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Fostering appropriate behaviour in rehabilitant orangutans (*Pongo pygmaeus*)

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Abstract

Rehabilitation centres in Indonesia and Malaysia accommodate displaced orangutans (*Pongo pygmaeus* and *P. abelii*) and aim to facilitate their release into the wild by developing in them the skills that are necessary for survival. Regular forest excursions are provided but their efficacy in improving learning of appropriate behaviours is unknown. We observed forty rehabilitating orangutans from the Orangutan Care and Quarantine Centre during three forest excursions each to determine whether their behaviour fostered the development of survival skills. In total 38% of their time was spent in locomotion, particularly quadrupedal arboreal travel (13%), walking (8%), climbing (7%) and vine-swinging (4%). 26.5% of their time was spent 5 m or more from the ground, at heights up to 25 m. Arboreal activities were more common early in the excursions and interaction with care-givers more common later (hour 1: 0.3% of time; hour 5: 0.9% of time). Animals of lower body weight were significantly more likely to engage in arboreal movement, locomotion in general, eating of bark and leaves, and social play, and less likely to eat insects. Those that had been at the Centre the longest were less likely to perform arboreal activities and significantly more likely to be found standing and at ground level, than those that were there for a shorter time. During this study, many forest food items were consumed, particularly leaves and fruit, but also invertebrates and bark. Little time was spent in sexual behaviour, tool use, nest building or socially-mediated learning, but social play occupied almost 6% of their time. We conclude that regular excursions into the forest are likely to assist in the development of locomotion and feeding skills for survival in rehabilitating orangutans, but special attention is needed to encourage nest building, social activities and arboreal activity. Animals least likely to benefit are heavy animals and those that have been captive for a long time.

Introduction

As orangutan habitat (*Pongo pygmaeus* and *P. abelii*) decreases rapidly across Indonesia and Malaysia, the number of orphaned orangutans entering rehabilitation centres continues to increase (Russon 2009a). The majority of orangutans enter as infants or juveniles (Russon 2009a) and when they are considered ready for reintroduction to the wild, they are released to suitable areas of the remaining forest. It may take many years for wild orangutans to become semi-independent in foraging and nesting skills by weaning at 7-8 years of age and ecologically skilled by independence at 11 years of age (van Noordwijk & van Schaik 2005; Russon 2006). Additionally, habitat destruction across the orangutan's natural range has reduced the number of potential release sites, forcing rehabilitation centres to accommodate large numbers of potentially releasable animals (Buckland 2005). Post-release survival of orangutans is difficult to assess due to wide dispersal and inhospitable terrain, but is believed to be affected by preparedness of the animal and release site suitability (Rijksen & Meijaard 1999). Reported survival rates vary widely between reintroduction attempts, but a survey of data sourced from all existing rehabilitation centres (Russon 2009a) suggests a range of 20-80% with a realistic average of 40%. The main aspects of the rehabilitation that are likely to affect post-release success are post-release support, animal preparation and site choice (Yeager 1997; Russon 2009a). Providing opportunities to develop survival skills during short-term forest excursions is therefore expected to increase survival, but this has not been systematically evaluated. The critical skills for successful orangutan rehabilitation are considered to be food location and recognition, food processing techniques, arboreal locomotion and safe resting postures, nest building, and appropriate behaviour with conspecifics and other species (Orangutan Conservation and Reintroduction Workshop 2002; Grundmann 2006).

Foraging techniques for procurement of complex foods require a level of cognitive development and orangutans may require two or more years post-release before they are sufficiently advanced, with continuing skill development through to adulthood (Russon 1998; 2006). The orangutan diet varies considerably across its range due to natural habitat variations, seasonal fluctuations and habitat disturbance by external factors e.g. logging (Russon 2009b). In turn, habitat quality affects feeding behaviour and population density. Feeding behaviour can also be affected by animal factors such as sex, with some evidence that adult orangutan males feed for longer, use larger home ranges, travel greater distances and are more efficient feeders than females (Utami et al. 1997; Bean 1999). Sexual dimorphism and feeding requirements are probably responsible for these sex differences (Bean 1999; Key & Ross 1999; van Schaik et al. 2009), however Harrison (2009) reported no sex differences in feeding behaviour in the population at Sebanggau, Central Kalimantan. Additionally, body size can influence the ability to obtain or eat some specialised food species (e.g. Neesia fruit) or food parts (Bean 1999; van Schaik & Knott 2001). Food recognition skills appear to be attained slowly in ex-captive orangutans, and the acquisition of novel foods may be facilitated through observation of conspecifics (Russon 2002). Released rehabilitant orangutans in Sumatra have been shown to spend less time feeding and more time travelling than their wild counterparts, which may be related to food provisioning (Russon 2009a). Age and relevant experience are important in determining suitability for release, since juvenile primates usually display lower foraging success than adults (Janson & van Schaik 2002).

