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Recapturing the canopy: stimulating Bornean orang-utan (*Pongo pygmaeus*) natural locomotion behaviour in a zoo environment

Tom S. Roth[1], Thomas R. Bionda[2] and Elisabeth H.M. Sterck[1,3]

[1]Animal Ecology, Utrecht University, Utrecht, The Netherlands
[2]Apenheul Primate Park, Apeldoorn, The Netherlands
[3]Ethology Research, BPRC, Rijswijk, The Netherlands
Correspondence: Elisabeth HM Sterck, Padualaan 8, Room O211, 3584 CH UTRECHT, The Netherlands; E.H.M.Sterck@uu.nl

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Abstract
Orang-utans are the largest mainly arboreal animal: wild orang-utans rarely come to the forest floor. In contrast, the locomotion behaviour of captive orang-utans encompasses more time on the ground and they spend less time on locomotion than their wild conspecifics. Moreover, their most frequently employed climbing postures differ from those of wild orang-utans. More natural locomotion behaviour may be stimulated by the design of appropriate enclosures. This study aimed to investigate how the design of orang-utan enclosures influences locomotion behaviour both quantitatively (i.e. time spent above ground and on locomotion) and qualitatively (i.e. types of movement). We collected continuous focal samples from 11 captive Bornean orang-utans (*Pongo pygmaeus*) at Apenheul Primate Park (Apeldoorn, The Netherlands). During the study, Apenheul offered two types of outdoor enclosures to their orang-utans: horizontal trunk enclosures with a relatively high number of large-diameter, horizontal tree trunks; and multiple rope enclosures with a relatively high number of small-diameter ropes. The results showed that the orang-utans' quantitative locomotion behaviour was more natural in the horizontal trunk than in the multiple rope enclosures: they spent less time on the ground and more time on above-ground locomotion. However, the orang-utans' qualitative locomotion behaviour seemed more natural in the multiple rope enclosures than in the horizontal trunk enclosures. This indicates that both horizontal trunks and small-diameter substrates are required to stimulate natural quantitative and qualitative locomotion behaviour. Zoos can apply our recommendations to stimulate natural locomotion behaviour in captive orang-utans, which may improve their physical condition and thereby increase their wellbeing.

Introduction

Welfare of zoo animals may be improved by promoting natural behaviour (Newberry 1995; Maple 2007). The quality of the physical environment of captive animals may contribute to the amount of natural behaviour performed depending on its characteristics (Taylor et al. 2005; Maple 2007). First, the environment should mimic the natural situation of animals as much as possible (Young 2003). Second, enrichment can motivate animals to use their physical environment in a more natural way. Promoting natural behaviour in captive animals also conforms with the goal of zoos to educate visitors about the natural environment and the life history of their animals (Patrick et al. 2007; Hosey et al. 2013). Therefore, promoting natural behaviour will be beneficial for both animals and zoos.

The orang-utan (*Pongo* spp.) is the largest arboreal mammal (Thorpe and Crompton 2009). Their arboreal habits may result from predator avoidance (Cant 1987), while foraging success and reproduction depend on above-ground positional behaviour (Cant 1992). Orang-utans comprise two species: the Sumatran (*Pongo abelii*) and the Bornean orang-utan (*Pongo pygmaeus*; Goossens et al. 2009). Both species are adapted to living in an arboreal environment: they possess long forelimbs with large hands and long fingers and short hindlimbs with hand-like feet, which facilitate quadrumanous locomotion through the forest canopy (Delgado and van Schaik 2000). Bornean orang-utan males are more terrestrial than Sumatran orang-utan males (Cant 1987), but even Bornean males spend more than 86 percent of time above the ground (Thorpe and Crompton 2009).

Captive orang-utans may differ from wild conspecifics in their quantitative locomotion behaviour: it has been suggested that captive orang-utans spend a larger amount of time resting and staying on the ground than wild orang-utans, and spend

Table 1. Focal animals present at Apenheul Primate Park during the study.

Name	Sex	Year of birth	Observation time				
			Horizontal trunk enclosures		Multiple rope enclosures		
			Morning	Afternoon	Morning	Afternoon	Total
Amos	Male	2000	0:35:34	0:48:21	0:33:16	0:45:00	2:42:11
Binti	Female	2000	0:32:14	0:40:07	0:41:02	0:47:28	2:40:51
Dayang	Female	2005	0:48:45	0:34:56	0:41:11	0:45:00	2:49:52
Josje	Female	1992	0:35:55	0:31:33	0:52:09	0:40:37	2:40:14
Kevin	Male	1982	0:33:59	0:49:45	0:45:00	0:45:00	2:53:44
Merah	Female	2006	0:42:53	0:35:56	0:48:31	0:37:57	2:45:17
Radja	Female	1962	0:53:21	0:36:15	0:30:03	0:32:24	2:32:03
Samboja	Female	2005	0:40:37	0:46:39	0:47:19	0:36:15	2:50:50
Sandy	Female	1982	0:38:42	0:32:47	0:49:08	0:41:59	2:42:36
Silvia	Female	1965	0:49:12	0:36:18	0:32:04	0:30:00	2:27:34
Wattana	Female	1995	0:37:19	0:45:42	0:38:20	0:33:08	2:34:29
Average			0:41:38	0:39:32	0:40:46	0:39:51	2:41:47

