Terrestriality in the bornean orangutan (Pongo pygmaeus morio) and implications for their ecology and conservation

by Yaya Rayadin

RESEARCH ARTICLE

Terrestriality in the Bornean Orangutan (*Pongo pygmaeus morio*) and Implications for Their Ecology and Conservation

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Aside from anecdotal evidence, terrestriality in orangutans (*Pongo* spp.) has not been quantified or subject to careful study and important questions remain about the extent and contexts of terrestrial behavior. Understanding the factors that influence orangutan terrestriality also has significant implications for their conservation. Here we report on a camera trapping study of terrestrial behavior in the northeastern Bornean orangutan, *Pongo pygmaeus morio*, in Wehea Forest, East Kalimantan, Indonesia. We used 78 non-baited camera traps set in 43 stations along roads, trails, and at mineral licks (sepans) to document the frequency of orangutan terrestriality. Habitat assessments were used to determine how terrestrial behavior was influenced by canopy connectivity. We compared camera trapping results for *P. p. morio* to those for a known terrestrial primate (*Macaca nemestrina*), and another largely arboreal species (*Presbytis rubicunda*) to assess the relative frequency of terrestrial behavior by *P. p. morio*. A combined sampling effort of 14,446 trap days resulted in photographs of at least 15 individual orangutans, with females being the most frequently recorded age sex class ($N = 32$) followed by flanged males ($N = 26$ records). *P. p. morio* represented the second most recorded primate ($N = 110$ total records) of seven primate species recorded. Capture scores for *M. nemestrina* (0.270) and *P. p. morio* (0.237) were similar and almost seven times higher than for the next most recorded primate, *P. rubicunda* (0.035). In addition, our results indicate that for orangutans, there was no clear relationship between canopy connectivity and terrestriality. Overall, our data suggest that terrestriality is relatively common for the orangutans in Wehea Forest and represents a regular strategy employed by individuals of all age−sex classes. As Borneo and Sumatra increasingly become characterized by mixed-use habitats, understanding the ecological requirements and resilience in orangutans is necessary for designing optimal conservation strategies. Am. J. Primatol. 75:1129–1138, 2013. © 2013 Wiley Periodicals, Inc.

Key words: Indonesia; *Pongo pygmaeus morio*; terrestriality; wehea forest; camera traps; conservation

INTRODUCTION

Orangutans are only found on the islands of Borneo and Sumatra and exhibit considerable geographic variation in their biology and behavior [Wich et al., 2009]. Orangutans are divided into two closely related species, the Bornean orangutan (*Pongo pygmaeus*) and Sumatran orangutan (*Pongo abelii*) [Groves, 2001]. Bornean orangutans are further divided into three subspecies (the northwestern Bornean orangutan, *Pongo pygmaeus pygmaeus*; the central Bornean orangutan, *Pongo pygmaeus wurmbi*, and the northeastern Bornean orangutan, *Pongo pygmaeus morio*) [Groves, 2001]. This geographic variation is thought to reflect adaptations to different ecological conditions across Borneo and Sumatra [e.g., Marshall et al., 2009; Taylor & van Schaik, 2007; Van Schaik et al., 2009; Wich et al., 2012], with the forests of eastern Borneo generally recognized as the most

resource-scarce and of the lowest quality in the region. The northeastern Bornean orangutan subspecies, *P. p. morio*, seems to have developed adaptations to these

conditions of extreme scarcity (e.g., smaller brain size, a shorter interbirth interval, more robust jaws) [Singleton et al., 2009; Taylor, 2006, 2009; Taylor & van Schaik, 2007; Van Schaik et al., 2009], and some have suggested these adaptations may even increase the resilience of *P. p. morio* to anthropogenic habitat disturbance [Husson et al., 2009; Marshall et al., 2009].

Both species of orangutan are described as predominantly arboreal [e.g., Thorpe & Crompton, 2009]. However, one significant behavioral difference that has been noted between the species is in the amount of terrestriality exhibited. Terrestriality appears to be rare among Sumatran orangutans, possibly due to the presence of a large ground predator, the Sumatran tiger (*Panthera tigris sumatrae*) [Cant, 1987; Manduell, pers. comm., April 2013; Sugardjito & van Hooff, 1986]. In contrast, terrestriality has been reported from several well-studied Bornean orangutan populations. This behavior seems to be most common in flanged adult males [Delgado & van Schaik, 2000; Galdikas, 1979; ME. Harrison, pers. comm., April 2013; MacKinnon, 1974; Manduell, pers. comm., April 2013; AJ. Marshall, pers. comm., April 2013; Oram, pers. comm., April 2013; Rodman, 1979; Tuttle, 1986]. The contexts of terrestrial behavior appear to be obtaining food resources [e.g., fallen fruit, shoots, soil; MacKinnon, 1974] or traveling. In oil palm concessions, orangutans have been seen coming to the ground to eat young oil palm fruit and in mining concessions and oil palm and Acacia plantations, orangutans have been observed moving on the ground between fragmented forest patches (Rayadin, unpublished data). Some researchers report that flanged males spend a substantial amount of time traveling on the ground [MacKinnon, 1974; ME. Harrison, pers. comm., April 2013; Manduell, pers. comm., April 2013; AJ. Marshall, pers. comm., April 2013], possibly because their large body size makes it more energetically efficient for them to travel long distances on the ground rather than in the trees [Cant, 1987].

