RESEARCH ARTICLE

Why Do Orangutans Leave the Trees? Terrestrial Behavior Among Wild Bornean Orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan

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Orangutans (genus *Pongo*) are the largest arboreal mammals, but Bornean orangutans (*P. pygmaeus spp.*) also spend time on the ground. Here, we investigate ground use among orangutans using 32,000 hr of direct focal animal observations from a well-habituated wild population of Bornean orangutans (*P. p. wurmbii*) living in a closed-canopy swamp forest at Tuanan, Central Kalimantan, Indonesia. Ground use did not change with increasing observation time of well-habituated individuals, suggesting it was not an artifact of observer presence. Flanged males spent the most time on the ground (ca. 5% of active time), weaned immatures the least (around 1%). Females and immatures descended mainly to feed, especially on termites, whereas flanged males traveled more while on the ground. Flanged males may travel more inconspicuously, and perhaps also faster, when moving on the ground. In addition, orangutans engaged in ground-specific behavior, including drinking from and bathing in swamp pools. Supplementary records from 20 ground-level camera traps, totaling 3986 trap days, confirmed the observed age-sex biases in ground use at Tuanan. We conclude that ground use is a natural part of the Bornean orangutan behavioral repertoire, however it remains unclear to what extent food scarcity and canopy structure explain population differences in ground use. Am. J. Primatol.   © 2015 Wiley Periodicals, Inc.

Key words: Borneo; orangutan terrestriality; *Pongo pygmaeus wurmbii*; ground travel; direct observation; camera trapping

INTRODUCTION

Orangutans (genus *Pongo*) are the only great apes found outside of Africa and are the largest habitually arboreal mammals. There are two recognized species of orangutans, *P. abelii* in Sumatra and *P. pygmaeus* in Borneo [Brandon-Jones, 2004; Nater et al., 2011]. Both orangutan species have very slow life histories, with late ages at first reproduction and extremely long interbirth intervals [Galdikas and Wood, 1990; Wich et al., 2004; Knott et al., 2009]. Their arboreality contributes to their low extrinsic mortality by keeping them out of reach of most natural predators [Jones, 2011; van Schaik & Isler, 2012]. Indeed, orangutans in Borneo—where tigers (*Panthera tigris*) have been extinct for millennia—are known to occasionally come down to the ground in natural forests [Wallace, 1869]. In contrast, terrestrial behavior among Sumatran orangutans—where the range of extant tigers overlaps almost the entire range of orangutans [Chundawat et al., 2011, Singleton et al., 2008]—has hardly ever been observed [Thorpe and Crompton, 2009]. Other possible selective pressures to maintain an arboreal lifestyle include a relatively lower exposure to (intestinal) parasites and other pathogens by being away from the ground, and more recently, a lower risk of exposure to human activity [Ancrenaz et al., 2014; Woodford et al., 2002].

Many behavioral studies have noted terrestrial activity among orangutans [e.g. MacKinnon, 1974]. In the Bornean studies, the large-bodied flanged

males are reported to travel more frequently on the ground than females or smaller unflanged males [Galdikas, 1979; Rodman, 1979; Thorpe & Crompton, 2009], whereas Sumatran flanged males do not use the ground [Thorpe & Crompton, 2006], except in emergencies, such as when fleeing from an opponent [Cant, 1987; van Schaik, 2004]. Travelling terrestrially may be beneficial for several reasons, including a reduced risk of falling if a supporting tree or branch breaks [Kehoe & Chan, 1986; Kraft et al., 2014]. Terrestrial travel is also thought to be energetically cheaper than arboreal travel, even for an ape anatomically adapted to arboreal travel [Cant, 1987; Begun & Kivell, 2011; Loken et al., 2013], and because the cost of climbing is directly proportional to body size [Thorpe et al., 2007], this would explain the observed ground-use bias towards the large flanged males. This economical travel option may allow flanged males to offset certain costs associated with their secondary sexual characteristics (for instance, their inability to keep up with fleeing females), and thus diminish the advantages of the unflanged stage [van Schaik et al., 2009; Dunkel et al., 2013]. Therefore, the Borneo—Sumatra contrast in predation pressure and degree of terrestriality may have affected inter-island differences in social organization and patterns of male developmental arrest.

This argument assumes that the animals' behavior is not influenced by the presence of human observers. Thus, an observed orangutan may use the ground less in the presence of an observer because the observer is perceived as a threat [Loken et al., 2013], or alternatively over time may come to use the ground more in the presence of an observer because their presence is perceived as an indication that the ground is safe [Grundmann, 2006; Russon et al., 2009].

Three recent studies have sought to investigate and quantify orangutan terrestrial behavior using indirect observation through ground-level camera traps. Loken et al. [2013], Ancrenaz et al. [2014], and Loken et al. [2015] reported frequent detection by camera traps of Bornean orangutans on the ground at several sites, including varying types of forest subjected to varying degrees of human disturbance. These camera-trap studies have convincingly shown that in the absence of human observers, (flanged) males use the ground rather frequently. However, the other age-sex classes were also recorded to be on the ground, albeit less frequently in most [Ancrenaz et al., 2014; Loken et al., 2015], but not all sites [Loken et al., 2013].

The frequency of ground use found in these camera-trap studies has led to much speculation about the proximate reasons why wild orangutans descend to the ground. If the forest structure allows, orangutans are capable of crossing considerable gaps in the canopy by tree swaying, which is often energetically less costly than descending to the ground and climbing up again [Thorpe et al., 2007; Manduell et al., 2011]. Thus, terrestriality for the sole purpose of crossing canopy gaps should rarely be efficient. Nevertheless, some recent studies have emphasized terrestriality especially to cross gaps in the forest [Ancrenaz et al., 2014; Rijksen & Meijaard, 1999] and have even suggested that once individuals are used to using the ground to cross canopy gaps, this would enable them to disperse across open terrain in fragmented habitat [Ancrenaz et al., 2014]. Alternatively, orangutans' ground use is not forced by canopy gaps, but used to travel over longer distances in continuous forest [Galdikas, 1979; Rodman, 1979] or to acquire terrestrial (fallback) food, water, or minerals [Cant, 1987; MacKinnon, 1974; Matsubayashi et al., 2011].

To identify the major causes of terrestriality, we present direct observational and camera-trap data of ground use (defined as any time during which an orangutan is in contact with the ground) among Bornean orangutans (*Pongo pygmaeus wurmbii*) of a mostly habituated natural population, inhabiting a peat-swamp forest without major canopy gaps. We first investigated whether the behavioral data show a strong bias due to habituation or observation difficulties. Then we examined the behavioral, environmental and spatial correlates of ground use. Finally, we summarize the evidence of orangutan ground use from camera traps in our study area.

