1 DOWN FROM THE TREETOPS - RED LANGUR (PRESBYTIS RUBICUNDA)

2 TERRESTRIAL BEHAVIOUR

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Abstract

- 12 Using direct observations and camera traps at eight sites across Indonesian Borneo we show
- how red langurs (*Presbytis rubicunda*) are more terrestrial than previously believed, regularly
- coming to the ground. This unusual behaviour has been found at 6 of the 8 sites surveyed. We
- 15 find that red langurs come to the ground more frequently in disturbed forests, specifically
- ones which have been impacted by logging, fire and hunting, though more data are needed to
- 17 confirm this as a direct correlation. We also found a trend towards decreased ground use with
- increased elevation of the habitat. When on the ground, red langurs are predominantly
- engaged in feeding (50% direct observations, 61% camera traps) and travelling (29% direct
- 20 observations, 13% camera traps). Red langurs are found on the ground throughout the day, at
- 21 similar times to activity periods of the apex predator, the Sunda clouded leopard (Neofelis
- 22 diardi). We suggest that ground use by red langurs could be an adaptation to disturbed forest
- 23 to exploit additional food sources and to facilitate travel.

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Introduction

- Habitat conversion, degradation and loss continues at a rapid rate in many tropical forests and
- 27 has mixed effects on forest animal diversity (van Niewstadt et al. 2001, Wells et al. 2004,
- Meijaard et al. 2005, Wilcove et al. 2013). The effects of logging also change over time and
- 29 is the subject of increasing research. Species composition in logged forests approaches that of
- unlogged forests just a few decades after logging has ceased (Brodie et al. 2014; Danielsen
- and Heegaard 1994; Slik et al. 2002). Selectively logged forests are becoming an increasingly
- dominant component of many tropical landscapes. Yet, the conservation value of selectively
- 33 logged tropical forests is less well studied (Samejima et al. 2012, Burivalova et al. 2014,
- 34 Ehlers Smith 2014, Bernard et al. 2016) than those of more dramatic land cover changes,

such as deforestation driven by fire, agriculture or tree-plantation developments (Wilson & Wilson 1975, Estrada & CoatesEstrada 1996, Oka et al. 2000, Slik et al. 2002, O'Brien et al. 2003, Meittinen et al. 2012). What is less studied, is the impact on animal behaviour, and if novel behaviours e.g. coming to the ground, are a result of disturbance or actually a previously understudied part of a normal behavioural repertoire (Miller 2002, Zuberbuhler & Jenny 2002, Campbell et al. 2005, Mourthé et al. 2007, Loken et al. 2013, 2015, Ancrenaz et al. 2014, Ashbury et al. 2015)

Terrestrial behaviour in arboreal primates is recorded from many sites and has been attributed to socio-ecological factors such as food acquisition and aggression avoidance, and/or the anthropogenic effects of habituation to observer presence and habitat disturbance (Campbell et al. 2005, Mourthé et al. 2007). Increased terrestriality in arboreal primates is thought to increase the risk of predation (Miller 2002, Ancrenaz et al. 2014) and disease (Chapman et al. 2005) which has implications for the conservation of many threatened primate species. Increased use of the ground may be an indicator of lower quality habitat (Wells et al. 2004) or could indicate a broader behavioural repertoire and ability to make use of different space (Ancrenaz et al. 2014).

The Asian colobines of Genus *Presbytis* are small-bodied (~6kg), gracile monkeys restricted to the tropical rainforests of Southeast Asia (Oates et al. 1994) and are almost entirely arboreal (Davies and Oates 1994). Indeed, *Presbytis* monkeys are poorly adapted to terrestriality, with a low inter-membral index (Fleagle 1999) and relatively very long hindlimbs and phalanges, meaning they move quadrupedally on the ground and indicating a strong adaptation to arboreality (Strasser 1992). Relative to their close relatives the *Trachypithecus* monkeys, which have shorter hindlimbs, *Presbytis* monkeys engage in less quadrupedal walking, favouring arboreal leaping (Fleagle 1977, 1978, Strasser 1992). However, when investigating positional behaviour in Delacour's langurs Workman and Schmitt (2011) found no real morphological adaptation to living on limestone karsts but more flexibility of behaviour. Eighty % of locomotion was on rocks, but there was barely any leaping (4%). Workman and Schmitt (2011) suggest that the generalised locomotor capabilities of cercopithecids allows them this behavioural flexibility despite morphology (Workman and Schmitt 2012).

- The red langur, *Presbytis rubicunda*, is endemic to Borneo and the adjacent island of
- 69 Karimata (Medway 1970) and occupies the majority of the habitat types across the island
- 70 (Davies 1984, Supriatna et al. 1986, Marshall 2010). From two ecological studies at different
- sites and habitats, *P. rubicunda* is not known to descend to the forest floor (Supriatna et al.
- 72 1986) except for rare occasions to engage in geophagy (Davies & Baillie 1988, Davies et al.
- 73 1988, Rawson & Tuong Bach 2011). However this species has increasingly been reported on
- cameras traps placed on the ground, though these studies present encounter rates only and do
- not discuss behaviour (Giman et al. 2007, Samejima et al. 2012, Loken et al. 2013, Cheyne et
- 76 al. 2015, 2016).

- 78 In Sabangau peat-swamp forest, Central Kalimantan, we recorded *P. rubicunda* engaging in
- 79 terrestrial behaviour through researcher observation and remote observation using camera
- trapping over an 18-month period. In 7 other sites where these primates are not habituated,
- we used camera traps which were placed for 30-160 days.
- We looked at these data to address the following questions:
- 1. Were red langurs predominantly using the ground to travel, as might be expected in
- heavily disturbed forests?
- 2. If travel was not the primary activity, what behaviours were red langurs engaged in on
- the ground?
- 3. Which age/sex class was using the ground more? If access to food was a driving
- influence we may expect adults to use the ground more, and younger animals to avoid
- the ground due to predation risks.
- 90 4. Was frequency of ground use affected by logging, burnt forest, habitat type and
- 91 presence of hunting?
- 92 5. Is terrestrial behaviour affected by season?
- Here, we detail the circumstances under which terrestrial behaviour was observed and discuss
- 94 the ecological and conservation implications.