Unflanged males and females, particularly females with infants, are generally reported as being reluctant to come to the ground and thus exhibit terrestrial behavior far less often. However, this pattern may not be universal. Females have been seen coming to the ground to utilize resources, such as water sources and termites [Manduell, pers. comm., April 2013; Oram, pers. comm., April 2013]. MacKinnon [1974] noted that females and juvenile *P. p. morio* sometimes traveled briefly on the ground at Ulu Segama in northeastern Borneo, and Manduell et al. [2011] noted that at Sabangau in southern Borneo (*P. p. wurmbii*), "sub-adult males and adolescent females have also been observed occasionally to travel substantial distances over the ground" (p. 349).

Despite these anecdotal observations, the degree of terrestriality in Bornean orangutans has not been systematically studied and important questions about the contexts and determinants of orangutan terrestriality remain. Is this behavior confined to large-bodied flanged males, or are smaller-bodied individuals (e.g., unflanged males and females) also frequently terrestrial [cf Manduell et al., 2011]? Across age–sex classes, is terrestriality generally confined to short trips to the ground to acquire resources or do individuals frequently travel on the ground? Do individuals mainly employ terrestrial behavior in areas with poor canopy connectivity [Oram, pers. comm., April 2013; Rayadin, unpublished data] or is this behavior employed in a variety of habitat types? An important factor influencing terrestriality is likely energetics; terrestrial locomotion could be more energy efficient, particularly for large individuals traveling over long distances, and thus increase foraging efficiency [Cant, 1987]. However, the determinants of terrestriality in orangutans are difficult to elucidate without quantitative information about the ecological contexts in which this behavior is employed. Locomotion and habitat use are critical components of a species' ecology, and understanding terrestriality in orangutans has important implications for understanding their behavioral adaptations and strategies under different environmental conditions. This information can be integrated into comparative studies that will allow us to understand how differences in habitat quality and other environmental factors have shaped the morphology and behavior of orangutans across their geographic range [Van Schaik et al., 2009].

One reason there are little quantitative data on orangutan terrestriality may be that the presence of observers (required for long-term behavioral study) inhibits terrestrial behavior [Cant, pers. comm., March 2013; Oram, pers. comm., April 2013]. Camera traps offer a possible alternative for studying at least some aspects of the behavior of these elusive apes. This technology has been used extensively to study population density and abundance of elusive mammals [e.g., Kawanishi & Sunquist, 2004; Kays & Slauson, 2008; O'Connell et al., 2011; Treves et al., 2010; Wilting et al., 2012]. If deployed properly they can also provide information about habitat use and behavior without requiring behavioral follows of study animals, as has been demonstrated by a number of recent studies with primates [e.g., Head et al., 2012; Olson et al., 2012; Pebsworth et al., 2012; Tan et al., 2013].

Here we report on a camera trapping study of terrestrial behavior in the northeastern Bornean orangutan, *P. p. morio*, in Wehea Forest in East Kalimantan, Indonesia. The aim of this study was to shed light on the causes and possible determinants of terrestrial behavior in *P. p. morio* by collecting quantitative data on the frequency of terrestriality

by different age–sex classes and on the behavioral and ecological contexts in which terrestriality occurs. Clarifying the degree and contexts of orangutan terrestriality and the capacity for ecological flexibility is also crucial for designating priority habitat and designing optimal conservation management plans.

METHODS

Study site

Wehea Forest (01°32′46″N, 116°46′43″E), located in East Kutai District, East Kalimantan, Indonesia, contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests currently classified as logging concessions. Wehea Forest is within a logging concession, but this concession is currently inactive and all logging ceased in the mid-1990s. Old logging roads, which have not been maintained since logging stopped in the forest, are very overgrown but still exist and were utilized for this study. Wehea Forest is currently protected by an agreement between a local community and the local government, and paperwork has been submitted to change its status to a Protection Forest (Hutan Lindung).

