

1 **DOWN FROM THE TREETOPS – RED LANGUR (*PRESBYTIS RUBICUNDA*)**  
2 **TERRESTRIAL BEHAVIOUR**

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9 Key words: langur, terrestriality, logging, camera traps

10

11 **Abstract**

12 Using direct observations and camera traps at eight sites across Indonesian Borneo we show  
13 how red langurs (*Presbytis rubicunda*) are more terrestrial than previously believed, regularly  
14 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  
16 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  
18 increased elevation of the habitat. When on the ground, red langurs are predominantly  
19 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.

24

25 **Introduction**

26 Habitat conversion, degradation and loss continues at a rapid rate in many tropical forests and  
27 has mixed effects on forest animal diversity (van Nieuwstadt et al. 2001, Wells et al. 2004,  
28 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  
30 unlogged forests just a few decades after logging has ceased (Brodie et al. 2014; Danielsen  
31 and Heegaard 1994; Slik et al. 2002). Selectively logged forests are becoming an increasingly  
32 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,

35 such as deforestation driven by fire, agriculture or tree-plantation developments (Wilson &  
36 Wilson 1975, Estrada & Coates-Estrada 1996, Oka et al. 2000, Slik et al. 2002, O'Brien et al.  
37 2003, Meittinen et al. 2012). What is less studied, is the impact on animal behaviour, and if  
38 novel behaviours e.g. coming to the ground, are a result of disturbance or actually a  
39 previously understudied part of a normal behavioural repertoire (Miller 2002, Zuberbuhler &  
40 Jenny 2002, Campbell et al. 2005, Mourthé et al. 2007, Loken et al. 2013, 2015, Ancrenaz et  
41 al. 2014, Ashbury et al. 2015)

42

43 Terrestrial behaviour in arboreal primates is recorded from many sites and has been attributed  
44 to socio-ecological factors such as food acquisition and aggression avoidance, and/or the  
45 anthropogenic effects of habituation to observer presence and habitat disturbance (Campbell  
46 et al. 2005, Mourthé et al. 2007). Increased terrestriality in arboreal primates is thought to  
47 increase the risk of predation (Miller 2002, Ancrenaz et al. 2014) and disease (Chapman et al.  
48 2005) which has implications for the conservation of many threatened primate species.  
49 Increased use of the ground may be an indicator of lower quality habitat (Wells et al. 2004) or  
50 could indicate a broader behavioural repertoire and ability to make use of different space  
51 (Ancrenaz et al. 2014).

52

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

67

68 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  
71 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  
74 camera traps placed on the ground, though these studies present encounter rates only and do  
75 not discuss behaviour (Giman et al. 2007, Samejima et al. 2012, Loken et al. 2013, Cheyne et  
76 al. 2015, 2016).

77

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  
80 trapping over an 18-month period. In 7 other sites where these primates are not habituated,  
81 we used camera traps which were placed for 30-160 days.

82 We looked at these data to address the following questions:

- 83 1. Were red langurs predominantly using the ground to travel, as might be expected in  
84 heavily disturbed forests?
- 85 2. If travel was not the primary activity, what behaviours were red langurs engaged in on  
86 the ground?
- 87 3. Which age/sex class was using the ground more? If access to food was a driving  
88 influence we may expect adults to use the ground more, and younger animals to avoid  
89 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?

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

95

## 96 **Study Species**

97 *P. rubicunda* is physiologically adapted for folivory (Bauchop and Martucci 1968), although  
98 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  
100 mixed-sex group, with extra males forming all-male bands or ranging alone (Davies 1984;  
101 Supriatna et al. 1986; Ehlers Smith et al. 2013b). Currently listed as Least Concern on the

102 IUCN Red List, this species inhabits the same forests as the four species of Bornean gibbons  
103 (all listed as Endangered on the IUCN Red List (Geissmann & Nijman 2008a, b, c, Nijman et  
104 al. 2008)) and the Bornean orangutan (listed as Critically Endangered (Ancrenaz et al. 2016)).  
105 Red Langurs are being upgraded to Red List Endangered across their range based on a recent  
106 review predicting an estimated population reduction of over 50% when considering the past  
107 30 years and habitat change due to draining of peat swamps, logging and burning into the  
108 next 15 years (totalling 45 years which is approximately 3 generations (Cheyne et al.)). Age  
109 of first reproduction for red langurs is not confirmed but is estimated to be between 7-20yrs  
110 based on other langur species (Harley 1990). Between 2000 and 2010 the species experienced  
111 a mean 10% habitat occupancy reduction across all subspecies; *P. r. chrysea* experienced a  
112 ~21% habitat occupancy reduction (Ehlers Smith 2014a). Where the species persists, there is  
113 hunting and collection for the wildlife trade and for human consumption. A large part of the  
114 species range is in peat swamp - an extremely threatened ecosystem.

