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Coming down from the trees: Is terrestrial activity in Bornean orangutans natural or disturbance driven?

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The orangutan is the world's largest arboreal mammal, and images of the red ape moving through the tropical forest canopy symbolise its typical arboreal behaviour. Records of terrestrial behaviour are scarce and often associated with habitat disturbance. We conducted a large-scale species-level analysis of ground-based camera-trapping data to evaluate the extent to which Bornean orangutans *Pongo pygmaeus* come down from the trees to travel terrestrially, and whether they are indeed forced to the ground primarily by anthropogenic forest disturbances. Although the degree of forest disturbance and canopy gap size influenced terrestriality, orangutans were recorded on the ground as frequently in heavily degraded habitats as in primary forests. Furthermore, all age-sex classes were recorded on the ground (flanged males more often). This suggests that terrestrial locomotion is part of the Bornean orangutan's natural behavioural repertoire to a much greater extent than previously thought, and is only modified by habitat disturbance. The capacity of orangutans to come down from the trees may increase their ability to cope with at least smaller-scale forest fragmentation, and to cross moderately open spaces in mosaic landscapes, although the extent of this versatility remains to be investigated.

The Bornean orangutan *Pongo pygmaeus* is the largest arboreal species in the world and its survival is linked to forest habitat^{1,2}. Despite the orangutan's iconic value and millions of dollars spent annually on its conservation³, the species is declining throughout its range. In Borneo, more than 70% of orangutans occur in



fragmented multiple-use and human-modified forests that have lost many of their original ecological characteristics^{4,5}. The consequences of these drastic habitat changes on orangutan survival, behaviour and ecology are only just starting to be documented^{3,4,6,7}. Some authors have proposed that forest degradation may force the species to the ground more frequently^{8,9}. We can suppose that increased terrestriality would increase predation risk, interactions with and persecution by humans, and exposure to novel pathogens. On the other hand, terrestrial behaviour could also facilitate movement and, therefore, dispersal, especially in degraded or fragmented landscapes as a result of natural or man-made processes. It could also create new opportunities to access different food sources¹⁰. Ultimately, a better understanding of the drivers of orangutan terrestriality and how this influences dispersal and movement is important for designing effective landscape management strategies for maintaining viable meta-populations of this species in Borneo⁴.

Most studies of orangutan locomotion have been based on direct observations^{11,12}. However, orangutans may be reluctant to come to the ground in the presence of human observers, and remote camera traps present an opportunity to overcome this potential bias⁸. We conducted a large-scale species-level analysis of ground-based camera-trapping data to evaluate the extent to which Bornean orangutans travel terrestrially and to investigate possible drivers for this behaviour.

Results

Altogether we collected camera-trapping data from 16 study areas from Sabah (Malaysia) and East and Central Kalimantan (both Indonesia), for which reliable orangutan density estimates were available (Table 1). Pictures were collected between June 2006 and March 2013, and included data from all months of the year. The total

Table 2 | AIC summaries for zero-inflated Poisson regression of photo-counts of orangutans; models for the probability of coming to the ground as a function of forest class (for), camera trap placement (cam) and orangutan density (dens), or no covariates (0), conditional on best photographic frequency model containing all covariates. For definition of forest classes and camera trap placement, see Methods

Model	No. parameters	AIC	delta AIC	AIC weight
for + dens	16	2550.120	0.000	0.533
for + cam + dens	18	2550.783	0.664	0.364
cam + dens	13	2554.802	4.683	0.055
For	15	2555.798	5.678	0.032
for + cam	17	2557.085	6.965	0.016
Dens	11	2565.759	15.640	0.000
Cam	12	2567.900	17.781	0.000
0	10	2573.684	23.565	0.000

dataset encompassed 159,152 trap days at 1,409 independent camera-trap stations.