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Study Species

- 97 P. rubicunda is physiologically adapted for folivory (Bauchop and Martucci 1968), although
- a large amount of its diet comprises seeds of unripe fruits (Supriatna et al. 1986; Davies
- 99 1991; Marshall et al. 2009; Ehlers Smith et al. 2013a). The social unit is the single-male
- mixed-sex group, with extra males forming all-male bands or ranging alone (Davies 1984;
- Supriatna et al. 1986; Ehlers Smith et al. 2013b). Currently listed as Least Concern on the

IUCN Red List, this species inhabits the same forests as the four species of Bornean gibbons (all listed as Endangered on the IUCN Red List (Geissmann & Nijman 2008a, b, c, Nijman et al. 2008)) and the Bornean orangutan (listed as Critically Endangered (Ancrenaz et al. 2016)). Red Langurs are being upgraded to Red List Endangered across their range based on a recent review predicting an estimated population reduction of over 50% when considering the past 30 years and habitat change due to draining of peat swamps, logging and burning into the next 15 years (totalling 45 years which is approximately 3 generations (Cheyne et al.)). Age of first reproduction for red langurs is not confirmed but is estimated to be between 7-20yrs based on other langur species (Harley 1990). Between 2000 and 2010 the species experienced a mean 10% habitat occupancy reduction across all subspecies; *P. r. chrysea* experienced a ~21% habitat occupancy reduction (Ehlers Smith 2014a). Where the species persists, there is hunting and collection for the wildlife trade and for human consumption. A large part of the species range is in peat swamp - an extremely threatened ecosystem.

Study Grids

We present data from our long-term site in Sabangau and from 7 other sites surveyed for durations ranging from 30-180 days. In two of the short-term sites (Murung Raya and Mungku Baru), the camera-trap survey areas were considerably smaller due to access and time limitations (Table 1). The study sites differ in habitat type, altitude, size and human pressures which also impacted the size of the area surveyed by the cameras (Cheyne et al. 2016). The number of functional trap nights is presented (i.e. one camera operating for one calendar night is one trap night, 44 cameras operating for one calendar night is 44 trap nights. Functional trap nights account for the number of trap nights with deductions made for when individual cameras were not functioning (Andrew Royle et al. 2009, Cheyne et al. 2016).

Table 1 Summary of habitat and climactic characteristics of each study area. Min and Max a.s.l. refer to placement of cameras not the overall altitude of the study area. # Cameras have been in place in Sabangau since May 2008 but for the purposes of comparison only data from a 6-month period were used.

Grid	Central latitude	Central Longitude	Total survey days	Total number of cameras stations (* indicates cameras were in pairs)	Trap nights (number of active survey nights)	Min a.s.l (m)	Mean a.s.l (m)	Max a.s.l (m)	References
Bawan	1.605550°	113.991090°	78	63*	4146	35	72	93	(Harrison et al. 2012, Wanelik et al. 2013)
Belantikan	1.529640°	111.361660°	114	50*	4583	19	72	109	(Sapari et al. 2005)
Kutai	0.528546°	117.444857°	101	48*	3269	41	152	246	(Rodman 1977)
Lesan	1.591214°	117.142854°	195	70*	5548	64	212	344	(The Nature Conservancy 2011)
Mungku Baru	-1.650790°	113.750120°	187	44	6840	30	60	80	(Harrison et al. 2010)
Murung Raya	0.299046°	114.432248°	40	10	558	80	150	231	(Cheyne et al. 2012; McConkey and Chivers 2004)
Sabangau #	-2.321480°	113.899730°	185	30*	5487	12	29	30	(Morrogh-Bernard et al. 2003, Cheyne 2010)
Sungai Wain	1.085150°	116.835000°	83	79*	4729	35	69	86	(Rustam et al. 2012, Stark et al. 2012, Bersacola et al. 2014, Gilhooly et al. 2015)

Unlogged areas were sampled in all study grids. Four grids had forest which was logged >20 years ago. Due to the size of area surveyed, all grids crossed several habitat types and all were affected by some level of disturbance. Burnt refers to areas where vegetation has been cleared by fire in the last ≤ 15 years and is recovering (Figure 1).

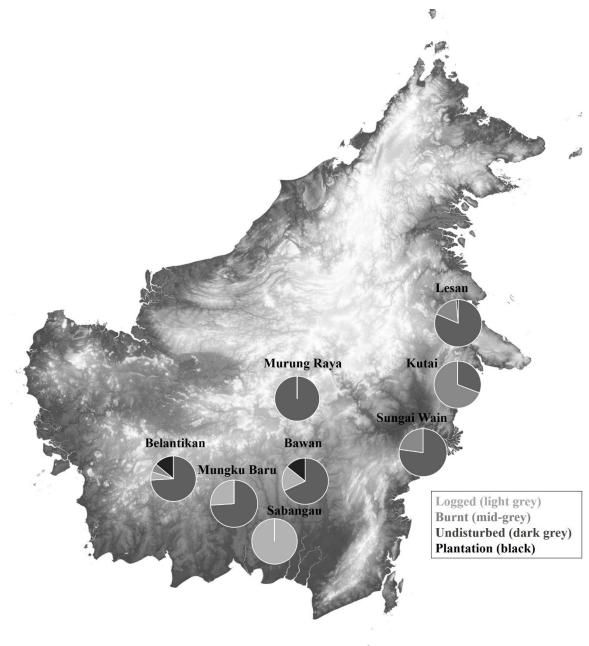


Figure 1 Map of the study region in Indonesian Borneo showing for each study grid the proportion of camera stations in logged (light grey), burnt (mid-grey), undisturbed (dark grey) and plantation (black) forest. The elevation model is from Google Earth. White shading indicates high elevation; dark grey shading indicates low elevation. See Supplementary Information for a map detailing exact study grid location.

Methods

- 141 Direct Observations (Sabangau only)
- We collected data on four habituated groups between March 2010 and January 2017 as part of a long-term ecological study of *P. rubicunda*. We followed groups from the morning sleeping tree until the evening sleeping tree and collected instantaneous behavioural data on a focal adult female every five minutes, including activity and height of the focal animal. We collected feeding data on a focal adult female at the instant the behaviour began until it
- stopped, including food item species; part eaten, and height or position of the food item (for
- full details of observation methods see (Ehlers Smith and Ehlers Smith 2013; Ehlers-Smith et
- 149 al. 2013a, b).

