		YL		
Rhamnaceae	<i>Zyzyphus angustifolius</i>	L	Sd	YL	FB	
Rubiaceae	<i>Uncaria</i> sp.	L	Sd	YL		
	<i>Ixora havilandii</i>	T	Sd			
Sapindaceae	<i>Xerospermum</i> sp.	T	Sd	YL		
Sapindaceae	<i>Nephellium lappaceum</i>	T	Sd			
Sapotaceae	<i>Madhuca mottleyana</i>	T	Sd	YL, ML	FB	
	<i>Palaquium pseudorostratum</i>	T		YL		
	<i>Palaquium cf. xanthochyllum</i>	T		YL		
	<i>Palaquium ridleyi</i>	T	Sd	YL	FB	
	<i>Palaquium cochlearifolium</i>	T	Sd		FB/F	
	<i>Planchonella cf. maingayi</i>	T	Sd			

TABLE I. Continued

Family	Species <sup>1</sup>	Plant type <sup>2</sup>	Fruit part <sup>2</sup>	Leaf <sup>2</sup>	Flower <sup>2</sup>	Pith <sup>2</sup>
Sterculiaceae	<i>Sterculia rhooidifolia</i>	T		YL		
	<i>Sterculia</i> sp.	T	Sd			
Tetrameristaceae	<i>Tetramerista glabra</i>	T	Sd			
Theaceae	<i>Ternstroemia magnifica</i>	T	Sd	YL		
Unknown	“Bajakah Kalalawit Merah Daun Kecil”	L		YL		
	“Pahakung”	Epi		YL		
	Fungi (7 spp)					
	Invertebrates (2 spp)					
	Water					
Total # food items			40	38	9	8

<sup>1</sup>c.f. = Very similar to the named species in the CIMTROP/Wanariset herbariums but identification could not be confirmed for certain due to absence of critical flowering/fruitlet part, complex genus taxonomy and/or inadequate reference descriptions. Names in “quotation marks” could not be assigned a Latin name and are presented in the local Dayak language.

<sup>2</sup>T, tree; L, Liana; CL, climber; Epi, epiphyte; Sd, seed; Pu, pulp; Sk, skin; Wh, whole fruit; YL, young leaf; ML, mature leaf; FB, flower bud; F, flower; P, pith.

(Table II). The mature leaves of *D. bantamensis* and the young leaves of *Xanthophyllum ellipticum* together contributed ~5% of the diet, but were mainly selected at the end of the dry season and the onset of the wet season, although fruit availability was neither unusually high nor low at these times (Table II and Fig. 1). No other leaf species featured consistently in the diet.

Indeed, the focal group consumed leaves consistently less than expected based on their relative availability, indicating that despite the monkeys’ physiological adaptation for folivory, leaves are not a preferred food for red langurs in Sabangau. Instead, the specialized gut morphology appears more important in facilitating the processing of the high seed content in the diet. Flowers were similarly unpreferred, and were also consistently of low importance in

the overall diet. Consistent with our first hypothesis that fruit would be the preferred food class in Sabangau, the group consumed fruit (seeds) in consistently higher proportions than expected based on its relative availability, indicating that fruit in the form of seeds is a preferred food in this habitat. The majority of the most important species in the diet were also the most highly selected based on their relative availability, with the notable exception of *M. leptopoda* seeds, which was ranked fourth in importance in the diet, but 23rd for preference (Table II).

Consistent with our second hypothesis that fruit would form a larger proportion of the overall diet in Sabangau than in forests on mineral soils, frugivory in *P. rubicunda*, in the form of granivory, was indeed higher in Sabangau peat-swamp forest than in masting dipterocarp forest sites (Fig. 2) [Davies

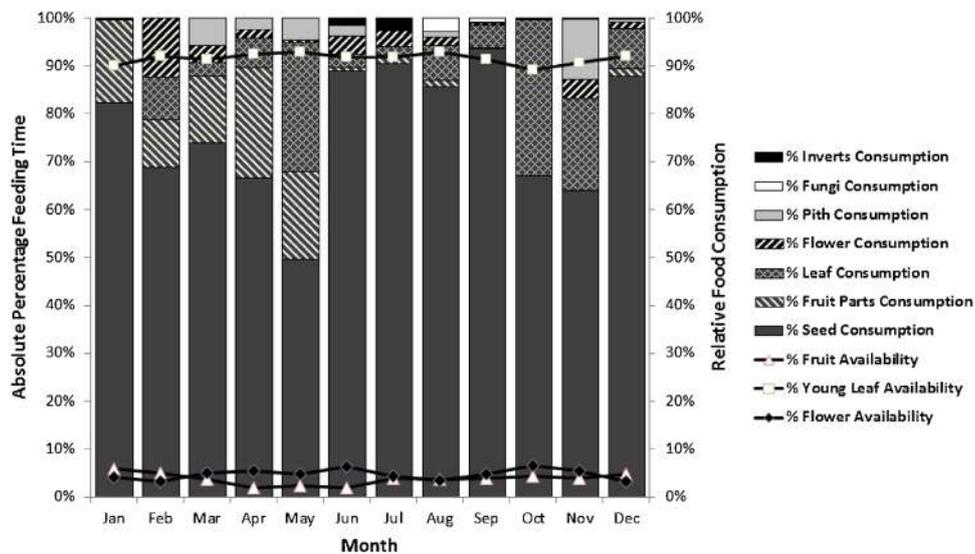


Fig. 1. Absolute proportion of feeding time by *P. rubicunda* in Sabangau on all food classes compared to the relative availability of those that could be quantified and measured for productivity (i.e. fruits, flowers, and leaves).

TABLE II. Annual and Monthly Dietary Importance, Plus Preference Scores and Ranks of *P. rubicunda* Species-Specific Food Items Contributing 1% of the Annual Diet, Listed in Order of Mean Monthly Consumption

Family	Species	Food item	Mean monthly % of feeding time	SD	Preference index	Preference rank	Monthly Consumption											
							Jan %	Feb %	Mar %	Apr %	May %	Jun %	Jul %	Aug %	Sep %	Oct %	Nov %	Dec %
Euphorbiaceae	<i>Neoshoerthia kingii</i>	Seed	20.9	24.1	0.2335	2	10.8	0.6	0.8	2.1	8.9	5.3	5.0	9.6	66.6	58.3	38.0	44.4
Sapotaceae	<i>Palaquium cochlearifolium</i>	Seed	10.6	15.0	0.2812	1	44.7	0.0	0.6	0.0	0.0	4.4	24.8	24.2	24.1	4.4	0.0	0.0
Euphorbiaceae	<i>Blumeodendron tokbrai</i>	Seed	8.1	14.9	0.1503	4	5.1	43.4	35.7	4.9	0.0	0.0	1.0	1.5	1.3	0.0	4.1	0.0
Annonaceae	<i>Mezetta leptopoda</i>	Pulp	5.9	8.9	0.0169	24	17.0	0.0	17.7	23.0	12.9	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Apocynaceae	<i>Willughbeia</i> sp.	Seed	4.4	6.6	0.0767	8	0.3	0.0	0.0	3.3	4.0	16.6	16.0	12.8	0.3	0.1	0.0	0.0
Icacinaeae	<i>Stemonorus cf. scorpiodes</i>	Seed	4.1	6.7	0.1018	7	2.6	4.7	0.9	0.0	0.0	5.5	19.5	16.0	0.0	0.0	0.0	0.0
Fabaceae (Leguminosaeae)	<i>Koempasia malaccensis</i>	Seed	3.3	5.7	0.1301	6	0.0	0.0	0.0	0.0	7.1	15.4	0.0	3.2	0.0	0.0	0.0	13.6
Lauraceae	<i>Litsea cf. rufo-fusca</i>	Seed	3.0	7.0	0.0695	9	0.0	0.0	0.0	0.2	0.0	24.0	2.7	8.1	0.0	0.0	0.0	0.5
Myristicaceae	<i>Horsfieldia crassifolia</i>	Seed	2.9	4.4	0.0140	26	0.5	12.8	5.8	0.2	0.0	4.2	0.0	0.0	0.0	0.0	1.5	10.1
Ebenaceae	<i>Diospyros bantamensis</i>	Mature Leaf	2.7	4.4	0.0140		0.0	0.0	0.0	0.0	0.0	0.0	2.7	5.0	1.1	15.2	4.6	3.7
Sapotaceae	<i>Madhuca motleyana</i>	Seed	2.4	4.4	0.0533	11	0.0	0.0	7.4	13.1	7.5	0.0	0.0	0.0	0.0	0.6	0.0	0.0
Loganiaceae	<i>Fragaria</i> sp.	Seed	2.4	4.8	0.1928	3	0.0	0.0	3.6	12.3	12.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polygalaceae	<i>Xanthophyllum ellipticum</i>	Young Leaf	2.3	4.5	0.0533		0.0	0.0	0.0	0.9	7.0	0.0	0.1	0.0	0.0	14.7	4.6	0.0
Menispermaceae	<i>Fibraura tinctoria</i>	Bud	1.6	1.5	0.0533		0.3	3.3	0.8	0.5	0.5	3.1	3.3	1.7	0.0	0.0	4.2	1.3
Sterculiaceae	<i>Sterculia</i> sp.	Seed	1.5	4.7	0.1400	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.4	1.7
Sapotaceae	<i>Palaquium ridleyi</i>	Seed	1.5	3.1	0.0364	15	0.0	0.0	0.0	0.0	0.5	0.0	9.0	1.1	0.0	0.0	0.0	7.2
Apocynaceae	<i>Dyera lowii</i>	Pith	1.5	3.5	0.0364		0.0	0.0	3.4	0.0	0.0	0.2	0.0	1.2	0.0	0.1	12.2	0.7
Rubiaceae	<i>Uncaria</i> sp.	Seed	1.3	4.1	0.0020	33	0.0	0.0	0.0	14.2	0.0	0.5	0.0	0.0	0.0	0.5	0.0	0.0
Fabaceae (Leguminosaeae)	<i>Archidendron borneensis</i>	Seed	1.2	2.4	0.0695	10	0.6	0.0	0.0	8.4	1.3	0.0	0.0	0.0	0.0	1.8	0.0	1.7
Fabaceae (Leguminosaeae)	<i>Adenantha pavonina</i>	Seed	1.1	2.6	0.0425	13	0.2	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	1.4	8.7
Unknown epiphyte	"Pahakung"	Young leaf	1.1	3.9	0.0425		0.0	0.0	0.0	0.0	13.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Moraceae	<i>Parartocarpus venenosus</i>	Seed	1.1	1.7	0.0331	16	4.6	0.0	0.0	0.0	0.0	0.0	1.3	4.3	0.4	0.0	2.1	0.0
Anisophyllaceae	<i>Combretocarpus rotundatus</i>	Seed	1.1	2.1	0.0261	21	0.0	0.0	5.7	5.2	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lauraceae	<i>Litsea cf. resinosa</i>	Seed	1.0	1.8	0.0262	20	2.7	4.7	0.0	0.0	0.0	0.0	0.5	4.3	0.2	0.0	0.0	0.0
Chrysobalanaceae	<i>Licania splendens</i>	Pulp skin	1.0	2.5	0.0470	12	0.0	8.1	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

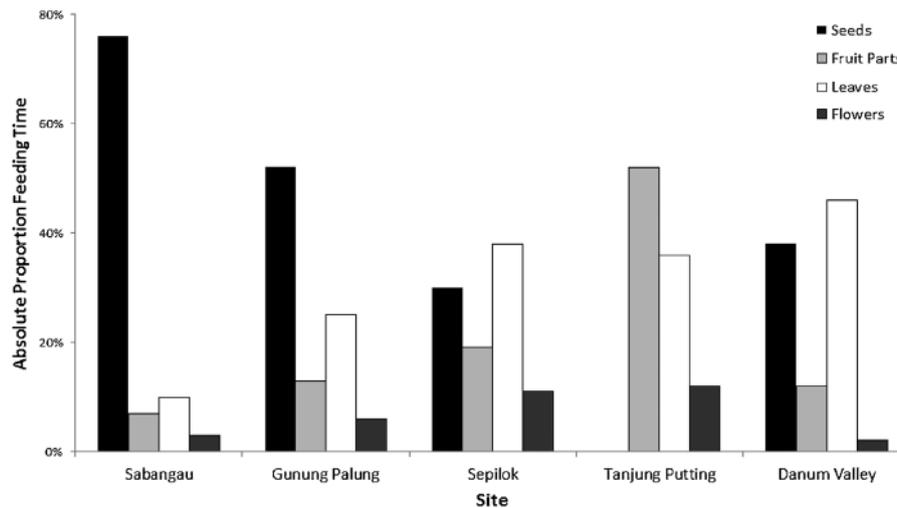


Fig. 2. Dietary composition of *P. rubicunda* across research sites on Borneo based on absolute consumption of major food classes. Data from this study, Gunung Palung [Marshall, 2004], Sepilok [Davies et al., 1988], Tanjung Puting [Supriatna et al., 1986], Danum Valley [Hanya & Bernard, 2012]. Supriatna et al. [1986] did not distinguish between seeds and other fruit parts.

et al., 1988; Hanya & Bernard, 2012; Supriatna et al., 1986]. Although Salafsky [1988] recorded equally high levels of fruit-eating in Gunung Palung National Park, West Kalimantan during a 9-month study period in which masting took place, the proportion of fruit-eating as recorded from a 5-year study at the same site was lower (Fig. 2) [Marshall, 2004]. These discrepant findings suggest that the wide temporal gaps between fruiting periods in masting forests require longer studies that include the protracted low fruit periods experienced in these habitats to provide accurate overall accounts of primate diets in these habitats [Marshall, 2004].

*P. rubicunda* in Sabangau did not appear to use fallback foods during the study period. That is, none of the major food classes showed patterns of consumption that were negatively correlated with availability of fruit, the preferred food class. By contrast, young leaves of *Spatholobus macropterus* (Leguminosae: liana) were both the most important dietary item overall (28% of all feeding bouts) and classified as a fallback food for a population of *P. rubicunda* at Danum Valley, Sabah, as consumption was negatively correlated with the availability of fruit, the preferred food class [Hanya & Bernard, 2012]. Red langurs in Sepilok, Sabah were also reported to be highly selective feeders, consuming seeds and other fruit parts (30% and 19% of total annual diet, respectively) disproportionately often relative to their availability in the environment [Davies et al., 1988]. Young and mature leaves comprised 37% and 1% of their overall diet respectively, and were eaten extensively outside of peak fruiting periods (in which consumption of seeds and other fruit parts rose to >85% of the monthly diet), indicating a reliance on leaves as fallback foods [Davies et al., 1988]. Thus our results are consistent

with our third hypothesis that reliance on fallback foods would be lower, or non-existent, in Sabangau Forest compared to masting forests. Further, fruit consumption was not significantly correlated with fruit availability, indicating that red langur diet in Sabangau was not constrained by availability of the preferred food class during our study period. Similarly, there was no significant relationship between orangutan fruit availability and energy intake for adult female and unflanged male orangutans in Sabangau (although there was for flanged males [Harrison et al., 2010]), suggesting that fruit availability may not be an accurate predictor of primate energy intake in the peat-swamp environment where fruit is consistently available year-round (Fig. 1). By contrast, fruit consumption by *P. rubicunda* in the masting dipterocarp forests of Danum Valley [Hanya & Bernard, 2012] and Sepilok [Davies et al., 1988] increased with fruit availability, suggesting that consumption of preferred foods by *P. rubicunda* in dipterocarp forests is dependent on availability, because of their rarity in the environment [Davies et al., 1988].

We acknowledge the potential limitation in inferring definitive dietary trends from the limited sample size in this study [Marshall & Wrangham, 2007]. We further acknowledge the potential limitations in the method used to assess food production in our phenology plots, as by recording production by presence/absence, one may over or underestimate actual availability, and thus variation in food availability resulting from interspecific differences in crop size (and even nutrient content) may be masked. There is also a potential limitation in drawing definitive conclusions regarding the diet of *P. rubicunda* in tropical peat-swamp forests from a single continuous year of data, as supra-annual

seasonal variations in food resource availability can cause fluctuations in primate dietary intake [Janson & Chapman, 1999; Oates, 1987]. Because fruit consumption in Sabangau was independent of fruit availability, however, we believe that the data presented here are likely to be representative of the true overall longitudinal diet of *P. rubicunda* in peat-swamp forests.

### Implications for Understanding Colobine Feeding Ecology

It is possible that the relatively small body size and concomitant limitation to the efficiency of foregut fermentation in *P. rubicunda* influences the diet and degree of folivory, and particularly the exploitation of mature leaves, as it does for another small-bodied colobine, *Procolobus verus* [Oates, 1988]. The relatively larger small intestine found in the smaller bodied colobines instead permits more efficient digestion of fruit parts [Chivers, 1994]. The greater fermenting potential in the larger stomachs of *Trachypithecus* monkeys, with which many *Presbytis* populations are sympatric, is consistent with their more folivorous diet [Bennett & Davies, 1994; Chivers, 1994]. This difference in degree of frugivory may contribute to niche separation between these two genera [Caton, 1999]. The consistent availability of nutrient-rich fruits/seeds in Sabangau peat-swamp forest does, however, appear to support high population densities of *P. rubicunda* relative to those found in forests on mineral soils throughout Borneo [Blouch, 1997; Ehlers Smith & Ehlers Smith, 2013; Marshall, 2010]. Indeed, the limiting factor to population density in Sabangau appears to be the availability of preferred fruit/seed-bearing stems, as *P. rubicunda* was present in high densities in habitat sub-classes where large ( $\geq 20$  cm DBH) trees with preferred fruits were abundant, but absent from a habitat sub-class in which large, preferred fruit-bearing stems were present at very low densities [Ehlers Smith & Ehlers Smith, 2013]. Our observation here that feeding bout length is positively correlated with feeding tree DBH is in line with this suggestion.

While this Sabangau focal group was more consistently frugivorous/granivorous than other *P. rubicunda* populations, and colobine monkeys in general, there is a marked seasonal variation in some species that seems to belie their folivorous adaptations and highlight the ability of the forestomach to effectively digest fruit parts and seeds in particular [Kay & Davies, 1994; Kirkpatrick, 1999]. For example, the diets of *Rhinopithecus avunculus* and *Nasalis larvatus* also consist of a high proportion of fruits (~60%) when seasonally available [Bennett & Sebastian, 1988; Boonratana & Le, 1998; Oates, 1994], and *Trachypithecus pileatus* and *T. johnii* also prefer fruits when in season [Oates et al., 1980; Stanford, 1991]. African colobine diets similarly

undergo seasonal shifts as *Colobus satanas* and *C. guereza* select seeds and whole fruits, respectively, over young leaves when they become abundant [Fashing, 2001; Oates, 1994]. In areas of high anthropogenic disturbance where a variety of cultivated fruits are consistently available, *Semnopithecus vetulus nestor* exploits this resource virtually year-round [Dela, 2007], but it appears that for most colobine species in natural environments, leaves are exploited as fallback foods when preferred fruits are unavailable. What is notable in the peat-swamp population of *P. rubicunda*, then, is the consistently high importance of fruit, and particularly seeds, in the diet across the year, facilitated by relatively low fluctuations in fruit availability that appear to negate reliance on fallback foods.

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### **Appendix 3**

**Ehlers Smith DA**, Ehlers Smith YC, Cheyne SM (2013b). Home-range use and activity patterns of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesian Borneo. *International Journal of Primatology* 34: 957–972.

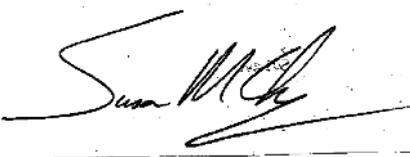
Concept and design: DA Ehlers Smith; Data collection: DA Ehlers Smith, YC Ehlers Smith; Data analysis: DA Ehlers Smith, YC Ehlers Smith; Manuscript preparation: DA Ehlers Smith, YC Ehlers Smith, SM Cheyne

## Co-Author Statement

**Ehlers Smith DA**, Ehlers Smith YC, Cheyne SM (2013b). Home-range use and activity patterns of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesian Borneo. *International Journal of Primatology* 34: 957–972.

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I, co-author Susan M. Cheyne, confirm that David Ehlers Smith made the stated contributions to this publication.

Signature 

Date 23<sup>rd</sup> October 2014

# Home-Range Use and Activity Patterns of the Red Langur (*Presbytis rubicunda*) in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesian Borneo

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**Abstract** Knowledge of a species' ranging patterns is vital for understanding its behavioral ecology and vulnerability to extinction. Given the abundance and even distribution of leaves in forested habitats, folivorous primates generally spend less time feeding; more time resting; have shorter day ranges; and require smaller home ranges than frugivorous primates. To test the influence of frugivory on ranging behavior, we established the activity budget and home-range size and use in a highly frugivorous population of the Borneo-endemic colobine, *Presbytis rubicunda*, within Sabangau tropical peat-swamp forest, Central Kalimantan, and examined relationships between fruit availability and ranging patterns. We collected 6848 GPS locations and 10,702 instantaneous focal behavioral scans on a single group between January and December 2011. The group had the largest home-range size recorded in genus *Presbytis* (kernel density estimates: mean =  $108.3 \pm \text{SD } 3.8$  ha,  $N = 4$  bandwidths). The annual activity budget comprised  $48 \pm \text{SD } 4.0\%$  resting;  $29.3 \pm \text{SD } 3.9\%$  feeding,  $14.2 \pm \text{SD } 2.5\%$  traveling, and  $0.4 \pm \text{SD}$

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0.4% social behaviors. Mean monthly day-range length was the highest recorded for any folivorous primate ( $1645 \pm \text{SD } 220.5 \text{ m/d}$ ). No significant relationships existed between ranging variables and fruit availability, and ranging behaviors did not vary significantly across seasons, potentially owing to low fluctuations in fruit availability. Our results suggest that colobine monkeys maintain larger than average ranges when high-quality food resources are available. Their extensive range requirements imply that protecting large, contiguous tracts of habitat is crucial in future conservation planning for *Presbytis rubicunda*.