The site has a varied topography, characterized by steep ravines, multiple ridges, and runoff streams. Elevations vary from 250 m in the east, where the main logging activity took place, to 1,750 m in the west, where the primary forest occurs. Wehea Forest is characterized by lowland dipterocarp, sub-montane, and montane forests with mean total annual rainfall amounting to 3,000 mm and a mean 24 h temperature of 27°C. A dry season typically runs from June to September and the rainy season is from November to February. Wehea Forest lies within a center of richness for primate species [Meijaard & Nijman, 2003] and ten species of nonhuman primates have been previously reported from the site: the northeastern Bornean orangutan (*P. p. morio*), Bornean gibbon (*Hylobates funereus*), red langur (*Presbytis rubicunda*), Miller's grizzled langur (*Presbytis hosei canicrus*), white-fronted langur (*Presbytis frontata*), silvered langur (*Trachypithecus cristatus*), pig-tailed macaque (*Macaca nemestrina*), long-tailed macaque (*Macaca fasicularis*), slow loris (*Nycticebus coucang*), and the Western tarsier (*Tarsius banancus*). Research is currently underway in Wehea Forest to estimate population densities for *P. p. morio*, *H. funereus*, *P. rubicunda*, and *P. h. canicrus*.

Camera Traps

In March 2012, 68 non-baited cameras were set in pairs, or stations, along old logging roads, trails, and at one mineral lick (sepan). This station array covered an approximate area of 38 km^2 (Fig. 1). The cameras used were Bushnell Trophy Cams ($N = 60$) and Reconyx HC500 ($N = 8$) cameras. An additional ten Bushnell Trophy Cams were added in May, seven set along roads and three at a second sepan, bringing the total number to 78 cameras set across 43 camera trap stations and resulting in a sampling effort of 14,446 trap days. All cameras remained at the same locations until this study concluded in October 2012.
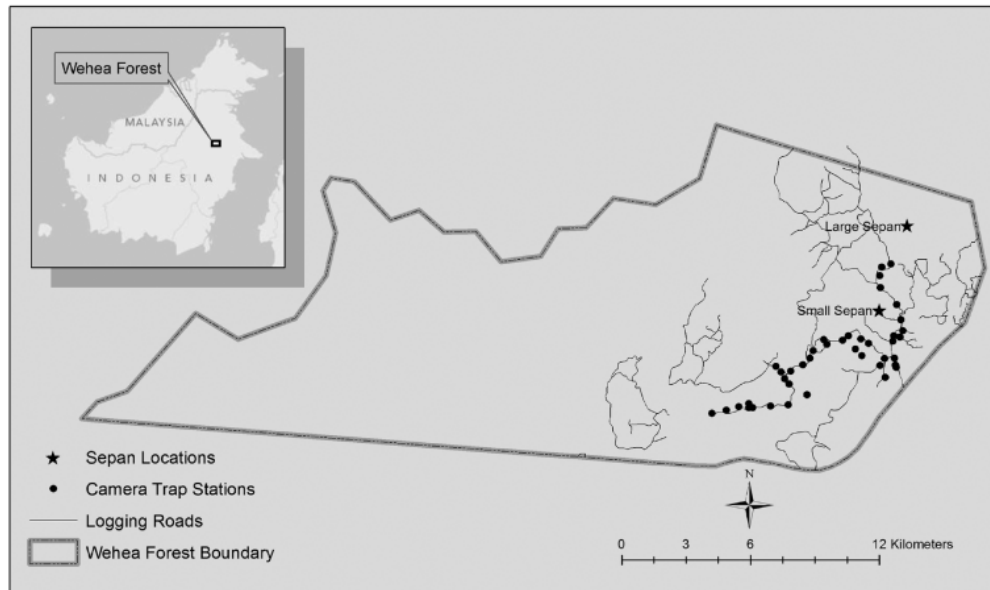

Fig. 1. Location of camera-trap stations in Wehea Forest. Insert shows the location of Wehea Forest on the island of Borneo.

Of the 43 camera trap stations used from May onwards, five were located along trails, two at sepans, and the remaining 36 along old logging roads. All cameras were placed on trees ∼50 cm from the ground and fitted with a plastic cover above and a bed of leaves below to protect against rain and mud. Each camera was set to take three pictures per trigger, with a reset time of 1 sec. Cameras were checked a total of three times, in the middle of May, the beginning of July, and again in October, at the conclusion of the study. At each visit, non-functioning cameras were replaced with new cameras, batteries were changed and the SD card storing the photos was removed from the camera and replaced by a new card.