Camera Trapping

Following Cheyne et al. (2016) Cuddeback Capture IR® (Cuddeback Digital, Non-Typical) camera traps were placed along established trails and, where possible, watering areas, located so as to maximise the success rate of photographic 'detections' (Wilting et al. 2006; Gordon and Stewart 2007; Cheyne et al. 2013). Two cameras were placed opposite each other, 7 to 10 m apart to create a paired station at each location with the aim of photographing each flank of the animal simultaneously (Brodie & Giordano 2012). In Murung Raya and Mungku Baru only one camera was placed at each location (Cheyne et al. 2015). The passive infrared sensors were set at about 50 cm height off the ground and on a tree to record the majority of biodiversity present in the study areas (Cheyne, Stark, et al. 2013, Adul et al. 2015, Cheyne et al. 2017). The Capture IR cameras use an infrared flash to minimise disturbance to wildlife and reduce trap avoidance (O'Connell et al. 2011). There are some logging roads in some of the study areas, all cameras were placed along established trails at cross-roads and near fallen logs or man-made boardwalks, which may facilitate felid movements during the flooded wet

The grids were surveyed consecutively except for Sabangau which was surveyed concurrently with the Kutai and Lesan grids. Cameras were ideally set in a grid system with ± 0.5 - 1km between camera stations. This layout was not possible in Bawan due to the disturbed nature of the forest and issues of water accessibility when setting the cameras thus the cameras were placed along established trails. A General Linear Model with general contrasts and survey effort as a covariate was performed to assess the impact of logging age

season (Gordon & Stewart 2007, Cheyne & Macdonald 2011, Cheyne, Stark, et al. 2013).

(number of years since logging occurred), presence of hunting and fire on the presence of red langurs on the ground

RESULTS

Frequency of Encounters on the Ground

We recorded 82 counts (0.32% of all focal observations) of ground use by the focal individual at the instantaneous data point, characterised by four distinct behaviours (Total data points 25,502 (taken at 5-min intervals following (Ehlers Smith et al. 2013b)): feeding = 50, travelling = 29, resting = 20 and social behaviour = 1. We further catalogued 31 of the 82 occasions of the focal individual feeding from the ground independent of the instantaneous point over 100 minutes by breakdown of time and food types consumed on the forest floor by the focal individual: water from the ground = 17 (25mins), water from Nepenthes = 5 (10mins), Fungi = 10 (50mins), Pith = 6 (13mins), Leaves = 2 (4mins) and Unknown = 41 (103mins). Images and videos of Red langurs on the ground were obtained from in 6 of the 8 sites (a total of 78 independent images/videos). Red langurs were confirmed present in the 2 remaining sites (Rodman 1977, Bersacola et al. 2014) but the langurs were not seen on the ground (Table 2).

Table 2 Number of independent photos of red langurs on the ground across all sites as detected by the cameras. 0 = not detected.

	Habitat	Total Images/Sightings	Logging status/age	Fire	Hunting
Bawan 2010	Lowland Dipterocarp/ Ombrogenous Peat- swamp Forest (PSF) mosaic	3	Current	Y	Y
Bawan 2012	Lowland Montane/Lowland Dipterocarp (LM/LD)	8	Current	Y	Y
Sabangau*	Lowland Dipterocarp (LD)	3	> 10	Y	Y
Murung Raya	Lowland Montane	1	> 10	N	Y
Kutai	Lowland Dipterocarp	0	> 10	N	Y

Sungai Wain	Lowland Montane. Pristine and remote	0	> 20	N	N
Mungku Baru	Ombrogenous PSF	21	> 20	Y	Y
Lesan	Lowland Dipterocarp/Alluvial PSF	40	> 20	N	Y
Belantikan		1	> 20	Y	Y

* Sabangau data are from the 6-month comparison survey period, data in brackets are numbers from the full 7 years of survey (Adul et al. 2015).

Images of all age sex classes and of multiple individuals at the same time were obtained (Figure 2).

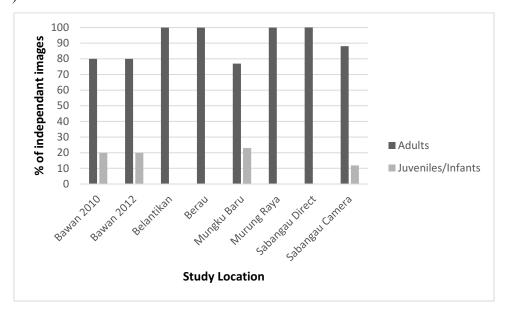


Figure 2 Age classes of the individual red langurs on the ground.

Red Langur Behaviour on the Ground

Red langurs predominantly used the ground for travelling and feeding across study sites (Figure 3). Feeding was classified when the langurs were holding food items or clearly seen to have food in their mouth. Travelling was classified as any movement and resting where the animals are not in motion. Social activity was classified as any interaction between 2 or more individuals and direct gaze at the cameras was classed as looking at the camera.

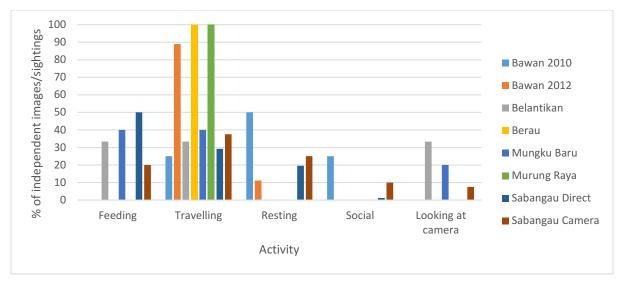
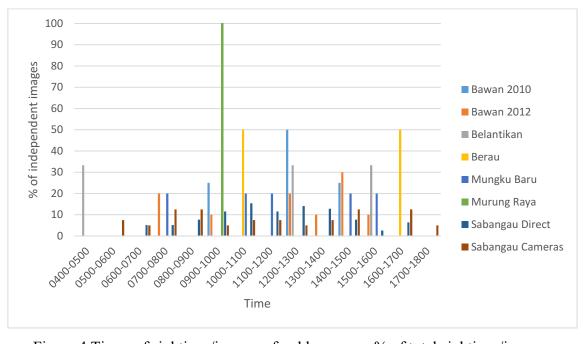


Figure 3 Sightings/images of red langurs engaged in each activity % of total sightings/images.

Red langurs came to the ground throughout the active period with peaks between 1000-1100h, 1200-1300h and 1400-1500h though there is variation between sites (Figure 4). These times of greatest terrestrial behaviour are not significantly affected by the behaviour being performed on the ground (Friedman ANOVA: $\chi^2 = 0.74$, n = 6, d.f. = 4, p = 0.69).



 $Figure\ 4\ Times\ of\ sightings/images\ of\ red\ langurs\ as\ \%\ of\ total\ sightings/images.$

Of the 8 sites only 5 had cameras present consecutively across wet and dry seasons (Kutai, Lesan, Mungku Baru. Sabangau and Sungai Wain). Only 3 of those sites had images/sightings of red langurs on the ground: Lesan = 2 (1 wet season, 1 dry season); Mungku Baru = 21 (12 wet season, 9 dry season) and Sabangau = 40 (24 wet season, 16 dry season).

