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Down from the treetops: red langur (*Presbytis rubicunda*) terrestrial behavior

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Abstract

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 behavior has been found at six of the eight sites surveyed. We 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 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 traveling (29% direct observations, 13% camera traps). Red langurs are found on the ground throughout the day, at similar times to activity periods of the apex predator, the Sunda clouded leopard (*Neofelis diardi*). We suggest that ground use by red langurs could be an adaptation to disturbed forest to exploit additional food sources and to facilitate travel.

Keywords Langur · Terrestriality · Logging · Camera traps

Introduction

Habitat conversion, degradation, and loss continues at a rapid rate in many tropical forests and 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 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 logged tropical forests is less well studied (Samejima

et al. 2012; Burivalova et al. 2014; 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 and Wilson 1975; Estrada and 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 behavior, and if novel behaviors, e.g., coming to the ground, are a result of disturbance or actually a previously understudied part of a normal behavioral repertoire (Miller 2002; Zuberbuhler and Jenny 2002; Campbell et al. 2005; Mourthé et al. 2007; Loken et al. 2013, 2015; Ancrenaz et al. 2014; Ashbury et al. 2015)

Terrestrial behavior 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

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indicate a broader behavioral repertoire and ability to make use of different space (Ancrenaz et al. 2014).

The Asian colobines of genus Presbytis are small-bodied (~6 kg), 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, favoring arboreal leaping (Fleagle 1977, 1978; Strasser 1992). However, when investigating positional behavior in Delacour's langurs Workman and Schmitt (2012) found no real morphological adaptation to living on limestone karsts but more flexibility of behavior. Eighty % of locomotion was on rocks, but there was barely any leaping (4%). Workman and Schmitt (2012) suggest that the generalized locomotor capabilities of cercopithecids allow them this behavioral flexibility despite morphology (Workman and Schmitt 2012).

The red langur, *Presbytis rubicunda*, is endemic to Borneo and the adjacent island of Karimata (Medway 1970) and occupies the majority of the habitat types across the island (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. 1986) except for rare occasions to engage in geophagy (Davies and Baillie 1988; Davies et al. 1988; Rawson and 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 behavior (Giman et al. 2007; Samejima et al. 2012; Loken et al. 2013; Cheyne et al. 2015a, b, 2016).

In Sabangau peat-swamp forest, Central Kalimantan, we recorded *P. rubicunda* engaging in terrestrial behavior through researcher observation and remote observation using camera trapping over an 18-month period. In seven 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 behaviors 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 increased predation risks.

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- 4. Was frequency of ground use affected by logging, burnt forest, habitat type and presence of hunting?
- 5. Is terrestrial behavior affected by season?

Here, we detail the circumstances under which terrestrial behavior was observed and discuss the ecological and conservation implications.

Study species

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 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 and 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 Vulnerable 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 (totaling 45 years which is approximately three generations (Cheyne et al. 2017). Age of first reproduction for red langurs is not confirmed but is estimated to be between 7 and 20 years 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 2014). 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 seven other sites surveyed for durations ranging from 30 to 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 44 trap nights. Functional trap nights account

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Table 1 Summary of habitat and climactic characteristics of each study area

Grid	Central latitude	Central longitude	Total survey days	Total number of cameras sta- tions	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 ^a	4146	35	72	93	Harrison et al. (2012), Wanelik and Abdulazis Cheyne (2013)
Belantikan	1.529640°	111.361660°	114	50 ^a	4583	19	72	109	Sapari et al. (2005)
Kutai	0.528546°	117.444857°	101	48 ^a	3269	41	152	246	Rodman (1977)
Lesan	1.591214°	117.142854°	195	70 ^a	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. (2015b), McConkey and Chivers (2004)
Sabangau ^b	- 2.321480°	113.899730°	185	30 ^a	5487	12	29	30	Morrogh- Bernard et al. (2003), Cheyne (2010)
Sungai Wain	1.085150°	116.835000°	83	79 ^a	4729	35	69	86	Rustam and Tsuyuki (2012), Stark et al. (2012), Bersacola et al. (2014), Gilhooly et al. (2015)

Min and max a.s.l. refer to placement of cameras not the overall altitude of the study area

^aCameras were in pairs

^bCameras have been in place in Sabangau since May 2008 but for the purposes of comparison only data from a 6-month period were used

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).

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 \leq 15 years and is recovering (Fig. 1).

Methods

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



Fig. 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 shad*-

and collected instantaneous behavioral data on a focal adult female every 5 min, including activity and height of the focal animal. We collected feeding data on a focal adult

female at the instant the behavior began until it stopped,

ing indicates high elevation; *dark grey* shading indicates low elevation. See Supplementary Information for a map detailing exact study grid location

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 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 maximize the success rate of photographic 'detections' (Wilting et al. 2006; Gordon and Stewart 2007; Cheyne et al. 2013a, b). Two cameras were placed opposite each other, 7–10 m apart to create a paired station at each location with the aim of photographing each flank of the animal simultaneously (Brodie and Giordano 2012). In Murung Raya and Mungku Baru only one camera was placed at each location (Cheyne et al. 2015a, b). 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 et al. 2013a, 2017; Adul et al. 2015). The Capture IR cameras use an infrared flash to minimize 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 season (Gordon and Stewart 2007; Cheyne and Macdonald 2011; Cheyne et al. 2013a).