a smaller amount of time on above-ground locomotion (Isler and Thorpe 2003; Maple 1980). This difference may be due to enclosure characteristics. First, captive orang-utans are often confronted with enclosures that are substantially different from the natural habitat (e.g. rigid furniture, uniform substrate type and diameter), which may result in reduced locomotion. Second, they may have a reduced motivation to climb, because they do not have to avoid predators and climb to find food. Third, habituation may reduce locomotion, because captive animals become too familiar with the climbing opportunities in their enclosure (Isler and Thorpe 2003).

The fact that captive orang-utans spend more time on the ground and climb less can have important welfare consequences. First, because terrestrial locomotion exerts different force on muscles and joints than arboreal locomotion, captive orang-utans may develop muscular and/or skeletal adaptations that negatively influence their climbing ability (Isler and Thorpe 2003). Second, orang-utans experience low metabolic rates and therefore low energy needs, which is probably an adaptation to food scarcity in the wild (Pontzer et al. 2010; Russon 2010). However, in a captive setting these low energy needs make orang-utans vulnerable to overfeeding and obesity (Pontzer et al. 2010; but see Pontzer et al. 2016). Therefore, stimulating captive orang-utans to spend a significant amount of their time on climbing and above-ground locomotion will contribute to their health.

Stimulating natural behaviour in captive orang-utans should take their natural movement preferences into account. First, wild orang-utans prefer climbing in the part of the canopy that provides the most continuous horizontal stratum (Thorpe and Crompton 2005; Manduell et al. 2011). Therefore, a large number of horizontal connections in their enclosure may increase their quantitative locomotion behaviour. Second, most locomotion types of wild orang-utans are associated with climbing supports with a diameter smaller than 20 centimetres, with the exception of quadrupedal walking and vertical climbing/descending (Thorpe and Crompton 2009). Therefore, replacing small diameter substrates with large diameter trunks may have a negative impact on qualitative locomotion behaviour. Thus, it may be that environmental enrichment efforts should aim to increase not only substrate type, but variability in substrate diameter, to maximise animal wellbeing. Third, wild orang-utans will aim to minimise their travel costs (Thorpe et al. 2007). Large-diameter supports may be a preferred support type over small-diameter supports like ropes, because they decrease the costs of locomotion (Thorpe et al. 2009). In addition, horizontal movement is generally less costly than vertical movement (Hanna and Schmitt 2011), and vertical movement may only be conducted when rewarding.

The aim of this study was to investigate the influence of these two different types of outside enclosures on the quantity of orang-utan locomotion and the quality of orang-utan locomotion. To this end, we performed research at Apenheul Primate Park (Apeldoorn, The Netherlands). Apenheul Primate Park offered two different types of outdoor enclosures for Bornean orang-utans in 2015: one type with a more horizontal stratum of large tree trunks, referred to as the horizontal trunk enclosures, and one type with a relatively large number of climbing supports with a low diameter, referred to as the multiple rope enclosure. Continuous focal samples from 11 captive Bornean orang-utans were conducted. Because the horizontal trunk enclosures were newly constructed, we also tested for habituation. Outcomes of this study can help to identify the effects of the physical environment on orang-utan locomotion, and therefore contribute to the welfare of captive orang-utans.

Methods

Subjects and housing

The study was conducted at Apenheul Primate Park in spring 2015. Apenheul housed 11 adult Bornean orang-utans: two flanged males and nine females (Table 1). Two infant males were not observed.

The orang-utans were housed in four separate inside enclosures, each connected to an outside enclosure consisting of two small islands (Figure 1). Every morning, the orang-utans could choose which of the enclosures they preferred to spend their day in, by seeking visual contact with their caretakers. All individuals were allowed to spend the day together, except the two flanged males. During the study, the orang-utans lived in different subgroups of between two and five individuals. Subgroups consisted mainly of relatives, such as mothers and offspring, and sometimes an adult male. The orang-utans took part in a feeding presentation for the visitors once a day from about 1445 to 1500h.

The individuals had free access to both inside and outside enclosures. Every outside enclosure consisted of two small islands (Figure 1). Islands E, F, G and H were reconstructed in the