Camera Trap Analysis

All photos of primates taken from March to October 2012 were first categorized by species. We then analyzed these photographic records to determine how often *P. p. morio* were photographed relative to other primates on (1) trails and old logging roads, (2) at sepans, and (3) in both areas. We examined the use of trails and roads separately from use of sepans (mineral licks) because sepans are areas largely devoid of trees and primates must descend to the ground to use these areas. Furthermore, primates are known to use sepans to supplement minerals in their diet by drinking the mineral rich water [Blake et al., 2010; Lhota et al., 2012; Matsubayashi et al., 2007, 2011].

The number of records of each species was calculated as the number of photos taken with >1 hr. interval between photos at each station. If an individual/species was seen at a station multiple times within an hour, this was treated as one record. The percent of primate records represented by each species was calculated from the total records (road + sepan) and from all stations ($N = 43$). A capture score for each primate was computed from the percent of total stations (e.g., 28 of 43 total stations recorded *M. nemestrina*) that recorded a given primate multiplied by the percent of total records represented by that primate (e.g., 113 *M. nemestrina* records out of 302 total primate records). A relative encounter score was based on the relative encounter rate for each species. Encouter rates were calculated by asking a set of well-trained field assistants and researchers ($N = 6$) to rank each primate species with a number that reflected how often they perceived encountering each species in Wehea Forest. Each field assistant and researcher spent at least 500 hr in Wehea Forest conducting primate behavior and survey research between 2010 and 2012 and were not affiliated with this camera trapping study. The final rank of each species was then calculated as the mean of scores for that primate given by all participants. This is meant only as a rough estimation of the relative abundance of primate species in Wehea Forest.

The number of different *P. p. morio* individuals captured was determined by carefully studying and comparing all photographs of *P. p. morio* ($N = 658$). These determinations were completed by an observer experienced in identifying wild primate individuals based on variation in physical appearance (Spehar). Records (sets of photographs from the same capture) were first divided into age−sex class categories (flanged male, unflanged male, female with juvenile, female without juvenile, juvenile, and adult of indeterminate sex) based on external genitalia if visible, secondary sexual characteristics (cheek flanges, throat pouch, cape of hair on back, and elongated nipples), and body size and shape. Photographs were then examined for cues to individual identity, noting characteristics for each of the following categories: body size; hair color, and quality (e.g., thick, thin, and any bald patches); facial features (prominance of brow ridges; prognathism; angle and size of nostrils and mouth; overall shape of face; etc.), shape of hair on head, and any other identifying features (e.g., elongated nipples, marks or scars, distinctive body posture). If the individual's face and/or some other clearly identifying mark (e.g., a distinctive injury) was not visible in a photograph, we did not attempt to identify that individual. After this initial assessment was performed, photographs were placed side-by-side for comparison to determine if the same individual had been captured at multiple stations and to ensure that no individual was counted more than once. This process was completed in its entirety from the beginning two separate times by Spehar to maximize confidence in the assessment.

Habitat Assessment and Analysis of Terrestriality

In order to determine how terrestrial behavior was influenced by canopy gaps we measured and rated canopy connectivity for each camera trap station. For this and other analyses related to orangutan terrestriality, we compared our results for orangutans to those for two other primate species: *M. nemestrina*, a species that is known to be largely terrestrial [Caldecott, 1986] and *P. rubicunda*, a species that is primarily arboreal but is ocassionally seen on the ground [Spehar, unpublished data]. These two species were incorporated into our analysis because they allow us to assess how frequently orangutans use the ground relative to other known terrestrial and arboreal primates, and thus draw conclusions about the extent of *P. p. morio* terrestriality in Wehea Forest.

Canopy connectivity was assessed in the area 5 m on either side of each camera trap and directly between each paired camera trap at each station by a single observer (Loken). Habitat characteristics such

as the presence of boughs, branches or lianas of sufficient size to be used by primates for crossing gaps were recorded and a canopy connectivity rating was created based on visual estimates of the minimum distance measured between these support attributes [Manduell et al., 2011, 2012; Thorpe & Crompton, 2006; Thorpe et al., 2007]. Pictures were taken of the canopy from various angles at each camera trap station and cross referenced with notes to determine a final connectivity rating of low, medium or high for each station (Table I).

These canopy connectivity ratings were based on the frequency of gap crossings for *H. muelleri*, *P. pygmaeus*, and *M. fascicularis* [Cannon & Leighton, 1994; Manduell et al., 2012]. Our canopy connectivity rating of low was based on Cannon & Leighton's [1994] observation of a maximum gap crossing of 9 m by *H. muelleri* and that gaps of 5–9 m were crossed in each layer of the canopy. Based on extensive behavioral observations of *P. rubicunda* and *P. h. canicrus* in Wehea Forest (Spehar, unpublished data) we believe that *P. rubicunda, P. h. canicrus* and *P. cristata* would be able to cross similar distances to *H. funereus*. Connectivity ratings of medium and high were based on Cannon & Leighton's [1994] maximum gap crossing widths for *M. fascicularis* and Manduell et al.'s [2012] mean observed gap crossing sizes (0.96–2.59 m) for various *P. pygmaeus* age/sex classes respectively. All stations located along old logging roads and trails had canopy support attributes of sufficient size for primate gap crossing and a gap width less than 9 m.