The number of sightings each month was generally higher in the dry season though the average number of sightings and images per month taken as an average was not significantly different (10.63 wet season and 9.25 dry season, $\chi^2 = 22.01$, p > 0.05. Figure 5).



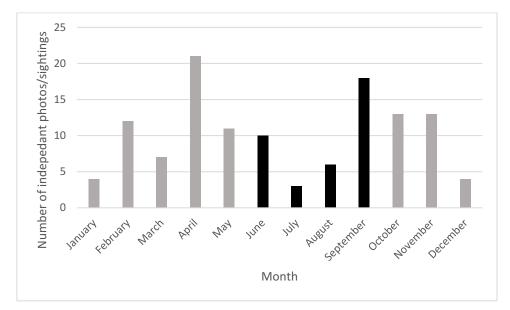


Figure 5 Number of sightings/images of red langurs per month. Grey bars represent wet season, black bars represent dry season.

Habitat and Disturbance

There is a correlation between habitat/altitude and number of images obtained. While we recognise that factors such as different forest types/structure, food availability and animal diversity likely important determinants affecting their terrestrial behaviours, red langurs do appear to be coming to the ground more frequently at low altitudes (Figure 6). Though this correlation does not suggest causality. It might be that the study sites at lower altitudes were different from the others in other aspects (presence of predators, vegetation structure etc.). The possible influence of altitude was added as a proxy for the variation in forest structure but also there are some suggestions that predation pressure could be higher in higher

altitudes, due to an increased presence of clouded leopards (Macdonald, David Bothwell et al.).

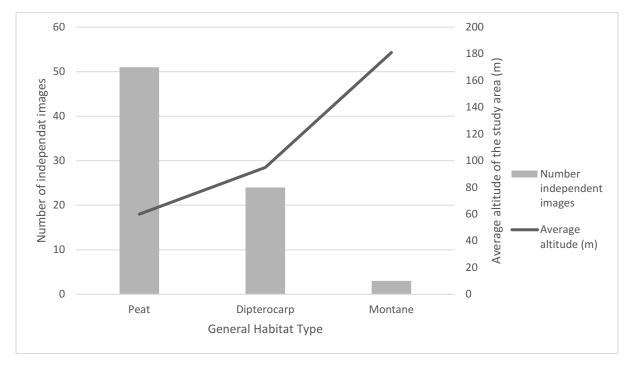


Figure 6 Number of sightings/images of red langurs in each habitat type compared to the altitude of the study site.

Of the 78 images/sightings on the camera traps 4% (3 images) were in forests unaffected by fires and 96% (75 images) were obtained in areas where the forests had experienced at least one fire event. A possible reason for the langurs making use of the ground could be impacts of logging. Using logging data obtained for these areas (Cheyne et al. 2016) we assessed the number of images of red langurs on the ground as a function of total primate images and compared this to this logging history of the area at a broad scale. The GLM predicted that the age of logging model most consistently explains presence of red langurs on the ground (F = 5.1, p = 0.036), followed by fire F = 6.4, p = 0.04). The presence of hunting model did not explain any of the variation F = 4.3, p = 0.08, (Figure 7).

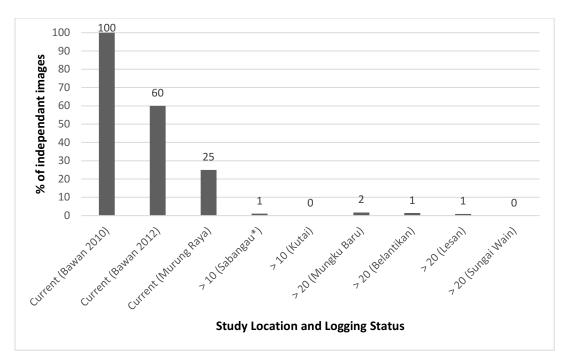


Figure 7 Comparison of % of red langur images as a function of all primate images with logging status.

DISCUSSION

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Red Langur Behaviour on the ground

Asian colobines are infrequently recorded on the ground and are poorly adapted to terrestrialism. Colobines do use the ground for feeding e.g., geophagy, drinking water and eating fungi but in the absence of long-term data regarding this behaviour it is important to investigate other drivers for terrestriality (McKey et al. 1981, Davies & Oates 1994, Rawson & Tuong Bach 2011). Arboreal primates may descend to the ground in more disturbed habitats and in the presence of researchers (to whom they are habituated) in order to flee (Ehardt et al. 2005). The degree of terrestrial behaviour may be related to habituation and has implications for conservation owing to vulnerability from predation/disease/parasite transmission (Hart 2007, Matsuda et al. 2008, Morino 2011, Hilser et al. 2014). Predation rate is difficult to evaluate, and may not be a limiting factor, but the few data which are available on gibbons (primates of a similar size) suggest that there is a predation risk (Uhde & Sommer 2002, Hart 2007, Morino 2011, Clarke et al. 2012, Burnham et al. 2013, Wilcox et al. 2017). Hunting pressure was measured by presence of hunters on the camera traps and is a rough proxy for pressure of human hunting. Most hunters were observed in Bawan forest, where red langurs were observed on the ground. As monkeys are infrequently targeted by human hunters they may come to the ground more frequently (Marshall et al. 2006, Meijaard et al.

2012). Species that travel along the ground and live in more open forests are more prone to predation (by other animals and humans; Rudran 1973; Stanford 1989). Predation of arboreal primates by other animals is hardly ever reported in SE Asia (Davies 1984, Burnham et al. 2012) and much lower than African forests (Aldrich-Blake 1970, Busse 1977). Pythons appear to have a minimal influence on predators (Whitten 1980). Forest monkeys travel and forage on the ground far more in the absence of leopards (Struhsaker 2000). The monkeys on the islands do so much more frequently in the absence of leopards. In areas where people hunt primates colobine populations may be reduced (Bennett and Sebastian 1988).

Age/sex class ground use

The use of the ground does not appear to be restricted to one age class or sex though adults are recorded on the ground more than younger animals, perhaps due to increased predation risk. Adults may use the forest floor more often than that in juveniles simply because juveniles are more vulnerable than adults in terms of their body size, though this has not been borne out from data on orangutans in the same forests (Ancrenaz et al. 2014). Additionally, clouded leopards in the study sites are predominantly active between 1100 and 1600h (Adul et al. 2015, Cheyne et al. 2016), similar times to when the red langurs are most active on the ground indicating that predation risk may not be an explanatory factor.