METHODS

Study Site

Behavioral data were collected from July 2003–2010 on the natural population of Bornean orangutans in the Tuanan Orangutan Research Area, Mawas Reserve, Kalimantan Tengah, Indonesia (2° 09' S; 114° 26' E). The entire study area (approx. 7.5 km^2) is homogenous peat-swamp forest, which has previously been subjected to selective logging, but had had (as of 2003) at least 5 years to recover [van Schaik et al., 2005]. There is an approximately 200×200 m grid of narrow research trails over the entire study area. A few main trails have narrow raised wooden boardwalks for part or all of their length in order to facilitate observers' travel efficiency. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates and adhered to the legal requirements of Indonesia.

Data Collection

Individual focal data were collected from 2003 to 2010 in accordance with standardized field methods [http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html], including activities and heights recorded at 2 min intervals [see also Dunkel et al., 2013; van Noordwijk et al., 2012]. Orangutans

observed to use the boardwalks were not scored as being on the ground. Location points were taken every half hour on a hand-drawn map that was later digitized (early years), or with a handheld Garmin GPSMAP 78 series GPS unit (later years). Both methods involve a certain amount of error (approximately $+/-$ 10 m), however, because of the large spatial scale in which orangutans move, as well as the nature of our questions, it is unlikely that this error measure has influenced our analysis.

Focal individuals could not always easily be followed without disturbing them once they were travelling on the ground through dense vegetation. Therefore, we included all focal activity data as long as the individual was followed for at least 3 hr, to reduce the bias in the data due to the focal being "lost" on the ground. However, we used all data covering at least a half hour to calculate the speed of movement during travel bouts and to assess space use.

In total, the dataset covers over 32,300 hr of focal observation on all age-sex classes of orangutans (plus an additional 5585 hr on pre-weaned offspring sampled together with their mothers) by an experienced team. In the current analyses, we distinguish between "immatures"—all weaned immatures, whether ranging in association with their mother or independently; "adolescent females"—ranging independently, sometimes sexually active, but nulliparous; "adult females"—all parous females (almost all accompanied by offspring); "unflanged males"—sexually mature males without cheek pads; "flanged males"—sexually mature males with fully developed secondary sexual features. In addition, some analyses were done on the dependent, pre-weaned offspring (infants) with known ages.

The monthly fruit abundance index was measured as the percentage of trees (in a phenology plot of over 1500 trees) bearing fruit [cf. Marshall et al., 2009]. Rainfall was measured daily at camp and minimum and maximum temperatures were measured daily at a fixed location in the forest, 50 m from the forest edge.

Twenty camera traps (Bushnell TrophyCam, 8 MP model) were installed throughout the study area, with at least 700 m between each one. The traps were active for a total of 3986 camera-trap days, between February 2010 and February 2012. The camera traps were programmed to take two photos, 10 seconds apart, whenever movement was detected. One "camera-trap record" refers to a set of two photos, and no camera-trap records of orangutans occurred at the same station on the same day, thus all records were considered independent. Fifteen of these cameras (3174 camera-trap days) were installed facing research trails at a height of 60–80 cm off the ground. The five additional cameras were located facing the raised boardwalks (812 camera trap days). All orangutan records ($N = 31$) were extracted and the age-sex classes of the orangutans in the photos were determined.

To control for possible observer effects, we analyzed changes in individuals' time spent on the ground over the 7-year period, as the orangutans were presumably becoming increasingly habituated to observer presence. In order to control for observation biases due to losing focal orangutans prior to the end of a full-day follow, we totaled and compared the number of times that focal individuals were followed to their night nests, lost prior to building a night nest, and lost when they were moving on the ground prior to building a night nest.

Spatial Data Analysis

Exact locations were known for every instantaneous data point falling on the hour and the half hour, as well as morning, day, and night nests. Approximate locations were calculated for every activity data point (2 min interval), by equally distributing the distance between the nearest preceding and subsequent location points.

In order to investigate general ground-use spatial patterns, a grid cell analysis was first performed: all location points were overlaid onto a grid of cells measuring 200×200 m. Thus, the total time spent in each area (grid cell) could be compared with the time spent on the ground in each area. Second, all location points were overlaid with a map of the trail system and any points within 5 m of a trail were categorized as "on trail" (the 5 m buffer zone was included in order to accommodate mapping and GPS error). This allowed for a comparison of orangutans' ground use on versus off trails.

Average travel speed was calculated for all follows lasting at least 3 hr by dividing the follow path length (measured between all subsequent half-hour points) by the duration of the follow. The overall travel speed during follows that did not include any movement on the ground were then compared to the overall travel speeds of follows which did include at least some movement on the ground. A second more detailed analysis of distance travelled during specific bouts of movement included data from any follow lasting at least 30 min, using the 2 min location points approximated between half-hour location points. A "travel bout" was defined as a 30 min period in which the individual's activity was "Move" (locomotion in some way or other) during at least 10 (out of a maximum of 15) behavioral data points. Travel bouts began at the time and location of the first point where the point sample activity was "Move" and ended 30 min later, regardless of the temporal distribution of the $10+$ "move points" during that time. If an orangutan continued to travel, and had at least 10 move points in the next 30 min, this was classified as a second travel bout. The distance traveled during these bouts was measured as the total distance travelled, from 2 min point to 2 min point, from the beginning to

the end of the 30 min. Travel bouts were then classified as having occurred entirely through the trees or as having included at least some ground travel, and the travel bout distances for the two groups were compared.

Statistical Analyses

All data were analyzed using χ^2 tests, Pearson's correlations, Kruskal–Wallis tests, and Wilcoxon signed-rank tests. For the Kruskal–Wallis and the time budget (activity and food items) Wilcoxon signed-rank tests, all data for each individual throughout the entire study period were summed, and individuals' scores were grouped by age-sex classes. For the kiss squeak analysis, as well as the average travel speed and the travel bout distance Wilcoxon signed-rank tests, each individual's mean scores were used, grouped by age-sex class where applicable (using median scores did not affect any of the conclusions). Thus, in order to avoid pseudo-replication in the data due to repeated sampling of the same individuals, each individual is represented by one data point in the analyses comparing time budgets, kiss squeak frequencies, travel distances, and speeds. Where simple statistical tests were not applicable, we have presented our results using descriptive statistics or as anecdotes. Camera-trap data are all described quantitatively, as were data investigating whether or not individuals' ground-use frequencies changed significantly over time as they became increasingly habituated to human observer presence.

RESULTS
Potential Biases and Habituation Effects

Long-term data consistently suggest that even habituated orangutans seem wary to descend to the ground when observers are present, and emit "kiss squeaks"—apparently toward observers—more frequently when they are close to or on their way to the ground than when they are higher up in the canopy. In order to analyze kiss squeak frequency without habituation level as a confounding factor, we used only data collected from 2006 to 2010, i.e. after 2–3 years of habituation, on the 7 most frequently encountered and thus, most habituated females. For each follow series lasting 5–10 days, the proportion of 2 min intervals when the focal was on or at <5 m from the ground and emitted a kiss squeak and the proportion of 2 min intervals when the focal was >5 m off the ground and emitted a kiss squeak was calculated. Even though observers always attempted to remain at a respectful distance, these females kiss squeaked significantly more often when they were <5 m above the ground than when they were >5 m above the ground (Wilcoxon signed-ranks test: $Z = 28, P < 0.05, N = 14, r = -0.54$).