We then calculated a "ground use" score as a measure of how often *P. p. morio, P. rubicunda*, and *M. nemestrina*, were terrestrial at camera trap stations located along old logging roads and trails with different canopy cover and connectivity. Ground use scores were computed for each of our three canopy connectivity ratings using the variables "station success," "record success," and "station proportion." Station success was computed from the percent of stations that recorded the species for a given connectivity rating, while record success was computed as the percent of total species records for a

given connectivity rating. The multiplied result was then divided by station proportion, the percentage of total stations in a connectivity category, to obtain the ground use score. This score reflects the chance of recording the species at an individual camera trap in a particular canopy connectivity category, as well as the capture rate of species at camera traps located in a particular connectivity category. We should note that our ground use score may reflect not only the relative ground use by each species but also the relative abundance of each species within that particular canopy connectivity category. Therefore, comparison across species should be treated with some caution.

All research conducted was in compliance with the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates, was approved by Simon Fraser University's Office of Research Ethics and Animal Care Committee and UW Oshkosh's Institutional Animal Care and Use Committee, and adhered to Indonesian legislation. Research permits were approved by the Indonesian Ministry of Research and Technology (RISTEK).

RESULTS

A total of 2,149 primate photos were taken on old logging roads, trails and at sepans in Wehea Forest between March and October 2012 (Table II). A total of 302 independent records of primate species were recorded on both roads/trails and at sepans, and 218 records were recorded on roads/trails only. *M. nemestrina* was the most frequently photographed primate in Wehea Forest ($N = 113$ records) and was recorded at 31 of 43 stations while *P. p. morio* was the second most photographed primate ($N = 110$ records) and was recorded at 28 of 43 stations. When considering only records from roads/trails, *M. nemestrina* accounted for 49.5% of primate records ($N = 108$ records) and *P. p. morio* accounted for 34.9% of primate records ($N = 76$ records). However when considering records from roads/trails and sepans, the number of records for *M. nemestrina*

TABLE I. Description of Canopy Connectivity Ratings Used for Analysis of Forest Structure and Terrestriality for *P. p. morio, M. nemestrina*, and *P. rubicunda* in Wehea Forest

Canopy connectivity rating	Description
Low	Low connectivitiy (gap size 5–9 m), *P. rubicund* very likely able to cross and *P. p. morio* and *M. nemestrina* very likely not able to cross
Medium	Medium connectivity (gap size 3–5 m), *P. rubicund* able to cross, *P. p. morio* possibly able to cross, and *M. nemestrina* very likely not able to cross
High	High connectivity (gap size 0–3 m), *P. rubicunda, P. p. morio*, and *M. nemestrina* very likely able to cross

Categories were created using locomotor data provided by Cannon & Leighton's [1994] maximum and preferred gap crossing widths for *H. Muelleri* (9 m) and *M. fascicularis* (3.5 m) and Manduell et al.'s [2012] mean observed gap crossing sizes (0.96–2.59 m) for various *P. pygmaeus* age/sex classes.

TABLE II. Camera Trapping Results for all Primates Recorded Along Roads and at Sepans in Wehea Forest From March to October 2012

Species	Scientific name	Total photos	Road only records	Total records (road + sepan)	% of total records	Capture score	Relative encounter score
Pig-tailed macaque	*Macaca nemestrina*	1,054	108	113	37.4	0.270	5.33 ± 0.47
Orangutan	*Pongo pygmaeus morio*	658	76	110	36.4	0.237	4.33 ± 0.56
Red langur	*Presbytis rubicunda*	171	19	38	12.6	0.035	1.33 ± 0.19
Miller's grizzled langur	*Presbytis hosei canicrus*	168	0	26	8.6	0.004	5.75 ± 0.57
Long-tailed macaque	*Macaca fascicularis*	84	8	8	2.6	0.002	5.00 ± 0.42
Bornean gibbon	*Hylobates funereus*	13	6	6	2.0	0.0009	1.67 ± 0.19
White-fronted langur	*Presbytis cristata*	1	1	1	0.3	0.0001	4.58 ± 0.61

($N = 113$ records, 37.4%) and *P. p. morio* ($N = 110$ records, 36.4%) were similar and by far the most frequently captured primate (Table II and Fig. 2). Capture scores for *M. nemestrina* (0.270) and *P. p. morio* (0.237) were also similar and almost seven times higher than the primate with the next highest capture score, *P. rubicunda* (0.035; Table II). The two primates with the highest relative encounter scores were *P. rubicunda* (1.33 ± 0.19) and *H. funereus* (1.67 ± 0.19) while *M. nemestrina* (5.33 ± 0.47) had the second lowest relative encounter score. There was not a significant correlation between our capture and relative encounter scores (Spearman rank correlation, $n = 7$, $r_s = 0.14$, $P > 0.05$).