**Keywords** Activity budget · Borneo · Colobinae · Folivore · Kernel density estimates · Utilization distribution

## Introduction

A home range is defined as the area in which an animal spends its adult life in search of food and caring for its offspring, but excludes peripheral excursions (Burt 1943; Jolly 1985). Identifying how animals divide their activities throughout the day and year offers insight into their interaction with the environment and their strategies for maximizing energetic and reproductive success (Defler 1995). Knowledge of a species' home-range size and ranging and activity patterns is vital for understanding its behavioral ecology, habitat requirements (Nkurunungi and Stanford 2006; Singleton and van Schaik 2001), and vulnerability to extinction (Haskell *et al.* 2002). In turn, such insights provide baseline data for conservation management initiatives (Bekoff and Mech 1984; Biebouw 2009; Haskell *et al.* 2002).

The size of an animal's home range is dependent on a variety of factors including seasonality, climatic and astronomical variables (Altmann and Altmann 1970; Li *et al.* 2005; Ren *et al.* 2009; Stigg and Stolba 1981), food resource distribution and phenology (Basabose 2005; Bennett, 1986; Boinski, 1987; Clutton-Brock 1977; Kinnaird and O'Brien 2000; Li 2001; Suarez 2006), population density and group size (Chapman and Chapman 2000; Dias and Strier 2003), and body size and mass (Chapman and Pavelka 2005; Clutton-Brock and Harvey 1979; Harestad and Bunnell 1979). Temporal and spatial variations in food sources particularly affect primate ranging and activity budget, and have an ultimate influence on home-range size and shape (Basabose 2005; Li *et al.* 2010; Wallace 2006; Watts 1998).

Primate ranging, then, is typically considered to be a trade-off between energy obtained and energy expended in the foraging process. Home-range sizes are generally larger in frugivorous primates than in folivorous primates, as fruits tend to be more patchily distributed (Clutton-Brock and Harvey 1977; Richard 1985). Given the abundance and relatively even distribution of leaves in forested habitats, folivores generally spend less time feeding, more time resting, and have shorter day ranges and require smaller home ranges than frugivores and insectivores (Clutton-Brock and Harvey 1977; Dasilva 1992). Socio-ecological theory proposes that group living provides benefits such as predator avoidance, but as group sizes increase, so too does intragroup feeding competition and the need for larger home ranges and day-range lengths; thus group size is likely limited by intragroup competition as dictated by the availability of food resources (Dunbar 1988; Janson 1992). The existence of

the “folivore paradox,” however, as many folivorous primate species live in relatively small groups despite their abundant food resources, suggests that social factors such as infanticide avoidance and other stresses associated with living in large groups exert a limiting pressure on group size (Steenbeck and van Schaik 2001).

The folivorous Colobinae of Asia and Africa display considerable variation in home-range size and ranging patterns among genera, species, and populations, although ranges are generally <100 ha (Fashing 2011; Kirkpatrick 2011). Species with larger home ranges tend toward lower population densities (Yeager and Kirkpatrick 1998). For example, *Rhinopithecus*, living in more temperate zones, occupy the largest home ranges at low population densities (>3500 ha; Bleisch *et al.* 1993; Li *et al.* 2000), and their range use is dependent on the sparse distribution of food resources and seasonal shifts in diet from leaves in summer to bark and flowers in winter (Kirkpatrick *et al.* 1999; Li *et al.* 2010). Colobine day-range lengths are similarly linked to the availability of food resources; species such as *Presbytis rubicunda* (Davies 1984), *P. siamensis* (Bennett 1986), and *Semnopithecus dussumieri* (Newton 1992) travel the farthest distances when fruits are available. By contrast, *Trachypithecus pileatus* travels the shortest distances when mature leaves are predominant in the diet (Stanford 1991).

Colobines with a greater degree of frugivory in their diet have larger home ranges than those that eat less fruit; e.g., *Nasalis larvatus* maintains relatively large home ranges (>770 ha) in mangroves where >55% of the diet comprises fruit (Bennett and Sebastian 1988), but ranges are smaller in peat-swamp forests (130–220 ha), where fruit consumption is less (11–40%; Boonratana 1994; Yeager 1990). The genus *Presbytis*, confined to peninsular Malaysia and the Sunda Islands, is considered less well adapted for folivory than other colobines (Bennett and Davies 1994), and much variation exists in home-range sizes within the 11 species that comprise the genus (13–99 ha; Kirkpatrick 2011; Supriatna *et al.* 1986; Watanabe 1981). *Presbytis rubicunda*, endemic to Borneo, lives in single-adult male multifemale groups ranging from 3 to 10 individuals (Davies 1984; Ehlers Smith and Ehlers Smith 2013; Supriatna *et al.* 1986), and has the largest home range size recorded within the genus (33–99 ha; Supriatna *et al.* 1986), and is also the most frugivorous of the Asian colobines (Ehlers Smith *et al.* 2013).

In 2010, we began an ecological study of *Presbytis rubicunda* in the nonmasting Sabangau tropical peat-swamp forest, Central Kalimantan, and discovered that fruit was consistently available throughout the year and was the preferred food, as selection was consistently disproportionately high relative to its availability across the same study period (Ehlers Smith *et al.* 2013) and dominated the mean annual diet (>83%, mainly in the form of seeds; Ehlers Smith *et al.* 2013). Population density was also relatively high within the genus (17.5 individuals/km<sup>2</sup>; Ehlers Smith and Ehlers Smith 2013). We here aimed to establish the activity budget and home-range size and use by this population. Given the high consumption of fruit in this population, we predicted that 1) the home-range size would be high relative to that of other tropical-living colobine monkeys; 2) day range would be high relative to other tropical-living colobine monkeys, and 3) day-range and active period length, and behaviors in the activity budget pertaining to foraging, i.e. feeding and traveling, would positively correlate with fruit availability as a potential driver of ranging behaviors (Ehlers Smith *et al.* 2013).

## Methods

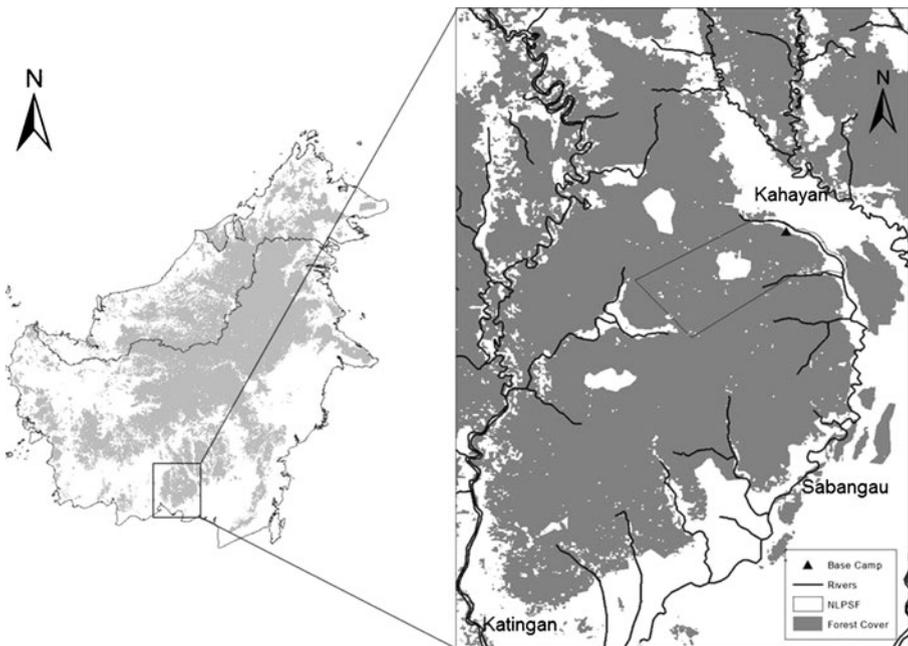
### Ethical Note

We acquired all the relevant permits and visas for the research from the Indonesian Institute for Research and Technology and adhered to Indonesian legislation. Our research was purely observational in nature.

### Study Site and Focal Subjects

The research was conducted as part of the Orangutan Tropical Peatland Project (OuTrop) – Center for the International Cooperation in Sustainable Use of Tropical Peatlands (CIMTROP) multidisciplinary research project within the 500 km<sup>2</sup> Natural Laboratory for the Study of Peat-Swamp Forest in the northern Sabangau Forest, Central Kalimantan, Indonesia (2°19'S and 113°54'E; Fig. 1), located 20 km southwest of the provincial capital, Palangka Raya. Because much of the lowland forests of Borneo have now been cleared (Curran *et al.* 2004; Miettinen *et al.* 2011), Sabangau represents the largest contiguous lowland rain forest block remaining on Borneo (Fig. 1) and is classified as a true ombrogenous tropical peat-swamp forest as the nutrient influx is obtained exclusively from aerial precipitation, i.e., rain, aerosol, and dust (Page *et al.* 1999).

Rainfall floods the forest floor for 8 mo of the year and the wet season typically spans November–May. We monitored the temperature and rainfall each day at 06:00



**Fig. 1** Location of the Natural Laboratory for the Study of Peat-Swamp Forest (NLPSF) within Sabangau tropical peat-swamp forest and Borneo. Forest cover is shaded gray, nonforested areas white. Derived from Miettinen *et al.* (2011).

and 18:00 h using a minimum–maximum thermometer situated inside the forest and a rain gauge situated at the base camp. During the study period (January–December 2011), the mean day and night temperature was  $26.2 \pm \text{SD } 1.0^\circ\text{C}$  and annual rainfall was 3406 mm (monthly rainfall range, 20–508 mm).

We collected home-range data on a single mixed-sex focal group between January and December 2011. The group comprised seven individuals (one adult male, three adult females, and three juvenile males) between January and July and five individuals between July and December after the death of one of the adult females and the subsequent disappearance of her juvenile offspring (Ehlers Smith and Ehlers Smith 2013). We followed the focal group from the morning sleeping tree to the evening sleeping tree for 3–11 d/mo ( $N = 84$  days; mean = 7 d/mo), for an annual total of 924.6 contact hours ( $N = 12$  mo; mean =  $77.1 \pm \text{SD } 25.2$  h/mo).

## Data Collection

*Home-Range and Behavioral Data Collection* On encountering the focal group, we obtained an initial geographic location using hand-held Garmin 60C Sx Global Positioning System (GPS) units, and thereafter took points of the group's location every 5 min until the follow concluded, either by the monkeys' entering an evening sleeping tree or the researchers no longer being able to locate the group. We obtained a total of 6848 GPS location points for the focal group during the study period.

We recorded focal-animal data (Altmann 1974) on a single adult female member of the group every 5 min in conjunction with a GPS location. We selected an individual adult female as the focal target before the beginning of the follow on the basis of ensuring an even balance between focal individuals and minimizing observer bias. This individual was then closely followed for the rest of the day. Focal females were readily identifiable by individual distinguishing characteristics of overall body sizes, nipple lengths, and shape of tails (Ehlers Smith *et al.* 2013). To describe the activity budget of behaviors, we recorded seven classes of data, including 1) the primary activity, which was divided into five categories: feeding (manipulating, masticating or swallowing food items); resting (all periods in which the focal individual was inactive); traveling (locomotor behavior that resulted in a change in spatial position); social behaviors (all activities involving interaction between the focal and any other individual); and unknown (any scan in which the focal individual could not be seen to determine the behavior); 2) the secondary activity, which explained how the primary activity was achieved, e.g., primary activity = feeding: secondary activity = eating seeds; primary activity = resting: secondary activity = sitting in tree; primary activity = traveling: secondary activity = quadrupedal running; primary activity = social behaviors: secondary activity = food share; 3) height of the focal individual in tree/substrate by 5 m categories, e.g., 1–5 m, 6–10 m; 4) height of the tree/substrate by the same 5 m categories; 5) distance of the focal individual to other adults in group by 10 m categories; 6) assessment of forest condition by mean height of canopy and canopy percentage, and 7) a unique GPS location tag, specific to each follow. We also recorded continuous feeding data on the focal individual (Ehlers Smith *et al.* 2013), for which we documented the species, food type, and food item during all feeding bouts  $\geq 30$  s and tagged, enumerated, and obtained GPS locations of all feeding stems. We defined the active period as the time the focal first emerged from the morning sleeping tree until all activity had ceased in the evening sleeping tree.

**Fruit Availability** We monitored food availability for *Presbytis rubicunda* in six plots (total area = 2.4 ha) located within and adjacent to the focal group's home range. We identified, tagged, measured, and enumerated all trees  $\geq 10$  cm diameter at breast height (DBH) and all lianas and figs  $\geq 3$  cm DBH and each month recorded all ripe and unripe fruits on tagged stems (mean no. of stems sampled/month =  $1593 \pm$  SD 10.2 trees). We direct readers to Ehlers Smith *et al.* (2013) for a detailed account of our fruit phenology method.

## Data Analysis

**Home-Range Analysis** We converted all GPS points into decimal degrees and then GIS shapefiles using the DNR GPS program v.6.0.0.11 (DNR, 2011). All shapefiles were projected into the UTM WGS\_1984 49S coordinate projection. We used the Geospatial Modeling Environment suite v.0.7.1.0 (Beyer 2012) to determine home-range size based on fixed-kernel density estimates (KDE; Worton 1989). KDE provides insight into area usage within home ranges by providing a probability density function (Silverman 1986) that corresponds to an animal's utilization distribution (Kernohan *et al.* 2001; van Winkle 1975; Worton 1987). KDE is sensitive to the various bandwidth values (Seaman *et al.* 1999; Silverman 1986), the objective algorithms applied to determine both the distance between the kernel and an evaluation point in the environment, and the contribution of the kernel to the overall density estimate at a location. Of the numerous bandwidth methods available, the least-squares cross-validation method is sensitive to sample size (Gitzen and Millspaugh 2003; Gitzen *et al.* 2006; Kie *et al.* 2010). Second-generation methods, including the plug-in and smooth cross-validation algorithms, which control for these known issues, have improved performance (Beyer 2012). We used four bandwidth algorithms on Gaussian kernels: least-squares cross-validation (LSCV), plug-in estimator (PLUGIN), biased cross-validation (BCV), and smooth cross-validation (SCV; Gitzen and Millspaugh 2003). We modeled home-range size using 90% volume contours and core-range size using 50% volume contours (Horner and Powell 1990; Powell 2000), and, for comparison, we also calculated the minimum convex polygon (MCP; Boyle *et al.* 2009). We calculated day-range length as the sum of the lengths recorded between GPS points from the morning sleeping tree to the evening sleeping tree, as displayed in ArcGIS v.10 (ESRI 2011).

**Behavioral Analysis of the Activity Budget** For behavioral analysis we discarded any follow  $< 6$  h to avoid potential bias resulting from short follow lengths (Harrison *et al.* 2009); thus we obtained a total of 4316 behavioral scans for adult female 1 ( $N = 12$  mo; mean =  $359.6 \pm$  SD 267.3 scans/mo), 5115 scans for adult female 2 ( $N = 12$  months; mean =  $426.3 \pm$  SD 100.9 scans/mo), and 1271 scans for adult female 3 ( $N = 6$  months; mean =  $211.8 \pm$  SD 176.4 scans/mo). Behaviors varied in a similar way between the three focal adult females across study months; thus we pooled the data set (total 10,702 focal sample scans between January and December 2011,  $N = 12$  mo; mean  $891 \pm$  SD 303.7 scans/mo).

We calculated the activity budget as the frequency score of a behavioral activity, i.e., resting, feeding, traveling, social, unknown) /total number of behavioral activity

scores per month, and then calculated the mean percentage that each activity contributed to the overall activity budget across the 12 mo. We similarly calculated the mean monthly day-range length, activity period length, height of focal in a substrate, and substrate height, and subsequently calculated annual means from each of these data sets. We tested for significant differences in the mean monthly activity budget scores and monthly day-range lengths across the two seasons (wet and dry; *t*-test, after Kolmogorov–Smirnov test determined data were normally distributed).

We tested potential relationships between the availability of the preferred food items (as potential drivers of ranging behaviors) and ranging behavior variables, including day-range length, activity period, and behaviors pertaining to foraging, i.e., feeding, traveling, through Pearson’s correlational tests after determining that the data sets were normally distributed by Kolmogorov–Smirnov test.

## Results

### Home-Range and Core-Range Sizes

The four bandwidth estimators predicted a home-range size of 104.9–112.0 ha for the focal group ( $N = 4$  bandwidths, mean  $108.3 \pm \text{SD } 3.8$  ha) and a core-range size of 45.1–48.7 ha ( $N = 4$ , mean  $47.0 \pm \text{SD } 1.9$  ha; Table I, Fig. 2). There was relatively little variation between bandwidth calculations of home-range estimates (Table I), although the BCV and LSCV bandwidths predicted a larger range than did the second-generation SCV and PLUGIN algorithms (Table I). At 134.3 ha, home-range size as calculated by MCP was larger than that calculated by KDE.

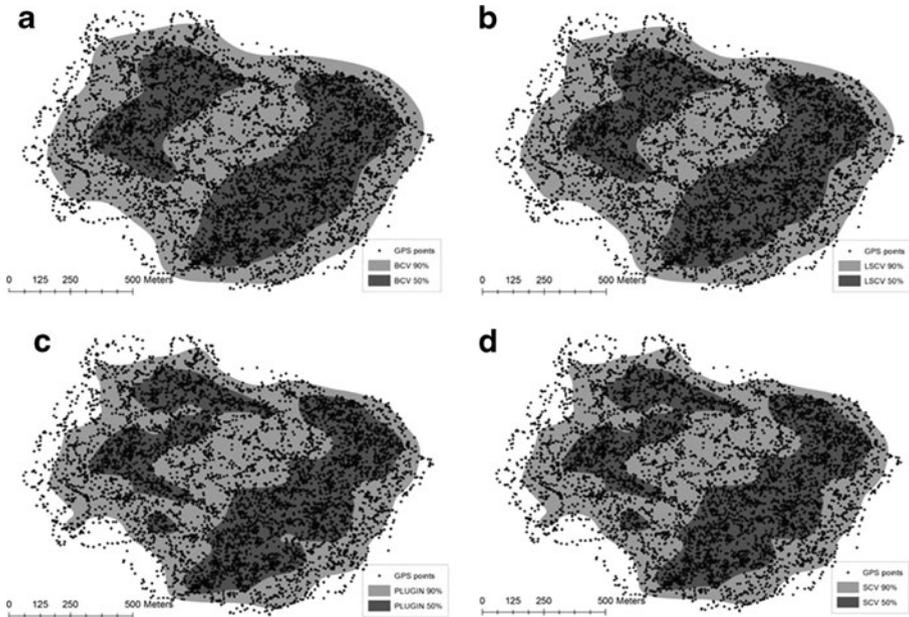
### Activity Budget and Ranging Patterns

The activity budget of the focal group was divided into  $48.0 \pm \text{SD } 4.0\%$  resting (range = 41.6–54.2%),  $29.3 \pm \text{SD } 3.9\%$  feeding (range = 22.6–37.7%),  $14.2 \pm \text{SD } 2.5\%$  traveling (range = 9.8–19.6%), and  $0.4 \pm \text{SD } 0.4\%$  engaged in social behaviors (range = 0.0–0.6%; Fig. 3). Across the study period, the behavior was unknown for  $8.2 \pm \text{SD } 3.6\%$  of scan samples (range 4.5–17.7%; Fig. 3). There were no significant differences in time spent feeding (*t*-test:  $T = -1.514$ ,  $df = 10$ ,  $P = 0.161$ ); feeding ( $T = -0.995$ ,  $df = 10$ ,

**Table I** Home-range (90% volume contours) and core-range (50% volume contours) sizes of a focal group of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest between January and December 2011, as calculated by kernel density estimates (KDE)

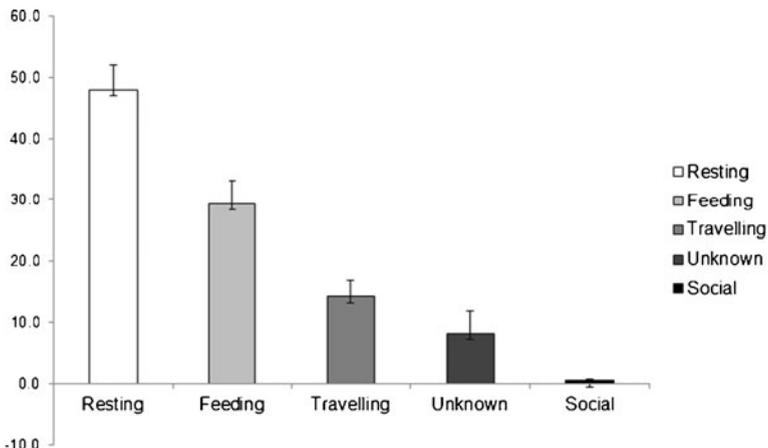
	BCV		LSCV		PLUGIN		SCV		90%		50%	
	90%	50%	90%	50%	90%	50%	90%	50%	Mean	SD	Mean	SD
ha	112.0	48.7	111.1	48.6	104.9	45.1	105.0	45.5	108.3	3.8	47.0	1.9

KDE based on four bandwidth algorithms: biased cross-validation (BCV); least-squares cross-validation (LSCV); plug-in estimator (PLUGIN), and smooth cross-validation (SCV).



**Fig. 2** Home range (90% volume contours) and core range (50% volume contours) of the focal group of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest between January and December 2011, as calculated by kernel density estimates (KDE) using the (a) biased cross-validation (BCV); (b) least-squares cross-validation (LSCV); (c) plug-in (PLUGIN); and (d) smooth cross-validation (SCV) bandwidth algorithms (see main text).

$P = 0.343$ ) or traveling ( $T = 1.326$ ,  $df = 10$ ,  $P = 0.214$ ) across the two seasons. Mean monthly day-range length was  $1645 \pm SD 220.5$  m/d (range = 1341–2041 m/d) and the mean daily activity period was  $11.0 \pm SD 0.4$  h (range = 10.4–11.6 h), beginning  $8 \pm SD 12.0$  min after sunrise (range = –10.1 to +28.0 min after sunrise; mean 05:29 h,  $\pm SD 1.2$  h, range = 05:02–06:00 h) and ending  $56.5 \pm SD 17.1$  min before sunset (range = 37.0–



**Fig. 3** Annual activity budget of behaviors, with standard deviation bars, of the focal group of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest between January and December 2011.