We also looked for bias in the observational data due to terrestrial behavior. Focal individuals were "lost" before they made a night nest in 17% of all 3215 follows. This was most often because the focal individuals were on the ground and could not be followed through thick vegetation where visibility is low but following too closely would disturb them and human locomotion is necessarily slow ($N = 331$ times, or 60% of the lost cases). However, flanged males were much more frequently lost overall, and they were also twice as often lost while on the ground than females, immatures or unflanged males ($\chi^2 = 272.81$, $df = 4, P < 0.001$; see Fig. 1).

To examine whether focal orangutans gradually change their patterns of terrestriality in the presence of observers (i.e. long-term habituation effect), we compared the yearly proportion of ground use after 2–3 years of habituation, for four adult females for whom we had at least 200 hr of focal data per year during multiple years. Figure 2 shows that there was no consistent pattern in time spent on the ground as these individuals became increasingly familiar with human observer presence over the years. Thus, the observations of the well-habituated individuals provided relatively unbiased estimates of their natural ground use. However, we did not include data collected on unhabituated individuals, trying to flee or hide from observers or giving distress vocalizations for extended periods.

Frequency and Behavioral Correlates of Ground Use

Tuanan orangutans spent, on average, 2.29% of the total focal observation time on the ground. When including only those individuals for whom there is over 200 hr of data (total: $N = 25$; immatures: $N = 2$; adolescent females: $N = 2$; adult females: $N = 8$; unflanged males: $N = 6$; flanged males: $N = 7$), there is a significant difference between age-sex classes in the proportion of time spent on the ground
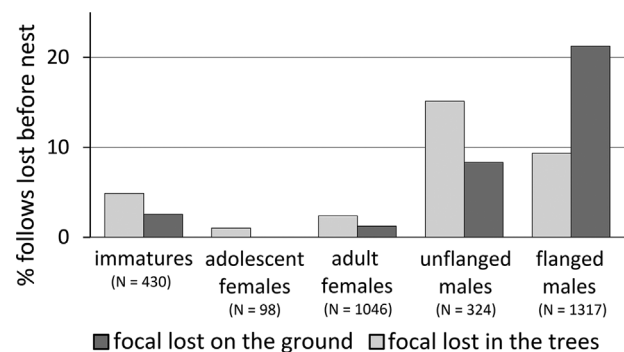

Fig. 1. The percentage of follows in which the focal individual was lost in the trees (light gray) and lost on the ground (dark gray) before making a night nest. The total number of focal follows started (either from morning nest or found during the day) is indicated per age-sex class.
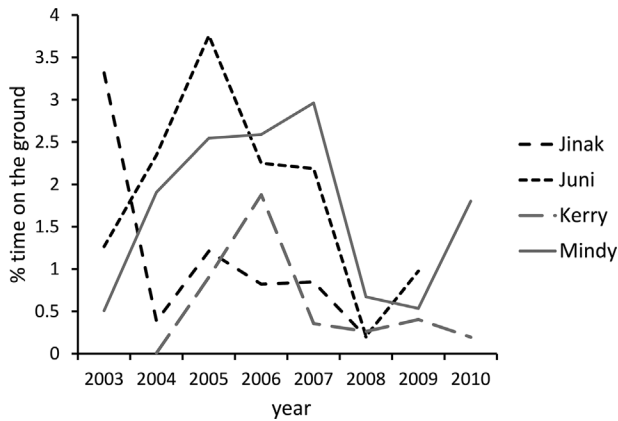
Fig. 2. The percentage of time spent on the ground by habituated females for whom >200 hr of focal data was available for at least 4 different years (all individuals, as well as the combined Pearson correlations are not significant, $P > 0.10$).
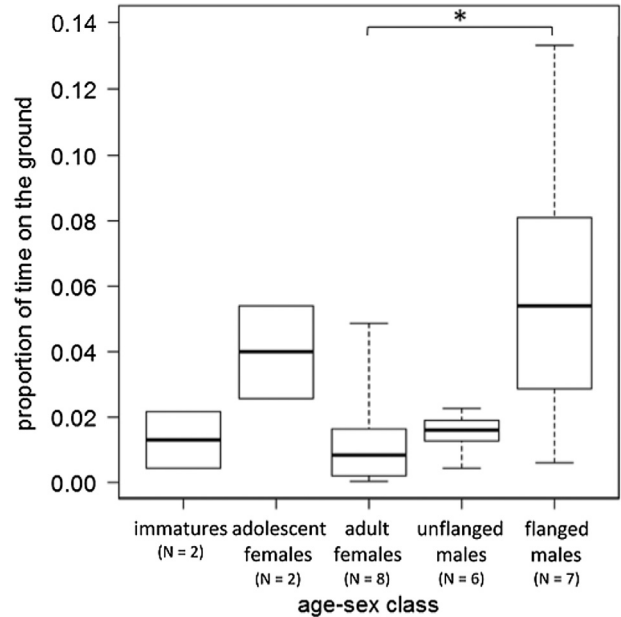

Fig. 3. The proportion of time during which individual habituated focal individuals were on the ground, by age-sex class. Center lines represent medians and whiskers extend to the maximum and minimum values of the data ($^{*}P < 0.05$).

(Kruskall–Wallis test: $H(4) = 11.85$, $P < 0.05$) and post-hoc tests reveal that the only significant difference is between adult females and flanged males: flanged males spent significantly more time on the ground than did adult females (Fig. 3). Note, that other pairings' differences were likely not significant primarily because of the small number of included individuals in the immature ($N = 2$) and adolescent female ($N = 2$) age-sex classes.

When the study started in 2003, an adult female (Sumi) with a young offspring was found in the logged and burned area adjacent to the study forest. Since there were only a few (mostly dead) trees still standing in her presumed original home range, this female mostly foraged and moved on or close to the ground in the dense and low recovering vegetation (this also made it difficult to follow her without being too close, so the sample is likely an underestimate of her actual time on, or close to, the ground). Over the next three years, this female moved completely into the forested study area, where she spent only ca 1% of her time (close to the average for mothers with dependent offspring) on the ground vs. >12% of her time on average during her first full year of being studied. Thus, her initially high use of the ground was forced upon her by the circumstances, whereas she became more arboreal and avoided being on the ground again when she had the opportunity.