Habitat and Disturbance

Higher quality foods (leaves containing higher protein but lower fibre) may be more available in disturbed forests (Ehlers-Smith et al. 2013, Matsuda et al. 2013), and there are also potentially more shade-tolerant plants on the ground in disturbed forests (Estrada & CoatesEstrada 1996, Munoz et al. 2006, Anderson et al. 2007). Thus, red langurs may have more opportunities to come down to the ground in these habitats. These findings are preliminary and require further investigation to find correlations, unless the use of the ground is unrelated to habitat disturbance. Only one site (Sungai Wain) has no regular encroachment for hunting and this site did not yield any images of red langurs on the ground. With these data, it is not possible to determine any relationship between hunting presence and frequency of ground use by red langurs. There was no obvious influence of season on the frequency with which red langurs came to the ground either from direct observational data or from the camera traps. However, the impacts of hunting, logging and

fire have been observed for other species (Brodie et al. 2014, Cheyne et al. 2016), highlighting the need to investigate this more fully for red langurs.

The more recently disturbed areas (recent logging) had more frequent occurrences of red langurs on the ground, perhaps due to increased loss of large trees and/or canopy connectivity as has been seen for gibbons (Cheyne, Thompson, et al. 2013). Thus, this behaviour could be a potential indicator of habitat quality. Selective logging is likely to influence the ecology of P. rubicunda as the practise removes the largest trees, upon which feeding (Ehlers Smith et al. 2013a), distribution Ehlers Smith and Ehlers Smith, 2013), and sleeping sites (Ehlers Smith 2014b) are dependent. Given the increased incidences of terrestrial behaviours in logged forests and the frequency with which feeding behaviours were associated with terrestriality, it is likely that terrestrial foraging forms an important part of the behavioural ecology of P. rubicunda in logged forests. Consequently, there is an increased risk associated with parasite transmission through increased time on the ground (Chapman et al. 2005) and predation for populations in logged forests; despite the success of logging concessions in maintaining overall forest cover in comparison to protected areas (Ehlers Smith 2014a), logged forests could be sub-optimal habitat for P. rubicunda populations therein. However more data and longer studies are needed so we can only conclude that this species does come to the ground more often in logged forest. Why red langurs do this remains unclear, as are any impacts on long term population viability.

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362	
363	REFERENCES
364	Adul, Ripoll Capilla B, Limin SH, Cheyne SM. 2015. Felids of Sebangau: Camera trapping
365	to estimate activity patterns and population abundance in Central Kalimantan,
366	Indonesia. Biodiversitas 16:151–155.
367	Adul, Ripoll Capilla B, Limin SH, Cheyne SM (2015) Felids of Sebangau: Camera trapping
368	to estimate activity patterns and population abundance in Central Kalimantan, Indonesia.
369	Biodiversitas 16:151–155
370	Aldrich-Blake FP. (1970) Problems of social structure in forest monkeys. In: Crook JH (ed)
371	Social behaviour in birds and mammals. Academic Press, London, p 79-101
372	Ancrenaz M, Gumal M, Marshall A., Meijaard E, Wich SA, Husson S (2016) Pongo
373	pygmaeus. IUCN Red List Threat Species
374	Ancrenaz M, Sollmann R, Ambu L, Bernard H, Bohm T, Brodie J, Cheyne S., Fredriksson G,
375	Gardner P, Goossens B, Harrison M, Hearn A., Khee Lee S, Loken B, Macdonald D.,
376	Matsuda I, Meijaard E, Mohamed A, Ross J, Samejima H, Spehar S, Stark D, Wich S,
377	Wilting A (2014) Coming down from the trees: Is terrestrial activity in Bornean
378	orangutans natural or disturbance driven? Sci Rep 4:1-5
379	Anderson J, Cowlishaw G, Rowcliffe JM (2007) Effects of forest fragmentation on the
380	abundance of Colobus angolensis palliatus in Kenya's coastal forests. Int J Primatol
381	28:637–655
382	Andrew Royle J, Nichols D. J, Ullas Karanth K, Gopalaswamy AM (2009) A hierarchical
383	model for estimating density in camera-trap studies. J Appl Ecol 46:118-127
384	Ashbury AM, Posa MRC, Dunkel LP, Spillmann B, Atmoko SSU, Schaik CP van,
385	Noordwijk MA van (2015) Why do orangutans leave the trees? Terrestrial behavior
386	among wild Bornean orangutans (Pongo pygmaeus wurmbii) at Tuanan, Central
387	Kalimantan. Am J Primatol 77
388	Bauchop T, Martucci R (1968) Ruminant-like digestion of the langur monkey. Science (80-)

389	161:698–699
390	Bennett EL, Sebastian A (1988) Social organization and ecology of proboscis monkeys
391	(Nasalis larvatus) in mixed coastal forest in Sarawak. Int J Primatol 9:233-256
392	Bernard H, Rayner B, Matsuda I, Hanya G, Wearn OR, Wong A, Ahmad AH (2016) Species
393	Richness and Distribution of Primates in Disturbed and Converted Forest Landscapes in
394	Northern Borneo. Trop Conserv Sci 9:1-11
395	Bersacola E, Smith DAE, Sastramidjaja WJ, Rayadin Y, Cheyne SM (2014) Population
396	density of Presbytis rubicunda in a small primary Dipterocarpp forest in East
397	Kalimantan, Indonesian Borneo. Asian Primates J 4:16–26
398	Brodie J, Giordano A (2012) Density of the Vulnerable Sunda clouded leopard Neofelis
399	diardi in a protected area in Sabah, Malaysian Borneo. Oryx 46:427-430
400	Brodie JF, Giordano A., Zipkin E., Bernard H, Jayasilan M-A, Ambu L (2014) Correlation
401	and Persistence of Hunting and Logging Impacts on Tropical Rainforest Mammals.
402	Conserv Biol 29:110–121
403	Burivalova Z, Şekercioğlu C., Pin Koh L (2014) Thresholds of Logging Intensity to Maintain
404	Tropical Forest Biodiversity. Curr Biol 24:1893–1898
405	Burnham D, Bearder SK, Cheyne SM, Dunbar R, Macdonald DW (2012) Predation by
406	mammalian carnivores on nocturnal primates: is the lack of evidence support for the
407	effectiveness of nocturnality as an anti-predator strategy? Folia Primatol 83:236-251
408	Burnham D, Bearder SK, Cheyne SM, Dunbar RIM, MacDonald DW (2013) Predation by
409	Mammalian carnivores on nocturnal primates: Is the lack of evidence support for the
410	effectiveness of nocturnality as an antipredator strategy? Folia Primatol 83
411	Busse CE (1977) Chimpanzee predation as a possible factor in the evolution of red colobus
412	social organization. Evolution (N Y) 31:907–911
413	Campbell C, Aureli F, Chapman C, Ramos-Fernández, G Matthews K, Russo S, Suarez S,
414	Vick L (2005) Terrestrial Behavior of Ateles spp.
415	Chapman C, Gillespie TR, Goldberg TL (2005) Primates and the Ecology of Their Infectious
416	Diseases: How will Anthropogenic Change Affect Host-Parasite Interactions? Evol
417	Anthropol 14:134 –144
418	Cheyne SM (2010) Behavioural ecology and socio-biology of gibbons (Hylobates albibarbis)
419	in a degraded peat-swamp forest. In: Supriatna J, Gursky SL (eds) Indonesian Primates.
420	Springer, New York, p 121–156
421	Cheyne SM, Adul, Veen, F JF Van, Ripoll Capilla B, Boyd N, Maimunah S (2017) First
422	record of the bay cat in mosaic heath/peat-swamp forest, Kalimantan, Indonesia. Cat