Table III provides the summary data of individual orangutan records for this study. Flanged males were recorded on old logging roads and trails the most frequently of all individual age–sex classes ($N = 26$ records); however, when all females are considered together (females with juveniles and females without juveniles), they were recorded on old logging roads

Fig. 2. Percent of total records for each primate species recorded along roads/trails and at sepans in Wehea Forest from March to October 2012.

and trails more than flanged males ($N = 32$ records). Flanged males represented the most frequently recorded age/sex class at the sepans ($N = 20$ records) with young males representing the second and only other age/sex class photographed at sepans. The minimum number of separate individuals recorded (that could be identified with 100% confidence) was 15. However, individuals could be identified for only 75 out of 112 or 67% of records.

For all species examined (*P. p. morio*, *P. rubicunda*, and *M. nemestrina*), ground use scores across the different canopy connectivity categories (low, medium, and high) did not differ significantly (Fig. 3, $X^2 = 0.27$, df $= 4$, $P = 0.99$), suggesting that we were not significantly more likely to capture a species in one canopy connectivity category than another. However, some differences in patterns between species can be detected; *M. nemestrina* were more likely to be captured in areas with a canopy connectivity rating of high ($N = 12$ stations), while *P. p. morio* and *P. rubicunda* were more likely to be captured in areas with a canopy connectivity rating of medium ($N = 11$ stations). In addition, we recorded a large difference in the ground use score between *P. p. morio* (0.472) and *M. nemestrina* (0.973) in areas with a canopy connectivity rating of high (Table IV and Fig. 3).

DISCUSSION

A possible critique of our results is that the differences in capture scores between species (Table II) do not reflect more or less frequent use of the ground but simply differences in abundance between species in Wehea Forest. Although abundance certainly influences how frequently species are captured on camera traps, we believe it cannot explain all of the differences in capture scores between species in this study. We do not have absolute abundance and density estimates for the primate species in Wehea Forest, but after over 3 years of intensive work with the primate community at the site (Spehar, unpublished data) we are able to make broad statements regarding the relative
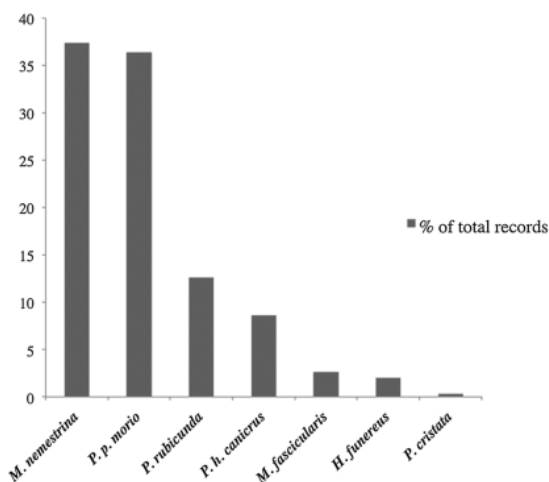
TABLE III. Individual *P. p. morio* records for Each Age/Sex Class and Numbers of Confirmed Individuals Recorded Along Roads and at Sepans

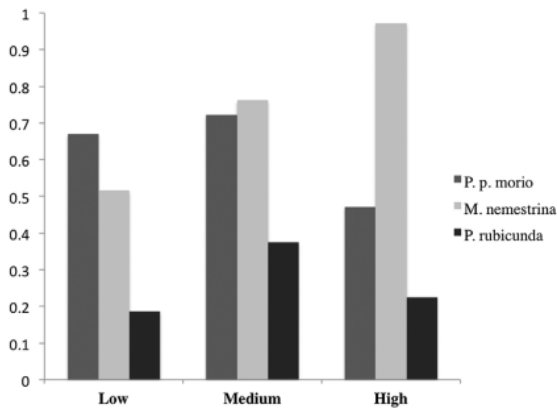| Age/sex class	No. of confirmed individuals	Total records (road + sepan)	Road only records	% of road only records
Flanged male	5	46	26	34.2
Unflanged male	4	25	11	14.5
Female without juvenile	2	10	10	13.2
Female with juvenile	4	22	22	29.0
Juvenile of indeterminate sex	—	5	5	6.6
Adult of indeterminate sex	—	2	2	2.6