115

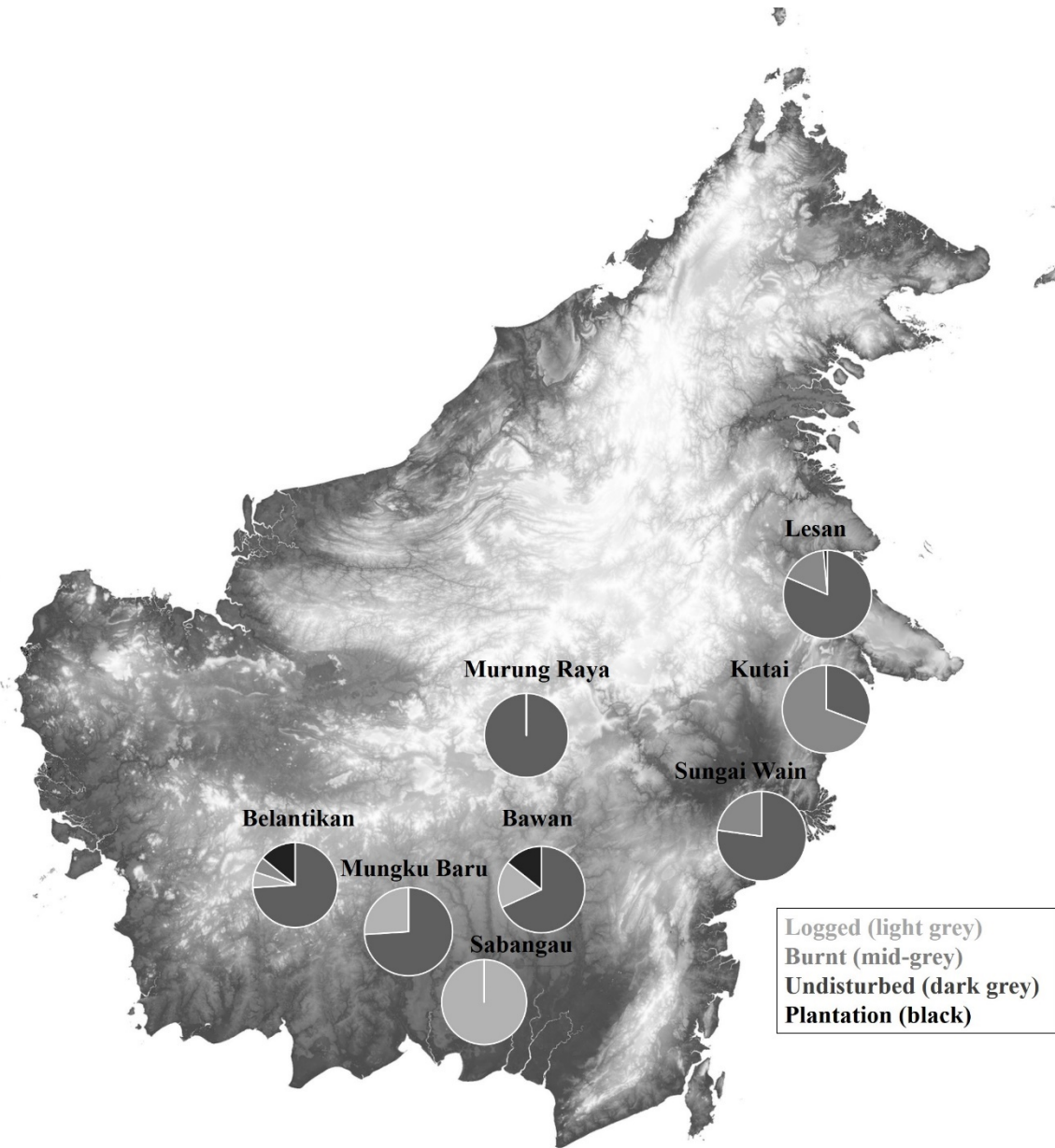
#### 116 **Study Grids**

117 We present data from our long-term site in Sabangau and from 7 other sites surveyed for  
118 durations ranging from 30-180 days. In two of the short-term sites (Murung Raya and  
119 Mungku Baru), the camera-trap survey areas were considerably smaller due to access and  
120 time limitations (Table 1). The study sites differ in habitat type, altitude, size and human  
121 pressures which also impacted the size of the area surveyed by the cameras (Cheyne et al.  
122 2016). The number of functional trap nights is presented (i.e. one camera operating for one  
123 calendar night is one trap night, 44 cameras operating for one calendar night is 44 trap nights.  
124 Functional trap nights account for the number of trap nights with deductions made for when  
125 individual cameras were not functioning (Andrew Royle et al. 2009, Cheyne et al. 2016).

126 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  
 127 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-  
 128 month period were used.

<b>Grid</b>	<b>Central latitude</b>	<b>Central Longitude</b>	<b>Total survey days</b>	<b>Total number of cameras stations (* indicates cameras were in pairs)</b>	<b>Trap nights (number of active survey nights)</b>	<b>Min a.s.l (m)</b>	<b>Mean a.s.l (m)</b>	<b>Max a.s.l (m)</b>	<b>References</b>
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)

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



133  
134 Figure 1 Map of the study region in Indonesian Borneo showing for each study grid the  
135 proportion of camera stations in logged (light grey), burnt (mid-grey), undisturbed (dark  
136 grey) and plantation (black) forest. The elevation model is from Google Earth. White shading  
137 indicates high elevation; dark grey shading indicates low elevation. See Supplementary  
138 Information for a map detailing exact study grid location.