We also compared activity budgets and diet composition on the ground versus in the trees. This analysis only included individuals for whom we have at least 200 hr of data and who were observed to spend at least 1 hr on the ground (immatures: $N = 2$; adolescent females: $N = 2$; adult females: $N = 6$; unflanged males: $N = 6$; flanged males: $N = 7$). A comparison of focal individuals' activity budgets when on the ground versus in the trees (Fig. 4) shows that adolescent and adult females, as well as immatures, spent a greater proportion of time

feeding and a smaller proportion of time resting when on the ground. Indeed, this difference was significant for adult females (Wilcoxon signed-ranks test: (feeding) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$; (resting) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). Flanged males spent a greater proportion of time moving when on the ground (Wilcoxon signed-ranks test: $Z = 28$, $P < 0.05$, $N = 14$, $r = -0.65$), and reduced their proportion of time spent resting when on the ground (Wilcoxon signed-ranks test: $Z = 2$, $P < 0.05$, $N = 14$, $r = -0.53$). Unflanged males had the same activity profile in the trees and on the ground.

The diet composition of all age-sex classes while on the ground differed from that when up in the trees: all orangutans spent much more time feeding on insects, mostly termites, which are found in decaying wood (Fig. 5). This difference was significant for flanged and unflanged males (Wilcoxon signed rank tests: (flanged males) $Z = 28$, $P < 0.05$, $N = 14$, $r = -0.65$; (unflanged males) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). In addition, all orangutans more often drank water while on the ground, even though water was sometimes also obtained from treeholes. Wilcoxon signed rank tests showed that this difference was significant for adult females ($Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$), flanged males ($Z = 27$, $P < 0.05$, $N = 14$, $r = -0.58$), and unflanged males ($Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). With the exception of immatures, individuals also tended to spend more time feeding on vegetative plant parts (mostly mature leaves and stems for *Ficus spp.*, pith of *Pandanus spp.* and *Zingiberacea*) while on the ground, although this contrast was not significant for any age-sex class.
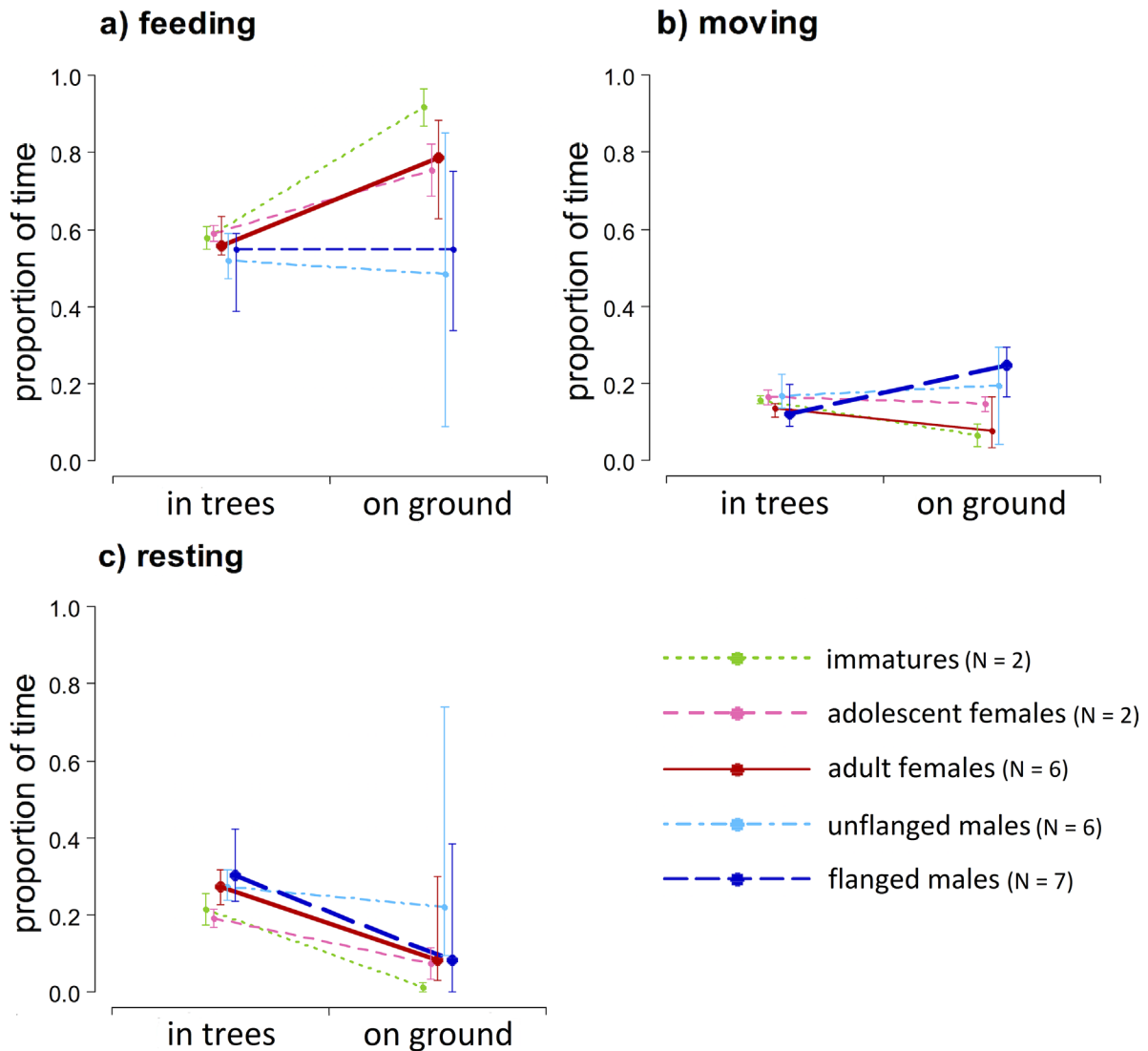
a) feeding

b) moving

c) resting

immatures (N = 2)

adolescent females (N = 2)

adult females (N = 6)

unflanged males (N = 6)

flanged males (N = 7)

Fig. 4. The difference in proportion of time that focal individuals spent feeding (**a**), moving (**b**), and resting (**c**) while in the trees versus on the ground, by age-sex class. Proportion of time spent engaging in each activity is of the total proportion of time spent on that substrate (ground or trees). Thicker lines denote significant differences ($P < 0.05$).

It is important to note that most food items usually found on the ground can also be found in—or at least easily carried up into—the trees, and therefore do not actually require orangutans to stay on the ground during or after collection. Indeed, all food items except for termites, soil, and water, were more often consumed while in the trees than while on the ground, when considering absolute, rather than proportional, amount of time spent feeding on the items. Indeed, termites—which were the overall most-consumed food item while on the ground—were consumed more often in the trees than on the ground by all adult females, all unflanged males, one flanged male, all adolescent females, and all immatures. Water was more often drank while in the trees than while on the ground by 2 adult females,

2 flanged males, 1 unflanged male, and 2 immatures. Of those individuals observed to consume soil ($N = 11$), 2 (both of whom were adult females) consumed it in the trees, rather than on the ground.