Fig. 3. Terrestriality scores for *P. p. morio*, *M. nemestrina* and *P. rubicunda* for each canopy connectivity rating.

encounter rates of the different species (quantified in our relative encounter score for each species). We found that the relative encounter score and the capture score of species are not correlated (Table II), indicating that capture rates were not determined solely by relative abundance at the site. Some of the species that have the highest relative encounter scores and appear to be most abundant in Wehea Forest (i.e., red langurs and gibbons) had the lowest

capture scores, while species that had much lower relative encounter scores (notably, pig-tailed macaques, and orangutans) had the highest capture scores. It is possible that the elusiveness of species influenced relative encounter scores (e.g., encounter rates might be exceptionally low for Miller's grizzled langurs because this species is very cryptic and difficult to spot in a dense forest environment). However, the fact that the two most commonly encountered primates at the site (red langurs and gibbons) were almost never captured on camera traps indicates that capture rate does not reflect only abundance but also how frequently that species uses the ground. It is for this reason that, although we are aware of the inherent limitations of this study, we feel comfortable making preliminary inferences about orangutan terrestriality using these data.

Previously, terrestrial behavior in Bornean orangutans was assumed to be uncommon and generally employed primarily as a means of acquiring resources on the ground [e.g., ME. Harrison, pers. comm., April 2013; MacKinnon, 1974; Manduell, pers. comm., April 2013;], although some researchers have described flanged males regularly traveling on the ground, in some cases for long distances [Galdikas, 1979; ME. Harrison, pers. comm., April 2013; Manduell, pers. comm., April 2013; AJ. Marshall, pers. comm., April 2013; Oram, pers. comm., April 2013]. Terrestrial behavior also seemed

TABLE IV. Ground Use Scores for *P. p. morio*, *M. nemestrina*, and *P. rubicunda* Recorded at Camera Trap Stations With Various Canopy Connectivity Ratings Along Old Logging Roads and Trails in Wehea Forest

Species	Canopy connectivity rating	Total records	Stations with records	Station success % stations with records	Record success % of total records	Ground use score
Pongo pygmaeus morio	Low	31	13	0.722	0.408	0.671
	Medium	27	6	0.545	0.355	0.722
	High	18	7	0.583	0.237	0.472
Macaca nemestrina	Low	40	11	0.611	0.370	0.516
	Medium	27	9	0.818	0.250	0.762
	High	41	9	0.750	0.380	0.973
Presbytis rubicunda	Low	7	4	0.222	0.368	0.186
	Medium	7	3	0.273	0.368	0.375
	High	5	3	0.250	0.263	0.225

to be confined largely to flanged males [Galdikas, 1979; MacKinnon, 1974], although a handful of anecdotal observations suggested that other age−sex classes also occasionally travel on the ground [Manduell et al., 2011]. The results of our camera trapping study, which represent the first published attempt to quantify orangutan terrestriality, show that Bornean orangutans in Wehea Forest are captured via camera trap on the ground almost as often as the only primarily terrestrial primate found at the site, the pig-tailed macaque (*M. nemestrina*), and far more often than other primates in Wehea Forest that are of equal or greater abundance and known to be largely arboreal (Table II and Fig. 2). Furthermore, our data suggest that terrestrial behavior is not confined primarily to flanged males whose large body size may cause them to have trouble finding adequate support in the trees, and who may be less concerned about predators on the ground, as had been previously suggested [Galdikas, 1979; MacKinnon, 1974; Rodman, 1979; Tuttle, 1986]. Smaller-bodied individuals (e.g., females and un-flanged males) are also frequently terrestrial (Table III). Interestingly, our data show that females are terrestrial almost as often as flanged males. The fact that adult females with young were captured twice as often as females without young is likely because adult female orangutans will typically always be accompanied by an infant, rather than any actual differences in ground use between females with and without infants. Finally, the fact that multiple individuals (at least 15 total) of all age−sex classes could be identified from our orangutan camera trap photos demonstrates that these records do not represent a handful of "rogue" individuals but repeated behavior by multiple individuals. Overall, our data suggest that terrestriality in the orangutans in Wehea Forest is not an occasional behavior employed only by certain classes of individual, but instead represents a regular strategy employed by individuals of all age−sex classes.