Orangutans were recorded on the ground in all forest classes, indicating that terrestrial activity occurs regardless of habitat disturbance. Nevertheless, the regression model revealed that forest class, camera-trap placement and orangutan density influenced the photographic frequency and the probability of orangutans coming to the ground (Table 3, Figure 1 A–C). Photographic frequencies were significantly higher beneath large canopy gaps than under closed canopy (Figure 1A & 1B, Table 3). In 428 out of 641 orangutan records the sex-age class could be reliably determined (see Methods). We observed females alone 27 times, females with clinging

Table 1 | Summary statistics for orangutan camera trapping data from Borneo used in the present analysis. For definition of forest classes, see Methods

No	Study site	Status ¹	State	No of stations	No of trap days	No of records	Forest class	Orangutan density [ind/km ²]	Density reference
1	Bawan Forest	CFR	Central Kalimantan, Indonesia	65	2,064	2	REC-RIL	2.15	30
2	Croker Range Park	NP	Sabah, Malaysia	35	3,999	0	PRIM & VOL	1.0	5
3	Danum Valley Conservation Area	TPA	Sabah, Malaysia	198	20,223	51	PRIM	1.0	5
4	Deramakot Forest Reserve	CFR	Sabah, Malaysia	144	10,532	25	VOL & OLD-RIL	1.5	5
5	Lower Kinabatangan Wildlife Sanctuary	WS	Sabah, Malaysia	128	19,602	179	VOL	1.1–3.9 ²	31
6	Kuamut Forest Reserve	CFR	Sabah, Malaysia	38	1,949	2	REC-CL	0.1–1.4 ²	5
7	Kutai National Park	NP	East Kalimantan Indonesia	53	3,310	42	VOL	1.0–1.3 ²	Spehar, pers. com.
8	Maliau Basin	TPA	Sabah, Malaysia	27	5,232	0	PRIM & OLD-REC	0.1	5
9	Malua Forest Reserve	CFR	Sabah, Malaysia	107	9,730	40	REC-CL	1.3–1.6 ²	5
10	Sabangau Peat Swamp Forest	NP	Central Kalimantan, Indonesia	58	26,722	49	OLD-RIL	1.7	32
11	Segaliud Lokan Forest Reserve	CFR	Sabah, Malaysia	67	3,452	19	OLD-CL & REC-RIL	1.2	5
12	Kulamba Wildlife Reserve	WR	Sabah, Malaysia	4	252	2	VOL	2.3	5
13	Tabin Wildlife Reserve	WR	Sabah, Malaysia	283	28,462	104	VOL	1.3	5
14	Tangkulap Forest Reserve	CFR	Sabah, Malaysia	100	6,057	37	OLD-CL	0.6	5
15	Ulu Segama Forest Reserve	CFR	Sabah, Malaysia	61	9,829	13	OLD-CL	1.1–1.4 ²	6
16	Wehea Forest	CFR	East Kalimantan, Indonesia	41	7,737	76	OLD-RIL	1.1	Loken, pers. com.
TOTAL				1,409	159,152	641			

¹CFR = Commercial Forest Reserve; NP = National Park; TPA = Totally Protected Area; WS = Wildlife Sanctuary; WR = Wildlife Reserve.

²Density varied between areas.



Table 3 | Model-averaged parameter estimates from zero-inflated Poisson regression of photographic frequencies of orangutans against forest class (PRIM, VOL, RIL-OLD, CL-OLD, RIL-REC, CL-REC, see Methods for abbreviations), camera trap placement (closed canopy, small gap, large gap) and orangutan density. Primary forest and closed canopy were reference categories in the regression

Parameter	Coefficients	Estimate	SE	Lower CI	Upper CI	z value	p value
Frequency (log scale)	Intercept	-5.017	0.227	-5.462	-4.572	22.098	<0.001
	β (VOL)	0.053	0.242	-0.423	0.528	0.217	0.828
	β (RIL-OLD)	-1.064	0.300	-1.653	-0.475	3.542	<0.001
	β (CL-OLD)	-0.229	0.302	-0.821	0.363	0.758	0.448
	β (RIL-REC)	-0.578	1.165	-2.862	1.706	0.496	0.620
	β (CL-REC)	-0.313	0.332	-0.963	0.337	0.943	0.346
	β (small gap)	0.220	0.152	-0.079	0.518	1.443	0.149
	β (large gap)	0.412	0.179	0.061	0.762	2.300	0.021
	β (density)	0.372	0.106	0.166	0.579	3.529	<0.001
	Intercept	1.694	0.337	1.033	2.355	5.022	<0.001
Probability (logit scale)	β (VOL)	-0.423	0.330	-1.070	0.224	1.283	0.200
	β (RIL-OLD)	-1.643	0.456	-2.537	-0.749	3.603	<0.001
	β (CL-OLD)	-0.871	0.380	-1.615	-0.127	2.294	0.022
	β (RIL-REC)	1.070	1.420	-1.714	3.854	0.754	0.451
	β (CL-REC)	-0.353	0.456	-1.247	0.542	0.773	0.439
	β (small gap)	-0.461	0.300	-1.050	0.127	1.538	0.124
	β (large gap)	-0.025	0.398	-0.805	0.756	0.062	0.951
	β (density)	-0.587	0.217	-1.013	-0.162	2.706	0.007