Mothers may be more likely than other adult age-sex classes to carry termite-infested logs up into the trees. Such "termite-logs" are often shared - that is, mothers tolerate and actively enable co-feeding by their offspring. Independently mobile offspring seemed reluctant to spend time on the ground and tended to stay behind in the trees, or climbed back up faster, when their mothers were on the ground. Figure 6 shows the proportion of time that a dependent offspring was on the ground when his/her mother was, and the proportion of time that a mother was on the ground when her dependent
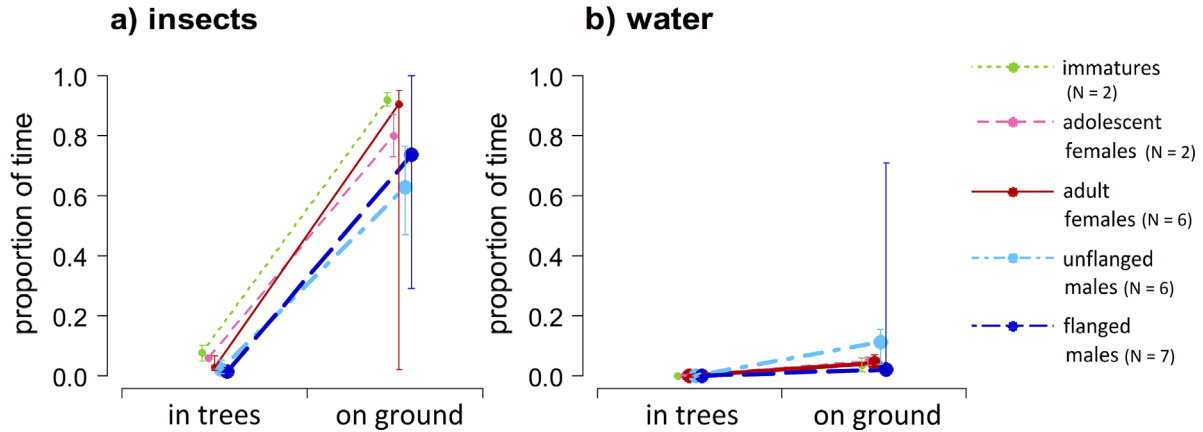
a) insects

b) water

Fig. 5. The difference in proportion of time that focal individuals spent feeding on insects (**a**), and water (**b**), while in the trees versus on the ground, by age-sex class. Proportion of time spent feeding on each item is of the total proportion of time spent feeding while on that substrate (ground or trees). Thicker lines denote significant differences ($P < 0.05$).

offspring was, broken down by age of the offspring. As offspring matured, they were increasingly likely to follow less closely and stay up in the trees when their mothers descended to the ground, and offspring were hardly ever on the ground without their mothers until they were at least 5 years old. In addition, even though it seems much easier for a small infant to move around on the ground than in the trees, dependent immatures up to age of 4–5 years were consistently more likely to be clinging to their mothers while on the ground than while in the trees during maternal moving, feeding and resting (Fig. 7).

In contrast, some social conditions seem to encourage leaving the trees. Orangutans fleeing from conspecifics, either in response to an agonistic encounter or as a form of preventive distancing, sometimes choose to descend to the ground and then quickly move away: in 44% (28 out of 62) of observed events of fleeing, the fleeing individual did so on the ground (Fig. 8).

After an individual fled from a conspecific on the ground, the association (proximity within 50 m) ended in 96% of the 28 cases, compared to only 68% of the 34 events when an individual fled through the trees ($\chi^2 = 6.71$ Yates corr, $df = 1$, $P < 0.01$). Furthermore, during her first years in the study area, the above-mentioned female, Sumi, disappeared over the ground whenever she encountered another orangutan, especially one of the resident females.

Environmental Correlates of Ground Use

Monthly rainfall in the Tuanan swamp forest is highly variable within and between years [van Noordwijk et al., 2013]. On average, the least rain falls in August and September (<100 mm/month) and the most rain falls in December to April (>300 mm/month). However, there was no relationship between the amount of rain in the previous 60 days or 30 days (intended as a proxy measure for
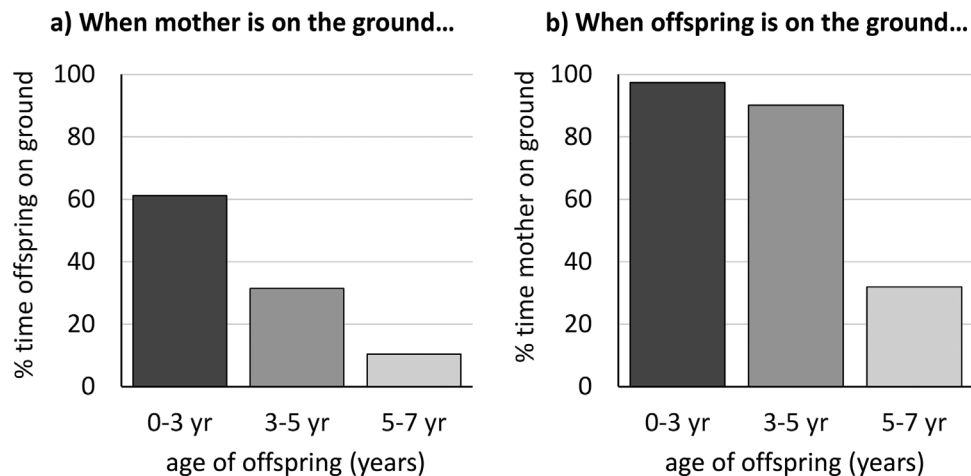
a) When mother is on the ground...

b) When offspring is on the ground...

Fig. 6. The percentage of time that a dependent offspring was on the ground while his/her mother was on the ground (**a**), and the percentage of time that a mother was on the ground when her dependent offspring was on the ground (**b**), by offspring age class.
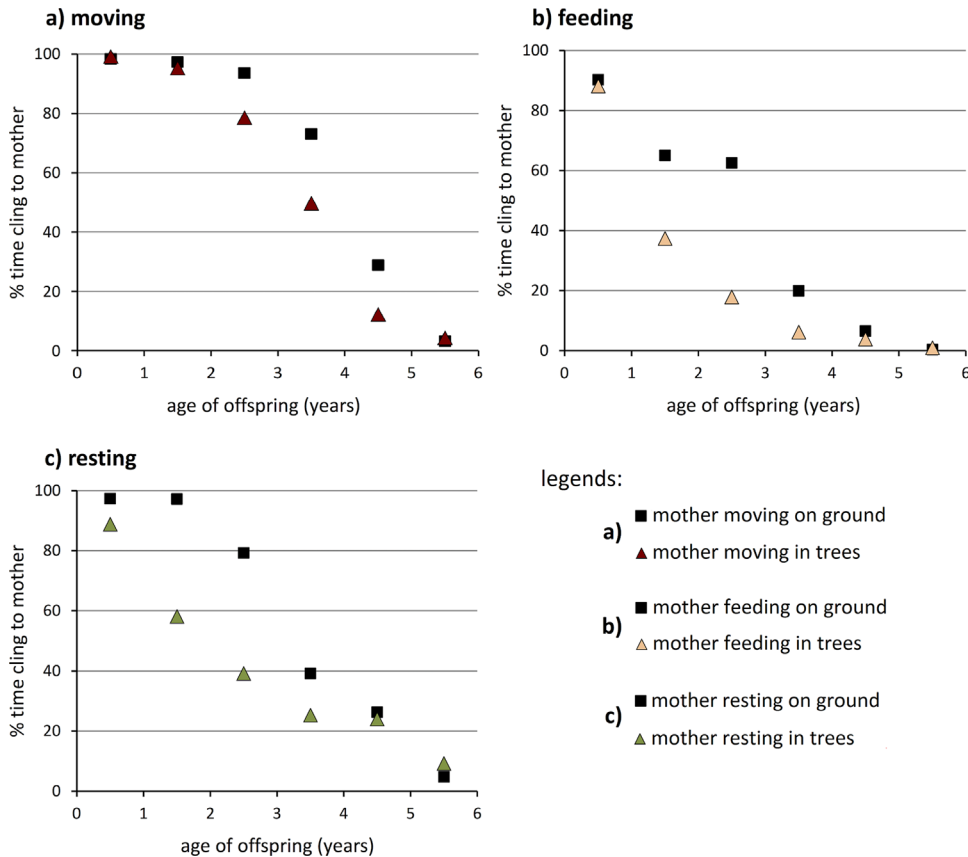
Fig. 7. A comparison of the percentage of time that a dependent offspring was clinging to his/her mother during moving (**a**), feeding (**b**), and eating (**c**), while his/her mother was on the ground versus while she was in the trees, by offspring age.