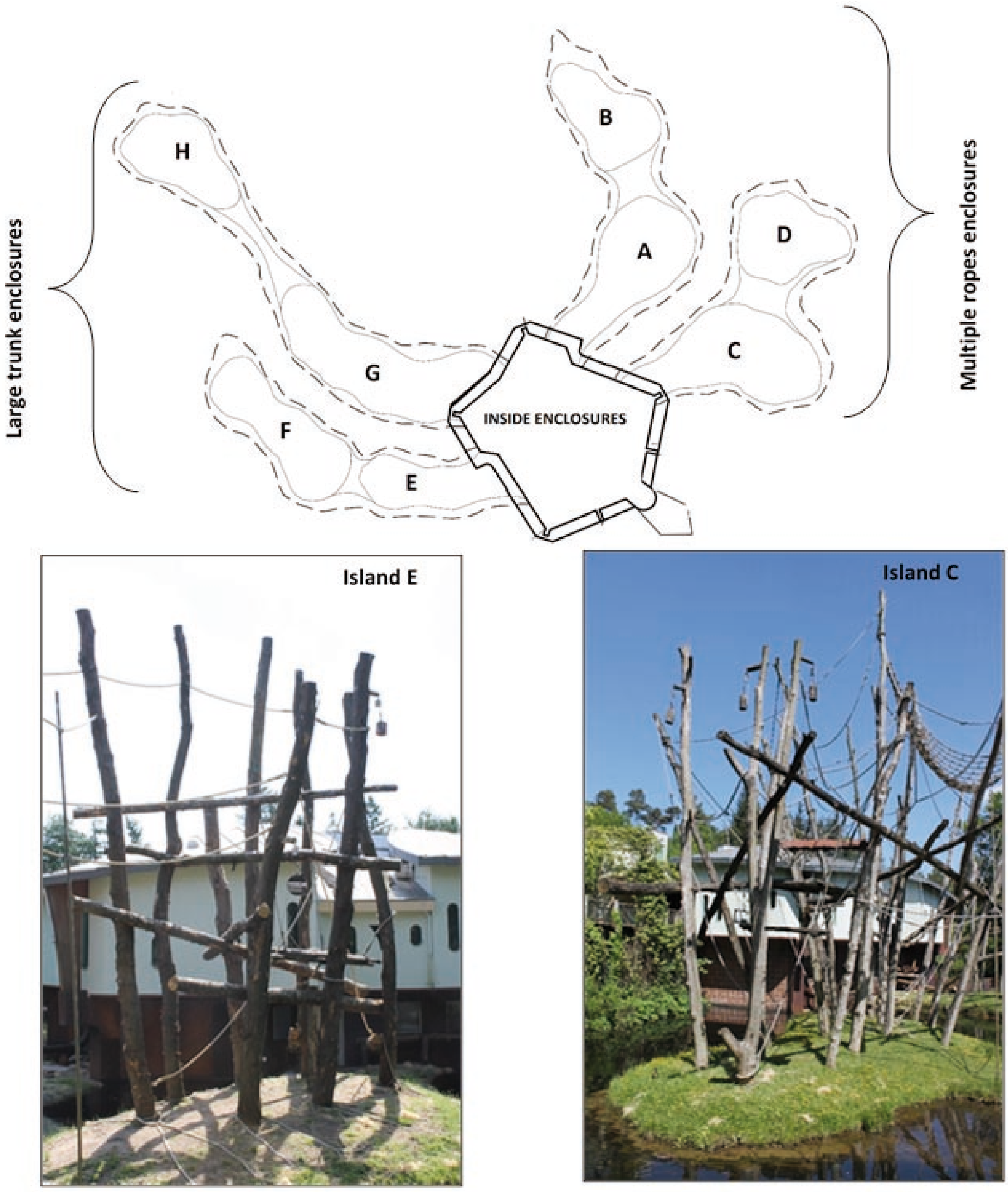

Figure 1. Schematic drawing of the orang-utan outside enclosures in Apenheul Primate Park, and an example of both enclosure types. Island E is an example of a large trunk enclosure, while island C represents a multiple ropes enclosure.

winter of 2014–2015 and were characterised by a relatively small number of ropes and a relatively high number of horizontal tree trunks. These islands will be referred to as the “horizontal trunk enclosures” (Figure 1, island E). In contrast, islands A, B, C and D were characterised by a large number of ropes and a relatively low number of horizontal trunk connections. These islands will be referred to as the “multiple rope enclosures” (Figure 1, island C). Furthermore, all islands contained feeding enrichment, resting spots and nesting material. The bottom of three of the outside enclosures (A, B, C, D, G and H) contained grass, while E and F did not have full grass cover and were mainly characterised by a dusty and sandy cover.

Differences between the enclosures

The horizontal trunk enclosures were designed to contain fewer ropes and more horizontal tree trunks (>30 cm in diameter) than the multiple rope enclosures, because wild orang-utans prefer climbing in the part of the canopy with the most continuous horizontal stratum (Thorpe and Crompton 2005; Manduell et al. 2011). The horizontal trunks were fixed at heights ranging from 1 metre to 11 metres. We counted the number of tree trunks and number of ropes between two fixing points on the eight different islands of the two enclosure types (Table 2). The horizontal trunk enclosures contained higher proportions of large diameter horizontal trunks, i.e. trunks with an inclination below 45° of true

Table 2. The number of horizontal trunks, loose ropes and ropes on every island. In addition, the proportion of horizontal trunks/total trunks and the proportion of loose ropes/total ropes. The multiple rope enclosures contain more ropes and a higher proportion of loose ropes, while the horizontal trunk enclosures contain both more and a higher proportion of horizontal trunks.