babies or with walking young 63 and 25 times, respectively, unflanged males 48 times, and flanged males 265 times. We recorded flanged males significantly more often than expected based on their proportion in the population (see Methods) ($\chi^2 = 32.050$, df = 1, $p < 0.001$), suggesting they are more terrestrial than unflanged males, and females. Only 15 orangutan records were obtained during night time (before 0600 h and after 1800 h).

Discussion

Overall, Bornean orangutan terrestrial activity appears more common than previous anecdotal observations suggested⁸, which indicates that the species exhibits a flexible and varied repertoire of locomotion. This is supported evolutionarily: the potential ancestors and fossil relative taxa of *Pongo*, are thought to have used more ground locomotion than the current *Pongo*^{14,15}. This, in turn, has led to the suggestion that ancestral orangutans may have been able to cover larger distances on the ground^{13,16}. It should be noted that

the data used in the present analysis come predominantly from the subspecies *P. pygmaeus morio* in northeastern Borneo and there is the potential for regional differences in the species' response to forest characteristics driven by differences in ecological circumstances¹³. For example, an analysis of raw model residuals by study site (Supplementary Information) showed stronger negative outliers for photographic counts from the Sabangau peat swamp (i.e., subspecies *P. p. wurmbi*) than from other sites, suggesting that swamp habitat may reduce terrestriality in orangutans. Further, preliminary data indicate that the Sumatran orangutan *Pongo abelii* is much less terrestrial, possibly because of the presence of tigers *Panthera tigris* as potential predators, which are absent from Borneo¹.

Our analysis shows that the degree of terrestriality is modulated by forest structure. This suggests that anthropogenic canopy disruptions will increase terrestrial activity in orangutans, but habitat disturbance is not the only driver for this behaviour. Indeed, both photographic frequencies and probabilities of coming to the ground