standing water) with the proportion of time individuals spent on the ground per focal follow ($N = 3428$ days, $N = 3456$ days, respectively).

Average monthly maximum temperature in the forest (28.8°C) varied little (range of monthly average: 28.1°C in January to 29.5°C in September). Focal individuals were occasionally seen standing or sitting in standing water on the ground, splashing themselves or even rubbing themselves with wet leaves. In total, 14 different individuals representing
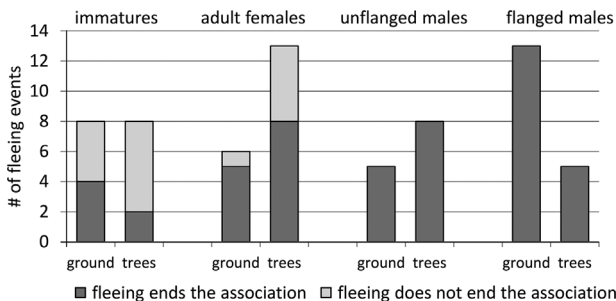

Fig. 8. The number of observed fleeing events (from conspecifics) through the trees and on the ground, comparing cases that did not result in the termination of the association (distance between conspecifics remained within 50 m) (light gray) and those that did end the association (dark gray).

all age-sex classes were observed to do this at least once. Even though these individuals seemed to cool off this way, the maximum temperature (measured at a fixed location) was barely higher on days with this "bathing" behavior than on days without it (average during focal follows with "bathing" T_{max} $29.10 \pm SD$ 1.64°C, $N = 32$ versus average during focal follows without "bathing" T_{max} $28.72 \pm SD$ 1.58°C, $N = 3706$) and well within the measuring error of our thermometers. Thus, although many different Tuanan orangutans seem to use standing water for apparent comfort behavior, the frequency of this is very low (at least in the presence of observers) and not clearly related to weather conditions.

During periods of food scarcity, orangutans may be expected to increase their time spent on the ground, either in order to collect fallback foods or to save energy by travelling longer distances over the ground. However, there was no consistent effect of fruit availability on the proportion of time that individuals spent on the ground, using the averages per age-sex class (based on at least 50 hr) per month. Adolescent females (the age-sex class with the smallest sample) are the only age-sex class to show a significant correlation. However, it is in a direction opposite to the expected one: as fruit availability

increased, the time they spent on the ground also increased (Pearson's $r = 0.695$, $N = 12$ month samples of ≥ 50 hr, $P < 0.05$). Most age-sex classes with larger samples (including immatures, unflanged, and flanged males) showed the expected negative trends, as did lumping all class samples together, but all these were non-significant, (Pearson's $r = -0.080$, $N = 198$ month samples, $P > 0.10$).

Spatial Distribution of Ground Use, and Speed of Ground Travel

Orangutans spent time on the ground in all parts of the study area, and overall, did not favour ground use in particular areas. There was a postive correlation between the total number of location recordings and the number of on-the-ground location recordings in each grid cell of the study area (Pearson's $r = 0.69$, $N = 282$, $P < 0.001$). There were two noticeable outliers—grid cells in which orangutans spent more time than expected on the ground. In these cells (which are adjacent), orangutans spent a relatively high proportion of time feeding on termites (66.2%, 84.5%). This suggests that the spatial distribution of termites has a large influence on the spatial distribution of orangutan ground use.

Overall, orangutans were within 5 m of a research trail in 8.4% of all on-the-ground observations, and in 9.0% of all above-ground observations. Flanged males were occasionally observed to move on the ground along trails; however, there were no significant differences between ground use on and off trails for flanged males or any other age-sex class, except for independent immatures, who were significantly less likely than expected to be on a trail when on the ground ($\chi^2 = 4.79$, $df = 1$, $P < 0.05$).

Among flanged males, the overall speed of travel during follows of at least 3 hr which did not include any ground travel was significantly lower than for those which did include at least some ground travel (Wilcoxon signed-rank test: $Z = 10$, $P < 0.005$, $N = 32$, $r = -0.57$). Furthermore, among flanged males, the distance travelled during 30 min travel bouts was significantly farther during bouts that did include some ground travel than bouts which took place entirely through the trees (Wilcoxon signed-rank test: $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$) (Fig. 9). It is important to note, however, that even the distances travelled by flanged males during 30 min travel bouts that took place entirely on the ground (no travel through the trees at all) ($N = 3$, range = 97–498 m) do not exclusively exceed the maximum distance travelled by a flanged male during a 30 min move bout taking place entirely through the trees (428 m). No other significant relationships between speed or distance travelled and movement on the ground were found for any age-sex class, over entire follows or during specific travel bouts.
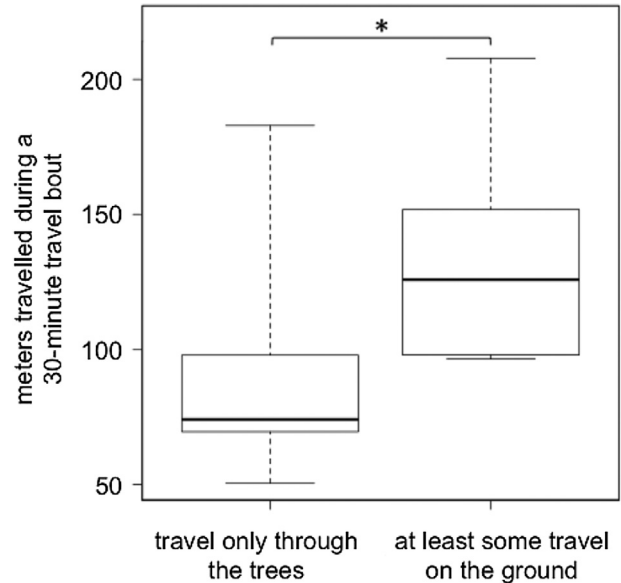

Fig. 9. The difference in distances travelled during 30-min travel bouts which occurred entirely through the trees versus those which included some ground use, for flanged males only ($N = 6$). Center lines represent medians and whiskers extend to the maximum and minimum values of the data (*$P < 0.05$).