423	News 65:48
424	Cheyne SM, Ehlers Smith D., Nijman V, Traeholt C Presbytis rubicunda. IUCN Red List
425	Threat Species
426	Cheyne SM, Höing A, Houlihan PR, Kursani, Rowland D, Zrust M (2015) Report on the
427	large mammals of the Uut Murung Region, Central Kalimantan, Indonesia. J Indones
428	Nat Hist 3:38–45
429	Cheyne SM, Macdonald DW (2011) Wild felid diversity and activity patterns in Sabangau
430	peat-swamp forest, Indonesian Borneo. Oryx 45:119-124
431	Cheyne SM, Sastramidjaja WJ, Muhalir, Rayadin Y, Limin SH, Macdonald D. (2016)
432	Mammalian Communities as indicators of disturbance across Indonesian Borneo. Glob
433	Ecol Conserv 7:157–173
434	Cheyne SM, Stark D, Limin SH, Macdonald DW (2013) First Estimates of Population
435	Ecology and Threats to Sunda Clouded Leopards (Neofelis diardi) in a Peat-swamp
436	Forest, Indonesia. Endanger Species Res 22:1–9
437	Cheyne SM, Thompson CJH, Chivers DJ (2013) Travel adaptations of gibbons Hylobates
438	albibarbis (Primates: Hylobatidae) in a degraded secondary forest, Indonesia. J Threat
439	Taxa 5:3963–3968
440	Cheyne SM, Zrust M, Hoeing A, Houlihan PR, Rowland D, Rahmania M, Breslin K (2012)
441	Barito River Initiative for Nature Conservation and Communities (BRINCC)
442	Preliminary Report. BRINCC Expedition, Palangka Raya, Indonesia
443	Clarke E, Reichard UH, Zuberbühler K (2012) The anti-predator behaviour of wild white-
444	handed gibbons (Hylobates lar). Behav Ecol Sociobiol 66:85-96
445	Danielsen F, Heegaard M (1994) The impact of logging and forest conversion of lowland
446	forest birds and other wildlife in Seberida, Riau Province, Sumatra In: Sandbukt OW
447	(ed) Proceedings of NORINDRA Seminar. Indonesian Institute of Sciences. Jakarta,
448	Indonesia., p 59–60
449	Davies AG (1984) An ecological study of the red leaf monkey (Presbytis rubicunda) in the
450	dipterocarp forests of Sabah, northern Borneo. University of Cambridge, Cambridge
451	Davies AG (1991) Seed-eating by red leaf monkeys (Presbytis rubicunda) in dipterocarp
452	forest of northern Borneo. Int J Primatol 12:119-144
453	Davies AG, Baillie I (1988) Soil-eating by red leaf monkeys (Presbytis rubicunda) in Sabah
454	northern Borneo Biotropica 20:252–258
455	Davies AG, Bennett EL, Waterman PG (1988) Food selection by two south-east Asian
456	colobine monkeys (Presbytis rubicunda and P. melalophos) in relation to plant

457	chemistry Biol J Linn Soc 34:34–56
458	Davies GA, Oates JF (1994) Colobine monkeys: Their ecology, behaviour and evolution
459	(GAD and JFO, Eds.). Cambridge University Press, Cambridge
460	Ehardt CL, Jones TP, Butynski TM (2005) Protective status, ecology and strategies for
461	improving conservation of Cercocebus sanjei in the Udzungwa Mountains, Tanzania. Int
462	J Primatol 26:557–583
463	Ehlers-Smith DA, Ehlers Smith YC (2013) Population Density of Red Langurs in Sabangau
464	Tropical Peat-Swamp Forest, Central Kalimantan, Indonesia. Am J Primatol 75:837-847
465	Ehlers-Smith DA, Husson SJ, Ehlers Smith YC, Harrison ME (2013) Feeding ecology of red
466	langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory
467	in a non-masting forest. Am J Primatol 75:848-859
468	Ehlers Smith DA (2014) The effects of land-use policies on the conservation of Borneo's
469	endemic Presbytis monkeys. Biodivers Conserv
470	Ehlers Smith DA, Ehlers Smith YC, Cheyne SM (2013a) Home Range Use and Activity
471	Patterns of Red Langurs in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan,
472	Indonesia. Int J Primatol 34:957–972
473	Ehlers Smith DA, Ehlers Smith YC, Cheyne SM (2013b) Home-Range Use and Activity
474	Patterns of the Red Langur (Presbytis rubicunda) in Sabangau Tropical Peat-Swamp
475	Forest, Central Kalimantan, Indonesian Borneo. Int J Primatol 34
476	Estrada A, CoatesEstrada R (1996) Tropical rain forest fragmentation and wild populations of
477	primates at Los Tuxtlas, Mexico. Int J Primatol 17:759-783
478	Fleagle J (1977) Locomotor behavior and muscular anatomy of sympatric Malaysian leaf
479	monkeys Presbytis obscura and Presbytis melalophos. Am J Phys Anthropol 46:297-308
480	Fleagle JG (1978) Locomotion, posture, and habitat utilization in two sympatric Malaysian
481	leaf-monkeys (Presbytis obscura and Presbytis melalophos). In: Montgomery GG (ed)
482	The Ecology of Arboreal Folivores. Smithsonian Institution Press, Washington D.C
483	Fleagle JG (1999) Primate adaptation and evolution. Academic Press, San Diego and New
484	York
485	Geissmann T, Nijman V (2008a) Hylobates muelleri. IUCN Red List Threat Species
486	Geissmann T, Nijman V (2008b) Hylobates funereus. IUCN Red List Threat Species
487	Geissmann T, Nijman V (2008c) Hylobates abbotti. IUCN Red List Threat Species
488	Gilhooly LJ, Rayadin Y, Cheyne SM (2015) A Comparison of Hylobatid Survey Methods
489	Using Triangulation on Müller's Gibbon (Hylobates muelleri) in Sungai Wain
490	Protection Forest, East Kalimantan, Indonesia. Int J Primatol 36:567-582