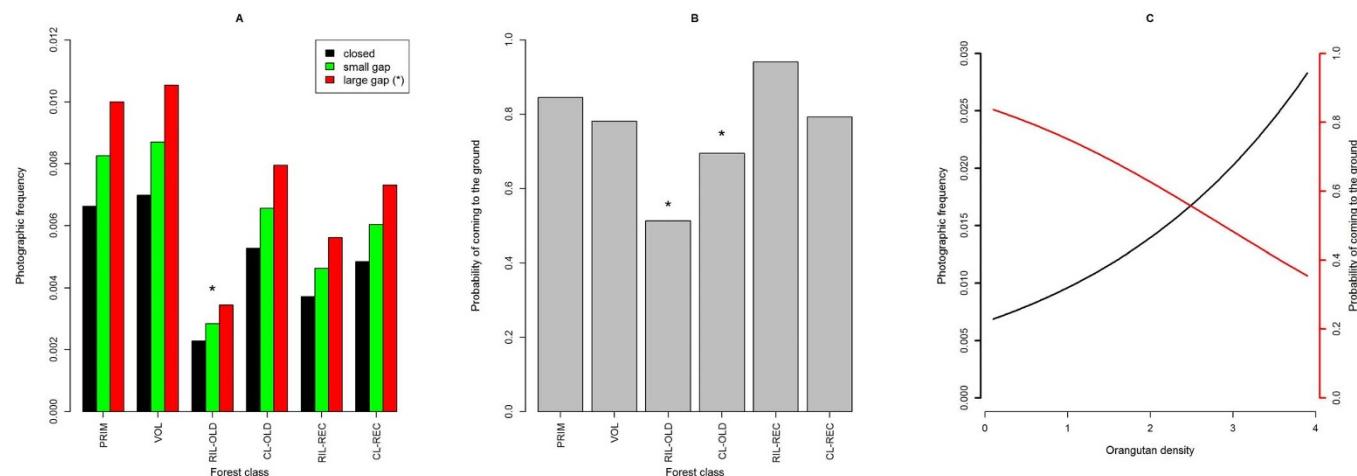


Figure 1 | (A) Photographic frequency (including different camera-trap placement categories) and (B) probability of orangutans coming to the ground for six different forest classes ordered from primary to recently heavily logged forest (PRIM = primary forest; VOL = very old conventionally logged forest >20 years ago; RIL-OLD = reduced impact logging 2–20 years ago; CL-OLD = conventional logging 2–20 years ago; RIL-REC = conventional logging within the last 2 years; CL-REC = conventional logging in the last 2 years). (C) Relationship of photographic frequency (black) and probability of orangutans coming to the ground (red) with orangutan density, plotted for primary forest, but patterns for other forest classes are equivalent.



were lowest in areas logged by reduced impact logging schemes between two and 20 years ago and not, as expected if terrestriality were determined by disturbance, in primary forests. This may be caused by a continuous lower canopy layer that develops after reduced impact logging and is relatively easy to travel through without coming to the ground to cross gaps. In contrast, the irregular canopy structure in primary forests and the large man-made gaps in forests recently logged using conventional logging methods may increase the energetic costs of arboreal locomotion¹¹, offering an explanation for similar terrestriality in these forest classes. Although our data also support the perception that terrestriality in orangutans is most prevalent in larger and heavier flanged males⁹, our camera trap data showed that all age-sex classes travel on the ground irrespective of habitat type.

The ability to cross forest gaps, especially for males, which are the dispersing sex^{17–19}, suggests that gene flow can occur even in disturbed and possibly fragmented habitats¹⁰. In addition to occasional advantages in travelling from place to place, terrestriality could enhance the possibilities for foraging for terrestrial resources, such as succulent shoots, termites or mineral clay^{10,20}. This may be particularly important during periods of habitat-wide fruit scarcity. Heightened orangutan terrestriality in human-modified landscapes and the resulting increase in contact with people creates new risks, such as increased susceptibility to hunting and exposure to new diseases, as great apes are vulnerable to many human diseases^{21,22}.

Our findings reinforce the importance of incorporating degraded forests recovering from logging disturbance into orangutan conservation strategies^{3,4,6}. The capacity of orangutans to come down from the trees may increase their ability to cope with at least smaller scale fragmentation¹⁰, and to cross moderately open spaces in mosaic landscapes, although the extent of this versatility remains to be investigated. In order to design conservation management strategies that will allow for the species to persist in anthropogenic landscapes, however, practitioners need to be mindful of the potential risks associated with terrestrial activities in orangutans. The “man of the forest” cannot be regarded as safely tucked away up in the trees.

Methods

Our analysis is based on a compilation of existing ground-based camera trapping data that had been collected at 16 sites in Borneo, mostly on the northern part of the island (Table 1).

Data base. To avoid inflated counts caused by repeated detections of the same individual, only one record per hour per camera site was included in the data analysis. We excluded all cameras that were placed at salt licks, and data from the orangutan rehabilitation site at Sepilok Forest Reserve, as we assumed that both factors could influence terrestrial behaviour (i.e., a particular resource for the former²⁰ and habituation to humans for the latter²³). To avoid spatial autocorrelation in the data, we only included camera-trap stations that were a minimum of 1 km apart from each other, assuming that orangutans do not move continuously along the ground over distances in the order of a kilometre¹⁰, so that events to come to the ground are independent at that scale. The independence of these observations would be compromised if orangutans routinely moved along the ground over 1 km. This assumption is backed by the observation that the *overall* (i.e. arboreal and terrestrial) maximum distance moved by orangutans within a day is in most cases below 1 km²⁴. Considering these restrictions all analyses are based on 641 independent orangutan records taken at 1,409 stations during 159,152 trap days (see Table 1).

Analysis. All analyses were performed in R, version 2.15.1²⁵.