Islands	Horizontal trunks	Proportion of total trunks	Loose ropes	Proportion of total ropes	Total ropes
Multiple rope enclosures					
A	10	0.34	19	0.86	22
B	5	0.29	18	0.90	20
C	10	0.36	19	0.79	24
D	7	0.33	21	1.00	21
Horizontal trunk enclosures					
E	9	0.53	2	0.18	11
F	11	0.42	4	0.25	16
G	14	0.42	5	0.28	18
H	18	0.51	4	0.20	20

horizontal. Moreover, the multiple rope enclosure contained more low diameter vertical (i.e. with an inclination above 45°) ropes and a higher proportion of loose-hanging ropes, i.e. loosely hanging between two fixation points, than in the enclosures characterised by horizontal trunks. Due to the design of the enclosures, the effect of substrate diameter and angle could not be disentangled.

Data collection and ethogram

Data were collected between 20 April 2015 and 12 June 2015. The observations were conducted in two timeslots: 1000–1300 and 1300–1600. Continuous focal sampling was used (Altmann 1974). Focal animals were observed for a maximum of 15 minutes, and observations shorter than 2 minutes were not used. After an observation, the focal animal was not observed for at least 30 minutes. Also, no observations were collected during the daily feeding presentation. The objective was to observe all 11 focal animals for at least 40 minutes in each timeslot and on each island type. However, due to weather conditions, it was not possible to reach this goal for each orang-utan in the different observation slots (Table 1).

First, the locomotion/posture type was noted, based on the ethogram of Thorpe and Crompton (2006) (Table 3). Locomotion types were scored directly if a focal animal started moving, but postures were only scored if an animal stayed in the same posture for at least 5 seconds. Second, we noted whether the focal animal was on the ground or above ground. Third, general behaviours, i.e. travelling (locomotion without other pursuits), resting (stationary behaviour without performing other activities), feeding (obtaining and consuming food) and other, were scored.

Statistical analysis

Data were analysed using IBM SPSS Statistics 20. To analyse the behavioural data, time data were converted to proportions of the total observation time or proportions of the total locomotion

Table 3. Locomotion types observed in this study. A posture within 45° of true vertical was considered orthograde, while a posture within 45° of true horizontal was considered pronograde. This ethogram is based on Thorpe and Crompton (2006).

Quadrupedal and tripedal walk	Locomotion with pronograde (horizontal) torso and 3 or four limbs contacting the support in a particular sequence.
Torso-orthograde suspensory locomotion	Suspensory locomotion with the body hanging and the torso orthograde (vertical). Body mass is mainly supported by the forelimbs.
Bipedal walk	Hindlimbs provide majority of support and propulsion and torso is orthograde (vertical). Includes both hand-assisted and unassisted bipedal walking.
Torso-pronograde suspensory locomotion	Suspensory locomotion with the body hanging and the torso pronograde (horizontal).
Bridge*	Torso-orthograde (vertical) gap crossing movement.
True vertical climb/descent	Ascent or descent within 22.5° of true vertical.
Angled climb/descent	Ascent or descent between 22.5° and 45° of true vertical.
Tree sway**	Oscillatory locomotion in which the focal uses its own weight to move a support that is fixed at the bottom, such as a tree, to reach another support.
Liana/vertical branch sway**	Oscillatory locomotion in which the focal uses its own weight to move a support that is fixed above the focal, such as a liana, to reach another support.

*=Thorpe and Crompton (2006) defined this as a pronograde movement. **=Thorpe and Crompton (2006) merged these categories into one locomotor mode, ‘sway’.