139

140 **Methods**

141 Direct Observations (Sabangau only)

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

150

151 Camera Trapping

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

166

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

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

175  
 176

177 **RESULTS**

178 Frequency of Encounters on the Ground

179 We recorded 82 counts (0.32% of all focal observations) of ground use by the focal  
 180 individual at the instantaneous data point, characterised by four distinct behaviours (Total  
 181 data points 25,502 (taken at 5-min intervals following (Ehlers Smith et al. 2013b)): feeding =  
 182 50, travelling = 29, resting = 20 and social behaviour = 1. We further catalogued 31 of the 82  
 183 occasions of the focal individual feeding from the ground independent of the instantaneous  
 184 point over 100 minutes by breakdown of time and food types consumed on the forest floor by  
 185 the focal individual: water from the ground = 17 (25mins), water from Nepenthes = 5  
 186 (10mins), Fungi = 10 (50mins), Pith = 6 (13mins), Leaves = 2 (4mins) and Unknown = 41  
 187 (103mins). Images and videos of Red langurs on the ground were obtained from in 6 of the 8  
 188 sites (a total of 78 independent images/videos). Red langurs were confirmed present in the 2  
 189 remaining sites (Rodman 1977, Bersacola et al. 2014) but the langurs were not seen on the  
 190 ground (Table 2).

191

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

	<b>Habitat</b>	<b>Total Images/Sightings</b>	<b>Logging status/age</b>	<b>Fire</b>	<b>Hunting</b>
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



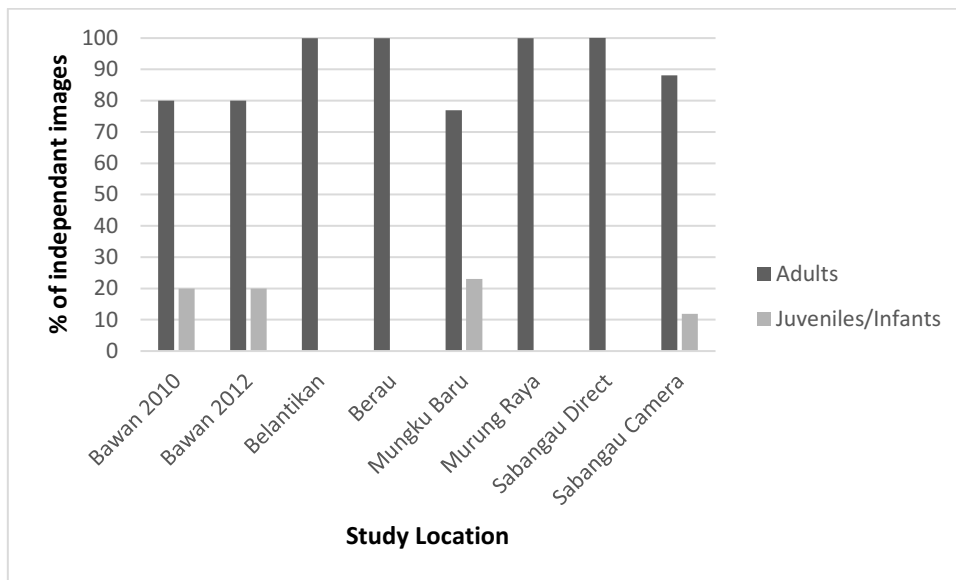
Sungai Wain	Lowland Montane. Pristine and remote	0	> 20	N	N
Mungku Baru	Ombrogenous PSF	21	> 20	Y	Y
Lesan	Lowland Dipterocarp/Alluvial PSF	40	> 20	N	Y
Belantikan		1	> 20	Y	Y