Terrestrial activity as a function of forest disturbance and density. We hypothesised that regional forest structure and camera-trap site specific canopy structure (also referred to as camera-trap placement), as well as orangutan density, could influence how often orangutans are photographed on the ground. We therefore classified forests into six classes, based on their current and past management history: 1. primary forest (PRIM; not disturbed); 2. very old conventionally logged forest (VOL; last logging more than 20 years ago); 3. old slightly logged forest (OLD-RIL; exploitation using reduced impact logging (RIL) practices between 2–20 years ago); 4. old heavily logged forest (OLD-CL; conventional logging practices 2–20 years ago); 5. recent slightly logged forest (REC-RIL; RIL within the last 2 years); 6. recent heavily logged forest (REC-CL; conventional logging in the last 2 years). We further categorized camera trap placement according to Loken *et al.*⁸ as under closed canopy (0–3 m gaps that orangutans are likely able to cross by tree swaying), small canopy gap (3–5 m gaps that

orang-utans might be able to cross by tree swaying), or large canopy gap (>5 m gaps that orang-utans are unlikely to cross by tree swaying). Gap size was determined post hoc based on field notes and photographs. We recognize that there might be some inherent error in classifying gap size post hoc, but the coarse classification of gap size should buffer most of that error. Orangutan densities were obtained from the literature and from unpublished data of the authors for each site (Table 1). We acknowledge that density estimates were obtained with different methods and that some of these methods are controversial; however, the estimates used here represent the best currently available data for these sites and are widely used to assess the status of the species.

To quantify the influence of the above variables on orangutan terrestriality, we compiled the number of orangutan records taken at each camera location and analysed the data using a zero-inflated Poisson (ZIP) regression²⁶. A ZIP model allows for overdispersion in counts in the form of excess zeros, which we observed in our data set. It is a Binomial-Poisson mixture that attempts to separate zero counts into structural zeros (sites where orangutans never come to the ground so that we can only observe a zero count) and sampling zeros (sites where orangutans do come to the ground but we happen to not record them there). The binomial component of the ZIP model estimates the *probability of coming to the ground* at a given camera trap station. The Poisson component of the ZIP model describes the number of records we expect to observe (referred to as the *photographic frequency*) at a camera trap, conditional on the species coming to the ground at all. Both parameters can be modelled as functions of covariates on the logit and log scale, respectively. We used station-specific survey effort (i.e., camera-trap days) as offset, and orangutan density, forest class, and camera-trap placement (characterised by station-specific canopy gap size) as model covariates.

We built a number of models, differing in the combination of explanatory covariates (forest class, canopy gap size and orangutan density), and used the Akaike Information Criterion (AIC) to select the most parsimonious ('best') model. Because we expect a direct relationship between the sampling effort at a camera-trap station and the number of pictures obtained, all models used the number of camera trap days each station was surveyed as an offset in the model for frequency.

To reduce the total number of candidate models, we first explored different models for the photographic frequency while holding the probability of coming to the ground constant (i.e. no explanatory variables of the probability of coming to the ground). Conditional on the best frequency model we then built candidate models for the probability of coming to the ground (Table 2). The best model for photographic frequency contained all three covariates. Conditional on this frequency model, the best overall model additionally contained effects of forest class and density on the probability of coming to the ground. The second-best model, which also included camera placement as a covariate on the probability of coming to the ground, only had a delta AIC relative to the best model of 0.66 and was therefore essentially equally supported by the data (Table 2). Since we were unable to determine a single best model, we employed model averaging, where parameter estimates are obtained as a weighted average over all candidate models²⁷.

Age-sex classes on the ground. To investigate whether terrestrial behaviour is exhibited by all demographic classes (i.e. flanged males, unflanged males, females and females with offspring) we would have ideally run separate ZIP regressions for different classes, but identification of these classes was only possible with high certainty in about 50% of all camera trap records. We cannot assume that failure to identify the age-sex class occurs at random – it is much harder to distinguish a small male from a female, or ascertain that a female is with offspring, than it is to unambiguously identify a flanged male. The only analysis we conducted with respect to demographic class was, therefore, a comparison of the observed versus expected number of flanged male pictures using a Chi-square test. We expect a 50:50 male-female ratio in the orangutan population²⁸; within the males, on Borneo there are typically 1.6:1 flanged to unflanged males^{28,29}. Thus, if all demographic groups came to the ground relative to their occurrence in the population, we would expect flanged male pictures to comprise 31% of our total sample. We considered all pictures in which the demographic group could not be identified as “not flanged male” – this is unlikely to be true since pictures that only show small part of an orangutan could be of a flanged male. However, this procedure guaranteed a conservative approach towards the question of whether flanged males come to the ground more frequently than expected.

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Author contributions

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