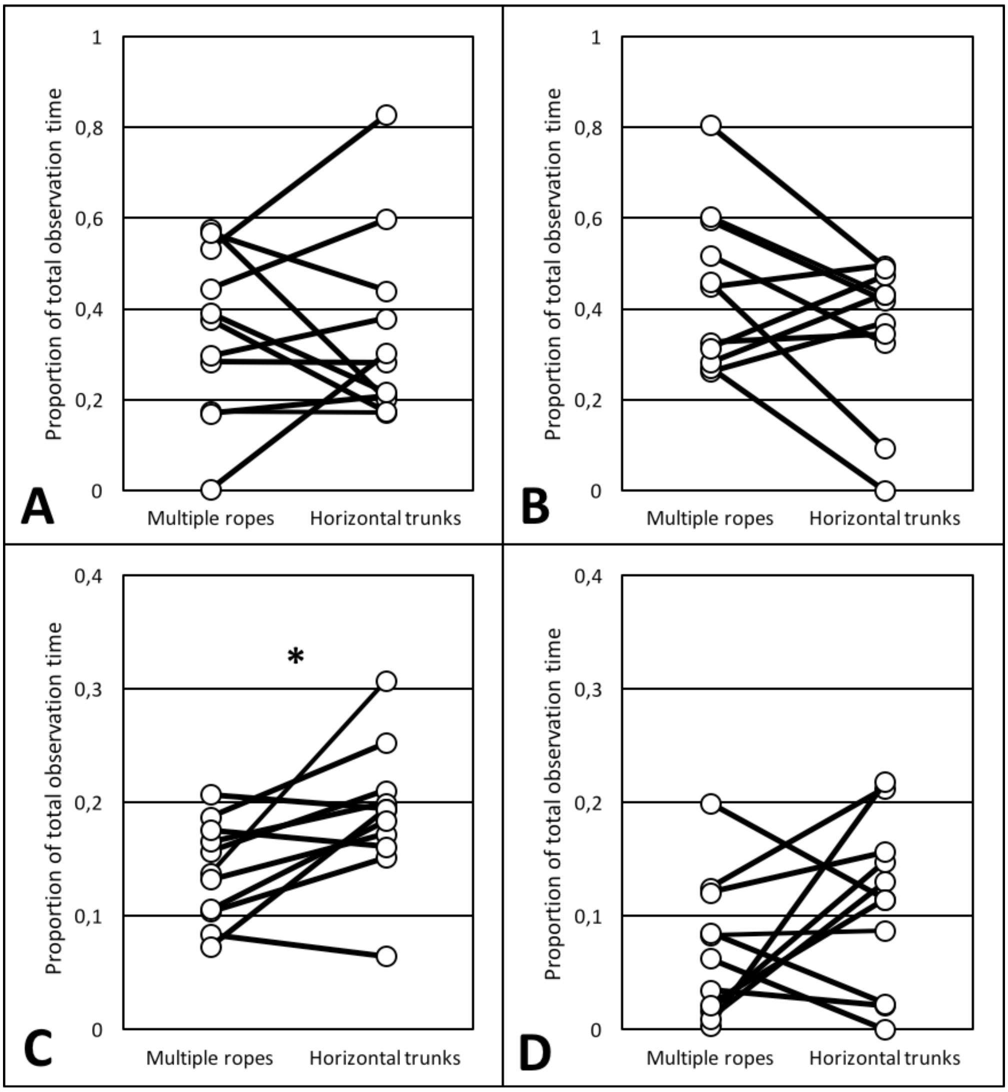

Figure 2. Proportion of the total observation time spent on resting (A), feeding (B), travelling (C) and other behaviour (D) per individual in the two different enclosures types. Asterisk (*) indicates significant differences between the two enclosure types (P<0.05).

time. Most behavioural data were analysed with a multi-factorial repeated measures ANOVA, using Pillai's trace statistic, to test for main effects of island and time, and an interaction effect of time*island.

Time budget and locomotion types were analysed using a paired t-test, or a Wilcoxon signed-rank test if the data were not normally distributed. For the time budgets and locomotion types, morning and afternoon data were combined. The comparisons for locomotion types (9 comparisons) were corrected using a Bonferroni correction, which changed the critical p-value to p=0.00556.

We also tested for habituation, because the horizontal trunk enclosures were new to the orang-utans. We combined morning and afternoon data of each enclosure type per week, and ran a linear mixed model to see whether quantitative locomotion behaviour (above-ground time and above-ground locomotion) differed between the weeks of the study. Data were transformed using an arcsine transformation (Whitlock and Schluter 2009). If habituation would occur, in the newly furnished horizontal trunk enclosures the orang-utans would spend more time on locomotion in the first weeks, and less in the later weeks of the study.

Results

Quantity of locomotion behaviour

First we analysed the data regarding the quantity of locomotion behaviour, encompassing time budget, time spent above ground, and time spent on above-ground locomotion. The time budget data (Figure 2) indicate that the orang-utans moved significantly more often in the horizontal trunk than in the multiple rope enclosures ($n=11$, $t=-2.928$, $p=0.015$). No significant differences were found for resting ($n=11$, $t=0,024$, $p=0.982$), feeding ($n=11$, $t=1.571$, $p=0.147$) and other behaviour ($n=11$, $t=-1.461$, $p=0.175$).

The proportion of total observation time spent above ground in different enclosure types and timeslots did not show a significant interaction effect ($F(1,10)=2.338$, $p=0.157$, $\eta^2=0.190$). Also, no significant results were found for differences between the timeslots ($F(1,10)=0.924$, $p=0.359$, $\eta^2=0.085$). However, the orang-utans spent a significantly larger proportion of time above-ground in the horizontal trunk than in the multiple rope enclosures ($F(1,10)=9.413$, $p=0.012$, $\eta^2=0.485$) (Figure 3a). Because of the reduced grass-cover on islands E and F, we tested whether quantity of above-ground time differed between these islands with islands