194

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

197

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



200

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

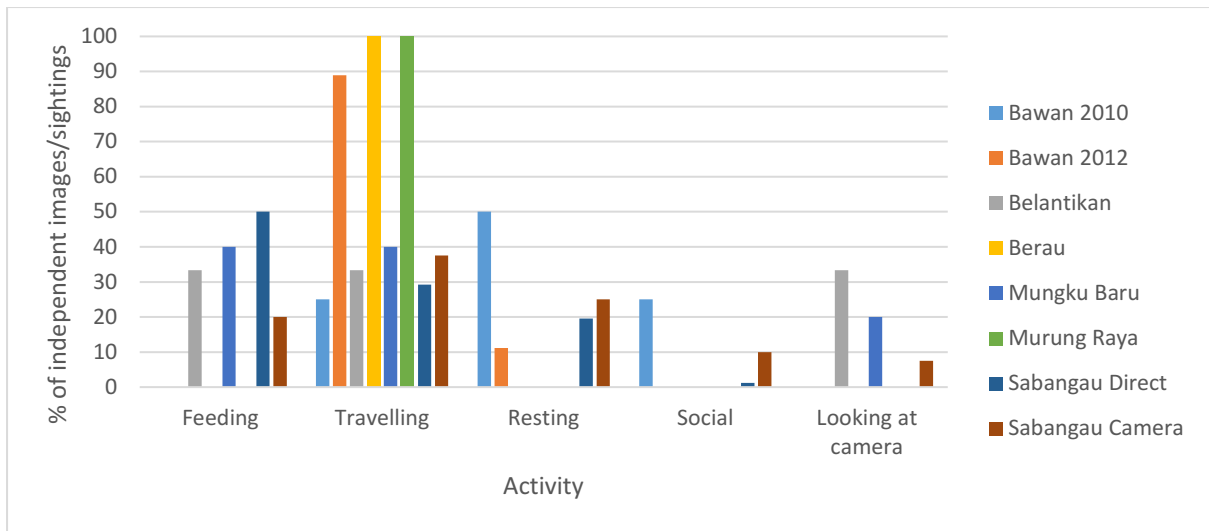
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203

#### 204 Red Langur Behaviour on the Ground

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

210



211

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

213

sightings/images.