87.4 min before sunset; mean 16:31 h  $\pm$  SD 1.1 h, range = 16:05–16:49 h). There was no significant difference across the two seasons in monthly day-range length ( $t$ -test:  $T = 1.500$ ,  $df = 10$ ,  $P = 0.165$ ), and no variation in the mean monthly height category of substrate used (11–15 m category), or in the mean height of individual category (16–20 m category).

Mean monthly fruit availability did not significantly correlate with either mean monthly day-range length or active period length. Further, fruit availability did not correlate with mean percentage time spent feeding, resting, or traveling. Active period length did not significantly correlate with percentage time traveling, feeding, or resting. Day-range length was, however, significantly correlated with percentage time traveling (Table II).

## Discussion

### Range Size

There are inherent problems when comparing home-range sizes across studies, as the various methods of determining range sizes often provide differing results (Boyle *et al.* 2009). Taking into account these concerns, however, the results of this study are consistent with our first prediction that home-range size would be high relative to that of other tropical-living colobines. With the exception of *Trachypithecus johnii* (65–250 ha), which occurs at relatively very high densities ( $>70$  individuals  $\text{km}^{-2}$ ; Kirkpatrick 2011; Poirier 1970), the focal group had the largest home-range size recorded within the genus *Presbytis* and its closest related (Roos *et al.* 2011) and sympatric genus, *Trachypithecus*. In fact, the core range of the focal group was larger than the total home-range sizes recorded for all other *Presbytis* (Kirkpatrick 2011). Of the Asian colobine groups that occupy larger home ranges (*Rhinopithecus*, *Semnopithecus schistaceus*, *S. dussumieri*, *Nasalis larvatus*), all occur at the lowest end of recorded population densities (2–11 individuals  $\text{km}^{-2}$ ; Bennett and Sebastian 1988; Boonratana and Le 1998; Curtin 1975; Dolhinow 1972; Ren *et al.* 2009; Table III). Of the African colobines, only

**Table II** Results of correlation analysis between ranging variables and fruit availability in *Presbytis rubicunda* in Sabangau tropical peat-swamp forest between January and December 2011

Variable $x$	Variable $y$	$R$ value	$P$ value
Fruit availability	Day range length	0.431	0.161
Fruit availability	Active period length	-0.305	0.336
Fruit availability	Time spent feeding	-0.495	0.102
Fruit availability	Time spent resting	0.278	0.381
Fruit availability	Time spent traveling	0.360	0.250
Active period length	Time spent traveling	-0.224	0.483
Active period length	Time spent feeding	0.179	0.577
Active period length	Time spent resting	0.322	0.307
Day range length	Time spent traveling	0.737	0.006

*Colobus angolensis* (2440 ha); *C. satanas* (573 ha), and *Piliocolobus tephrosceles* (114 ha) have larger ranges (Bocian 1997; Clutton-Brock 1975; Fashing 2011; Fashing *et al.* 2007; Table III). *Colobus satanas* also maintains relatively very low population densities (8 individuals km<sup>-2</sup>; Fleury and Gautier-Hion 1999), while at the Rwandan site *C. angolensis* seemed to be a rare case in which exceptionally high-quality food, in the form of mature leaves, permitted unusually high group sizes (>300 individuals), and in turn dictated huge ranges (Fashing *et al.* 2007; Fimbel *et al.* 2001; Table III). The overall trend within colobine feeding ecology suggests that the largest home-range sizes are determined either by very low food resource availability, which forces larger ranges and consequently limits population densities (Yeager and Kirkpatrick 1998), or the availability of high-quality food resources that permit large groups, which are consequently maintained through larger ranges (Fashing 2011; Kirkpatrick 2011; Table III). Although group sizes in this study population are average (7 individuals/group), at 17.5 individuals km<sup>-2</sup>, population density is relatively high within the genus (Ehlers Smith and Ehlers Smith 2013), indicating a degree of overlap in home ranges between groups, as colobine species tend toward home-range compression as population density increases (Dunbar 1987; Fashing 2011; Newton and Dunbar 1994;). Thus, the data obtained in this study suggests that the focal group were able to occupy some of the largest home ranges recorded because of the consistent exploitation and low variation in availability of high-quality food resources (Ehlers Smith *et al.* 2013).

Consistent with our second prediction that day-range length would be accordingly high relative to other tropical-living colobines, it appears that the focal group had the largest recorded mean monthly day range of all folivorous primates, including the African colobines ( $N = 17$ , range = 300–1212 m; Fashing 2011; Korstjens 2001; Sicotte and MacIntosh 2004) and the folivorous Atelinae of South America (*Alouatta*:  $N = 20$ , range = 123–1150 m; *Brachyteles*:  $N = 3$ , range = 630–1313 m; Dias and Strier 2003; Di Fiore and Campbell 2011; Estrada 1984). This is particularly noteworthy as colobine species with larger home ranges do not necessarily have correspondingly larger day ranges (Kirkpatrick 2011), and day-range length is typically low in colobine monkeys owing to the relative abundance and even distribution of leaves (Fashing 2011; Kay and Davies 1994). In the species with larger day-range lengths, food sources are either rare or patchily distributed in the environment (Davies 1984; Fleury and Gautier-Hion 1999), or fruit is predominant in the diet (Bennett 1986; Davies 1991; Newton 1992; Stanford 1991). The latter case is consistent with our focal group, for which >83% of the annual diet comprised fruit (Ehlers Smith *et al.* 2013).

### Activity Budget

Despite pronounced frugivory, we discovered no significant relationships between fruit availability and ranging patterns, including day-range length and daily activity length, or time spent feeding and traveling. This does not support our prediction that fruit availability, as a potential driver of ranging behaviors, would positively correlate with time spent engaged in ranging behaviors. The lack of significant correlations is potentially due to the relatively low fluctuations in fruit availability during both the study period (Ehlers Smith *et al.* 2013), and in tropical peat-swamp forests in general (van Schaik and Pfannes 2005), which may have either masked fruit availability as a potential driver of ranging behaviors, or freed the focal group from the effects and

**Table III** Relationships between range use and diet in colobines

Species	Site	Habitat	Population density (ind./km <sup>2</sup> )	Home-range size (ha)	Day-range length (m)	Percentage fruit in diet	Percentage leaves in diet	Study
<i>Presbytis rubicunda</i>	Sabangau	Peat swamp	17.5	108	1645	83.7	10.2	This study; Ehlers Smith and Ehlers Smith 2013; Ehlers Smith <i>et al.</i> 2013
<i>P. comata</i>	Kamojang	Montane tropical	11	38	500	14	65	Ruhiyat 1983
<i>P. hosei</i>	Lipad	Dipterocarp	ca. 26	35	740	19	78	Mitchell 1994
<i>P. potenziani</i>	Betumonga	Dipterocarp	11	34	540	32	55	Fuentes 1994
<i>P. rubicunda</i>	Sepilok	Dipterocarp	16.2	67	890	49	37	Davies 1984; Davies <i>et al.</i> 1988
<i>Trachypithecus johnii</i>	Kakachi	Evergreen forest	71	24		25	52	Oates <i>et al.</i> 1980
<i>T. obscurus</i>	Kuala lompat	Dipterocarp	87	17–33	560	35	58	Curtin 1976, 1980
<i>Nasalis larvatus</i>	Samunsam	Mangrove	6	770	485	58	41	Bennett and Sebastian 1988
<i>N. larvatus</i>	Kinabatangan	Peat swamp	34	220	910	11	74	Boonratana 1994
<i>Rhinopithecus beiti</i>	Wuyapiya	Conifer	7	2500	1310		ca. 6	Kirkpatrick <i>et al.</i> 1998
<i>R. brelichi</i>	Fanjingshan	Temperate broadleaf	11	3500	1290	15	71	Bleisch <i>et al.</i> 1993
<i>Semnopithecus dussumieri</i>	Orcha	Moist deciduous	3–6	ca. 375				Dolhinow 1972
<i>S. schistaceus</i>	Junbesi	Conifer/broadleaf	ca. 2	ca. 1275				Curtin 1975
<i>Colobus angolensis</i>	Nyungwe	Mixed tropical	>300(gr size)	2440		17	65	Fimbel <i>et al.</i> 2001; Fashing <i>et al.</i> 2007
<i>C. satanas</i>	Foret des Abeilles	Mixed tropical	8	573	510	50	38	Fleury and Gautier-Hion 1999

Adapted from Fashing (2011) and Kirkpatrick (2011).

constraints of seasonal fluctuations on ranging. Thus, during the study period in Sabangau, *Presbytis rubicunda* experienced only small seasonal shifts in their dietary composition, and consequently there was no significant variation in ranging patterns.

The overall activity budget of the focal group was less subject to seasonal changes, and more focused on feeding (29%) and traveling (14%) and less on resting (48%; Fig. 3) relative to that of other Asian colobines. For example, *Nasalis larvatus* spent 76% of its time resting and just 3.5% of its time traveling (Matsuda *et al.* 2009), whereas *Trachypithecus poliocephalus leucocephalus* spent 84% of its time resting in the summer and 57% in winter owing to seasonal changes in leaf availability (Huang *et al.* 2003). The activity budget of the focal group appeared to be similar to that of the more comprehensively documented African colobines, which spend a mean 50% of their time resting ( $N = 20$ , range = 32–61%), 28% of time feeding ( $N = 20$ , range = 19–45), and 13.5% of time traveling ( $N = 20$ , range = 2–25%; Fashing 2011).

From the phylogenetic perspective, colobine digestive physiology appears to have a profound effect on social behavior, as the abundance of food resources is thought to preclude intragroup aggression and food scrambles and the subsequent need for dominance interactions and appeasements (Yeager and Kool 2000). The almost complete absence of social activities between adults in the focal group is noteworthy, even in this highly frugivorous population, and consistent with that recorded in other, more folivorous Asian colobines (Bennett 1983; Kirkpatrick 2011; Poirier 1970; Fig. 3). We occasionally observed embracing behavior between the adult females (although it occurred too infrequently to be represented in the scan samples), but contact between the adult male and adult females occurred only during resting periods when they sat <1 m apart, and grooming behavior was absent. Instead, the tiny proportion of social behaviors in the activity budget represented interactions between the adult females and their offspring, namely nursing and food sharing.

## Conclusions and Conservation Implications

We have shown that in the largest remaining lowland forest-block on Borneo, the endemic *Presbytis rubicunda* used one of the largest ranges found in folivorous monkeys in tropical rain forests. The high levels of frugivory, facilitated by low fluctuations in fruit availability at the study site, potentially permitted a very large home range relative within the subfamily Colobinae, which is consistent with the findings that colobine monkeys have larger range requirements when high-quality food resources are available (Fashing *et al.* 2007; Fimbel *et al.* 2001). From a conservation perspective, much of the lowland forests on Borneo have either been cleared or are now comprehensively fragmented and degraded (Curran *et al.* 2004; Miettinen *et al.* 2011), and although much forest at elevation remains, densities in these habitats (>750 m asl) are so low they may be unable to support viable populations (Marshall 2010). The implications of the findings of this research, therefore, is that owing to their extensive range requirements, the identification and protection of larger and more contiguous tracts of rain forests are crucial considerations in any future conservation strategies for *Presbytis rubicunda*.

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## **Appendix 4**

**Ehlers Smith DA** (2014a). The effects of land-use policies on the conservation of Borneo's endemic *Presbytis* monkeys. *Biodiversity and Conservation* 23: 891-908.

# The effects of land-use policies on the conservation of Borneo's endemic *Presbytis* monkeys

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**Abstract** Despite supporting the highest biodiversity on Earth, tropical rainforests are undergoing intensive economic development. In particular, the island of Borneo has lost over 56 % of original lowland forest to resource extraction, fires, and illegal logging. Its rainforests contain 16 primate species, which serve as excellent ‘umbrella’ taxa for conservation initiatives. The genus *Presbytis* (Colobinae) is well represented across Borneo by four endemic species (*P. chrysomelas*; *P. frontata*; *P. hosei*, and *P. rubicunda*), but remains relatively understudied. Using ecological niche modelling, I calculated the distributions of the 12 Bornean *Presbytis* subspecies; evaluated habitat loss between 2000 and 2010, and examined the current land-use policies across remnant distributions. Subspecies experienced a mean 12.7 % (N = 12 sp.) habitat reduction over the 10 year period. 12.5 % of all habitats were allocated for conversion to oil palm and industrial tree plantations, while logging concessions accounted for a mean 26.3 % across distributions. While the current protected area networks encompassed an average 33.4 % of distributions, most PAs are underfunded, degraded and threatened by logging and mining operations. I therefore recommend priority gazetting of unallocated lands to new PAs within the distribution of *Presbytis chrysomelas* and *Presbytis hosei sabana*, which have experienced the highest forest loss in the last 10 years (22–50 %) and are critically endangered. Logging concessions appear to be at least as effective in maintaining forest cover as PAs and have the economic advantage for effective management, but may have detrimental effects to

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monkey populations. I recommend an urgent assessment of the effects of selective logging practices on species' persistence, and further recommend population surveys to quantify the populations of critically endangered and data deficient subspecies.

**Keywords** Borneo · Colobinae · Distributions · Forest loss · Protected areas

## Introduction

Tropical rainforests are undergoing intensive economic development (Carlson et al. 2012; Hansen et al. 2008; Page et al. 2002), despite supporting the highest biodiversity on Earth (Pimm and Sugden 1994). The island of Borneo in particular has lost more than 56 % of its original lowland forest, due to resource extraction, fires, and illegal logging (Curran et al. 2004; Geist and Lambin 2002; Langner et al. 2007; Miettinen et al. 2011). Since the 1980s, ~ 80 % of the forests of Kalimantan (Indonesian Borneo) alone have been allocated as federally-managed industrial timber-logging concessions (Curran et al. 2004). Additionally, in the last 10 years, the rate of forest clearance for oil-palm production has increased by 212 % to account for 31,640 km<sup>2</sup> of Kalimantan's total area; 90 % of such clearances occurred on forested land (Carlson et al. 2012).

Borneo also represents one of the global top 25 biodiversity hotspots under threat (Myers et al. 2000) and is home to 16 primate species, ten of which are endemic (Groves 2001; Munds et al. 2013). Given the high rate of habitat loss, much action has been taken to conserve the Bornean orangutan (*Pongo pygmaeus*), including efforts to stabilize populations and moratoriums on logging throughout known distributions (Soehartono et al. 2007), and comprehensive studies on its ecology (e.g. Morrough-Bernard et al. 2009; Wich et al. 2008), distribution (Husson et al. 2009) and conservation status (Wich et al. 2012). Such actions in turn serve as useful conservation surrogates for biodiversity within orangutan distributions (Bibby 1998; Margules et al. 2002).

Indeed, in addition to protection for their own sake, the primates, as a large, well-studied (Rowe 1996) and charismatic order (Mittermeier et al. 2012), make excellent 'umbrella' species for conservation initiatives (Soemarna et al. 1995; Kiester et al. 1996; Bibby 1998; Sowa et al. 2007). Primates of the genus *Presbytis* are more extensively distributed than the orangutan across Borneo, and are represented by 4 endemic species: *P. chrysomelas*; *P. frontata*; *P. hosei*, and *P. rubicunda*, but remain relatively understudied (but see Ampang and Zain 2012; Davies et al. 1988; Marshall 2010; Nijman 2010; Ehlers Smith and Ehlers Smith 2013). Locality data for *P. chrysomelas* and *P. frontata* in particular are scarce, and the taxonomic status of the genus is still disputed and in a state of flux (c.f. Groves 2001; Brandon-Jones et al. 2004; Brandon-Jones 2006; Meyer et al. 2011; Table 1).

Basic knowledge of a species' occurrence and distribution is an essential starting point for predicting extinctions as a result of habitat loss, and to subsequently devise strategies to focus conservation efforts (Margules and Pressey 2000; Groves 2003). Three types of species occurrence data exist: point localities, at which a species has been observed; extent of occurrences, as broad geographic ranges within which are all the localities that a species is recorded; and predicted distributions, in which the suitability of environmental conditions within a known extent of occurrence are assessed for the likelihood of species'

**Table 1** The taxonomy (after Groves 2001), IUCN Red List Threat Status and habitat requirements (Boitani et al. 2006) of the *Presbytis* monkeys of Borneo

Species	Authority	Status	Habitat <sup>a</sup>	Altitudinal limit (m asl)
<i>P. chrysomelas chrysomelas</i>	Müller 1838	CR A2cd	TWE, PS, FS	500
<i>P. chrysomelas cruciger</i>	Thomas 1892	CR A2cd	TWE, PS, FS	500
<i>P. frontata</i>	Müller 1838	VU A2cd	TWE	2,000
<i>P. hosei canicrus</i>	Miller 1934	EN A4cd	TWE	1,700
<i>P. hosei everetti</i>	Thomas 1892	VU A2cd	TWE	1,700
<i>P. hosei hosei</i>	Thomas 1889	DD	TWE	1,700
<i>P. hosei sabana</i>	Thomas 1893	EN A4cd	TWE	1,700
<i>P. rubicunda carinatae</i>	Miller 1906	DD	TWE, PS	N/A
<i>P. rubicunda chrysea</i>	Davis 1962	DD	TWE, PS	2,000
<i>P. rubicunda ignita</i>	Dollman 1909	LC	TWE, PS	2,000
<i>P. rubicunda rubicunda</i>	Müller 1838	LC	TWE, PS	2,000
<i>P. rubicunda rubida</i>	Lyon 1911	LC	TWE, PS	2,000

<sup>a</sup> TWE tropical wet evergreen forests on mineral soils, PS peat-swamp forest on regularly flooded soils, FS fresh-water swamp forests on regularly flooded soils (Boitani et al. 2006; Miettinen et al. 2011)

occupancy (Corsi et al. 1999; Guisan and Zimmermann 2000; Rondinini et al. 2006). If environmental and habitat requirements are known, ecological niche models can refine extent of occurrence data by omitting areas that are unsuitable (Rondinini et al. 2005, 2006), as these data representations often overestimate species' distributions (commission errors). In species for which an abundance of locality data-points are available, more sophisticated predictive niche modelling techniques are known to perform well, in which computer algorithms predict species' distributions based on a variety of environmental variables at multiple locations (e.g. Maximum Entropy, Phillips et al. 2006).

The high rate of habitat destruction, agricultural expansion and multiple land-use policies on Borneo is impetus for assessing the anthropogenic threats faced by the endemic and scarcely-documented *Presbytis* monkeys. In this study I aim to (1) present the distributions of the 4 species of Bornean *Presbytis* monkeys, and their respective subspecies, based on ecological niche modelling and a consensus of the literature; (2) evaluate the proportion of habitat loss for each subspecies over the 10 year period between 2000 and 2010; (3) calculate the current land-use policies throughout remnant distributions, and investigate the likely effects of these on the conservation status of each subspecies, and (4) make recommendations for conservation strategies to safeguard the persistence of each subspecies.

## Methods

### Study species

Genus *Presbytis* is a monophyletic taxon comprising at least 11 species restricted to the Greater Sunda Islands and the Malayan Peninsula (Meijaard and Groves 2004; Meyer et al. 2011). The genus is included in the colobine sub-family, which is distinct in the adaptation of its forestomach morphology, which facilitates folivory and granivory (seed eating; Chivers 1994; Kay and Davies 1994). *Presbytis* monkeys are among the most frugivorous

and granivorous colobines, and typically consume between 25 and 65 % fruit parts (Davies et al. 1988; Marshall 2010; Nijman 2010). Body sizes are relatively gracile and range from 5.6 to 8.2 kg (Rowe and Myers 2010). The genus is almost entirely arboreal, and, with the exception of *P. potenziani*, maintains groups of single-adult males and multiple-adult females and their offspring. Extra-group males form all-male bands or range alone (Davies and Oates 1994).

### *Presbytis chrysomelas*

*Presbytis chrysomelas* was recently elevated from a subspecies of *P. femoralis* (Groves 2001), and now comprises two of its own subspecies (Table 1). It has the most restricted distribution of the *Presbytis* monkeys and inhabits lowland tropical wet evergreen and swamp forests below 500 m above sea level (asl) in groups of 3–13 individuals (Ampang and Zain 2012; Boitani et al. 2006; Nijman et al. 2008a; Table 1). *P. chrysomelas* is considered critically endangered due to its low population size, restricted distribution and the high conversion rate of its habitat (Nijman et al. 2008b; Table 1).

### *Presbytis frontata*

*Presbytis frontata* is monotypic (Groves 2001; Table 1) and inhabits tropical wet evergreen forests on mineral soils in a broad distribution across the centre of the island at relatively low densities up to an elevation of 2,000 m asl (Meijaard and Nijman 2008; Table 1). It lives in relatively small groups of >6 individuals (Nijman 2001) and is classified as vulnerable due to hunting and habitat loss (Meijaard and Nijman 2008). *Presbytis frontata* is particularly cryptic and under-studied, and is known to freeze upon contact with humans (Nijman and Nekaris 2012).

### *Presbytis hosei*

The taxonomy of *Presbytis hosei* is under dispute and may actually contain up to three separate species (c.f. Nijman and Meijaard 2008a; Nijman 2010), but for simplicity it is treated here as one species comprising four subspecies (Groves 2001; Table 1). *Presbytis hosei* occurs in tropical wet evergreen forests on mineral soils up to 1,700 m asl in the north and east of Borneo. Above this altitude, densities become much lower (Nijman 2010). Average group sizes range from 7 to 10 individuals, at variable densities from >1 to over four groups km<sup>-2</sup>. The threat assessment for the respective subspecies ranges from vulnerable to endangered, as a result of hunting and habitat loss (Nijman et al. 2008a; Table 1). *Presbytis hosei canicrus* is noteworthy as its status and distribution is currently under review. Lhota et al. (2012) confirmed the species' persistence in the Wehea Forest of the West Kutai district, and Brandon-Jones (1997) established that its range extends west beyond this region. Setiawan et al. (2009) suggested that the species may be absent in the Kutai National Park, its former population stronghold in the south of its range.