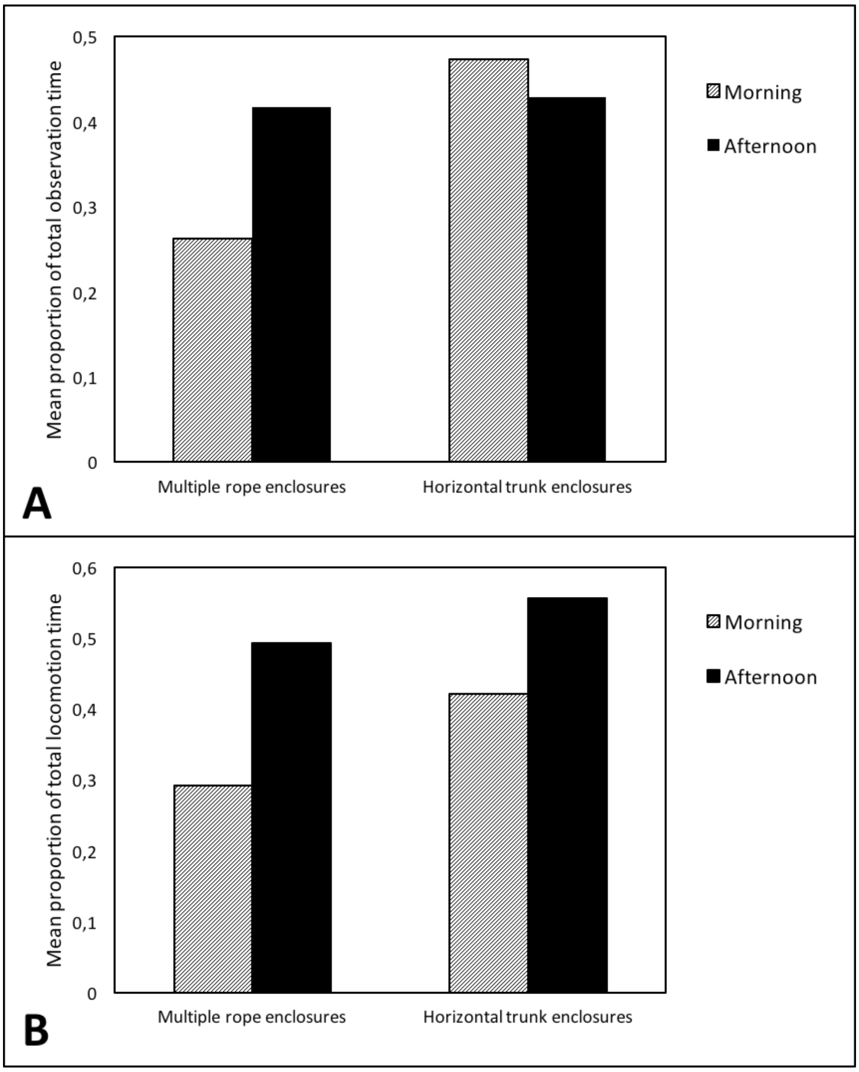

Figure 3. (A) Mean proportion of the total observation time spent above-ground in both enclosure types and both timeslots. The effect of enclosure type was significant ($F(1,10)=9.413$, $p=0.012$, $\eta^2=0.485$) (B) Mean proportion of the total locomotion time spent on above-ground locomotion. The effects of both enclosure type ($F(1,10)=6.415$, $p=0.030$, $\eta^2=0.391$) and timeslot ($F(1,10)=10.828$, $p=0.008$, $\eta^2=0.520$) were significant.

G and H. We found a tendency towards more time spent above-ground on the islands with reduced grass-cover ($n=11$, $t=2.086$, $p=0.064$). Moreover, the difference in proportion of time spent above-ground between the horizontal trunk islands with grass cover (islands G and H) and the multiple rope enclosures was not significant ($n=11$, $t=0.398$, $p=0.699$).

For the proportion of the total locomotion time spent on above-ground locomotion, we found no significant interaction effect ($F(1,10)=0.371$, $p=0.556$, $\eta^2=0.036$). However, we found a significant effect of both enclosure type ($F(1,10)=6.415$, $p=0.030$, $\eta^2=0.391$) and timeslot ($F(1,10)=10.828$, $p=0.008$, $\eta^2=0.520$): individuals spent more time on above-ground locomotion in the afternoon and in the horizontal trunk enclosures (Figure 3b).

To test for habituation, we tested whether the proportion of above-ground time and the proportion of above-ground locomotion declined during the seven weeks of data collection. We found no significant decrease during the study in proportion of time spent above-ground ($F(1, 34.527)=0.086$, $p=0.771$) and proportion of time spent on above-ground locomotion ($F(1, 31.555)=1.466$, $p=0.235$) in the horizontal trunk enclosures. However, we found a trend for a decrease in proportion of time spent above-ground ($F(1, 32.261)=3,765$, $p=0.061$) and the proportion of time spent on above-ground locomotion ($F(1, 32.549)=3.419$, $p=0.074$) in the multiple rope enclosures. Altogether, we found no evidence for habituation to the new (horizontal trunk) enclosures.

Quality of locomotion behaviour

To determine the influence of enclosure type on the quality of locomotion behaviour, the proportions of total locomotion time spent on different types of locomotion were analysed. Of all nine locomotion types, three differed significantly in their occurrence between the enclosures after Bonferroni-correction (Figure 4). In the multiple rope enclosures, the orang-utans moved a significantly larger proportion of their time by using liana sway (paired t-test, $n=11$, $t=4.297$, $p=0.002$). In the horizontal trunk enclosures, orang-utans made more use of quadrupedal/tripedal walking (paired t-test, $n=11$, $t=-3.833$, $p=0.003$) and torso-pronograde suspensory locomotion (Wilcoxon signed-rank test, $n=11$, $Z=-2.934$, $p=0.003$).