214

215 Red langurs came to the ground throughout the active period with peaks between 1000-

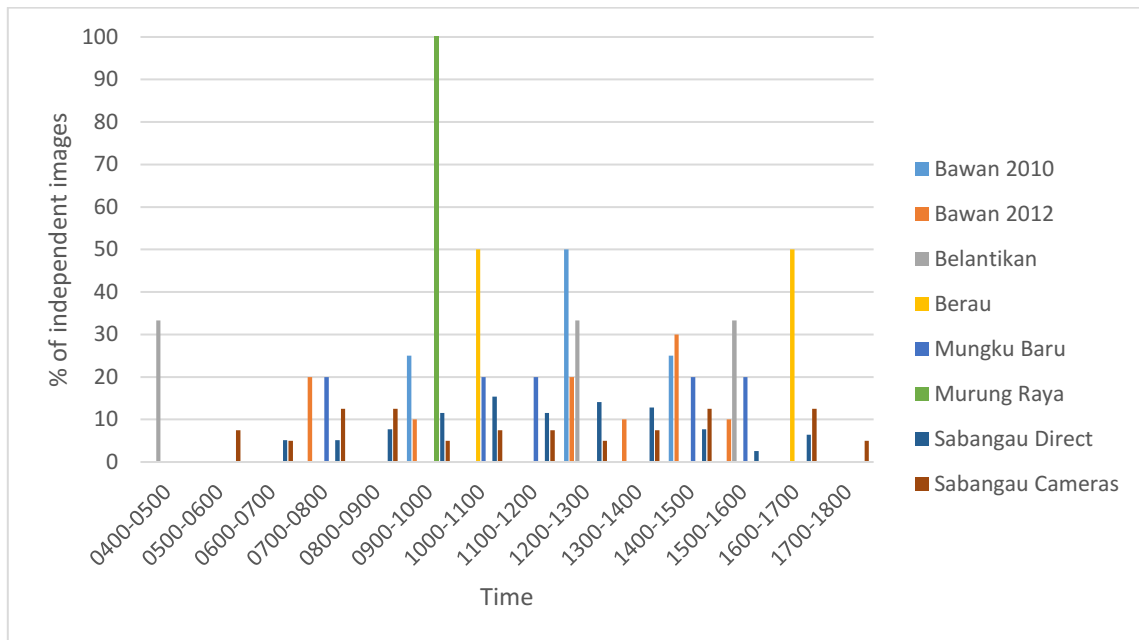
216 1100h, 1200-1300h and 1400-1500h though there is variation between sites (Figure 4). These

217 times of greatest terrestrial behaviour are not significantly affected by the behaviour being

218 performed on the ground (Friedman ANOVA:  $\chi^2 = 0.74$ ,  $n = 6$ ,  $d.f. = 4$ ,  $p = 0.69$ ).

219

220



221

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

223

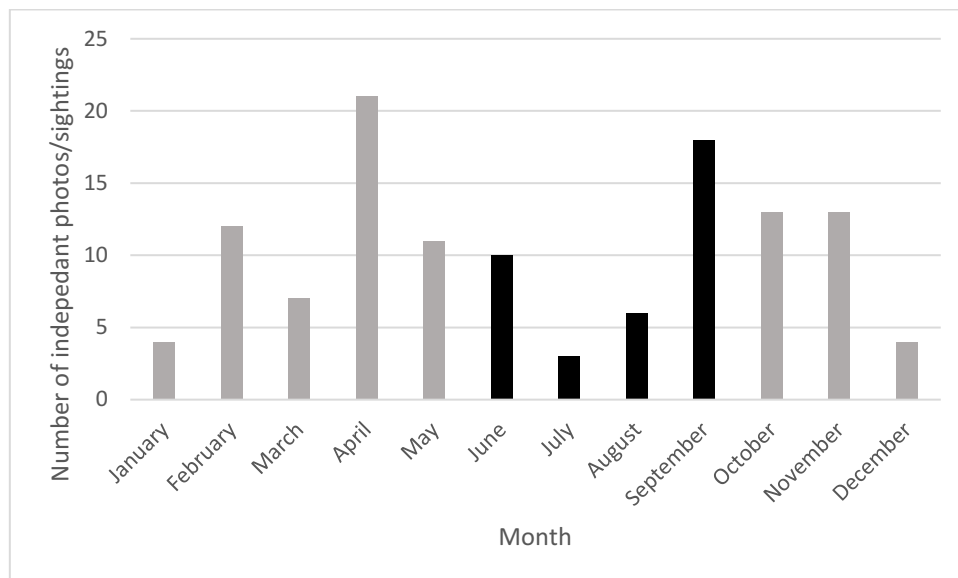
224 Of the 8 sites only 5 had cameras present consecutively across wet and dry seasons (Kutai,  
225 Lesan, Mungku Baru, Sabangau and Sungai Wain). Only 3 of those sites had  
226 images/sightings of red langurs on the ground: Lesan = 2 (1 wet season, 1 dry season);  
227 Mungku Baru = 21 (12 wet season,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