### *Presbytis rubicunda*

*Presbytis rubicunda* represents the most comprehensively-studied of the endemic *Presbytis* monkeys (c.f. Supriatna et al. 1986; Davies et al. 1988; Davies 1991; Marshall 2010; Hanya and Bernard 2012; Ehlers Smith and Ehlers Smith 2013; Ehlers Smith et al. 2013a,

b), contains five subspecies, and is considered the least threatened due to its broad distribution (Nijman and Meijaard 2008b; Table 1). It occurs at a range of densities, dependent on the availability of high-quality foods (Marshall 2010; Ehlers Smith and Ehlers Smith 2013), and typically comprises 3–10 individuals. *Presbytis rubicunda* occupies tropical swamp and wet evergreen forests on mineral soils up to 2,000 m asl, although it is likely populations above 700–800 m asl are at such low densities that they are non-viable (Marshall 2010).

### Species' distribution modelling

Given the state of flux that exists within the taxonomy of the genus, historical locality records assigned to the subspecies treated here are of dubious accuracy and practicality. Furthermore, sufficient locality data were lacking for the subspecies to perform advanced predictive niche modelling. Therefore, I used ecological niche modelling on the known extent of occurrence data-sets for each primate subspecies, which represents a consensus of the available locality data.

I used ArcGIS v10 (ESRI 2011) for all modelling. I accessed primate species' extent of occurrence data from "All The World's Primates" (Rowe and Myers 2010), land cover maps of Insular Southeast Asia from 2000 to 2010 produced by the CRISP project (Miettinen et al. 2011), and elevation data from the World Database on Protected Areas Consortium (WDPA 2006). I extracted by attribute the appropriate forest cover classes from the land cover maps of 2000 and 2010 for each subspecies according to its habitat requirements, as listed in the Southeast Asian Mammal Databank (Boitani et al. 2006; Table 1) which represents a consensus of the literature. For each subspecies I merged all habitat classes as appropriate, and then clipped the resultant layer by its recorded altitudinal limit. I then clipped each extent of occurrence layer by its species-specific habitat layer to produce a distribution layer, from which I then erased all rivers that bisected habitats as natural geographic barriers. I projected all data layers into the appropriate WGS 1984 UTM Zones of Borneo to facilitate accurate area calculations. The dissolve and multi-part to single-part functions were used to assign a unique identification to each polygon, and I then calculated the area of each polygon and subsequently deleted those smaller than 10 km<sup>2</sup> from the distribution model as too small to be a viable habitat patch.

Two of the 12 subspecies treated here warrant specific treatment: given the uncertainty of the distributional boundary of *P. h. canicrus*, I performed two boundary scenarios thus: (1) a minimum scenario based on the data provided by Lhota et al. (2012), and (2) a maximum scenario based on the data provided by Brandon-Jones (1997). The interim distributional region between the known boundary of *P. h. everetti* and *P. h. canicrus* is ascribed to an "unconfirmed" subspecies that is thought to exist in the area and may be one or the other subspecies (Nijman 2010). Similarly, taking into account the likelihood that populations of *P. rubicunda* are non-viable above 700–800 m asl (Marshall 2010), I performed two ecological niche model scenarios for each subspecies for whom distributions exceeded 700 m asl thus: (1) the maximum altitudinal limit recorded (2,000 m asl), and (2) the viable altitudinal limit (700 m asl).

### Land use projections

To assess the impacts of the current land-use allocations on the distributions of the 12 *Presbytis* subspecies, I used the data-set compiled by Wich et al. (2012) detailing the current major land uses including: (1) oil palm plantations (IOPP); (2) industrial tree

plantations (ITP); (3) logging concessions, and (4) the protected area (PA) networks. A comprehensive overview of these land-use allocations and how the data were compiled can be found in Wich et al. (2012). I overlaid each subspecies' distribution with each land-use data-layer to calculate the area and proportion that each allocation contributed to each overall distribution (Fig. 1).

#### *Industrial oil palm plantation concessions (IOPP)*

Oil palm plantation concessions are granted by the Indonesian and Malaysian governments at the local level for the conversion of natural forests and subsequent production of oil palm monocultures. In Malaysia, a minority of concessions are allocated from de-gazetted commercial forest reserves; the majority are issued in 'conversion' or 'production' forests, as is the case for Indonesian concessions. These data were unavailable for the Malaysian state of Sabah, and as such are not included in the analysis of land-use impacts on subspecies' whose ranges (*P. rubicunda chrysea*, *P. hosei sabana*) are located within that state (Wich et al. 2012).

#### *Industrial tree plantation concessions (ITP)*

The conversion of natural forested lands to ITPs is not considered deforestation in the United Nations Framework Convention on Climate Change, as they are legally defined as 'forest' (Sasaki and Putz 2009; Wich et al. 2012). In Indonesia, ITP are granted by the Ministry of Forestry and converted on lands classified as 'production forests'; in Malaysia the Forestry Department grants concessions on the equivalent 'commercial forest reserves' (Wich et al. 2012).

#### *Logging concessions in natural forests*

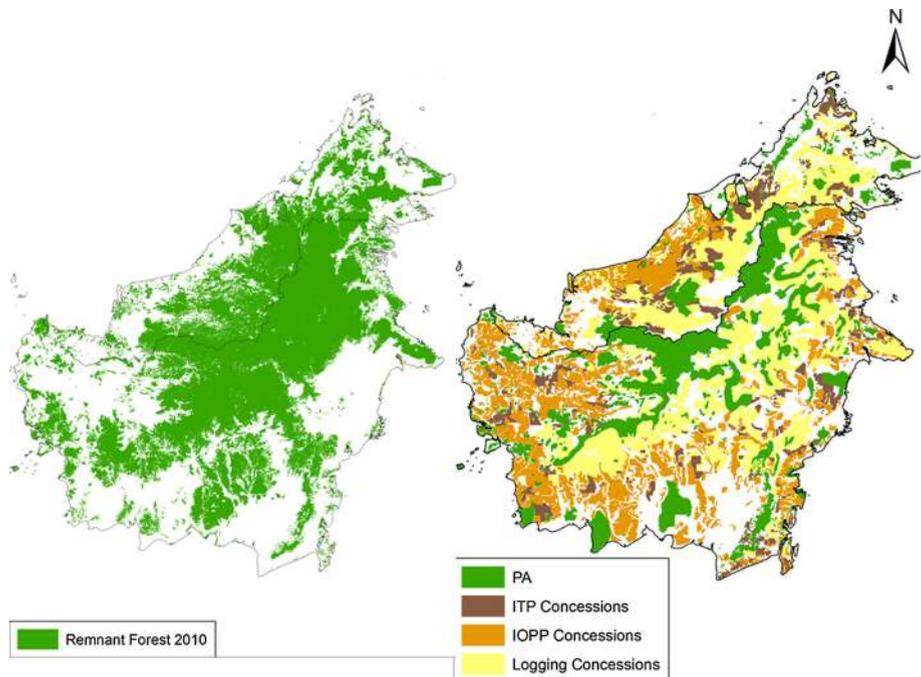
Logging concession licenses permit companies to extract natural timber products from the rainforests, although mandates of sustainable resource extraction prohibit deforestation through clear-felling (Wich et al. 2012).

#### *Protected areas (PAs)*

The gazettement of natural habitats into national parks; nature and wildlife sanctuaries; game and virgin jungle reserves; protection forests, and recreational parks prohibits logging and degradation of PAs (Wich et al. 2012). However, in reality, deforestation occurs in a large proportion of PAs on Borneo (Nellemann et al. 2007; Gaveau et al. 2013).

## Results

Taken at the specific level, *P. rubicunda* was distributed across the largest range of the *Presbytis* monkeys found on Borneo (>278,000 km<sup>2</sup>; Fig. 2), followed by *P. frontata* (>160,000 km<sup>2</sup>) and *P. hosei* (~130,000 km<sup>2</sup>). *Presbytis chrysomelas* had the most restricted distribution (~21,000 km<sup>2</sup>). *Presbytis rubicunda carinatae*, found only on the adjacent island of Karimata, had the smallest distribution at the subspecific level (130 km<sup>2</sup>). Of the mainland



**Fig. 1** Forest cover remaining on Borneo in 2010 (Miettinen et al. 2011) and the current land-use allocations, including Protected Areas (PA); Industrial Tree Plantations (ITP); Industrial Oil Palm Plantations (IOPP), and Logging Concessions (Wich et al. 2012)

subspecies, *P. chrysomelas cruciger* and *P. hosei hosei* occupied the smallest area (3,780 and 5,790 km<sup>2</sup>, respectively; Fig. 3). *Presbytis r. rubicunda* (>98,000 km<sup>2</sup>), *P. r. rubida* (>92,000 km<sup>2</sup>) and *P. r. ignita* (~66,000 km<sup>2</sup>) had the largest distributions (Table 2; Fig. 3).

Each of the 12 subspecies lost natural habitat through forest conversions between 2000 and 2010 (range 4.6–53.7 %) with the exception of *P. r. carimateae*, whose range is entirely gazetted as a PA (Table 2; Fig. 4). A third of the subspecies lost over 10 % of their natural habitat over the 10 year period. *Presbytis chrysomelas cruciger* experienced the highest rate of habitat loss (>50 %) habitat since 2000. The subspecies located in Sabah (*P. r. chrysea*, *P. h. sabana*) also lost substantial proportions of forested habitat in the 10 year period (21.1 % and 22.8 %, respectively; Table 2).

For most subspecies, logging concessions represented the largest allocation of land-use throughout distributions, followed by PAs (Table 2). Unallocated land accounted for >10 % of all allocations in 10 subspecies, and in the case of *P. h. hosei* as much as 50 % of land within its distribution was unallocated. For the majority of subspecies, ITPs were a minor allocation throughout distributions. In Central Kalimantan and Sarawak, IOPPs also comprised a substantial proportion of land use, but were not assessable for Sabah (Table 2).

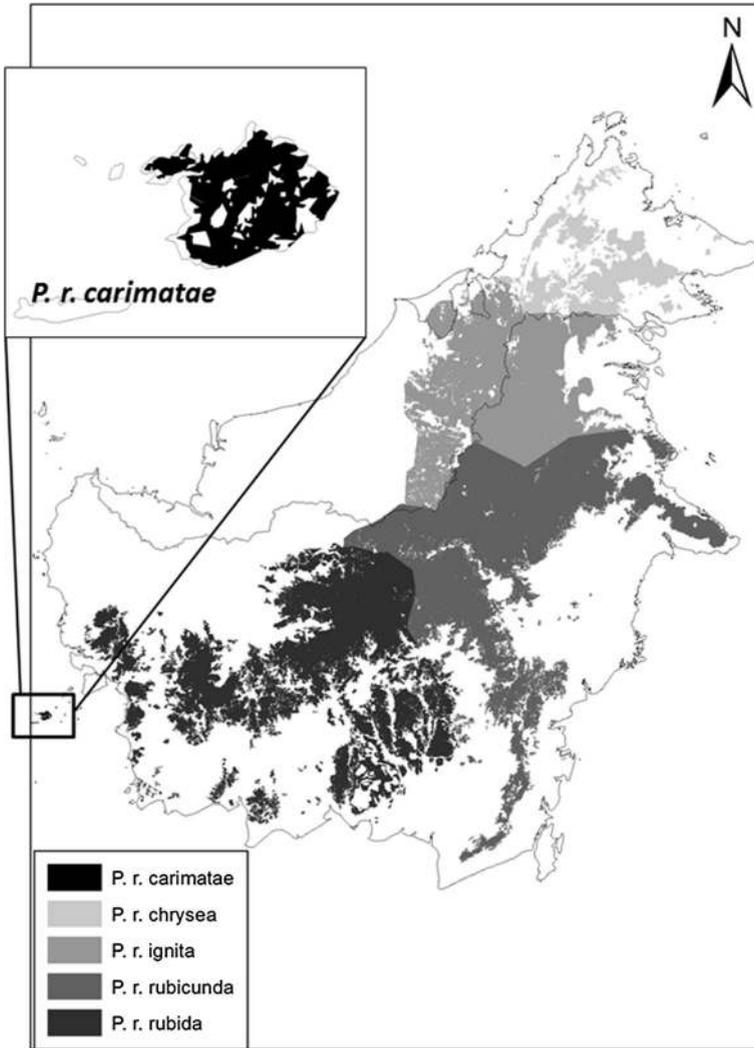
The overall distributions of *P. rubicunda* under 700 m asl were substantially lower in most cases, resulting in a general increase in the proportion of economic land-use allocations within distributions, and a complete decrease across all subspecies in PAs (with the exception of *P. r. carimateae*, for whom the entire distribution is protected), as much of the

**Table 2** The area of occupancy of all *Presbytis* spp. on Borneo as derived from land cover maps from 2000 and 2010 (Miettinen et al. 2011), and the current proportions of land-use allocations on 2010 distributions (Wich et al. 2012)

Species	Area of occupancy 2000	Area of occupancy 2010	Occupancy reduction (%)	Current IOPP concessions	Current ITP concessions	Current logging concessions	Current PAs (%)	Unallocated land
<i>P. c. chrysomelas</i>	18,860	17,190	8.9	1,540 (9.0 %)	190 (1.1 %)	3,630 (21.1 %)	6,890 (40.1)	4,940 (28.7 %)
<i>P. c. cruciger</i>	8,160	3,780	53.7	1,030 (27.3 %)	100 (2.7 %)	470 (12.4 %)	1,050 (27.7)	1,130 (29.9 %)
<i>P. chrysomelas</i>	27,020	20,970	22.4	2,570 (12.2 %)	290 (1.4 %)	4,100 (19.6 %)	7,940 (37.9)	6,070 (28.9 %)
<i>P. frontata</i>	171,220	160,280	6.4	5,310 (3.3 %)	8,570 (5.4 %)	59,880 (37.3 %)	55,250 (34.5)	31,270 (19.5 %)
<i>P. h. canicrus</i> MIN	8,600	7,200	16.3	490 (6.8 %)	400 (5.6 %)	3,680 (51.1 %)	1,100 (15.3)	1,530 (21.2 %)
<i>P. h. canicrus</i> MAX	12,710	11,340	11.8	580 (5.1 %)	800 (7.1 %)	6,120 (54.0 %)	1,760 (15.5)	2,080 (18.3 %)
<i>P. h. everetti</i>	59,340	55,570	6.4	2,480 (4.4 %)	6,000 (10.8 %)	23,010 (41.4 %)	16,490 (29.7)	7,590 (13.7 %)
<i>P. h. hosei</i>	6,240	5,790	7.2	230 (4.0 %)	710 (12.3 %)	460 (7.9 %)	1,450 (25.0)	2,940 (50.8 %)
<i>P. h. sabana</i>	28,380	21,920	22.8	830 (3.8 %)	1,770 (8.1 %)	13,250 (60.5 %)	4,100 (18.7)	1,970 (8.9 %)
<i>P. hosei</i>	142,760	129,820	9.1	5,500 (4.3 %)	9,410 (7.2 %)	55,810 (43.0 %)	36,970 (28.5)	22,130 (17 %)
<i>P. r. carinatae</i>	90	130	0	0	0	0	130 (100)	0
<i>P.r. chrysea</i>	26,710	21,080	21.1	N/A	1,770 (8.4 %)	13,530 (64.2 %)	3,660 (17.4)	2,100 (9.9 %)
<i>P. r. ignita</i>	69,150	65,980	4.6	2,780 (4.3 %)	6,080 (9.2 %)	22,460 (34.0 %)	20,340 (30.8)	14,320 (21.7 %)
<i>P. r. rubicunda</i>	106,580	98,980	7.1	4,130 (4.2 %)	2,120 (2.1 %)	40,410 (40.8 %)	32,440 (32.8)	19,880 (20.1 %)
<i>P. r. rubida</i>	105,710	92,210	12.8	11,980 (13.0 %)	4,200 (4.6 %)	26,510 (28.7 %)	26,570 (28.8)	22,950 (24.9 %)
<i>P. rubicunda</i>	308,240	278,380	9.7	18,890 (6.8 %)	14,170 (5.1 %)	102,910 (36.9 %)	83,140 (29.9)	59,270 (21.3 %)

N. B. The total figures for *P. hosei* include the area of occupancy ascribed to the unconfirmed species (Fig. 3)

Numbers in bold refer to the percentage of respective land-use policy on the total distribution



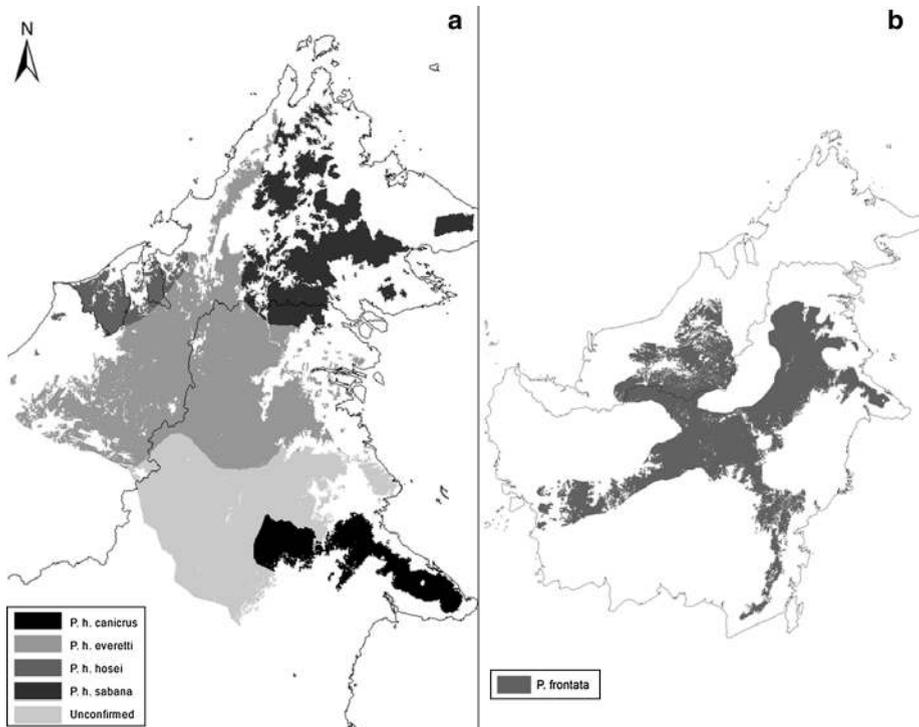
**Fig. 2** Distribution of all *Presbytis rubicunda* subspecies

PA network spans the central mountainous region (Table 3; Fig. 1). The maximum scenario for modelling the distribution of *P. h. canicrus* increased the area by  $\sim 4,000 \text{ km}^2$ .

## Discussion

### Distribution model caveats

The distributional modelling presented here represented a consensus of the known locality data and environmental and habitat requirements of the *Presbytis* monkeys on Borneo, and is the most comprehensive description of their distributions to date. Given the lack of locality data and the under-studied nature of the subject species, it is likely that both



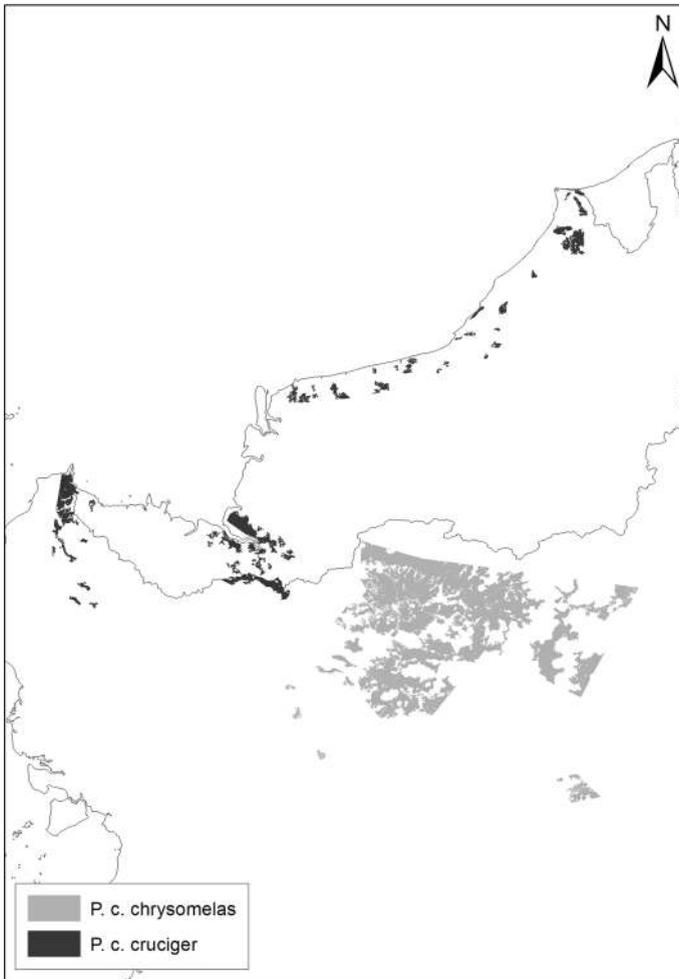
**Fig. 3** Distribution of (a) all *Presbytis hosei* subspecies including an unconfirmed subspecies between the known ranges of *P. hosei everetti* and *P. hosei canicrus*, based on the maximum scenario (Brandon-Jones 1997) and (b) Distribution of *P. frontata*

commission and omission errors featured in the model (Rondinini et al. 2006). Commission errors may have occurred within areas of occupancy that have not been surveyed, despite the removal of habitat known to be unsuitable. For example, large Bornean mammals exhibit irregular distributional patterns with large gaps in apparently suitable habitats, as a result of mutual exclusion through intra-genus competition and hunting pressures (Meijaard et al. 2005). Similarly, it is possible omission errors occurred in unsurveyed regions that lie beyond species' known geographical boundaries. However, given their understudied nature and the rapid habitat destruction occurring throughout their ranges, such an assessment of the anthropogenic threats facing Bornean *Presbytis* monkeys is urgently required and potential errors in the modelling process may be justified to this end.

#### Land-use impacts on the distribution of Bornean *Presbytis* monkeys

Oil palm plantations and ITPs have replaced vast tracts of lowland forest and fragmented remnant forest blocks (Carlson et al. 2012). Given their arboreal nature (Davies and Oates 1994), *Presbytis* monkeys cannot persist in deforested and converted habitats, and are unlikely to be able to cross denuded patches to disperse. Thus, land conversions for agricultural expansion likely pose the largest threat to the persistence of *Presbytis* monkeys.