491	Giman B, Stuebing R, Megum N, McShea WJ, Stewart CM (2007) A camera trapping
492	inventory for mammals in a mixed use planted forest in Sarawak. Raffles Bull Zool
493	55:209–215
494	Gordon CH, Stewart EA-M (2007) The use of logging roads by a solitary felid, the clouded
495	leopard. Cat News 47:12–13
496	Harley D (1990) Aging and reproductive performance in langur monkeys (Presbytis entellus)
497	Am J Phys Anthropol 83:253–261
498	Harrison ME, Cheyne SM, Husson SJ, Jeffers KA, Smallcombe J V, Ehlers Smith DA (2012)
499	Preliminary Assessment of the Biodiversity and Conservation Value of the Bawan
500	Forest, Central Kalimantan, Indonesia Orangutan Tropical Peatland Project, Palangka
501	Raya
502	Harrison M., Hendri, Dragiewicz M., Krisno J, Cheyne SM, Husson SJ (2010) Biodiversity
503	of the Mungku Baru Ulin Forest, Central Kalimantan, Indonesia. Orangutan Tropical
504	Peatland Project, Palangka Raya, Indonesia.
505	Hart D (2007) Predation on Primates: A biogeographical analysis. In: Gursky S, Nekaris KAl
506	(eds) Primate Anti-Predator Strategies. Springer, New York, USA, p 27-62
507	Hilser HB, Ehlers Smith DA, Morrogh-Bernard C H, Cheyne SM (2014) Creating
508	Connections: Integrating Health Monitoring Into Primate Conservation Management.
509	Biol Conserv
510	Loken B, Boer C, Kasyanto N (2015) Opportunistic behaviour or desperate measure?
511	Logging impacts may only partially explain terrestriality in the Bornean orang-utan
512	Pongo pygmaeus morio. ORYX 49
513	Loken B, Spehar S, Rayadin Y (2013) Terrestriality in the Bornean orangutan (Pongo
514	pygmaeus morio) and implications for their ecology and conservation. Am J Primatol
515	75:1129–1138
516	Macdonald, David Bothwell H, Hearn A, Cheyne, Susan M, Haidir I, Hunter L, Kaszta Z,
517	Linkie M, Macdonald E, Ross J, Cushman S Clouds over the hills: Deforestation and
518	large-scale plantations threaten an ambassador of Southeast Asian biodiversity (Neofelis
519	diardi), as revealed by multi-scale modeling and camera trapping. J Anim Ecol
520	Marshall AJ (2010) Effect of habitat quality on primate populations in Kalimantan: gibbons
521	and leaf monkeys as case studies. In: Gursky-Doyen S, Supriatna J (eds) Indonsian
522	Primates. Springer, New York, p 157–177
523	Marshall AJ, Ancrenaz M, Brearley FQ, Fredriksson GM, Ghaffar N, Heydon M, Husson SJ,
524	Leighton M, McConkey KR, Morrogh-Bernard HC, Proctor J, Schaik CP van, P. YC,

525	wich SA (2009) The effects of forest phenology and floristics on populations of
526	Bornean and Sumatran orangutans. In: Wich SA, Utami Atmoko SS, Mitra Setia T,
527	Schaik CP van (eds) Orangutans: Geographic Variation in Behavioral Ecology and
528	Conservation. Oxford University Press, Oxford, p 97–116.
529	Marshall AJ, Nardiyono, Engstrom LM, Pamungkas B, Palapa J, Meijaard E, Stanley SA
530	(2006) The blowgun is mightier than the chainsaw in determining population density of
531	Bornean orangutans (Pongo pygmaeus morio) in the forests of East Kalimantan. Biol
532	Conserv 129:566–578
533	Matsuda I, Tuuga A, Bernard H, Sugau J, Hanya G (2013) Leaf selection by two Bornean
534	colobine monkeys in relation to plant chemistry and abundance. Sci Rep 3:1873
535	Matsuda I, Tuuga A, Higashi S (2008) Clouded leopard (Neofelis diardi) predation on
536	proboscis monkeys (Nasalis larvatus) in Sabah, Malaysia. Primates 49:227-231
537	McConkey KR, Chivers DJ (2004) Low mammal and hornbill abundance in the forests of
538	Barito Ulu. Central Kalimantan, Indonesia. Oryx 38:439-447
539	McKey DB, Gartlan PG, Waterman FL, Choo FLS, Choo GM (1981) Food selection by black
540	colobus monkeys (Colobus satanus) in relation to plant chemistry. Biol J Linn Soc
541	16:115–146
542	Medway L (1970) The monkey of Sundaland: Ecology and systematic of the Cercopithecids
543	of a humid equatorial environment. In: Napier NH (ed) Old world monkeys: Evolution,
544	systematic and behaviour. Academic Press, New York, p 513-554
545	Meijaard E, Sheil D, Nasi R, Augeri D, Rosanbaum B, Iskandar D, Setyawati T, Lammertink
546	M, Rachmatika I, Wong A, Soehartono T, Stanley S, O'Brien T (2005) Life after
547	logging: reconciling wildlife forestry and production forestry in Indonesian Borneo.
548	CIFOR, Bogor, Indonesia
549	Meijaard E, Wich S, Ancrenaz M, Marshall AJ (2012) Not by science alone: why orangutan
550	conservationists must think outside the box. Year Ecol Conserv Biol 1249:29-44
551	Meittinen J, Hooijer A, Shi C, Tollenaar D, Vernimmen R, Liew S., Malins C, Page S. (2012)
552	Extent of industrial plantations on Southeast Asian peatlands in 2010 with analysis of
553	historical expansion and future projections. GCB Bioenergy 4:908-918
554	Miller L (2002) Eat or Be Eaten: Predator Sensitivity Foraging among Primates. Cambridge
555	University Press, Cambridge, UK
556	Morino L (2011) Clouded Leopard Predation on a Wild Juvenile Siamang. 1414:362–368
557	Morrogh-Bernard H, Husson S, Page SE, Rieley JO (2003) Population status of the Bornean
558	orang-utan (Pongo pygmaeus) in the Sebangau peat swamp forest, Central Kalimantan,