Evidence of Orangutan Ground Use From Camera Traps in Tuanan

Within the study area, orangutans were photographed by ground-level camera traps 19 times (on average 0.006 times per trap day). Over half (53%) of the Tuanan camera-trap records were of flanged males, while the age-sex classes of 8 orangutans in the remaining records (47%) could not be reliably determined, although, all were at least adolescent size and 4 were definitely not flanged males. This means that flanged males were recorded in a minimum of 53% and maximum of 77% of camera-trap records. The additional 5 camera traps directed at raised boardwalks recorded females with offspring at least 3 times and flanged males 7 times, out of a total of 12 records—for 0.015 records per trap day. Orangutans were significantly more likely to be recorded by camera traps facing the boardwalks than by those facing the trails ($\chi^2 = 5.39$, $df = 1$, $P < 0.05$).

DISCUSSION

Reasons for Ground Use in Tuanan

Although, until now, behavioral studies of wild Bornean orangutans have only reported terrestriality anecdotally, it is clear that ground use is within their natural behavioral repertoire. Consistent with early reports from other studies [e.g. Galdikas, 1979; MacKinnon, 1974], flanged male orangutans at Tuanan spent more time on the ground than any other age-sex class. Indeed, we found that flanged males were the most often lost age-sex class by

observers, often because they would descend to the ground, and thus our estimate of ground-use rate for flanged males is likely biased towards an underestimation. Furthermore, while flanged males often traveled along the ground, adult females primarily came to the ground to feed on certain resources, such as termites. We found no evidence of a strong spatial bias to orangutan ground use, except that orangutans forced to live in more open areas spent much time on the ground. Instead, orangutans did spend more time than expected on the ground where they could most often engage in termite feeding. Thus, ground use is not simply a response to canopy gaps or unsuitable habitat [cf. Ancrenaz et al., 2014], but occurs to satisfy specific needs.

Orangutans at Tuanan were observed to descend to the ground to collect, and sometimes consume, food items, including termites, water, and peat-soil/turf. In the homogenous peat-swamp forest at Tuanan, standing water is available and consumed throughout the study area, and there is no indication that it satisfies any nutritional/mineral needs aside from thirst (in contrast to drinking from salt lick pools as described for some other sites e.g. Matsubayashi et al. [2011]).

There is nonetheless strong evidence for an innate wariness of the ground. First, resting on the ground was extremely uncommon for orangutans other than flanged males. Second, even the most habituated adult female orangutans were more likely to kiss squeak when they are on their way to, or already on, the ground. Kiss squeaks are interpreted as both alarm and mobbing calls [Hardus et al., 2009] and alert others (mostly offspring) to watch out, but also warn potential predators (including human observers) that they have been noticed and will be chased if they come too close (Tuanan unpublished observations on humans and a dog). Lastly, small (unweaned) immature orangutans hardly ever descended to the ground alone, and even only rarely accompanied their mothers down to the ground, unless they could cling to her body. This apparent reluctance of small immatures to spend time on the ground, even when their mothers do, may explain why adult females did not spend significantly more time feeding on termites on the ground than up in the trees, while adult males, both flanged and unflanged, did. Thus, mothers may spend less time on the ground than would be efficient for themselves, to accommodate the needs of their young offspring. Indeed, adult females with dependent offspring are often observed to descend to the ground alone, and then carry a termite-infested log back up into the trees. These termites are then consumed in the canopy, where the offspring is allowed to co-feed.

The camera-trap data confirmed these observational findings. Immatures avoid coming to the ground on trails, supporting the notion that they only leave the trees when the attraction, i.e. feeding opportunity, is strong enough and not to travel or cross canopy gaps. Adult females with dependent offspring were recorded relatively more frequently on raised boardwalks than on trails, suggesting mothers with offspring avoided travelling on the ground when possible.

This pattern suggests that there may be a learned loss of fear over the course of an individual's life: as a young orangutan increasingly often accompanies its mother to the ground, grows in body size, and becomes more familiar with ground-based resources such as termites, terrestriality becomes a more regular component of its behavioral repertoire and its natural aversion to ground use is lessened. This indicates that regular ground use among Bornean orangutans may be a relatively recent addition to their behavioral repertoire, perhaps only since the extinction of tigers on the island (which may have occurred as recently as the early Holocene [Kitchener & Dugmore, 2000; Louys, 2014; Piper et al., 2007]). These learned behaviors have served to increase the feeding niche of all, as well as the mobility of male, orangutans.

This interpretation is bolstered by the fact that Bornean orangutans do not show obvious anatomical differences compared to their Sumatran counterparts, and thus lack any clear adaptation for terrestrial locomotion, such as the knuckle-walking capabilities of chimpanzees and gorillas. Indeed, since splitting from the common hominid ancestor, it is likely that orangutans' adaptations to arboreality have been further refined [Thorpe and Crompton, 2006].

Sumatran orangutans still share their range with tigers, and indeed rarely descend to the ground, except in social emergencies or to collect food and quickly carry it up into the trees [Rijksen, 1978; van Schaik, 2004; in the swamp forest of Suaq Balimbing habituated females spent <0.05% on the ground and even flanged males were <0.25% terrestrial: C. Schuppli, personal communication]. However, for both species, other predators such as clouded leopards, snakes, and wild pigs, are a potential threat to especially the smaller-bodied individuals, explaining their wariness to be on the ground (see Kanamori et al. [2012] for an example of a predation event on a juvenile orangutan). This wariness is less obvious among the large-bodied, and thus less vulnerable, flanged males, who even occasionally spend nights on the ground in Tuanan. Indeed, ground nesting by flanged males at Tuanan was observed 3 times during the study period ($N = 442$ follows to nest), but has been observed more frequently since (in the period of 2010–2012: 10 out of 197 follows to nest), with one male accounting for 9 of those nights. Individuals of other age-sex classes were never observed to nest on the ground, with the exception of the adult female whose home range was burned—she was observed to spend at least 4 nights

on the ground when she was still ranging in her original home range after it had been cleared (i.e. before she began to push her range into the adjacent forested area). Thus, the only individuals who ever nested (apparently) voluntarily on the ground were large-bodied flanged males.