As clear-felling within logging concessions is prohibited, it is possible that with effective management, concessions can contribute to species' persistence and appear to be



**Fig. 4** Distribution of all *Presbytis chrysomelas* subspecies

as successful as PAs in preventing total forest clearance (Putz et al. 2012; Wich et al. 2012; Gaveau et al. 2013). However, the actual response of Bornean *Presbytis* monkeys to the effects of logging within concessions is largely uncertain. For example, *P. rubicunda* has been variously reported as “neutral” (Bennett and Dahaban 1995) and intolerant to logging (Meijaard et al. 2008), with declines in population density as a result (Johns 1992; Blouch 1997). The tallest trees with the largest DBHs, which are targeted for selective logging practices, are important within the ecology of *P. rubicunda* and are used for feeding (Ehlers Smith et al. 2013a), predator avoidance (Nijman and Nekaris 2012) and sleeping sites (DA Ehlers Smith, unpublished data).

Johns and Skorupa (1987) predicted that a primate species’ ability to persist in disturbed habitats increases with its degree of folivory, although the most important factor in resistance to disturbance appears to be the ability to exploit leaves when, as a result of logging activities, fruits are scarce (Johns 1986; Meijaard et al. 2005). In this way, *Presbytis* monkeys have an

**Table 3** Viable area of occupancies and land-use allocations within distributions of *Presbytis rubicunda* ssp. below 700 m asl

	Area km <sup>2</sup> <700 m asl <sup>a</sup> (%)	Current IOPP concessions	Current IPT concessions (%)	Current logging concessions (%)	Current PAs (%)	Unallocated land (%)
<i>P. r. chrysea</i>	15,360 (72.7)	N/A	1,220 (7.9)	10,560 (68.8)	2,170 (14.1)	1,390 (9.1)
<i>P. r. ignita</i>	41,080 (62.3)	2,720 (6.6 %)	4,180 (10.2)	17,380 (42.3)	7,560 (18.4)	9,240 (22.5)
<i>P. r. rubicunda</i>	74,890 (75.7)	3,900 (5.2 %)	2,110 (2.8)	36,560 (48.8)	16,830 (22.5)	15,490 (20.7)
<i>P. r. rubida</i>	86,540 (93.9)	11,980 (13.8 %)	4,200 (4.9)	25,990 (30.0)	21,640 (25.0)	22,730 (26.3)

<sup>a</sup> Viable area of occupancy presented as a percentage of the maximum area of occupancy

Numbers in bold refer to the percentage of respective land-use policy on the total distribution

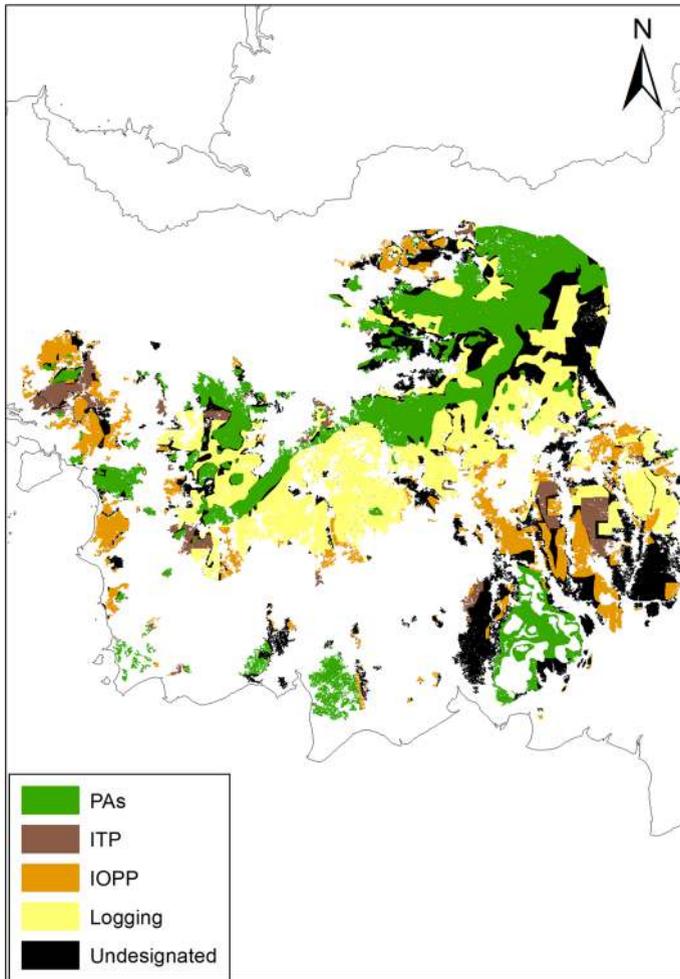
adaptive advantage. However, infant mortality due to starvation, lactational stress and abandonment often follows logging practices (Meijaard et al. 2005). Indeed, population density of *P. h. canicrus* appears to decline after logging events (Nijman 2000), with a possible time-lag between the onset of logging and population declines (Howell 2003). Meijaard et al. (2005) also noted that logging often results in an increase in hunting, which has a dramatic effect on *P. hosei* populations in Borneo's interior where traditional hunting practices persist (Nijman 2005). No data exist for the responses of *P. frontata* and *P. chrysomelas* to logging, but Meijaard et al. (2005) concluded that *Presbytis* ssp. would benefit from a more wildlife conscientious concession management policy (Fig. 5).

The long-term viability of habitats may be more secure if designated as PAs, as they are less likely to be de-gazetted than other land-use allocations (Wich et al. 2012; Gaveau et al. 2013). However, while current PA allocations also account for substantial areas within each distribution (28–38 %, Table 2), up to 80 % of all established PAs in Indonesia are degraded (Nellemann et al. 2007). Indeed, clearance of forests in PAs occurred at a similar rate as that in logging concessions (1.2 and 1.5 %, respectively) during the 10 year period (Gaveau et al. 2013), and severe logging occurs in as much as half of all PAs, in particular the Gunung Palung; Tanjung Puting; Danau Sentarum, and Kutai National Parks (Curran et al. 2004; Ministry of Forestry 2006). While PAs in Malaysia appear to be subject to lower rates of degradation and deforestation, they are subject to small-scale deforestation across the region where insufficient management resources are available (Wich et al. 2012).

While not a land-use policy *per se*, it is also worth discussing the detrimental effect that hunting has on *Presbytis* monkeys, as all species on Borneo are hunted for their meat and bezoar stones (visceral excretions of high economic value, used in traditional Asian medicines). For example, Nijman (2005) documented declines of up to 80 % in *P. hosei* in the Kayan Mentarang National Park following hunting for bezoar stones, and highlighted that although the protected forest remained in pristine condition, a lack of protection enforcement can result in drastic declines. Such hunting pressures can have profound influences on species' distributions, with local extinctions occurring within even remote and protected environments (Meijaard et al. 2005).

### Conservation implications

At the species level, each of the four endemic *Presbytis* monkeys lost substantial areas of natural habitat over the 10 year period between 2000 and 2010. Given the current land-use



**Fig. 5** An example of the land-use allocations across the distribution of *P. rubicunda rubida*

allocations, this trend will continue into the future. Indeed, if all economic allocations are exploited, between 45 and 65 % of remaining habitat will be under concession, and a minimum of 10 % will be destroyed outright (Table 2; Fig. 1).

*Presbytis frontata*, as a monotypic species with a broad distribution across the centre of the island where the largest concentration of PAs are situated, experienced the smallest habitat reduction in the 10 year period, and is the least affected by IOPPs (given the requirements of low elevation and slope for oil palm cultivation [Wakker 2004]). However, logging concessions accounted for over one-third of its remnant habitat (Table 2). At the subspecific level, only the habitat size of *P. r. carimatae* maintained stasis, suggesting efficient management of the PA of Karimata Island is in operation. However, populations of *P. r. carimatae* have not been conducted in 20 years (Yanuar et al. 1993) and the subspecies is considered data deficient on the IUCN Threat List (Nijman et al. 2008a), suggesting a resurvey should be considered a priority. Similarly, the uncertainty surrounding the area of occupancy of *P. h.*

*canicus* is impetus for further surveys to establish the subspecies' distribution patterns. The minimum modelling scenario predicts an area of occupancy of 7,200 km<sup>2</sup>, while the maximum predicts 11,300 km<sup>2</sup>, which would increase if the unconfirmed species that occupies the area toward the northern border with *P. h. everetti* is in fact *P. h. canicus*. Indeed, the subspecies occurs in the south-eastern portions of one of the largest, unfragmented forest-blocks remaining on Borneo (>55,000 km<sup>2</sup>) with few major geographic boundaries.

The largest habitat declines occurred in the subspecies with the most restricted distributions, particularly those in Sabah (Table 2). The most extreme case of distribution reduction occurred in the critically endangered *P. c. cruciger*, which lost over 50 % of its habitat in 10 years, while *Presbytis hosei sabana* and *P. r. chrysea* each lost over 20 % of their habitat in the same period, suggesting rapid population declines. Current economic land allocations are likely to have a particularly strong negative impact on the already threatened habitat of the critically endangered *P. c. chrysea*, as a further 30 % is due to be converted for OIPP and TIPs. Likewise, the huge logging concession allocations within the distributions of *P. h. sabana* and *P. r. chrysea* (60–65 % of total distributions; Table 2) may have negative impacts on their restricted populations (Meijaard et al. 2005; Howell 2003). Data for IOPPs in Sabah are unavailable, but given the large percentages of IOPP allocations in Sarawak (Table 2) and the large reduction in habitat over the last 10 years that has occurred in the Sabahan *Presbytis* subspecies, it is not unreasonable to assume that habitat conversion for current IOPPs is likely to be high, to the detriment of *P. h. sabana* and *P. r. chrysea* populations.

The current PA network accounts for over 20 % of subspecies' distributions in all but those that occur in Sabah. However, data show that the majority of PAs are too degraded and under-resourced to provide effective protection (Nellemann et al. 2007; Gaveau et al. 2013). Furthermore, the location of the majority of PA allocations is concentrated in the highlands, where in some cases, population densities are lower (*P. rubicunda*) or distributions do not occur (*P. chrysomelas*; Figs. 1, 2 and 4). These findings are consistent with the conclusions of Wich et al. (2012) that the current PA network is not optimally located and thus is likely insufficient for the long-term persistence of Bornean *Presbytis* monkeys.

Instead, huge proportions of each subspecies' distributions are currently not designated for economic allocation (Table 2). While the gazetting of these areas would, of course, increase the PA network (for example, ~30 % of the remnant 3,800 km<sup>2</sup> of habitat for *P. c. chrysea* is unallocated; if gazetted, the PA network of this critically endangered primate would increase to approximately 58 %), this does not guarantee species protection and persistence, due to the ineffective way PAs are currently managed (Nellemann et al. 2007). It is, in fact, possible that increasing the number of PAs within an already insufficiently funded PA network may be diluting, counterproductive and ultimately detrimental to species conservation. However, it is particularly clear that urgent action is required for the critically endangered species; the designation of a small PA on the unallocated lands to safeguard their persistence is likely to be more beneficial than no action at all. While logging concessions are better able to generate revenue than PAs, and appear at least as effective in preventing forest loss (Gaveau et al. 2013), the actual effects of logging on *Presbytis* populations living within concessions remain unclear, and may well have a negative effect (Nijman 2000; Howell 2003; Meijaard et al. 2005, 2008).

## Conclusions and recommendations

The threat to Borneo's endemic *Presbytis* monkeys through habitat destruction, disturbance and degradation is severe and sustained, and the trend is set to continue given current

land-use allocations (Wich et al. 2012). Between 2000 and 2010, the *Presbytis* subspecies of Borneo experienced a mean 12.7 % (N = 12; mean of each value for both scenarios of *P. h. canicrus* contributes to grand mean) habitat reduction, and 12.5 % of all habitats were allocated for conversion to IOPP and ITPs. While the current protected area networks encompassed an average 33.4 % of distributions, the majority of PAs are degraded and threatened by logging and mining operations (Nellemann et al. 2007). I therefore recommend priority gazetting of unallocated lands to PAs within the distribution of critically endangered *Presbytis chrysomelas* and *P. h. sabana*, which have experienced the highest forest loss in the last 10 years (22–50 %). Logging concessions, which may have detrimental effects to *Presbytis* monkey populations (Meijaard et al. 2005), accounted for a mean 26.3 % across distributions but appear to be at least as effective in maintaining forest cover as PAs (Gaveau et al. 2013). I therefore recommend an urgent assessment of the effects of logging practices on species' persistence, as concessions have an economic advantage for effective management over PAs. I further recommend population surveys to quantify the populations of the critically endangered *P. c. chrysea* and the data deficient *P. r. carinatae* and *P. r. chrysea*, and further surveys to establish the distributional boundaries of *P. h. canicrus* and *P. h. everetti*.

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## **Appendix 5**

**Ehlers Smith DA** (2014b). Preliminary evidence for the hired guns hypothesis and indirect mate defense in a wild group of red langurs (*Presbytis rubicunda*) in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesian Borneo. *Asian Primates Journal* 4 (2): 2–16.

# PRELIMINARY EVIDENCE FOR THE HIRED GUNS HYPOTHESIS AND INDIRECT MATE DEFENCE IN A WILD GROUP OF MAROON LANGURS *Presbytis rubicunda* (MÜLLER, 1838) IN SABANGAU TROPICAL PEAT-SWAMP FOREST, CENTRAL KALIMANTAN, INDONESIA BORNEO

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## ABSTRACT

Group-living primates enjoy numerous benefits, including effective resource defence from conspecifics in other groups. Resource contest often results in intergroup aggression, for which several hypotheses exist to explain its function: direct mate defence; direct food-resource defence; indirect food defence via 'hired guns'; mate attraction via infanticide, and indirect mate defence via male resource defence. I studied a focal group of Maroon Langurs *Presbytis rubicunda* in Sabangau tropical peat-swamp forest and examined the nature of intergroup aggression. Evidence supported direct mate defence in the majority of intergroup encounters. However, given that the resources in this frugivorous population may be defensible, and that most intergroup encounters occurred within their 'core range' of valuable resources, it is likely that the females in the group benefited from indirect resource defence as a result of aggression by the male as a 'hired gun'. The focal group was the subject of a takeover by an invading male. The post-takeover home range and core range overlapped pre-takeover ranges by 75% and 43% respectively and post-takeover, the group reused 47% of sleeping trees (N=14), suggesting that the invading male established himself in the territory of the resident females, who then continued to use the resources therein. The focal group also fulfilled three criteria proposed to predict indirect mate defence via male resource defence in colobine monkeys. Thus, it appears that indirect mate defence may have been employed by the invading male to obtain reproductive access to females. This study represents the first preliminary evidence for both indirect-resource-defence-via-hired-guns and indirect-mate-defence-via-resource-defence hypotheses in the genus *Presbytis*.

**Keywords:** aggression, colobinae, hired guns, intergroup encounters, mate defence, resource defence

## INTRODUCTION

Living in groups requires gregarious animals to coordinate their movements and make daily decisions regarding where, when and how to perform specific activities, incorporating the varying nutritional requirements and social and reproductive strategies of group members (Erhart & Overdorff, 1999; Conradt & Roper, 2005; Petit & Bon, 2010; Van Belle et al., 2013). Whatever differences in physiological and social needs, group-living primates receive numerous benefits, including increased vigilance and protection from predators, opportunities for social learning, and effective resource defence from conspecifics (Conradt & Roper, 2003; 2007).

Indeed, competition for resources can occur between individuals of different groups, and intergroup competition often results in aggression, which can influence both the behaviour and the social structure of primate groups (van Schaik & Janson, 2000), and have long-term consequences for individual fitness (Williams et al., 2004; Harris, 2010). However, resource competition does not adequately describe all aggressive intergroup encounters (IGEs); indeed, several hypotheses exist to explain the function of intergroup aggression by examining their nature and participants. The 'direct food-resource defence' hypothesis predicts that predominantly females cooperatively engage

in the aggressive defence of food resources within their territory (Wrangham, 1980), as female reproductive fitness is limited by access to food (Trivers, 1972). Alternatively, males can engage in 'direct mate defence', as male reproductive fitness is determined by access to females (Trivers, 1972; Wrangham, 1980). In this scenario, resident males aggressively repel invading males' attempts at mating, or 'herd' females away from invading males, forcing them to stay in the center of the group and preventing them from transferring to other groups (Davies, 1987; Stanford, 1991; Steenbeck, 1999). Direct mate defence potentially serves a second function of 'indirect food resource defence' for adult females and their offspring, as by repelling extra-group individuals, males are acting as 'hired guns' and securing food resources for other members of their group and themselves (Rubenstein, 1986; Wrangham & Rubenstein, 1986). In an additional strategy, an invading male may attempt "mate attraction via infanticide" by killing the offspring of female(s) he is trying to attract, to show the weakness of the father in his inability to protect his young, and also to rapidly gain reproductive access to females by terminating lactational amenorrhea (Hrdy, 1977; van Schaik, 1996; Steenbeck, 1999). Finally, males can also engage in 'indirect mate defence via male resource defence', by defending resources for a group of females in return for reproductive access, either by taking over a group of adult females and defending the resources from extra-group individuals within their range, or by defending a resource patch and attempting to attract females (resource defence polygyny; Emlen & Oring, 1977; Fashing, 2001).

Evaluating the validity of these explanations is problematic, however, as each hypothesis is not necessarily mutually exclusive (Rubenstein, 1986; Fashing, 2001). Male participation in aggressive IGEs has been traditionally viewed as evidence for the mate defence hypothesis, and female participation as evidence for resource defence. More recently, however, studies have begun empirically testing patterns of male and female participation in IGEs, and the results suggest that the strategies adopted are highly complex (Fashing, 2001; Harris, 2010; Fashing, 2011). Intergroup aggression and group takeovers have been particularly well-documented in African colobine monkeys (e.g. Onderdonk, 2000; Fashing, 2001; Harris & Montfort, 2003; Sicotte & MacIntosh, 2004; Saj & Sicotte, 2005; Sicotte et al., 2007), and males appear to play an important role in food-resource defence, both directly (Fashing, 2001; Sicotte & MacIntosh, 2004), and indirectly, as hired guns, during direct mate defence (Fashing, 2001).

Aggression is particularly evident during group takeover, when a resident male is replaced by an invading male. Group takeover is one strategy used by adult male colobines to gain reproductive access to females (e.g. Rudran, 1973; Saj & Sicotte, 2005; Sicotte et al., 2007), as many colobine societies are structured into single-male multi-female groups (Fashing, 2011; Kirkpatrick, 2011). Takeovers regularly involve aggression between the invading and resident adult male (e.g. Davies, 1987; Saj & Sicotte, 2005), and infanticide of resident infants by the invading male can occur (Curtin & Dolhinow, 1979; Sterck, 1995; Borries, 1997; Borries et al., 1999; Onderdonk, 2000; Sicotte et al., 2007). In Asian colobine monkeys, typically only males interact and show aggression during IGEs (Steenbeck et al., 1999), often with threatening displays, chases and "loud calls" (Steenbeck et al., 1999; Wich & Sterck, 2010). Such behaviours are not dependent on the proximity of food resources (Steenbeck, 1999), and this is often viewed as evidence for the mate defence hypothesis rather than resource defence hypothesis (van Schaik et al., 1992; Reichard & Sommer, 1997). Indeed, being folivores, colobine food resources tend to be more abundant and evenly distributed than those of frugivorous primates, although there is evidence to suggest that not all folivores' food resources are abundant, evenly spread and of low quality (Koenig et al., 1998; Koenig, 2000; Grueter et al., 2009). However, the socioecological model generally assumes frugivores' food resources to be scarcer, more patchily distributed, and therefore more defensible than those of folivores, meaning that for colobine monkeys, resource defence may not play such a crucial role in intergroup aggression (Mitani & Rodman, 1979). They may instead defend 'core ranges' of frequent use that contain particularly valuable resources within their larger home range (Oates, 1977). Within Asian colobine socioecology, however, the application of both indirect mate defence, and indirect resource defence through the use of hired guns, remains largely untested.

A population of Maroon Langur *Presbytis rubicunda* (Müller, 1838) in Sabangau tropical peat-swamp forest, Central Kalimantan is extremely frugivorous, with >83% of its annual diet comprising fruit parts (>75% comprises seeds, thus making it granivorous) (Ehlers Smith et al., 2013). It has the longest day-ranges recorded in any "folivorous" primate in their pursuit of these fruits (mean 1,645 m/day; Ehlers Smith et al., 2013b). This offers the potential for investigating the effect on intergroup encounter strategy of a preference for a more nutritiously valuable (Harrison, 2009 at this site), scarce (Ehlers Smith et al., 2013b), and there-

fore potentially defensible dietary resource (Wrangham, 1980) than is typical in colobine ecology. Despite their heavy reliance on seeds, however, this group is apparently non-female bonded, as social interactions between individuals are virtually absent (Ehlers Smith et al., 2013b).

*Presbytis rubicunda* is an Asian colobine endemic to Borneo (Medway, 1970) and is socially organized into single adult male multi-female groups ranging from three to ten individuals (Supriatna et al., 1986; Ehlers Smith & Ehlers Smith, 2013). Extra-group males form all-male bands or range alone (Supriatna et al., 1986; Davies, 1987; Ehlers Smith & Ehlers Smith, 2013). Group takeover in *Presbytis rubicunda* has been previously described from Sepilok, Sabah. In this case, an invading male aggressively formed a new group with the two nulliparous females of an original group and used some 20% of the original group's territory, while the parous female and a small juvenile male stayed with the deposed adult male (Davies, 1987).