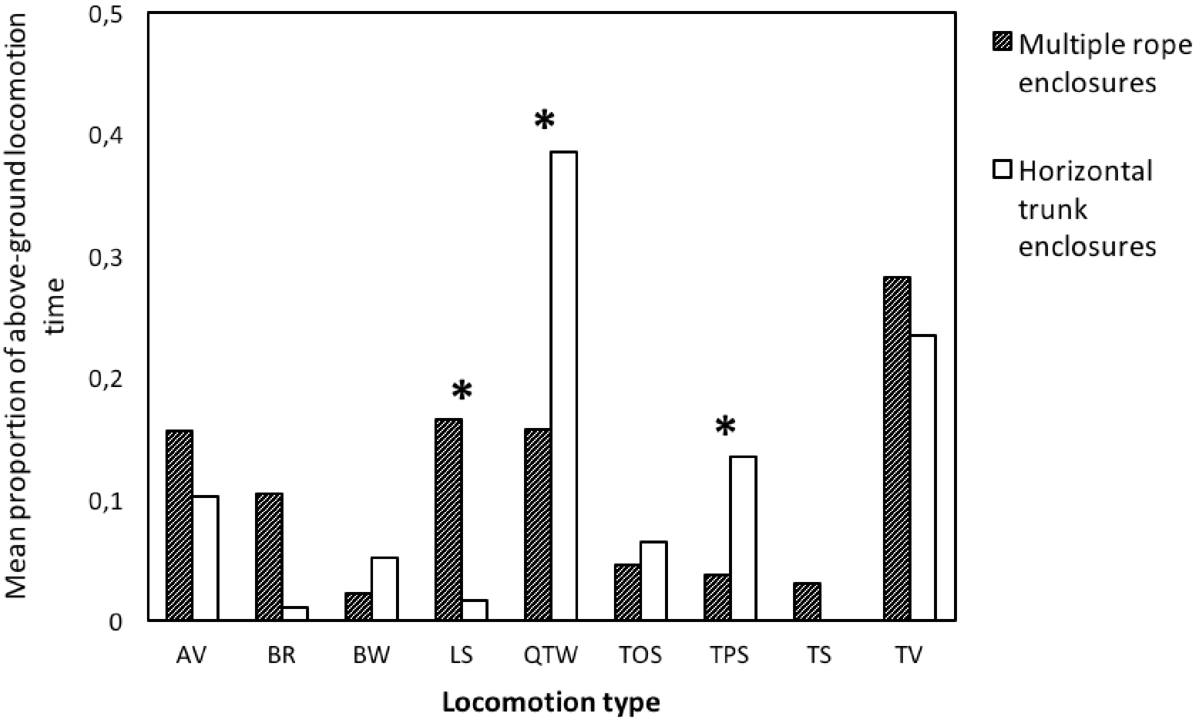

Figure 4. Mean proportions of above-ground locomotion time spent on different types of locomotion in the different types of enclosures. Asterisk (*) indicates significant differences between the two enclosure types after a Bonferroni-correction (P<0.0056). AV= angled vertical ascent/decline, BR=bridge, BW=bipedal walk, LS=liana sway, QTW=quadrupedal/tripedal walk, TOS=torso-orthograde suspensory locomotion, TPS=torso-pronograde suspensory locomotion, TS=tree sway,TV=true vertical ascent/descent. AV to TOS were analysed using paired t-tests, and TPS to TV were analysed using Wilcoxon signed-rank tests.

Discussion

The goal of this study was to determine what type of outdoor enclosure stimulated natural locomotion behaviour in captive Bornean orang-utans: horizontal trunk enclosures or multiple rope enclosures. The results suggest that enclosure type had a significant effect on both quantitative and qualitative locomotion behaviour: the large horizontal trunks promoted movement and above ground behaviour, but also quadrupedal walking, relatively rare in the wild, and moving while hanging under the support. The ropes stimulated swaying behaviour. Thus, enclosure furniture can stimulate movement and movement types.

Quantity of locomotion

As expected, the orang-utans travelled more, spent more time above the ground and spent more time on above-ground locomotion in the horizontal trunk than the multiple rope enclosures. We found no evidence for habituation to these new enclosures. This indicates that providing large horizontal trunks enhances natural quantitative locomotion behaviour. Alternatively, the reduced grass cover on islands E and F may have promoted time above the ground. Indeed, the orang-utans tended to spend more time above the ground on these two islands, and the difference between the enclosure types was no longer found. However, these additional analyses are based on a small data set. Therefore, it seems that an enclosure design with a high number of horizontal trunks, and possibly with an unattractive ground cover, stimulates a high quantity of locomotion in captive orang-utans.