Over the course of several hours, or even full days, flanged males travel faster when a proportion of their movement occurs on the ground. This is not seen for other age-sex classes, which may be because their terrestrial movement is often done in the context of searching for food and may therefore be much less unidirectional than that of larger males who are using the ground more for travel without inspecting foraging options. Because location points were only recorded every half-hour, the sinuosity of individuals moving around and searching for food on the ground was not measured. Interestingly, only 4% of adult females' 30 min travel bouts included any ground-travel (as compared to 22% for flanged males), showing that when adult females are engaging in relatively consistent movement (rather than that which is heavily interspersed with feeding, for example), they rarely include any ground travel.

Our analysis of distances traveled during 30 min travel bouts shows that flanged male orangutans are able to move quickly both on and off the ground but that there is an association between including at least some terrestrial locomotion and higher speeds. However, because flanged males travelling only through the trees were often able to reach travel speeds as fast or nearly as fast as those incorporating some ground-use, it is likely that factors other than simply the potential speed of travel have a large influence over whether or not an individual moves on the ground or in the canopy.

Although, Bornean orangutans do not show specific morphological adaptations for terrestrial locomotion, there is evidence that they are able to move relatively inconspicuously—even when moving quickly—along the ground. First of all, the relatively high rate at which focal individuals are lost by observers when on the ground, compared to when in the trees, demonstrates that it is much harder for humans to follow an orangutan who is moving along the ground than one who is moving through the trees. At Tuanan, orangutans on the ground hardly disturb or rustle the thick undergrowth when moving, the way that they disturb the trees when moving through the canopy. Thus, even a small distance of 5–10 m between the focal orangutan and its observers is often enough for observers to lose sight of the orangutan entirely.

Secondly, there is evidence that losing contact with an orangutan who is moving on the ground may not be only a human problem: orangutans fleeing from conspecifics on the ground were more likely to end the association than those fleeing through the trees. Thus, at least at Tuanan—where the forest is mostly made up of small, pliable trees—fleeing over the ground may be a more effective strategy to end unwanted associations with conspecifics than fleeing through the trees, which involves noisy and conspicuous movements such as tree swaying. This all indicates that in some closed canopy forests, orangutans' travel along the ground can be less conspicuous than travel through the trees, and social factors may greatly influence whether or not an orangutan chooses to travel on the ground. In Borneo, where competition between orangutan males can frequently turn violent [Dunkel et al., 2013], it is not surprising that males often seem to attempt to move around undetected by conspecifics.

Another common hypothesis to explain ground travel over longer distances by orangutans is based on the assumption that travel on the ground is more energy-efficient than through the trees, which may require frequent directional diversions in all three dimensions [Cant, 1987]. This would especially be true where canopy structure and connectivity are poor. Saving energy by moving along the ground could be especially beneficial for the large-bodied flanged males, and thus explain why they are the most likely age-sex class to move on the ground and why this ground-movement is associated with higher speeds and travel over longer distances. It has been suggested that microclimate might be an additional advantage of ground travel, e.g. Takemoto [2004] found that chimpanzees spent more time on the ground during the dry season and speculated that this helped them to stay cool and thus reduced their metabolic costs associated with thermoregulation. Measurements at Tuanan [Hermann, 2010] have shown that maximum temperature tends to be higher at the mid-canopy level (5 m or 10 m) than closer to the ground. It could therefore be speculated that, at least in the case of long-distance ground travel by the larger-bodied males, ground use increases when canopy temperature increases. However, the general patterns of ground use among Tuanan orangutans do not show a meaningful relationship with daily maximum temperature (measured at approximately 1.3 m off the ground). Furthermore, standing swamp water is also often used for bathing. Despite this behavior seeming to cool the orangutans off, it did not specifically occur on especially hot days. Thus, it is still unclear to what extent ground travel (and use in general) aids orangutans in reducing thermoregulatory costs.

One other potential explanation for ground travel, especially for the large-bodied males, is that it may reduce their risk of falling. Orangutans at Tuanan are occasionally observed to fall—either all the way from the canopy to the ground, or within the canopy from higher up to lower down—when supports break under their weight. Evidence of long bone fractures consistent with falls out of the

forest canopy has been found among great apes, including orangutans [Kehoe & Chan, 1986; Kraft et al., 2014]. This risk of injury from falling may be especially high for the heaviest orangutans, the flanged males, and thus may contribute to their more frequent ground travel.

Comparison With Other Sites

Our camera-trap data show that the frequency of orangutan terrestriality at Tuanan falls within the range of ground-use frequencies reported from other sites in Borneo [Ancrenaz et al., 2014]. Of all the camera-trap study sites, Tuanan is perhaps most comparable with the Sabangau study site, in terms of forest type (peat-swamp forest) and current and past management classification ("old and slightly logged forest"), as per Ancrenaz et al. [2014]. Orangutan density at Tuanan is approximately 3 times higher than at Sabangau, and the total camera-trap rate of capture at Tuanan is 3 times higher than at Sabangau. This suggests that orangutans in these two similar forests may be spending comparable amounts of time on the ground.

Interestingly, the rate of camera-trap captures of orangutans on the ground from the dryland, formerly selectively logged area in Wehea Forest [Loken et al., 2013, breakdown of counts reported in Ancrenaz et al., 2014] is almost twice that of Tuanan, despite an orangutan population that is 4 times less dense. This suggests that the orangutans (*P. p. morio*) living in Wehea Forest spend far more time on the ground than the orangutans (*P. p. wurmbii*) of Tuanan. Furthermore, the camera-trap study of Loken et al. [2015] demonstrates a propensity for ground use among various age-sex classes of orangutans, including adult females with and without dependent offspring. Indeed, in all 3 forest types, adult females accounted for 41% of camera-trap records, while flanged males accounted for 23–36% of records [Loken et al., 2015]. This suggests that in the areas studied by Loken et al. [2013, 2015], ground use by age-sex class may be different than among the Tuanan orangutans. Unfortunately, it is not yet possible to determine the relative contribution of structural factors (forest type, canopy structure, etc.), population/sub-species differences, or other factors, to this substantial observed difference. We suspect that food availability and distribution does play a role at this between-population scale.

In conclusion, we have shown that terrestriality is a normal component of the Bornean orangutan behavioral repertoire. In Bornean forests, even those with a relatively closed canopy, orangutans occasionally descend to the ground in response to unwanted associations, to retrieve attractive food sources (some of which, e.g. termite logs, may be carried up into the trees), and—especially in the case of flanged males—to travel. However, like Sumatran orangutans, Bornean orangutans do appear to have an innate fear of the ground. Unlike Sumatran orangutans, though, they gradually overcome this fear during ontogeny, although females never do so completely. The proportion of time spent on the ground differs between individuals and between populations, but for now the role of food scarcity, canopy structure, or other factors remains unclear.

The tendency of Bornean orangutans to come to the ground may better equip them to deal with forest degradation. In this respect, the Bornean orangutan may have more behavioral flexibility as to habitat use than Sumatran orangutans. This difference may enable Bornean orangutans to better cope in disturbed, fragmented, and human-dominated landscapes.

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