Here, I describe the nature of IGEs between a mixed-sex focal group of *P. rubicunda* and its neighbouring groups, and its subsequent takeover, in Sabangau tropical peat-swamp forest, Central Kalimantan. I aimed to examine the nature of the aggressive encounters and group takeover and the behaviour of both the new and remaining group members post-takeover, by testing the evidence for: direct mate defence; direct food-resource defence; indirect food resource defence via 'hired guns'; mate attraction via infanticide and indirect mate defence via male resource defence (Table 1). I predicted that:

1) If only direct mate defence occurred, only males should participate in intergroup aggression; male-male aggression should most likely be between a resident male and all-male bands/single male or incumbent males seeking to force females to transfer from one group to another, and the resident male should seek to protect the resident females and engage in herding behaviour to separate females and invading males; aggressive encounters would be just as likely to occur outside the 'core range' as inside (the core range is defined as the area in which the group spends >50% of its time (Ehlers Smith et al., 2013b), and is characterized by a high density of feeding trees (Ehlers Smith et al., 2013a) and sleeping trees).

2) If direct food-resource defence prevailed females should be more likely to participate in intergroup aggression; resident females should direct aggression to all invading group members, and aggressive encounters should be more likely to occur inside the core range.

3) If indirect resource defence via the 'hired guns' strategy occurred, resident males should participate in intergroup aggression toward extra-group males; females should avoid participation in the encounter; aggressive encounters should be more likely to occur within the core range.

4) If mate attraction via infanticide occurred, invading males should act aggressively toward resident females and attempt to kill their offspring; females with infants should attempt to avoid IGEs and behave defensively, and females would transfer to invading males that successfully achieved infanticide.

5) If indirect mate defence via male resource defence occurred, resident males should participate in intergroup aggression toward extra-group members; the male should defend resources within the territory for the benefit of the females to use.

## METHODS

### Study site and study subjects

The study was conducted as part of the Orangutan Tropical Peatland Project (OuTrop) – Center for the International Cooperation in Sustainable Management of Tropical Peatlands (CIMTROP) multi-disciplinary research project in the Natural Laboratory for the Study of Peat-swamp Forest. This is a 500 km<sup>2</sup> area within the Sabangau tropical peat-swamp forest, located between the Sabangau and Katingan rivers in Central Kalimantan, Indonesia (2°19'S and 113°54'E), and is contiguous with a larger landscape covering 8,750 km<sup>2</sup> of ombrogenous tropical peat-swamp forest between two major rivers. Detailed descriptions of the study site are published in Ehlers Smith & Ehlers Smith (2013).

The study subjects were a single, mixed-sex focal group of *P. rubicunda*, first identified in May 2010. Prior to October 2010, the group consisted of 8 individuals: 1 adult male, 3 adult females, 1 sub-adult male, and 3 very young infant males. In October 2010, the sub-adult male emigrated from the group. In July 2011, one of the adult females died and her juvenile offspring disappeared less than a month later. Thus, from July 2011 until the group was taken over by an invading male in May 2012, the group consisted of 5 individuals: the adult male, 2 adult females, and 2 juvenile males. Post-takeover, the group consisted of 3 individuals: the new invading male, and the 2 remaining adult females.

## Data collection

We habituated the focal study group, Group KB, between May and December 2010, to the stage where reliable feeding (Ehlers Smith et al., 2013a), ranging and behavioural data (Ehlers Smith et al., 2013b) could be recorded. From January 2011, we recorded instantaneous focal behavioural data every 5 minutes on a single adult female of the group (Altmann, 1974). We selected an adult female as the focal target before the beginning of the follow on the basis of ensuring an even balance between focal individuals and minimizing observer bias (Ehlers Smith et al., 2013a, b). This individual was then closely followed for the rest of the day. Focal females were readily identifiable by individual distinguishing characteristics of overall body sizes, nipple lengths and shape of tails (Ehlers Smith et al., 2013a). Using a team of two researchers, we recorded behavioural and ranging data including 1) primary behaviours (feeding, resting, traveling, social behaviours); 2) secondary behaviours (how the primary behaviour was achieved); 3) vocalizations including the loud call (a series of “kekekekeke” notes emitted by the adult male), alarm calls (a shorter burst of “keke-keke-keke” notes, emitted by the adult and sub-adult males, alarm “hiccups” (emitted by all members of the group, and “purr” (a contact call by the mother to her offspring); 4) height of focal animal in tree/bush by 5 m categories (1-5 m, 6-10 m etc.); 5) height of tree/bush by the same 5 m categories, and 6) a GPS location for each instantaneous behavioural sample, enumerated uniquely for each follow. We recorded continuous feeding data on the focal animal (Ehlers Smith et al., 2013a), for which we documented the species, food type and food item during all feeding bouts  $\geq 30$  seconds, and tagged, enumerated and obtained GPS locations of all feeding stems. We similarly tagged, enumerated and obtained GPS locations of all morning and evening sleeping-tree sites. Data collection was divided between the two researchers, with instantaneous behavioural and continuous feeding data recorded by the first researcher, and GPS locations and tree enumeration recorded by the second researcher.

Pre-takeover, we followed the group from morning sleeping-tree to evening sleeping-tree for 2-11 days each month from January 2011 until May 2012 with the exception of January and February 2012 when no data were collected (N=96 sleeping trees; mean=6.6 sleeping trees/month), for a total of 1070.9 hours (N=15 months; mean=71.4 $\pm$ SD 26.6 hour/month). Post-takeover, data collection occurred in all months between May 2012 and July 2013 with the exception of January, February and May 2013.

We followed the group from morning sleeping-tree to evening sleeping-tree for 1-11 days of those months (N=41 sleeping trees; mean=4.9 sleeping trees/month of data collection), for a total of 441.4 hours (N=11 months; mean=29.4 $\pm$ SD 30.5 hour/month of data collection).

## Data analysis

### *Intergroup encounter locations within home range and core range of Group KB*

I defined an intergroup encounter as an occurrence of 2 groups within 50 m of each other (Oates, 1977; Stanford, 1991). We obtained a GPS location at the onset of each intergroup encounter, and then at subsequent locations on the 5 minute instantaneous sample during encounters that lasted for longer than 5 minutes. I then converted these locations into ArcGIS shapefiles and overlaid them with the home range and core range of Group KB (90% and 50% volume contours, respectively, as determined using the Smooth Cross-Validation bandwidth estimator in kernel density estimates; Ehlers Smith et al., 2013b), to examine any patterns of interactions within these localities. Finally, I separated the locations involving encounters with known mixed-sex groups and all-male groups.

### *Post-takeover reuse of resources*

I calculated the home-range and core-range use by Group BD post-takeover using the Geospatial Modeling Environment suite v.0.7.1.0 and the Smooth-Cross Validation bandwidth (Beyer, 2012) to create a kernel density estimate of range utilization distribution, and selected 50% and 90% volume contours to represent the core range and home range, respectively (Ehlers Smith et al., 2013b). I then calculated the degree of overlap between the range-use by Group BD as a percentage of that used previously by Group KB (Ehlers Smith et al., 2013b).

To test for the defence of resources post-takeover, the home-range and core-range area, and suitable sleeping tree resources therein, should be reused. Sleeping-tree sites can be considered a defensible resource, as the abundance and selection of suitable sites can impact individuals' survival chances (Lutermann et al., 2010; Phoonjampa et al., 2010). Primates are often highly selective in their choices of sleeping-tree sites, as their locations and distributions can influence ranging patterns and foraging decisions (Spironello, 2001), and also offer protection against predators (Chapman, 1989). Individual trees are often reused if characteristics such as predator protection, structural safety and proximity to food resources are

desirable (Heymann, 1995; Reichard, 1998; Di Bitetti et al., 2000; Radespiel et al., 2003). To investigate sleeping site reuse post-takeover, I compiled a list of all sleeping tree tag numbers representing usage by both groups, and calculated the percentage of reuse by Group BD.

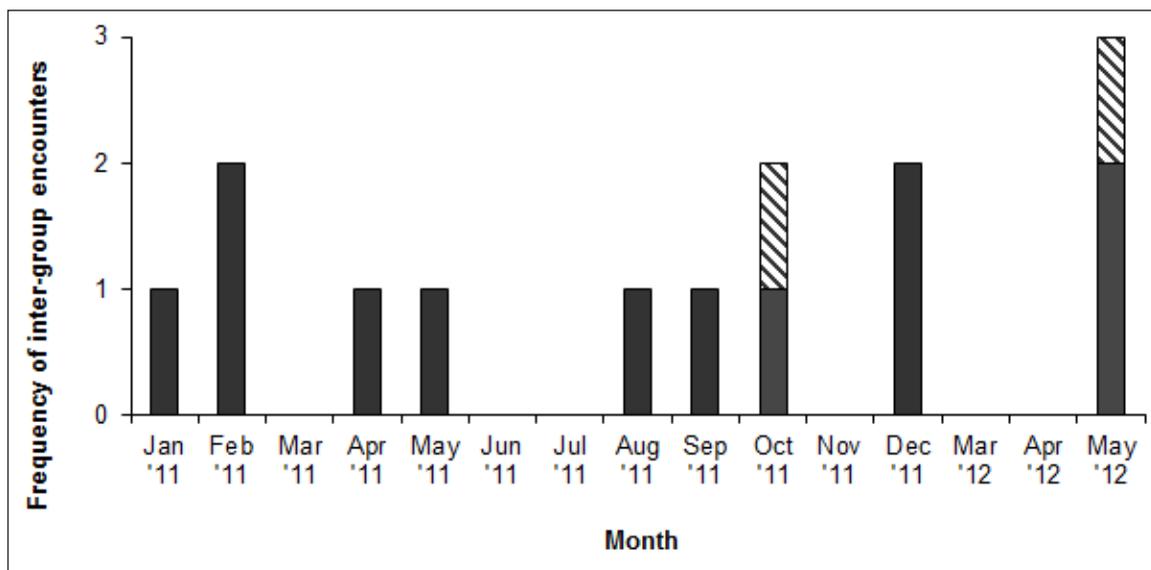
#### Location of feeding and sleeping tree sites

To analyze the locations of feeding and sleeping trees, I converted all GPS points of feeding and sleeping tree locations for Group KB into GIS shapefiles using the DNR GPS program v.6.0.0.11 (DNR, 2011) and projected all shapefiles into the UTM WGS\_1984 49S coordinate projection. I used the Geospatial Modeling Environment suite v.0.7.1.0 and the Smooth-Cross Validation bandwidth (Beyer, 2012) to create a kernel density estimate of the feeding tree utilization distribution, and selected a 50% volume contour to represent the feeding tree core-range. I then overlaid this core range with the focal group's total home- and core-range area, as determined previously through 90% and 50% volume contours (Ehlers Smith et al., 2013b), and calculated the percentage of overlap of these respective ranges. I also overlaid the sleeping tree sites with the core home- and feeding-ranges to calculate percentage of sleeping trees located within these localities.

## RESULTS

### Intergroup encounters between Group KB and other groups prior to takeover

A total of 13 IGEs were recorded between Group KB and other groups across 9 of the 15 months at a rate of 1 encounter per 82.4 observation hours Fig. 1 and Fig. 2a. Of these, 85% (N=11) were with neighbouring mixed-sex groups: 46% of encounters (N=5) occurred with Group GC to the east of Group KB's home range; 27% (N=3) occurred with Group GN to the west; 18% (N=2) occurred with Group TD to the south, and a single encounter occurred with Group TN, also to the south. Two encounters occurred with an all-male group consisting of two unknown adult males, deep within the western portion of the Group KB's core range Fig. 2a. In the first case, on 11 October 2011, Group KB had climbed into an evening sleeping tree and two unknown males approached from the west loud calling. No individuals of Group KB offered response and the two males retreated in the direction they had come. In the second case, on 10 May 2012, an adult male approached as Group KB were entering their evening sleeping tree in a similar location to the first case. The invading male was aggressively chased off by the resident male of Group KB, and no other member of the group responded.



Key: Solid=encounter with a mixed-sex group; Cross-hatch=encounter with an all-male group

**Fig. 1.** Frequency of intergroup encounters between Group KB and other groups of *Presbytis rubicunda* across the study period in Sabangau Tropical Peat-swamp Forest between January 2011 and May 2012.

### Aggression, herding and protective behaviours during IGEs

A total of 69% of encounters (N=9) involved aggressive chases by the adult males, and 85% of all encounters (N=11) involved loud calls. Only the adult males vocalized during IGEs. Two of these encounters lasted longer than 5 minutes across multiple locations: >20 minutes with Group GN and >15 minutes with Group TN (Fig. 2a). Both of these prolonged IGEs were aggressive, resulted in the retreat of the invading group, and occurred outside the core range.

Adult females were not recorded to instigate any aggressive chases, but were the recipients of aggressive chases from extra-group males in 23% (N=3) of encounters. 69% of all encounters occurred within the core range (N=9), and of these, 78% involved aggressive chases (N=7), and the invading groups retreated. 78% of encounters in the core-range were with mixed-sex groups (N=7), and of the two encounters with all-male groups within the core-range, one was aggressive (Fig. 2a).

Herding behaviour was not recorded during any intergroup encounter; however on 10 May 2012, herding behaviour was recorded prior to, but not during, an encounter with an unknown male. On 14 May 2012, the adult male was once again recorded herding Adult Female 1 and loud calling, but no physical contact was observed. No IGEs or other groups were recorded in proximity to the focal group on this day.

### Occurrence of adult male takeover

On 10 May 2012, we recorded the adult male of Group KB multiple times throughout the day approaching and running in a circular direction around both adult females of the group whilst loud calling. We recorded no physical contact but the females were positioned increasingly close to each other as the male ran around them, indicating a herding behaviour. Later that day, an unknown adult male approached Group KB, but was aggressively chased away by the resident adult male. After an encounter with Group TD on 15 May 2012, Group KB was no longer seen as a complete unit and the group was not encountered for the next four days. However, the composition of Group TD remained unchanged.

On 20 May 2012, we encountered and followed the two adult females travelling alone. Upon the next encounter with the adult females on 6 June 2012, a new, unhabituated adult male was seen travelling with the group. This new male was reluctant to approach

the research team but maintained proximity to the two adult females for most of the day. We subsequently followed this new group (named Group BD) over the following days, during which many loud calls were heard by both the new male and other males across the original territory of Group KB. Group BD now occupied the original territory and was using 8 of the established sleeping trees originally used by Group KB.

Between 27 and 29 May 2012, we encountered and followed the original adult male travelling with the two juvenile males of Group KB in the extreme south-east of their original territory and recorded a wound on the adult male's right leg. On 9 June 2012, we recorded new wounds across the lower right abdomen and right leg. By 14 June 2012, the youngest juvenile was no longer recorded with the adult male and elder juvenile. The deposed males were using only the south-eastern portion of their original home-range.

### Sleeping site selection

Group KB regularly revisited sleeping sites. We recorded 47 different individual trees used as sleeping sites over 96 follows that resulted in a sleeping tree. Nineteen sleeping trees were reused (40% reuse, range 2-9 revisits per tree). Group KB were highly selective in their choice of sleeping tree, using only 11 species of a total 200 that are available (~5%; S. Husson, unpublished data) (*Aglaiia rubiginosa* [Hiern] Pannell, *Calophyllum sclerophyllum* Vesque, *Combretocarpus rotundatus* [Miq.] Danser, *Dactylocladus stenostachys* Oliv., *Dipterocarpus borneensis* Slooten, *Dyera polyphylla* [Miq.] Steenis, *Koompassia malaccensis* Benth., *Nephelium lappaceum* L., *Palaquium leiocarpum* Boerl., *Shorea teysmanniana* Dyer ex Brandis, *Xylopia fusca* Maingay ex Hook.f. & Thomson; N=47 trees, mean height 21-25 m, range 16-30 m; mean DBH=56.6±SD 21.8 cm, range 27-96 cm).

Group BD similarly revisited their sleeping sites. We recorded 30 different individual trees used as sleeping sites over 41 follows that resulted in a sleeping tree. Seven sleeping trees were reused (23.3% reuse, range 2-6 revisits per tree). They selected 8 species for use as sleeping trees (some ~4% of those available; S Husson et al., unpublished data), including *Calophyllum sclerophyllum*, *Combretocarpus rotundatus*, *Dactylocladus stenostachys*, *Dipterocarpus borneensis*, *Koompassia malaccensis*, *Mezzettia parviflora* Becc, *Shorea teysmanniana*, and *Tetramerista glabra* Miq. (N=41 trees, mean height 21-25 m, range 21-30 m; mean DBH=54.1±SD 20.1 cm, range 28-83 cm).

As the focal individuals were solely adult females the sleeping tree reuse is reflected as such, with all adult females and their offspring using the same sleeping site. It is worth noting, however, that the adult male consistently slept separately, in trees located within 10 m of the group's sleeping site.

### Resource use, reuse and overlap

The total home range and core range of Group BD was 85.0 ha and 32.7 ha, respectively, and the total home range and core range of Group KB was 108 ha and 47 ha, respectively. The home range and core range of Group BD overlapped with that of Group KB by 75% and 43%, respectively (Fig. 2b). The core feeding-range used by Group KB constituted 36.6 ha, and overlapped with their core home-range by 79% (Fig. 3a). Of the 47 sleeping trees recorded in use by Group KB, 77% (N=36) were located within the core home-range, and 71% (N=32) occurred within the core feeding-range (Fig. 3b). Of 30 sleeping trees recorded in use by Group BD, 14 of them were also those of Group KB (47%).

## DISCUSSION

### Resource use

Post-takeover, Group BD maintained ~75% of Group KB's original home range and ~45% of their original core range (Fig. 2b); 47% of the sleeping tree resources were reused by Group BD. Sleeping site choice appeared to be highly selective in both groups, with only ~4-5% of species used as sleeping trees in comparison to the total species available (E. Husson et al., unpublished data). This is the first detailed description of sleeping site selection by *P. rubicunda*. Sleeping tree sites were selected within both the core feeding- and core home-range area in >70% of cases (Fig. 3b). Both their locations and percentage of reuse support the theory that sleeping sites are defensible resources that play an important role in primate ecology, by facilitating predator avoidance (Reichard, 1998; Radespiel et al., 2003) and maintaining proximity to food resources (Chapman, 1989; Li et al., 2013). It is also worth noting that no other groups were ever recorded using a sleeping tree established by the focal group.

All sleeping trees were representative of the tallest genera found in this habitat sub-class of Sabangau (Page et al., 1999; Morrogh-Bernard et al., 2003). Sabangau was subject to legal logging concession until the early 2000s (Page et al., 1999; Husson et al.,

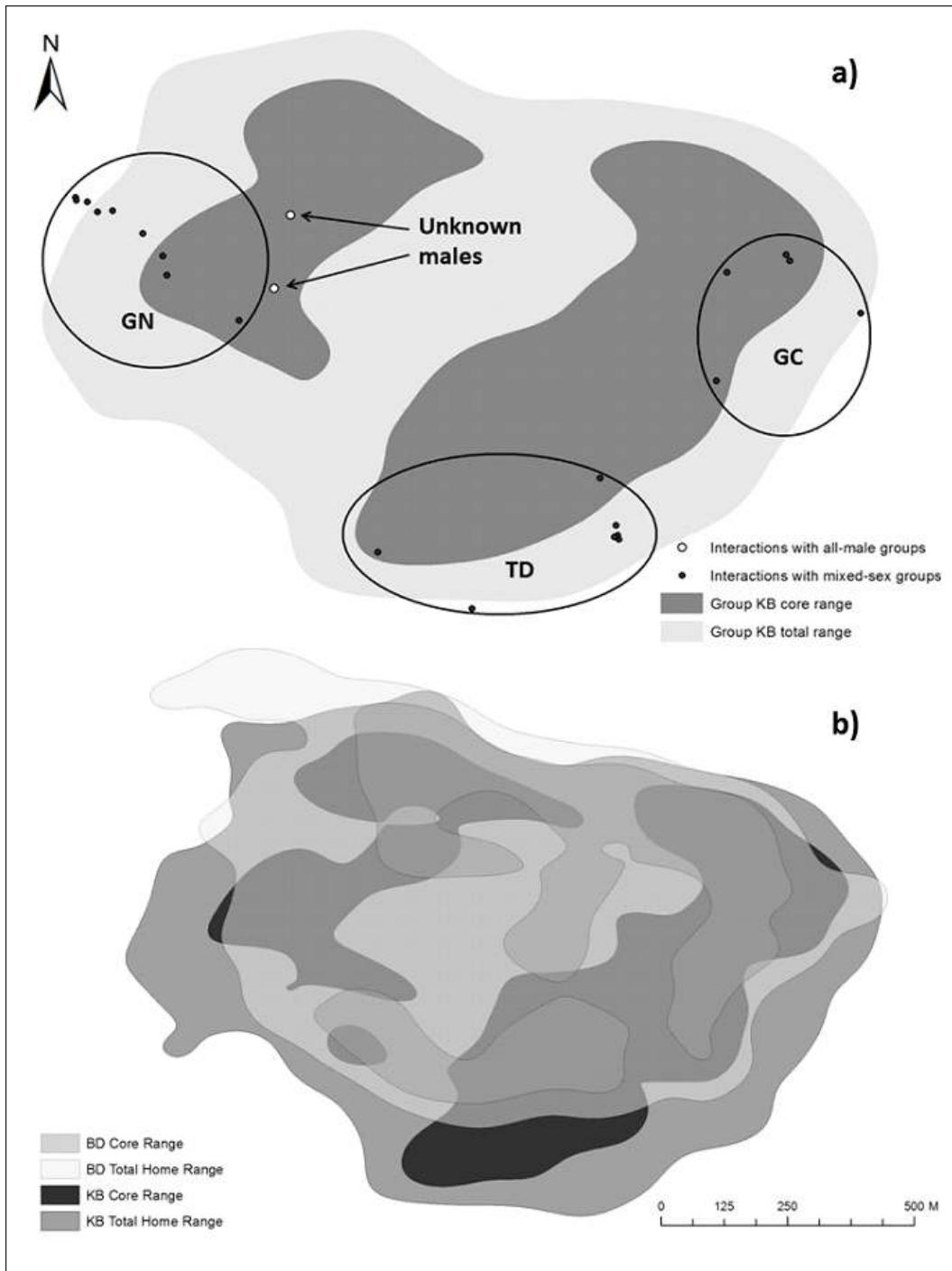
2002; Page et al., 2009), which targeted the largest and most economically valuable genera (e.g. *Shorea* spp., *Dipterocarpus* spp., Husson et al., 2002). Since legal concession ended, illegal loggers took over and were less discriminate in the species extracted, instead targeting all large trees regardless of genus (Page & Reiley, 2005). Consequently, suitable sleeping sites are less available, and therefore represent important resources to be defended at this site. This, in turn, has long-term conservation implications since the selection of sleeping sites can impact each individual's chances of survival and reproductive success (Lutermann et al., 2010; Phoonjampa et al., 2010).