229

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

233

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235

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

238

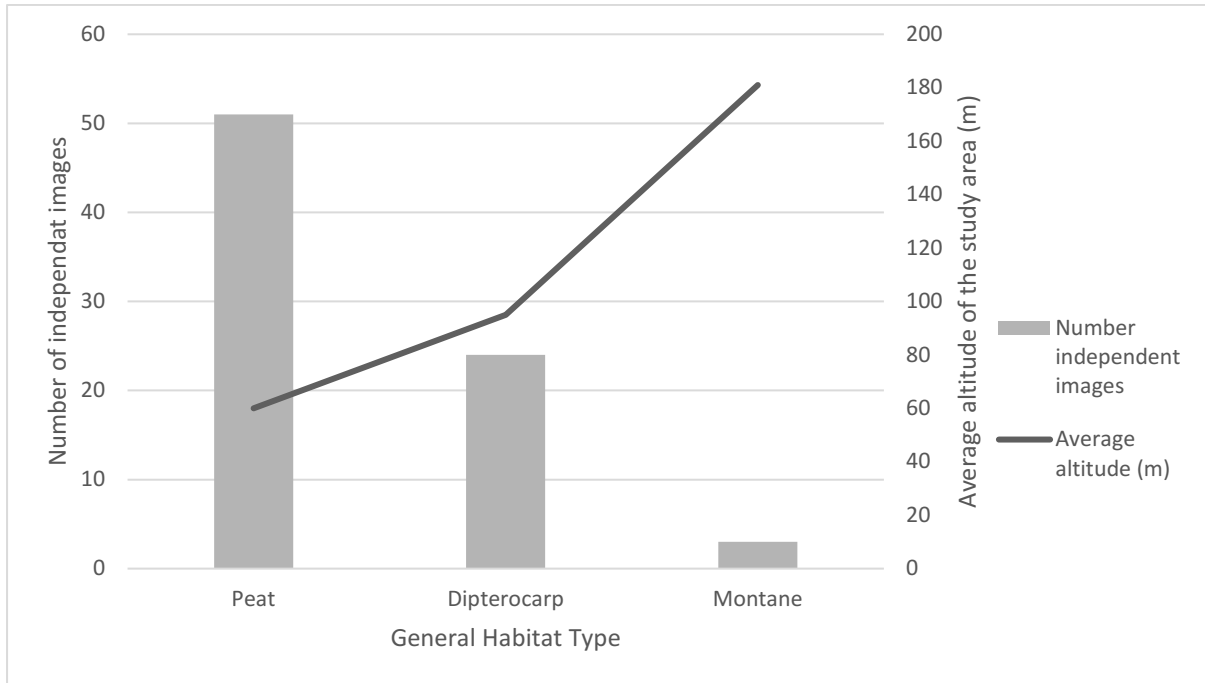
### 239 Habitat and Disturbance

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

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

250

251



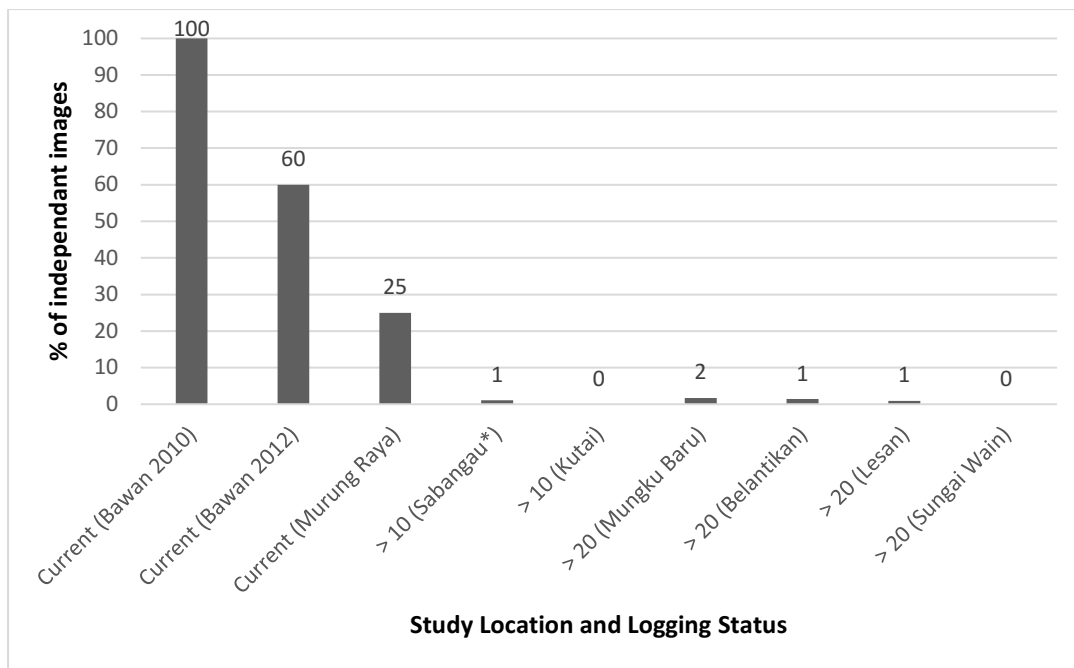
252

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

255

256 Of the 78 images/sightings on the camera traps 4% (3 images) were in forests unaffected by  
257 fires and 96% (75 images) were obtained in areas where the forests had experienced at least  
258 one fire event. A possible reason for the langurs making use of the ground could be impacts  
259 of logging. Using logging data obtained for these areas (Cheyne et al. 2016) we assessed the  
260 number of images of red langurs on the ground as a function of total primate images and  
261 compared this to this logging history of the area at a broad scale. The GLM predicted that the  
262 age of logging model most consistently explains presence of red langurs on the ground ( $F =$   
263  $5.1, p = 0.036$ ), followed by fire  $F = 6.4, p = 0.04$ ). The presence of hunting model did not  
264 explain any of the variation  $F = 4.3, p = 0.08$ , (Figure 7).

265



266

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

269

270 **DISCUSSION**

271 Red Langur Behaviour on the ground

272 Asian colobines are infrequently recorded on the ground and are poorly adapted to  
 273 terrestriality. Colobines do use the ground for feeding e.g., geophagy, drinking water and  
 274 eating fungi but in the absence of long-term data regarding this behaviour it is important to  
 275 investigate other drivers for terrestriality (McKey et al. 1981, Davies & Oates 1994, Rawson  
 276 & Tuong Bach 2011). Arboreal primates may descend to the ground in more disturbed  
 277 habitats and in the presence of researchers (to whom they are habituated) in order to flee  
 278 (Ehardt et al. 2005). The degree of terrestrial behaviour may be related to habituation and has  
 279 implications for conservation owing to vulnerability from predation/disease/parasite  
 280 transmission (Hart 2007, Matsuda et al. 2008, Morino 2011, Hilser et al. 2014). Predation rate  
 281 is difficult to evaluate, and may not be a limiting factor, but the few data which are available  
 282 on gibbons (primates of a similar size) suggest that there is a predation risk (Uhde & Sommer  
 283 2002, Hart 2007, Morino 2011, Clarke et al. 2012, Burnham et al. 2013, Wilcox et al. 2017).  