559	Indonesia. Biol Conserv 110:141–152
560	Mourthé I, Guedes D, Fidelis J, Boubli J, Mendes S, Strier KB (2007) Ground use by
561	northern muriquis (Brachyteles hypoxanthus). Am J Primatol 69:706-712
562	Munoz D, Estrada A, Naranjo E, Ochoa S (2006) Foraging ecology of howler monkeys in a
563	cacao (Theobroma cacao) plantation in Comalcalco, Mexico. Am J Primatol 68:127-142
564	Niewstadt MGL van, Shiel D, Kartawinata K (2001) The ecological consequences of logging
565	in the burned forests of east Kalimantan, Indonesia. Conserv Biol 15:1183-1186
566	Nijman V, Richardson M, Geissmann T (2008) Hylobates albibarbis. IUCN Red List Threat
567	Species 2008
568	O'Brien TG, Kinnaird MF, Nurcahyo A, Prasetyaningrum M, Iqbal M (2003) Fire,
569	demography and the persistence of siamang (Sympgylangus syndactylus: Hylobatidae)
570	in a Sumatran rainforest. Anim Conserv 6:115-121
571	O'Connell AF, Nichols JD, Karanth KU (2011) Camera Traps in Animal Ecology: Methods
572	and Analyses. Springer, New York
573	Oates JF, Davies AG, Delson E (1994) The diversity of living colobines. In: Davies GA,
574	Oates JF (eds) Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge
575	University Press, Cambridge, UK, p 45–73
576	Oka T, Iskandar E, Ghozali DI (2000) Effects of forest fragmentation on the behaviour of
577	Bornean gibbons. In: Guhardia E, Fatawi M, Sutisna M, Mori T, Ohta S (eds) Ecological
578	Studies: rainforest ecosystems of east Kalimantan: el Nino, drought, fire and human
579	impacts. Springer, London, p 229–241
580	Rawson B, Tuong Bach L (2011) Preliminary observations of geophagy amongst Cambodia's
581	Colobinae. Vietnamese J Primatol 5:41–46
582	Rodman PS (1977) Feeding behaviour of orang-utans of the Kutai Nature Reserve, East
583	Kalimantan. In: Clutton-Brook TH (ed) Primate Ecology: Studies of feeding and ranging
584	behaviour in lemurs, monkeys and apes. Academic Press, London, 381-413., London,
585	UK, p 171–209
586	Rudran R (1973) Adult male replacement in one-male troops of purple- faced langurs
587	(Presbytis senex senex) and its effect on population structure. Folia Primatol 19:166-192
588	Rustam, Yasuda M, Tsuyuki S (2012) Comparison of mammalian communities in a human-
589	disturbed tropical landscape in East Kalimantan, Indonesia. Mammal Study 37:299-311
590	Samejima H, Ong R, Lagan P, Kitayama K (2012) Camera-trapping rates of mammals and
591	birds in a Bornean tropical rainforest under sustainable forest management. For Ecol
592	Manage 270:248–256

593	Sapari I, Sadikin LA, Santoso E, Sadranto M (2005) Biodiversity, social, economy and
594	culture of communities in three villages of upstream Belantikan, Central Kalimantan.
595	Pangkalan Bun, Indonesia
596	Slik JWF, Verburg RW, P. K (2002) Effects of fire and selective logging on the tree species
597	composition of lowland dipterocarp forest in East Kalimantan, Indonesia. Biodivers
598	Conserv 11:85–98
599	Stanford CB (1989) Predation on capped langurs (Presbytis pileata) by cooperatively hunting
600	jackals (Canis aureus). Am J Primatol 19:53-56
601	Stark DJ, Nijman V, Lhota S, Robins JG, Goossens B (2012) Modeling population viability
602	of local proboscis monkey Nasalis larvatus populations: conservation implications.
603	Endanger Species Res 16:31–43
604	Strasser E (1992) Hindlimb proportions, allometry, and biomechanics in Old World Monkeys
605	(Primates, Cercopithecidae). Am J Phys Anthropol 87:187-213
606	Struhsaker T. (2000) The Effects of Predation and Habitat Quality on the Socioecology of
607	African Monkeys: Lessons from the Islands of Bioko and Zanzibar. In: Whitehead PF,
608	Jolly C. (eds) Old World Monkeys. Cambridge University Press, Cambridge (UK), p
609	393–430
610	Supriatna J, Manullang BO, Soekara E (1986) Group composition, home range, and diet of
611	the maroon leaf monkey (Presbytis rubicunda) at Tanjung Puting Reserve, Central
612	Kalimantan, Indonesia Primates 27:185–190
613	The Nature Conservancy (2011) Berau Forest Carbon Programme: Delivering Practical
614	Solutions to Support Development of a National-level REDD Framework in Indonesia.
615	Uhde NL, Sommer V (2002) Anti-predatory behaviour in gibbons (LE Miller, Ed.). Eat or be
616	Eaten Predat Sensitive Foraging Among Primates:268–291
617	Wanelik K, Abdulazis, Cheyne SM (2013) Note-, phase- and song-specific acoustic variables
618	contributing to the individuality of male duet song in the Bornean Southern gibbon
619	(Hylobates albibarbis). Primates 54:159–170
620	Wells K, Pfeiffer M, Lakim MB, Linsenmair KE (2004) Use of arboreal and terrestrial space
621	by a small mammal community in a tropical rain forest in Borneo, Malaysia. J Biogeogr
622	31:641–652
623	Whitten AJ (1980) The Kloss Gibbon in Siberut. University of Cambridge
624	Wilcove DS, Giam X, Edwards D., Fisher B, Koh L (2013) Navjot's nightmare revisited:
625	logging, agriculture, and biodiversity in Southeast Asia. Trends Ecol Evol 28:531–540
626	Wilcox CH, Supiansyah, Abdul Azis K, Zainuddin J, Rahman, Chevne SM (2017) Predator

627	Mobbing and Interspecies Cooperation: An interaction between gibbons, langurs and a
628	clouded leopard. Asian Primates J 6:20–26
629	Wilson CC, Wilson WL (1975) The influence of selective logging on primates and some
630	other animals in East Kalimantan. Folia Primatol 23:245-274
631	Wilting A, Fischer F, Bakar SA, Linsenmair KE (2006) Clouded leopards, the secretive top
632	carnivore of South-East Asian rainforests: their distribution, status and conservation
633	needs in Sabah, Malaysia. BMC Ecol 6:1–27
634	Workman C, Schmitt D (2012) Positional Behavior of Delacour's Langurs (Trachypithecus
635	delacouri) in Northern Vietnam. Int J Primatol 33:19-37
636	Zuberbuhler K, Jenny D (2002) Leopard predation and primate evolution. J Hum Evol
637	43:873–886
638	