### Intergroup encounters

Intergroup encounters were fairly evenly spread across the study period and involved mixed-sex groups in the majority of cases (Fig. 1). Adult males were the only aggressors, although adult females were occasionally the recipients of invading male aggression. The male-initiated aggression appears to affirm the first prediction that resident males would respond aggressively to invading males in the pursuit of direct mate defence. In the cases of invasions by single males or all-male bands, this prediction is particularly supported. Resident females were chased by invading males in several of the aggressive encounters, and in each case sought to avoid and flee the aggression. In most cases, the aggressive invading male held tenure of a mixed-sex group, which may have indicated an attempt to force the resident females to transfer groups. In each case, the resident male intervened to chase away the aggressor, and in at least one case, he appeared to herd his females before an aggressive encounter occurred. This provides further evidence for the first prediction that direct mate defence was the motivation behind the aggression.

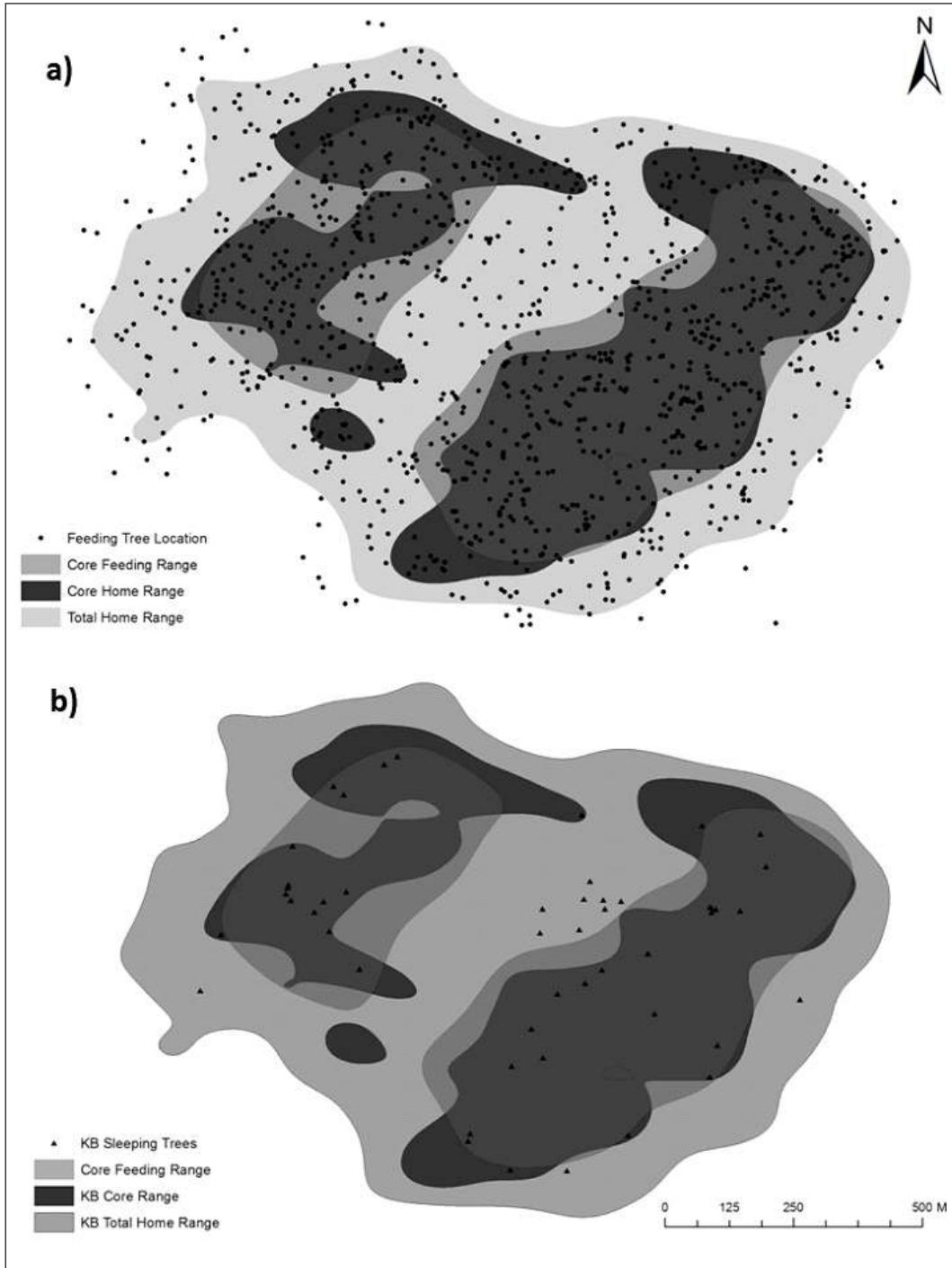
### Hired guns, resource reuse and indirect mate defence

One must be cautious when inferring evidence for hypotheses based on small sample sizes, such as those in this study. There is, however, the possibility for further explanation of the strategies employed, given that a) the main aggressors were males holding tenure over a mixed-sex group, and b) ~70% of aggressive encounters occurred in the core range of the focal group (Fig. 2a). Fruit is generally assumed to be more defensible than other food resources (Wrangham, 1980), and in the pursuit of fruit, which is rarer,



Note: the IGEs in the extreme top left (GN circle) and bottom right (TD circle) were respectively 20 minutes and 15 minutes in duration; thus multiple localities were recorded.

**Fig. 2.** Location of a) intergroup encounters between Group KB and surrounding groups of *Presbytis rubicunda* within the home range (90% density contour volumes) and core range (50% density contour volumes; Ehlers Smith 2013b) of Group KB between January 2011 and July 2012; and b) overlap of the core and total home-ranges of Group BD (light grey) and Group KB (dark grey) post-takeover between June 2012 and September 2013.



**Fig. 3.** Location of a) all feeding trees used by Group KB, core feeding-range (50% density contour volume) and overlap with core home-range; and b) all sleeping trees used by Group KB and overlap with core feeding- and home-ranges between January 2011 and May 2012 in Sabangau Tropical Peat-swamp Forest.

more patchily distributed and of high nutritional value, this population has the highest day-range length recorded in any folivorous primate (I refer here to the morphological adaptations of *P. rubicunda*, rather than the clearly granivorous nature of the study population; Ehlers Smith et al., 2013b). Evidence suggests that adult females lead group movements in their pursuit of nutrition (Salafsky, 1988; Stanford, 1990). Thus, females may have led their groups into the core range of Group KB to obtain high quality food resources, and incited aggressive IGEs between the resident and invading males. However, the second prediction that resource defence was the motivation behind aggression is not supported, as no females from either the resident or the invading groups participated in the aggression at any time. Instead, there is support for the third prediction that females may have benefitted from indirect resource defence, as males aggressively defended the females in their territory, and in turn, acted as hired guns in the defence of food resources in the core areas (Rubenstein, 1986). To the best of my knowledge, this represents the first preliminary evidence for this strategy in the genus *Presbytis*. Home-range data from the neighbouring groups, including the location and nature of IGEs, are unfortunately lacking here, but may further elucidate the context of encounter strategies and should be considered a priority for further research.

Again, with respect to caution when inferring support for a hypothesis based on a small sample size, there may also be preliminary evidence for the fifth prediction of indirect mate defence via male resource defence, as provided by the tenure change. After the successful deposit of the resident male of Group KB, the females transferred to the invading male, who then established tenure in the deposited male's territory and proceeded to defend ~75% of the original area and ~50% of the sleeping tree resources therein for the females to continue to reuse. Male-male aggression appeared to continue between the deposited and the invading adult male post-tenure change as new wounds were recorded in conjunction with a high frequency of loud calling for several days, indicating that tenure and territory had been aggressively established, and providing evidence for resource defence polygyny (Emlen & Oring, 1977). This formation of a group that contained the adult and juvenile males post-tenure-change is consistent with that reported in Sepilok, Sabah (Davies, 1987) where the deposited male maintained tenure of his parous females and his juvenile male offspring, and is likely a result of the independent status of the juveniles from their mothers.

Fashing (2001) presents a hypothesis to predict when male primates living in single-male multi-female groups are expected to employ the indirect mate defence strategy that describes 3 criteria: 1) "food must be limited and distributed in defensible patches (Wrangham, 1980; van Schaik, 1989); 2) groups must include relatively small numbers of females and/or females exhibiting oestrous asynchrony so that the females are virtually reproductively monopolizable; 3) females are expected to choose to mate with males that defend resources, and to transfer to other groups once the male in their group begins to defend resources poorly" (Fashing, 2001, 227-228). In the Sabangau population of *P. rubicunda*, each of these criteria are fulfilled, which strengthens the evidence found in the small sample size provided, and further supports the fifth hypothesis. Criterion 1 is fulfilled given that seeds and fruit parts constitute >80% of the annual diet (Ehlers Smith et al., 2013a) and that the focal group has the largest day range recorded in any 'folivorous' primate (mean 1,645 m per day; max 2,041 m per day), apparently in the pursuit of fruits (Ehlers Smith et al., 2013b). Criterion 2 is also fulfilled given females do not exceed 3 individuals per group (Ehlers Smith & Ehlers Smith, 2013) and females do not exhibit oestrous synchrony (DA Ehlers Smith, unpublished data). Evidence for criterion 3 is provided in the group takeover and transfer of the females to the invading male. Thus, this study also represents the first preliminary evidence of indirect mate defence via male resource defence in the genus *Presbytis* to the best of my knowledge.

## Conclusions

The evidence for direct mate defence as the motivation for aggressive IGEs was supported in the majority of cases. However, given that resources in this population may be defensible, and that most of the aggressive encounters occurred within the core range of the focal group, it is likely that the females of the group further benefitted from indirect resource defence as a result of the aggressive protection provided by the resident male as a hired gun. Post-takeover, the invading male established himself in the territory of the resident females, who then continued to use the resources therein. The study group fulfills the 3 criteria proposed by Fashing (2001) to predict indirect mate defence; thus, there is also preliminary evidence for indirect mate defence by the invading male in his pursuit of reproductive access to females. The findings of this study are consistent with the assertion that the hypotheses seeking to explain the nature of intergroup aggression in primates are not mutually exclusive.

**Table 1.** Overview of hypotheses to explain the nature of intergroup encounters, and evidence for the predictions in this study.

Hypothesis	Prediction	Evidence
1: Direct mate defence	Only males should participate in intergroup aggression; male-male aggression should most likely be between a resident male and all-male bands/single males; resident male should seek to protect the resident females, engage in herding behaviour; aggressive encounters just as likely to occur outside core range as inside	Yes - adult males were the only aggressors; aggression occurred between the resident group and all-male bands; apparent herding of females before aggressive encounter occurred but majority (~70%) of aggressive encounters occurred inside core range
2: Direct food defence	Females should be more likely to participate in intergroup aggression; resident females should direct aggression to all invading group members, and aggressive encounters should be more likely to occur inside the 'core range'	No
3: Indirect food defence via hired guns	Resident males should participate in intergroup aggression toward extra-group males; aggressive encounters should occur within the core range; no female participation	Yes - main aggressors were males holding tenure over a mixed-sex group; majority of the aggressive encounters occurred in core range of the focal group; no female participation in aggressive encounters
4: Mate attraction via infanticide	Invading males should act aggressively toward resident females and attempt to kill their offspring; females with infants should attempt to avoid IGEs and behave defensively, and females would transfer to invading males that successfully achieved infanticide	No
5: Indirect mate defence via male resource defence	Resident males should participate in intergroup aggression toward extra-group members; the male should defend resources within the territory for the benefit of the females to use	Yes - after deposal of the resident male, transference of females to invading male who established tenure in the deposed male's territory where reuse of resources occurred

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## **Appendix 6**

Bersecola E, **Ehlers Smith DA**, Sastramidjaja WJ, Rayadin Y, Cheyne SM (2014). Population density of *Presbytis rubicunda* in a small primary dipterocarp forest in East Kalimantan, Indonesian Borneo. *Asian Primates Journal* 4 (2): 16–26.

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## First Author Statement

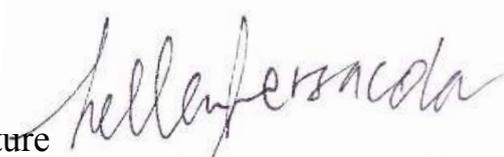
### Appendix 7

Bersacola E, **Ehlers Smith DA**, Sastramidjaja WJ, Rayadin Y, Cheyne SM (2014). Population density of *Presbytis rubicunda* in a small primary dipterocarp forest in East Kalimantan, Indonesian Borneo. *Asian Primates Journal* 4 (2): 16-26.

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I, Elena Bersacola, confirm that David Ehlers Smith made the stated contributions to this publication.

Signature



Elena Bersacola

Date 26 August 2014

# POPULATION DENSITY OF *Presbytis rubicunda* IN A SMALL PRIMARY DIPTEROCARP FOREST IN EAST KALIMANTAN, INDONESIAN BORNEO

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## ABSTRACT

Tropical rainforests on Borneo are rapidly shrinking due to human activities and related fires. Monitoring wildlife populations in their remaining habitats is crucial for developing effective conservation strategies. In 2012, we conducted surveys in Balikpapan Bay within the Sungai Wain forest, Indonesia, to estimate the population density of Maroon Langur *Presbytis rubicunda* (Müller, 1838). We surveyed Sungai Wain's primary core area using distance sampling of line transects, and assessed the vegetation structure using 100 m<sup>2</sup> square plots. We calculated density of *P. rubicunda* at 5.35 groups/km<sup>2</sup> (95% CI=3.4-8.43). Cluster size ranged between two and eight individuals and group size averaged 5.2 individuals (SE=1.4). The habitat within the core area of Sungai Wain appears suitable to support a high density of this colobine. Anthropogenic activities in the surrounding areas, as well as encroachment and illegal logging within the regenerating habitat, could become threats for *P. rubicunda* in Sungai Wain. This forest represents an important refuge for this primate in Balikpapan Bay. We recommend further surveys in degraded and regenerating forests to quantify the remaining suitable habitat for *P. rubicunda* in East Kalimantan.

**Keywords:** Colobinae, conservation, distance sampling, habitat, langur, refuge

## INTRODUCTION

Tropical rainforests in Southeast Asia have decreased massively since 1990 (Stibig et al., 2014). For example, between 2000 and 2010 the total forested area on Borneo decreased by 12% with a mean annual forest cover loss of 1.3% (Miettinen et al., 2011). Human activities such as logging, mining, habitat conversion for oil palm plantations, as well as an increase in magnitude of *El Niño* droughts and fires, are the driving causes of deforestation (Curran et al., 1999; Sodhi et al., 2004). Except for the Maroon Langur *Presbytis rubicunda* (Müller, 1838), all endemic primates of Borneo are considered threatened, and are classified as either Vulnerable, Endangered or Critically Endangered by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2013).

*Presbytis rubicunda* is believed to be widespread and may persist in degraded habitats; however, the population is decreasing due to habitat loss and hunting for medicine (Nijman & Meijaard, 2008). Densities of *P. rubicunda* in Kalimantan differ across habitats and study sites (Davies, 1984; McConkey & Chivers, 2004; Marshall, 2010; Nijman & Nekaris, 2012; Ehlers Smith & Ehlers Smith, 2013), but in disturbed habitats or at high elevations (>750 m) group densities of this species generally decrease and populations may not be viable (Blouch, 1997; Marshall, 2010).

In 2012, we conducted a survey in the Sungai Wain Protection Forest (SWPF), Indonesia. The SWPF is located within Balikpapan Bay, a large lowland ecosystem that extends to the Mahakam River, about 70 km

north of Sungai Wain (Wilson & Wilson, 1975; Stark et al., 2012). Part of the forest outside the SWPF was already selectively logged and encroached upon by humans in the 1970s (Wilson & Wilson, 1975), and was later affected by the *El Niño* fires in 1982-83 (Cleary & Genner, 2004). In 1998, subsequent fires were started at a nearby logging concession and quickly spread inside the SWPF (Fredriksson, 2002). The 1998 fires caused further change in the forest structure, reducing the primary habitat to a 40 km<sup>2</sup> core area. Most of the core area's surrounding habitat consisted of burned forest, with intact fragments along rivers (Fredriksson, 2002). It is likely that during and after the fires, primates and other animals relied on these intact fragments and the core area for refuge, thus altering their density and ranging patterns (S. Lhota, pers. comm.). Over the subsequent seven years following the 1998 fires, the vegetation structure and species composition of burned areas changed substantially (Fredriksson et al., 2006; Slik et al., 2011). Pioneer species such as *Macaranga gigantea* (Rchb.f. & Zoll.) Müll.Arg. dominated the landscape (Slik et al., 2008). Canopy cover and tree diversity began to increase in more recent years, and in 2010 there were indications that Malayan Sun Bears *Helarctos malayanus* (Raffles, 1821) were gradually moving back to the regenerating forest (Fredriksson et al., 2012).

According to the IUCN Red List of Threatened Species, the average density of *P. rubicunda* across Borneo is estimated to be 2.6 (SD  $\pm$  1.4) groups/km<sup>2</sup> (Nijman & Meijaard, 2008). No density estimate is available for *P. rubicunda* in the SWPF prior the 1998 fires; but surveys conducted there in 1999-2005 indicated a high density of this primate, with 3.3 groups/km<sup>2</sup> (Nijman & Nekaris, 2012). The aim of our study was to obtain a new population density estimate of *P. rubicunda* in the SWPF and identify possible conservation threats to the population present in the area. We also hope that our data help encourage local and national authorities to increase their efforts to protect the remaining forests of this region.

## METHODS

We acquired all the relevant permits and visas for the research from the Indonesian State Ministry of Research and Technology (RISTEK), adhering to Indonesian legislation. Our research was purely observational in nature. We collected data between May and July 2012.

## Study area

The SWPF (S1°16', E 116°54') occupies an area of approximately 100 km<sup>2</sup> (Fig. 1), and is located within the administrative area of Balikpapan, Kalimantan's second largest city and the second major oil production and commerce centre in Indonesia. The SWPF is categorised as *Hutan Lindung*, meaning that it does not have official protection but was established to be managed as a water catchment area for the oil company 'Pertamina' in Balikpapan. The SWPF is part of the Balikpapan Bay ecosystem, which consists of a network of freshwater rivers, marine waters, mangroves, dipterocarp as well as other non-mangrove forests (Stark et al., 2012). It is characterised by high biological diversity, and taxa present in Balikpapan Bay include Sunda Clouded Leopard *Neofelis diardi* (G. Cuvier, 1823), Proboscis Monkey *Nasalis larvatus* (Wurmb, 1787) and the Critically Endangered Mahakam River subpopulation of Irrawaddy Dolphin *Orcaella brevirostris* (Owen in Gray, 1866). Road construction, logging and the increase in magnitude of fires due to deforestation are major conservation threats in Balikpapan Bay, as animal populations and habitats are becoming increasingly fragmented. At present, the SWPF's core area is the largest lowland primary forest left in the south-eastern part of East Kalimantan (Fredriksson, 2002).

The study site (20 km<sup>2</sup>) lies within the northern part of the primary forest within the 40 km<sup>2</sup> core area. We used a system of thirteen parallel-line transects, which were already established prior to our study. The transects were set 70-600 m apart (average=286.8 m, SD=121.1) and were 1.70-2.06 km in length (Average=1.99 km, SD=0.11). The forest within the transect system was a mixture of humid and dry hilly dipterocarp forest, with occasional small swamp forest patches. The average annual rainfall in the SWPF is 2790 mm (Simbolon et al., 2012).