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 to 1 km 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 (number of years since logging occurred), presence of hunting and fire on the presence of red langurs on the ground. We ranked models based on the Akaike Information Criterion (AIC) values: models with the lowest AIC values were identified as the best output models.

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, characterized by four distinct behaviors [total data points 25,502 (taken at 5-min intervals following (Ehlers Smith et al. 2013a)]: feeding 50, traveling 29, resting 20 and social behavior 1. We further catalogued 31 of the 82 occasions of the focal individual feeding from the ground independent of the instantaneous point over 100 min by breakdown of time and food types consumed on the forest floor by the focal individual: water from the ground 17 (25 min), water from nepenthes 5 (10 min), fungi 10 (50 min), pith 6 (13 min), leaves 2 (4 min) and unknown 41 (103 min). Images and videos of red langurs on the ground were obtained from in six of the eight sites (a total of 78 independent images/videos). Red langurs were confirmed present in the two remaining sites (Rodman 1977; Bersacola et al. 2014) but the langurs were not seen on the ground (Table 2).

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

Red langur behavior on the ground

Red langurs predominantly used the ground for traveling and feeding across study sites (Fig. 3). Feeding was classified when the langurs were holding food items or clearly seen to have food in their mouth. Traveling was classified as any

Table 2 Number of independent photos of red langurs on the ground across all sites as detected by the cameras

	Habitat	Total images/ sightings	Logging status/age (years)	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 ^a	Lowland dipterocarp (LD)	3	> 10	Y	Y
Murung Raya	Lowland montane	1	> 10	Ν	Y
Kutai	Lowland dipterocarp	0	> 10	Ν	Y
Sungai Wain	Lowland montane, pristine and remote	0	> 20	Ν	Ν
Mungku Baru	Ombrogenous PSF	21	> 20	Y	Y
Lesan	Lowland dipterocarp/alluvial PSF	40	> 20	Ν	Y
Belantikan		1	> 20	Y	Y

0 =not detected. Fire and hunting: Y = has occurred and/or still occurring, N = has never occurred. Logging status: current = ongoing, > 10 = logging occurred more than 10 years ago but has stopped, > 20 = logging occurred more than 20 years ago but has stopped

^aSabangau 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)





Study Location

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



Fig. 4 Times of sightings/ images of red langurs as % of total sightings/images



movement and resting where the animals are not in motion. Social activity was classified as any interaction between two or more individuals and direct gaze at the cameras was classed as looking at the camera.

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

Of the eight sites, only five had cameras present consecutively across wet and dry seasons (Kutai, Lesan, Mungku Baru, Sabangau and Sungai Wain). Only three of those sites had images/sightings of red langurs on the ground: Lesan 2 (one wet season, one dry season); Mungku Baru 21 (12 wet season, nine 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, $\chi^2 = 22.01, p > 0.05$; Fig. 5).

Habitat and disturbance

There is a possible negative relationship between habitat/ altitude and number of images obtained (Pearson correlation p=0.09). While we recognize that habitat and mammalian guild structure, e.g., forest types/structure, food availability and animal diversity are likely important determinants affecting their terrestrial behaviors (Cheyne et al. 2016), red

25 Number of indepedant photos/sightings 20 15 10 5 0 November February September December october March APIII June 1J1H AUBUST 124 Januar Month 60 200 180 E 50 160 study area Number of independat images 140 40 120 the 30 100 j Number Average altitude 80 independent images 20 60 Average 40 altitude (m) 10 20 0 0 Peat Dipterocarp Montane General Habitat Type



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

langurs are recorded on the ground more frequently at low altitudes (Fig. 6). Though this trend 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 et al. 2018).

Of the 78 images/sightings on the camera traps 4% (three 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 (Fig. 7).

Discussion

Red langur behavior 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

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behavior it is important to investigate other drivers for terrestriality (McKey et al. 1981; Davies and Oates 1994; Rawson and 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 behavior 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. 2011). 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 and Sommer 2002; Hart 2007; Morino 2011; Clarke et al. 2012; Burnham et al. 2012; 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 were thought to have a minimal influence on predators (Whitten 1980). Longer-term studies and increased focus on predation does show that snakes and raptors are important predators of primates in the wild (Shine et al. 1998; Wiens and Zitzmann 1999; Fam and Nijman 2011; Matsuda et al. 2011; Tsuji et al. 2014, 2016) and in rescue centers (SMC pers. obs.).





Descending to the forest floor could be a defense strategy against aerial predators e.g., (Seyfarth and Cheney 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. 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 1600 h (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 from clouded leopards may not be an explanatory factor.

Habitat and disturbance

Higher quality foods (leaves containing higher protein but lower fiber) 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 and 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 et al. 2013b). Thus, this behavior could be a potential indicator of habitat quality. Selective logging is likely to influence the ecology of P. rubicunda as the practice removes the largest trees, upon which feeding (Ehlers Smith et al. 2013a), distribution (Ehlers Smith and Ehlers Smith 2013), and sleeping sites (Ehlers Smith 2014) are dependent. Given the increased incidences of terrestrial behaviors in logged forests and the frequency with which feeding behaviors were associated with terrestriality, it is likely that terrestrial foraging forms an important part of the behavioral 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 2014), 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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