

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⁻² (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⁻², 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. 9999:1–11, 2013. © 2013 Wiley Periodicals, Inc.

Key words: borneo; colobinae; distance sampling; folivore; habitat quality

INTRODUCTION

Tropical rainforests cover some 19.6 million km² 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 [Kronseider 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 km² [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 km², 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⁻² (*Colobus angolensis*) [Bocian, 1997] up to 315 ind km⁻² (*Colobus guereza*) [Davies, 1994] in Africa, and 1 ind km⁻² (*P. rubicunda*) [Marshall, 2010] up to 220 ind km⁻² (*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⁻² in the lowland forests of Peninsular Malaysia (*P. siamensis*) [Davies, 1994], but the majority of species' densities range between 11 and 26 ind km⁻² [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 ⁻² , 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., in press]. No other food types are preferred or used as fallback foods [Ehlers Smith et al., in press].

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 km² 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 km²) 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

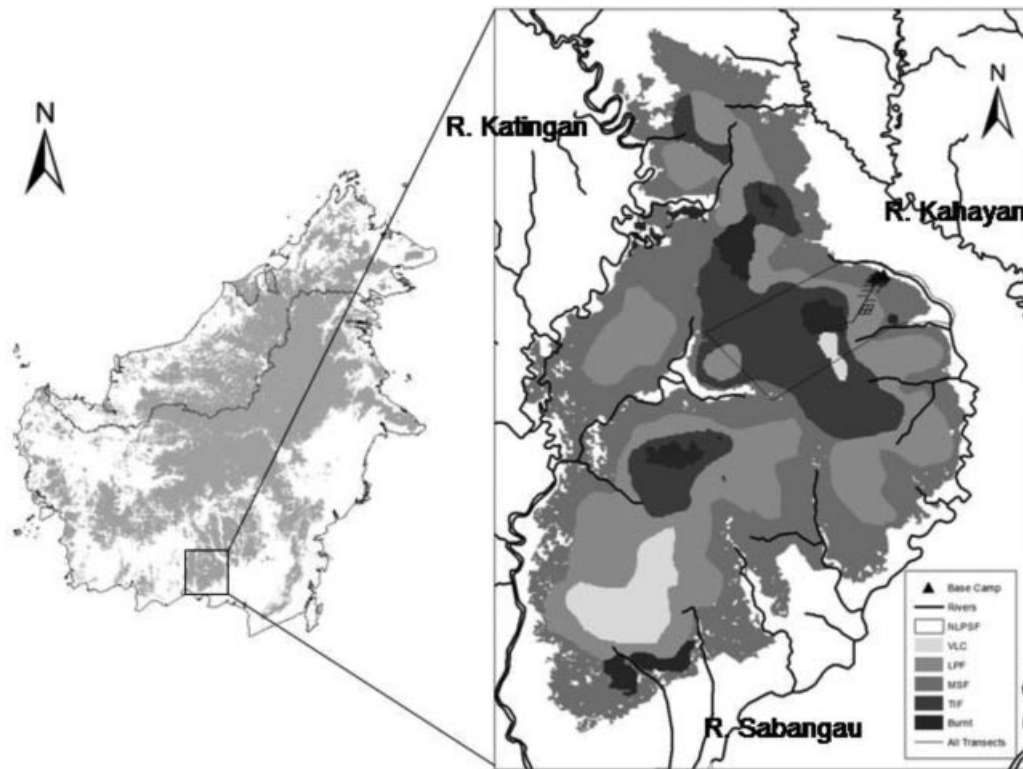
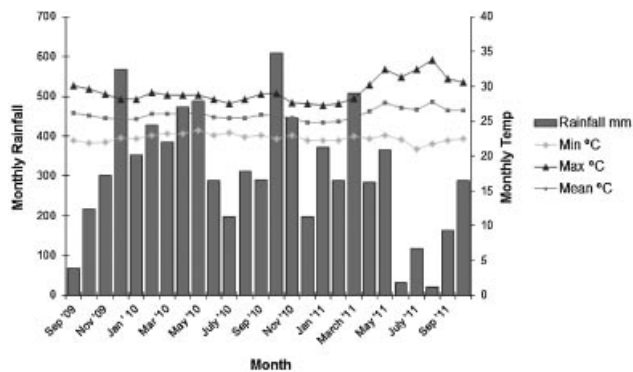


Fig. 1. Location of the Natural Laboratory for the Study of Peat-swamp Forest (NLPSF) within Sabangau and Borneo. MSF, mixed-swamp forest; LPF, low-pole forest; TIF, Tall-interior forest; VLC, very low-canopy forest. Gray shade = forest cover, white = non-forest. Derived from Miettinen et al. [2011b].



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., in press; 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 ²)
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>Comretocarpus</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 (ΔAIC , the difference between the minimum AIC and another key function model) was small enough ($\Delta AIC < 2$) 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., in press]. Fruit was selected disproportionately to its relative availability, and thus was the preferred food type [Ehlers Smith et al., in press]. 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., in press].

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 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 ^a	ΔAIC^b	Goodness of fit ^c			Group density ^e
					χ^2	df	PD ^d	
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 ^f	—	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

^aAkaike's Information Criterion.

^bDifference between key function AIC value and the selected (minimum) AIC value.

^cMeasured by chi-squared test [Buckland et al., 2001].

^dProbability of detection.

^eGroup density, 95% confidence interval (in parentheses) and coefficient of variation (sensitivity for detecting percentage change in the population between survey cycles).

^fModel 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 km^{-2} (95% CI, CV)	2.52 (1.56–4.08, 23.9)	
Population density, individuals km^{-2} (range)	17.51 (10.84–28.36)	
Biomass density, 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 ≥ 10 cm DBH and lianas ≥ 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 ≥ 10 cm DBH and lianas ≥ 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.^aNumber of encounters per group.

trees ≥ 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⁻² in the TPSFs of the Mentawai islands, Indonesia [Quinten et al., 2009], and *P. rubicunda* occurred at 2.5 ind km⁻² 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⁻²) 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., in press], 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 ≥ 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 ≥ 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., in press]. 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⁻²) 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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