## Study species

*Presbytis rubicunda* is a medium-bodied, gracile arboreal colobine (males 6.3 kg, females 6.0 kg; Davies & Payne, 1982) endemic to the island of Borneo and the adjacent Karimata Island (Nijman & Meijaard, 2008). They live in single-male, multi-female groups ranging from 3 to 12 individuals (Supriatna et al., 1986; Davies, 1987; Ehlers Smith & Ehlers Smith, 2013), and extra-group males typically form all-male bands or travel alone (Davies, 1987; Ehlers Smith & Ehlers Smith, 2013). *Presbytis rubicunda* has been observed mainly feeding on fruits, seeds and young leaves, with the proportions of consumption of these items vary-

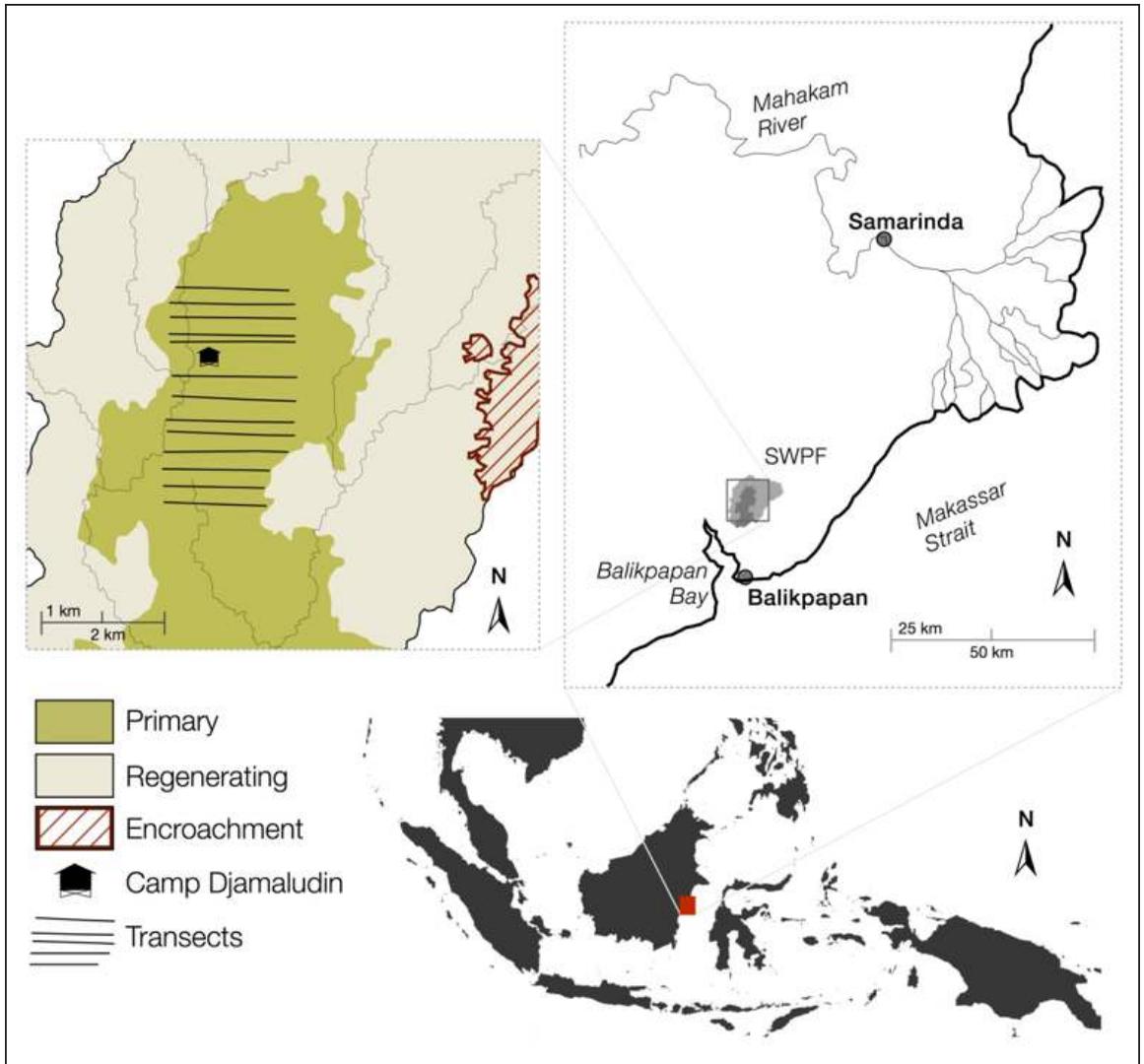


Fig. 1. Map and location of study site

ing across sites (Supriatna et al., 1986; Davies et al., 1988; Davies, 1991; Marshall, 2004; Hanya & Bernard, 2012; Ehlers Smith et al., 2013b). Home ranges of this species were reported at a number of sites, ranging from 0.33 ha in Tanjung Puting (Supriatna et al., 1986) to 108.3 ha in Sabangau Forest (Ehlers Smith et al., 2013a)

### Transect surveys

To monitor wild population trends over time and understand changes in ecological patterns, repeated surveys must be conducted using standardised methods. The importance of repetitive surveys using identical methods to identify a population trend is highlighted by previous studies (Mitani et al., 2000; Mbora & Meikle, 2004). Distance sampling is based on the

detection function  $g(y)$ , i.e., the statistical probability of seeing an object at a  $\geq 0$  m distance from the transect line (Buckland et al., 2001), and is considered an effective method for estimating and monitoring densities of various taxa, such as deer (Focardi et al., 2005), birds (Marques et al., 2007) and primates (Johnson et al., 2005; Ehlers Smith & Ehlers Smith, 2013). Analysis with the program DISTANCE (Thomas et al., 2010) enables users to choose different parameters to obtain a fit between the statistical model and the survey data.

We estimated population density of *P. rubicunda* using distance sampling on line transects (Buckland et al., 2001; Thomas et al., 2010). We walked thirteen parallel transects in two or three teams simultaneously, maintaining  $>750$  m distance between teams during all

surveys. All team members conducted prior practice surveys and one week of training on data collection with an established survey protocol. During surveys we measured distances visually, as the use of laser range finders could not provide us with true distances because of the dense structure of the forest. To ensure that distances were recorded precisely and to reduce researcher bias, we carried out distance training with the aid of a measuring tape and laser range finder every 4-5 days throughout the study period.

At each detection of *P. rubicunda* we collected the following data: group size, group spread, distance between the observer and the centre of the group, compass bearing of the centre of the group and the transect (later calculated to angle and then perpendicular distance), height above ground of observed animals, group composition and response behaviour to our presence. We recorded all data at the animals' initial location. As *P. rubicunda* is known to split into subgroups for foraging during the day (Supriatna et al., 1986), we considered all animals encountered within 100 m of the first detection as the same group, thus as a single sighting event. We walked two transects per team; one in the morning between 06:30 and 11:00

h and one in the afternoon between 13:30 and 18:00 h, at an average walking speed of ~1 km/h. We did not conduct surveys during midday hours, rainy days or strong wind as *P. rubicunda* becomes less active during these periods, thus reducing detectability (DA Ehlers Smith, pers. obs.). Where possible, we followed and observed the langurs until we could obtain full group counts. On 17 of such encounters we were able to observe groups gathering and remaining on emergent trees for approximately 20 minutes; thus were confident that all animals in the group were counted.

### Vegetation sampling

To measure habitat characteristics we established 73 plots, a sample size considered large enough to obtain a good representation of the habitat within the study site (Ganzhorn, 2003). Plots measured 10 m x 10 m, and were systematically located on both sides of transect lines at a minimum distance of 30 m from each other to ensure sampling independence. To assess vegetation structure we recorded the following data: diameter at breast height (DBH) of all the  $\geq 10$  cm DBH trees, height of all  $\geq 10$  DBH trees (measured on an ordinal scale: 1-5 m, 6-10 m, etc.) and total number of trees (Ganzhorn, 2003; Hamard et al., 2010).

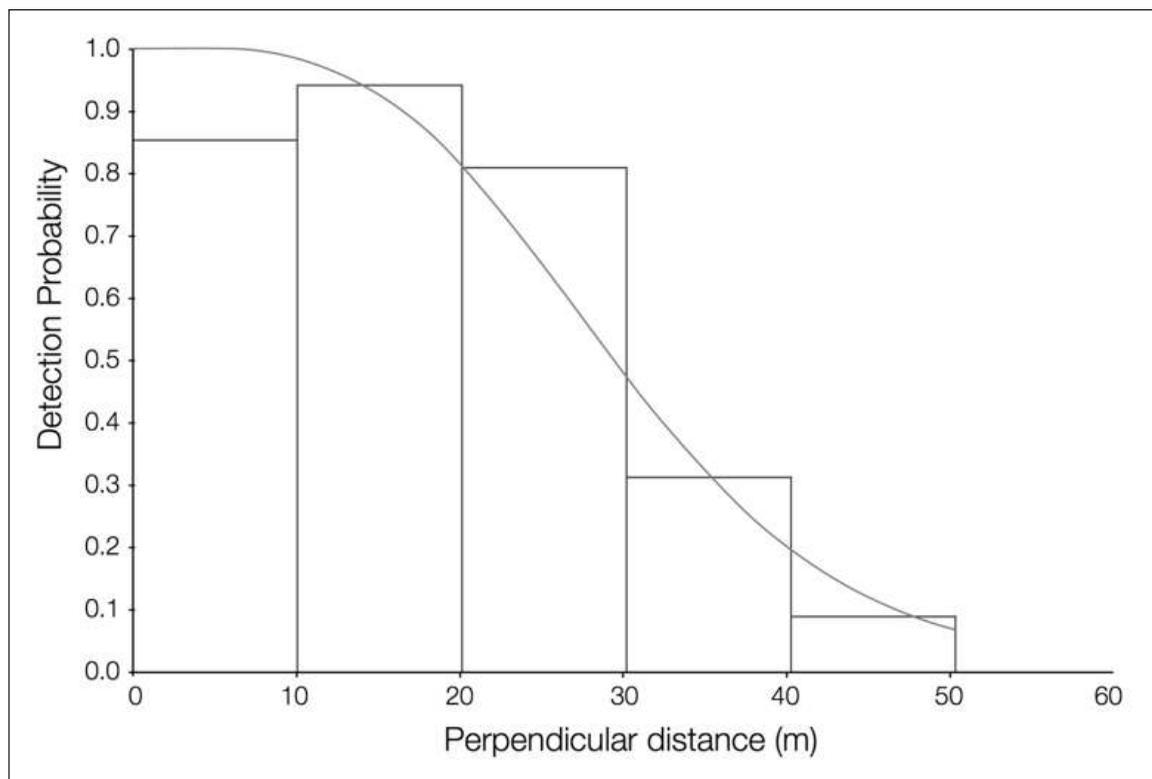


Fig. 2. Estimated detection function for *P. rubicunda* based on the best model computed in DISTANCE.

## Data analysis

We entered survey data into DISTANCE v. 6.0 (Thomas et al., 2010), and evaluated a number of models for selecting the one with the best fit. We analysed the survey data using three detection probability functions: uniform, half-normal and hazard rate, with and without cosine and simple polynomial adjustments. Upon a visual inspection of the sighting distances histograms (Fig. 2), we discarded the outermost observations by selecting a right truncation (32-50.4 m) to eliminate obvious outliers (Buckland et al., 2001). Cut points were maintained at equal sighting distance intervals. We used the Akaike's Information Criterion (AIC) and assessed the delta AIC as an indicator for selecting the model (Buckland et al., 2001; Burnham & Anderson, 2002).

To estimate the mean cluster size we used the size-bias regression computed by the software DISTANCE, which tests the observed cluster size against the estimated detection probability (Buckland et al., 2001). In addition, we considered that mean cluster size was likely to be underestimated due to the difficulty in detecting all animals in the group during census in a dense forest (Hassel-Finnegan et al., 2008). Therefore we calculated the average number of individuals/km<sup>2</sup> and abundance both with the mean cluster size (3.88, SE±0.25) as well as from the mean group size calculated from observations where full group counts were obtained.

## RESULTS

There was no significant difference in the number of observations of *P. rubicunda* ( $N_1=26$ ,  $N_2=26$ ,  $N_3=17$ ; chi-square:  $\chi^2(2)=2.348$ ,  $p=0.309$ ), and in the means of estimated perpendicular distances (ANOVA:  $F(2, 66)=0.211$ ,  $p=0.810$ ) across the three survey teams. The estimated cluster size did not differ across the three survey teams (Kruskal-Wallis:  $H(2)=0.884$ ,  $p=0.643$ ), as well as across transect lines (Kruskal-Wallis:  $H(12)=19.701$ ,  $p=0.073$ ). We also found no correlation between estimated perpendicular distances and cluster sizes ( $N=69$ ) (Spearman's:  $r_s=0.007$ ,  $p=0.956$ ), thus we concluded there was no inter-observer bias in the sighting data.

### Population density

We surveyed 13 line transects for a total effort of 207.12 km. During the surveys we observed 69 groups of *P. rubicunda*, with a mean encounter rate of 0.32 groups/km surveyed (95% CI=0.26-0.40). Observed mean cluster size was estimated to be 3.76 individuals (SE=0.20). Based on the size-bias regression computed by DISTANCE, the expected cluster size was estimated at 3.88 individuals (SE=0.25). All six models selected as the potential best ones displayed a delta AIC <2 (Burnham & Anderson, 2002). Differences between Akaike weights were minimal (<0.01). The half-normal key with cosine adjustments had the lowest AIC (195.13) and was thus chosen as the most suit-

**Table 1.** Density estimates obtained from various models as computed by DISTANCE v. 6.0

Model (adj., RT)	AIC	ESW	Density (groups/km <sup>2</sup> )	N	GOF K-S p	GOF Chi-sq p	Detection Probability
Half-normal (C, >50.4 m)	195.13	30.26	5.35 (3.4-8.43, 0.23)	415	-	0.461	0.6 (0.4-0.91, 0.21)
Half-normal (>32 m)	424.62	30.04	4.90 (3.43-7.01, 0.18)	370	0.913	0.477	0.94 (0.70-1.00, 0.15)
Half-normal (SP, 9%)	447.38	30.89	4.92 (3.74-6.47, 0.13)	374	0.916	0.873	0.91 (0.78-1.00, 0.07)
Half-normal (10%)	437.54	29.33	5.10 (3.57-7.29, 0.18)	386	0.838	0.366	0.87 (0.65-1.00, 0.14)
Hazard-rate (10%)	437.35	30.56	4.90 (3.77-6.37, 0.13)	381	0.911	0.491	0.9 (0.79-1.00, 0.07)
Uniform (10%)	436.61	33.82	4.43 (3.5-5.58, 0.11)	335	0.361	0.438	1.00 (1.00-1.00, 0.0)

Note: Densities are provided with the 95% confidence interval and the coefficient of variation.

RT=right truncation; AIC=Akaike's Information Criterion; ESW=effective strip width; N=abundance; GOF K-S p=goodness of fit Kolmogorov-Smirnov test; GOF Chi-sq p=goodness of fit Chi-square test; Cos=cosine adjustment; SP=simple polynomial adjustment

able model. It also showed a high goodness of fit value (0.461 chi-square tests of probability), with a detection probability of 0.6 (95% CI=0.4-0.91, Table 1). Density of *P. rubicunda* in the 20 km<sup>2</sup> pristine dipterocarp forest was estimated to be 5.35 groups/km<sup>2</sup> (95% CI=3.4-8.43) and 20.76 individuals/km<sup>2</sup> (95% CI=12.97-33.24) based on the half-normal/cosine.

We were able to obtain full group counts on 17 occasions, from which we calculated the mean group size to be 5.2 individuals, and the population density to be 27.82 individuals/km<sup>2</sup>.

### Other primates recorded

In addition to *P. rubicunda* within the study area we observed six individuals (two groups) of Bornean Orangutan *Pongo pygmaeus* (Linnaeus, 1760), 14 individuals (six groups) of Müller's Gibbon *Hylobates muelleri* Martin, 1841, ≥8 individuals (two groups) of Pig-tailed Macaque *Macaca nemestrina* (Linnaeus, 1766), ≥4 individuals (two groups) of Long-tailed Macaque *M. fascicularis* (Raffles, 1821) and four individuals (one group) of White-fronted Langur *Presbytis frontata* (Müller, 1838).

### Vegetation sampling

We recorded 653 trees in the primary forest in a total sampling area of 0.73 ha and computed vegetation variables (Table 2).

Of the total trees recorded, most trees (85%) were <20 m tall, a few (15%) were 20-40 m tall and a very few (0.2%) exceeded 40 m. The height of *P. rubicunda* above the ground (16-20 m) was significantly higher than the median vegetation height (11-15 m) (Mann-Whitney U=5369.5, p<0.001).

## DISCUSSION

Density of *P. rubicunda* within the 20 km<sup>2</sup> primary dipterocarp forest in Sungai Wain was relatively high within genus *Presbytis* (Kirkpatrick, 2012). Densities of Hose's Langurs *P. hosei* (Thomas, 1889) are reported to range from 5.5 individuals/km<sup>2</sup> in a young secondary forest to 18.9 individuals/km<sup>2</sup> in primary hill forest (Nijman, 2004). A density of 7.8 individuals/km<sup>2</sup> was estimated for Natuna Island Langur *P. natunae* (Thomas & Hartet, 1894) on Bunguran Island (Lammertink et al., 2003), and 13.5 individuals/km<sup>2</sup> were reported for Mentawai Langur *P. potenziiani* (Bonaparte, 1856) on Siberut Island (Watanabe, 1981).

Compared with previous distance sampling density estimates of *P. rubicunda* (Blouch 1997; Marshall, 2010; Ehlers Smith & Ehlers Smith, 2013), this study

**Table 2.** Vegetation characteristics within the primary forest in SWPF.

Vegetation attributes	SWPF primary forest*
Mean DBH (cm)	23.8 (± 0.8)
Density (stems/ha)	894.5 (± 27.5)
Proportion of ≥20 cm DBH trees (%)	38.4
Basal area (m <sup>2</sup> /ha)	59.7 (± 4.6)
Median tree height (m)	11-15
Canopy cover (%)	84.5 (± 1.90)

\* Values are given with standard errors.

showed the highest group density to date. Our mean group size and group density differ from those reported by Nijman & Nekaris (2012), most likely due to differences in methods of survey design and data analysis (Table 3). Our population density estimate, however, is comparable to that from the 1999-2005 surveys in the SWPF (Nijman & Nekaris, 2012). Thus at present, the Sungai Wain population of *P. rubicunda* appears to be stable within the primary forest. In Sarawak, similar population densities of *P. rubicunda* were found in the primary dipterocarp forests, where sympatric primate species assemblages coincided with those living in the SWPF (Blouch, 1997). These data suggest that undisturbed dipterocarp forests can support relatively high densities of *P. rubicunda*.

Between 2001 and 2012 it appears that there was an increase in tree density within the SWPF's primary habitat, with a slight bias towards larger trees. Our overall tree density (≥10 cm DBH) was double that found by Slik & Eichhorn (2003) in the same habitat in 2001. The proportion of ≥20 cm<sup>2</sup> DBH trees that we found in 2012 was 2.6 % higher than that reported by Slik & Eichhorn (2003). These are promising results for the conservation of *P. rubicunda* in the SWPF, as large trees represent a significant source of food for this colobine (Ehlers Smith et al., 2013b; Ehlers Smith & Ehlers Smith, 2013). A relatively high availability of large, preferred-food-bearing stems appears to play a crucial role for determining the presence of *P. rubicunda* (Ehlers Smith & Ehlers Smith, 2013). Within the mixed-swamp forest in Sabangau, Ehlers Smith et al. (2013b) found a positive correlation between fruiting tree DBH and the length of time that *P. rubicunda* spent feeding.

In the SWPF the majority of trees were well below 15 m high. In Barito Ulu vegetation height was found to be higher relative to the SWPF, with the mean height

**Table 3.** Comparison of density estimate of *P. rubicunda* across Borneo.

Study site	Forest type	Pop. density (ind/km <sup>2</sup> )	Group size	Survey method	Group size estimation method	Source
Sungai Wain Protection Forest, East Kalimantan, Indonesia	Primary dipterocarp forest	27.1	8.2	Line transect (4)	Complete counts from 54 groups observed during surveys	Nijman & Nekaris, 2012
Sungai Wain Protection Forest, East Kalimantan, Indonesia	Primary dipterocarp forest	27.8	5.2	Line transect (13), DISTANCE	Complete counts from 17 group encounters during survey	This study
Sabangau, Central Kalimantan, Indonesia	Peat swamp forest	17.5	7	Line transect (12), DISTANCE	Observation and complete counts of 7 groups	Ehlers Smith & Ehlers Smith, 2013
Gunung Palung NP, West Kalimantan, Indonesia	Alluvial bench	10.5	4.5	Line transect (2), DISTANCE	Observation during surveys	Marshall 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Lowland sandstone	5.9	2.9	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Freshwater swamp	7.8	5	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Peat swamp	2.5	3.8	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Lowland granite forest	7.3	3.8	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Upland granite forest	6.9	3.3	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Montane forest	1.24	3.2	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary dipterocarp forest	21.5	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary and secondary dipterocarp forest	20.8	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary and secondary heavily disturbed forest	5.4	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Barito Ulu, Central Kalimantan, Indonesia	Mixed lowland dipterocarp forest	8.4	4.3	Regular monitoring	Regular monitoring	McConkey & Chivers, 2004

Study site	Forest type	Pop. density (ind/km <sup>2</sup> )	Group size	Survey method	Group size estimation method	Source
Sepilok, Sabah, Malaysia	Lowland dipterocarp forest	18.9	7	Line transect	Observations during surveys across different sites in Sabah	Davies, 1984
Tanjung Putting Reserve, Central Kalimantan, Indonesia	Mixed lowland forest	9.8	6.1	Total group counts within study area	Observation and complete counts of 9 groups	Supriatna et al., 1986

Note: Where known, survey methods, number of transect lines in parentheses and software for analysis are indicated.

of trees ranging from 19 m in old secondary forest to 22.1 m in primary forest (Brearley et al., 2004). From the observations made during our survey, *P. rubicunda* appeared to prefer exploiting the canopy above the median vegetation height. In Sabangau Forest, *P. rubicunda* exclusively selected large, tall trees as sleeping sites ( $\geq 27$  cm DBH and  $\geq 16$  m tall trees [Ehlers Smith, 2014a]). In addition, Nijman & Nekarlis (2012) found that as a response to human presence, *P. rubicunda* fled upwards more often and would only use the ground or under-storey as a fleeing route on rare occasions. This species is therefore likely to rely on taller emergent trees to avoid predators and use the relatively high canopy to travel and feed. These findings might have important conservation implications, as selective logging causes a decrease in abundance of large trees and mean vegetation height (White et al., 1995; Okuda et al., 2003). To date, virtually no evidence is available on the effect of negative changes in habitat structure for *P. rubicunda*. In the SWPF, human encroachment and illegal logging are gradually increasing within the regenerating habitat. Meijaard et al. (2008) proposed that *P. rubicunda* is likely to be negatively affected by logging due to their diet consisting of mainly fruit and seeds. While *P. rubicunda* is able to increase leaf consumption when necessary, in logged areas and closer proximities to humans, colobines are also exposed to risks of disease (Gillespie & Chapman, 2008) and hunting (Nijman, 2005; Marchal & Hill, 2009).

Between 2000 and 2010 nearly 10% of the habitat occupied by *P. rubicunda* was lost due to habitat conversion (Ehlers Smith, 2014b). In 2012, logging concessions within the range of the subspecies present in the SWPF, *P. r. rubicunda* (Müller, 1838), accounted for 40.8% of the total remaining area (Ehlers Smith, 2014b). The relatively high abundance of *P. rubicunda* within the SWPF's primary habitat makes this forest an important conservation area for this species in East Kalimantan. At present, the SWPF is still connected to the ecosystem of Balikpapan Bay. Populations of *P. rubicunda* are present in Bukit Bangkirai Forest, a 15

km<sup>2</sup> rainforest approximately 6 km north of the SWPF, as well as along the coast of Balikpapan Bay. While the SWPF is becoming increasingly encircled by human activities, it remains unknown to what extent *P. rubicunda* is able to move between these areas.

We recommend further density assessments of *P. rubicunda* in regenerating and disturbed habitats across East Kalimantan. A focus on determining the primate carrying capacity of both primary and regenerating forests should also be considered. These investigations will provide us with the required information to quantify the remaining suitable habitat and develop further status assessments and conservation plans.

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