The difference in quantitative locomotion behaviour between the enclosure types may be related to the orang-utans' energy-efficient lifestyle, which causes them to minimise travel costs (Thorpe et al. 2007). Locomotion on large, horizontal trunks is probably less energy-demanding than vertical locomotion or climbing on flexible, small-diameter supports (Thorpe et al. 2009; Hanna and Schmitt 2011). Because of these low energetic costs, orang-utans in the horizontal trunk enclosures may have been more easily motivated to perform above ground locomotion. This also has implications for the use of flexible, small-diameter supports. Because climbing on these supports is costlier, orang-utans may only use them if they are highly motivated to reach a certain place, such as a preferred food source, a conspecific or a resting spot.

The larger time spent by the orang-utans on above-ground locomotion in the horizontal trunk enclosures than in the multiple rope enclosures corresponds with canopy use in wild orang-utans: they spend most of their time in the part of the canopy with the most continuous horizontal stratum (Sumatran orang-utan: Thorpe and Crompton 2005; central Bornean orang-utan: Manduell et al. 2011). Therefore, providing a continuous horizontal stratum may stimulate captive Bornean orang-utans to perform more natural quantitative locomotion behaviour.

Quality of locomotion

We found three significant differences in locomotion types performed in the different enclosures. The orang-utans performed significantly more quadrupedal/tripedal walking (QTW) in the horizontal trunk enclosures. In the wild, QTW is strongly associated with supports that have a diameter larger than 10 centimetres (Sumatran orang-utan: Thorpe and Crompton 2005). Therefore, the time spent on QTW in the horizontal trunk enclosures is probably due to the abundance of large-diameter support types. Quadrupedal walking is not common in wild orang-utans, e.g. Bornean orang-utans spent 8.5% of observation time performing QTW (Manduell et al. 2011), while in the horizontal trunk enclosures the orang-utans spent 39% of their above-ground locomotion time on QWT, and 16% in the multiple rope enclosures. Therefore, the quality of locomotion is not similar to wild orang-utans.

Furthermore, orang-utans spent significantly less time on liana sway (LS), and significantly more time on torso-pronograde suspensory locomotion (TPS: hanging) in the horizontal trunk than the multiple ropes enclosures. The low occurrence of liana sway in the horizontal trunk enclosures may result from the low number of loose-hanging ropes. In contrast, it is not clear why TPS was more common in the horizontal trunk enclosures, but it may be related to the tight ropes at various angles in the horizontal trunk enclosures, while loose ropes were almost absent. Both locomotion types contribute to a more wild quality of locomotion.

Captive and wild orang-utans differ in the locomotion types they use. The main difference between our captive orang-utans and wild ones concerns torso-orthograde suspensory locomotion (TOS). TOS is the most common locomotion type among wild Bornean orang-utans; the numbers vary from 48% of movement time (central Bornean orang-utan: Manduell et al. 2011), to 53% (travelling) and even 62% (during feeding) (northeast Bornean orang-utan: Cant 1987; Thorpe and Crompton 2006). This contrasts with the findings of this captive study, in which the orang-utans used TOS in less than 10% of the total locomotion time. The low prevalence of TOS in both enclosure types may result from the lack of the right support types. TOS is in often associated with small-diameter substrates, especially lower than 20 centimetres in diameter (Sumatran orang-utan and northeast Bornean orang-utan: Thorpe and Crompton 2009). These were available in the form of tight ropes, but in most cases these tight ropes were not horizontal, but slightly vertically oriented, or they were hanging loose, which makes it hard for orang-utans to perform TOS. In order to stimulate TOS, horizontal tight ropes or small-diameter trunks may be provided. Neither of these was available in large quantities in either type of enclosure.

When designing enclosures to stimulate natural qualitative locomotion behaviour, it is important to keep the energy-efficient locomotion behaviour of orang-utans in mind. Our results suggest that offering large horizontal trunks will increase quantity of locomotion, but this will mainly result in quadrupedal walking, which has low energy costs. However, costlier behaviours, such as TOS, are harder to stimulate. This costly behaviour may be promoted by making popular parts of the enclosure, such as food enrichment, only accessible by small-diameter supports. This will necessitate the use of costlier locomotion types for orang-utans if they want to reach the spot.

Conclusion

According to our results, orang-utans' quantitative locomotion behaviour was more natural in horizontal trunk enclosures, while their qualitative locomotion behaviour was more natural in multiple rope enclosures. Therefore, although offering captive orang-utans horizontal trunks leads to more natural quantitative locomotion, providing small-diameter supports may be required to improve natural qualitative locomotion behaviour. Horizontal trunks seem to motivate the orang-utans to perform above ground locomotion, but also stimulate quadrupedal walking, which is quite uncommon in wild orang-utans.

The current research was conducted in Apenheul, where the new horizontal truck enclosure was compared with the old multiple rope enclosure. While designed to promote locomotion, this only partly succeeded. Combining the features of the new and old enclosure may be optimal, yet this may have to include incentives to motivate orang-utans to use them. Therefore, additional research on this topic in other zoos is essential to determine which of our recommendations are crucial. Only then will we obtain the tools to compose enclosures that encourage natural behaviour in captive orang-utans and other great apes, that can be used to optimise their wellbeing.

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