 284 Hunting pressure was measured by presence of hunters on the camera traps and is a rough  
 285 proxy for pressure of human hunting. Most hunters were observed in Bawan forest, where red  
 286 langurs were observed on the ground. As monkeys are infrequently targeted by human  
 287 hunters they may come to the ground more frequently (Marshall et al. 2006, Meijaard et al.

288 2012). Species that travel along the ground and live in more open forests are more prone to  
289 predation (by other animals and humans; Rudran 1973; Stanford 1989). Predation of arboreal  
290 primates by other animals is hardly ever reported in SE Asia (Davies 1984, Burnham et al.  
291 2012) and much lower than African forests (Aldrich-Blake 1970, Busse 1977). Pythons  
292 appear to have a minimal influence on predators (Whitten 1980). Forest monkeys travel and  
293 forage on the ground far more in the absence of leopards (Struhsaker 2000). The monkeys on  
294 the islands do so much more frequently in the absence of leopards. In areas where people  
295 hunt primates colobine populations may be reduced (Bennett and Sebastian 1988).

296

### 297 Age/sex class ground use

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

306

### 307 Habitat and Disturbance

308

309 Higher quality foods (leaves containing higher protein but lower fibre) may be more available  
310 in disturbed forests (Ehlers-Smith et al. 2013, Matsuda et al. 2013), and there are also  
311 potentially more shade-tolerant plants on the ground in disturbed forests (Estrada &  
312 CoatesEstrada 1996, Munoz et al. 2006, Anderson et al. 2007). Thus, red langurs may have  
313 more opportunities to come down to the ground in these habitats.

314 These findings are preliminary and require further investigation to find correlations, unless  
315 the use of the ground is unrelated to habitat disturbance. Only one site (Sungai Wain) has no  
316 regular encroachment for hunting and this site did not yield any images of red langurs on the  
317 ground. With these data, it is not possible to determine any relationship between hunting  
318 presence and frequency of ground use by red langurs. There was no obvious influence of  
319 season on the frequency with which red langurs came to the ground either from direct  
320 observational data or from the camera traps. However, the impacts of hunting, logging and

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

323

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

341

342

343

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