Orangutans are typically arboreal and exhibit many morphological adaptations to arboreal locomotion [Cant, 1987; Thorpe & Crompton, 2006], which raises questions about the determinants of the frequent terrestrial behavior in these animals. In areas where canopy connectivity is poor, orangutans may have no choice but to travel on the ground, and one might expect that we would see terrestrial behavior far more frequently in these areas than in others. However, we did not find evidence for a strong relationship between canopy connectivity and how frequently orangutans were captured on the ground. Orangutans were captured on the ground most frequently at stations with medium canopy connectivity rating, followed closely by stations with low canopy connectivity rating, and least frequently at stations that had a high canopy connectivity rating (Table IV and Fig. 3). In addition, there was no

significant relationship between canopy connectivity and how often orangutans were captured on the ground in an area. This suggests that orangutans are not only terrestrial in areas where they may be forced to come to the ground due to large gaps in the canopy, but employ terrestrial travel as a strategy even in areas where it may be possible for them to find pathways for arboreal travel.

There are likely several interrelated factors influencing these patterns, in particular the energetic costs and benefits of arboreal versus terrestrial travel. Orangutans are the largest arboreal mammal, which presents special challenges to efficient travel in a complex arboreal environment [Cant, 1987; Thorpe & Crompton, 2006]. Orangutans are also subject to intense energetic constraints; most orangutans live in forests that are subject to unpredictable and extended periods during which their preferred food, fruit, is extremely scarce [Marshall et al., 2009]. Recent studies have suggested that orangutans are "low-energy specialists," [Harrison et al., 2010; Knott, 1998; Pontzer et al., 2010], exhibiting physiological and likely behavioral adaptations that allow them to conserve energy and survive these long periods of scarcity. In many cases, traveling on the ground may be the most energy-efficient choice for orangutans, even in areas with relatively continuous canopy. According to Cant [1987], who studied locomotor behavior of *P. p. morio* in East Kalimantan, "the ground is certainly continuous, and terrestrial travel per se is probably less laborious than arboreal travel because of the locomotor zigs and zags imposed by canopy structure. But a pattern of traveling on the ground and climbing up and down feeding trees may be costly in locomotor energy expenditure. The actual costs and benefits of such an alternative are likely to depend on the spatial distribution of the food patches that an animal uses" (p. 85). It may be that orangutans travel on the ground frequently in Wehea Forest because it is the most energetically efficient option, given the distribution of support structures and food resources at the site.

Our results have several important implications. First, they provide a challenge to our current understanding of the ecology of Bornean orangutans, suggesting they may not be as arboreal as has been suggested by previous studies. While we do not suggest that orangutans do not rely heavily on trees, our results support previous anecdotal observations that orangutans do travel on the ground and that travel on the ground is not limited to large flanged males but extends to all age−sex classes. However, we acknowledge that this study only includes the behavior of orangutans from one study site and that results may be influenced by uneven age−sex class ratios. Furthermore, our study subspecies, the northeastern Bornean orangutan (*P. p. morio*), lives in what is often regarded as the harshest orangutan habitat [Van Schaik et al., 2009]. Thus, the energetic

cost–benefits of arboreal versus terrestrial travel may be different for these orangutans than for orangutans living in habitats where resources are generally more abundant. Understanding the extent of terrestriality within the different orangutan species and subspecies is necessary in order to fully understand how ecology and phylogeny influence their foraging strategies. Only a broader cross-site comparison of orangutan terrestriality across their geographic range can resolve these issues.

Second, these results also have possible implications for orangutan conservation. They suggest that orangutans may be more capable than previously thought of using landscapes that may necessitate terrestriality (e.g., disturbed habitat that include substantial canopy gaps and roads). The islands of Borneo and Sumatra, which encompass the remaining range of wild orangutans, are becoming increasingly characterized by mixed-use habitats: a matrix of timber plantations, agro-forestry areas, mines, and remaining patches of natural forest separated by varying distances of non-forested habitat [e.g., Meijaard et al., 2011; Wich et al., 2008, 2012]. It has long been assumed that orangutans lack the resiliency to cope with widespread forest degradation, however, some recent studies [Meijaard et al., 2010] have found unexpectedly high orangutan densities in landscapes dominated by human activity (e.g., forestry and palm oil plantations), and have even observed orangutans moving extensively on the ground in these areas [Rayadin and Ancrenaz, unpublished data]. This suggests that, providing sufficient availability of food exists, orangutans may be able to use mixed-use landscapes that consist of natural and human altered habitats, at least in some cases.

We emphasize that we are not suggesting natural forests are not necessary for orangutan survival. The behavior of orangutans in highly modified landscapes and the long-term viability of orangutan populations living in these landscapes remains unknown and requires further study. However, our study, demonstrating extensive terrestriality by the orangutans of Wehea Forest, suggests that Bornean orangutans may be capable of greater ecological flexibility than previously thought.

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