Arboreal locomotion is an important skill necessary for survival in the wild and includes quadrumanous scrambling, brachiation, walking, vertical and angle climbing and vine swinging and tree swaying (to facilitate movement between trees) (Sugardjito & van Hooff 1986; Thorpe & Crompton 2006). As orangutans get heavier they use more tree-swaying and less brachiation and occupy lower forest zones more frequently (Sugardjito et al. 1996; Bean 1999). Body position during resting and locomotion is affected by the behavioural context, such as whether the animal is feeding or not (Thorpe & Crompton 2006). Despite their difference in size, both males and females climb to a similar extent, which comprises about 25% of all locomotion (Isler & Thorpe 2003). The duration of the journey may also influence locomotion method, since in Borneo it has been reported that adult males travelling for long periods prefer ground over arboreal travel (Galdikas 1978).

Nest building is an important skill to allow opportunities for safe resting, in which orangutans display hanging, standing, sitting and lying down postures (Sugardjito et al. 1986). Wild Sumatran orangutans may be proficient nest builders by three years of age (Van Noordwijk & Van Schaik 2005), but most orphaned orangutans are separated early from their mother and have few nesting skills. Both male and female wild orangutans build nests equally well, although males are more likely than females to reuse them (Ancrenaz et al. 2004). Although all wild orangutans build night nests, the rate of day nest building varies between sites and may be dependent on feed availability and habitat quality, and consequently whether the time and energy are available to engage in this activity (Felton et al. 2003; Morrogh-Bernard et al. 2003; Johnson et al. 2005). Studies of other skills, such as nest-building and social competence, are still required for rehabilitant or released orangutans, even though these are highly likely to affect post-release survival rates.

The orangutan's solitary nature is due primarily to low food density in the forest, however during periods of peak fruiting many animals may feed in close proximity (Sugardjito et al. 1987; Russon 1999). Social interaction with peers is especially important during the rearing of orphaned orangutans due to the absence of learning opportunities from the mother-infant bond (Grundmann 2006). Human-reared orphaned orangutans show a greater incidence of stereotyped behaviour patterns than mother-reared infants (Cocks 2007a). Release programmes usually involve simultaneous supervised release of several animals from one location, although in the wild individuals are widely dispersed and mostly comprise just a mother and her offspring or a small travel band (Galdikas 1985a; van Schaik 1999; Delgado Jr. & van Schaik 2000). The release of multiple animals provides more opportunity for social interaction, including play which is normal in the wild in juveniles, facilitating important developmental functions (Zucker et al. 1986). In the wild orangutans have a long period of dependence on their mother (van Noordwijk & van Schaik 2005), and it is unclear to what extent a lack of maternal care would impact on the development of skills required for survival (Yeager 1997). The intensive nature of rehabilitation is likely to increase abnormal and stereotyped behaviours, especially as a result of greater social pressures of living in a large group.

Although some previous studies have evaluated rehabilitant orangutan activity post-release (Russon 2009a), no published data exists on the behaviour shown by orangutans during the rehabilitation process. The aim of the current study was to observe the behaviour of juvenile, rehabilitating orangutans during forest excursions in preparation for eventual release, concentrating on the extent of survival-related behaviours. We hypothesised that although the rehabilitating population might show some or all of the behaviours considered important for post-release survival, these could be influenced by the sex, size and health of individuals.

Materials and Methods

We observed the behaviour of 40 orphaned, juvenile, Bornean orangutans over a five month period during the wet season at the Orangutan Foundation International's Orangutan Care and Quarantine Centre (OCQC) in Central Kalimantan, Indonesia. The Centre housed 268 orangutans in cages, with forest excursions for exercise and rehabilitation every two to four days. Orangutans were housed in eight groups, based on the weight and health of the animals. Conditions for orangutans to participate in the study were 1) being able to be safely taken to and returned from the forest, 2) not being scheduled for permanent release for at least 6 months and 3) being free of illness and not in quarantine at the study commencement. We selected the study subjects at random from a stratified sample of the age groups at the Centre. There were 4 animals of 5.0-10.0 kg, 16 of 10.1-15.0 kg, 10 of 15.1-20.0 kg and 10 of 20.1-25.0 kg, equally divided between males and females in each weight class. We classified the orangutans into three health categories, based on existing records: Good health (few or no problems); Moderate health (intermittent and/or mild problems in the past); and Poor health (had experienced serious problems in the past).

The study subjects were taken to two forest sites of approximately 26 and 100 ha for pre-release forest exposure every three days. Groups contained 10-15 animals each. A man-made hut was situated at the centre of the each excursion area. Six to eight care givers accompanied each group to ensure that the animals stayed close to their excursion site and to provide a midday feed of rice or fruit. We recorded behavioural observations during each five hour excursion period (0830 to 1330 h), however, if the weather was inclement the duration of the excursion was reduced by up to two hours. Excursions that prematurely ended within the first three hours were considered invalid and rescheduled for a different day. Two observers followed different orangutans. We verified inter-observer reliability three times, by both independently observing the behaviour of one individual and comparing data with 94.3%; 93.2%; 93.5% agreement between observers. We recorded behaviours known to be common and important to survival: feeding behaviour, nest building, play, solitary and social behaviour, locomotion and resting (Maple 1980; Zucker et al. 1986; Morrogh-Bernard et al. 2002). We also recorded stereotypic behaviours, predominantly sucking, because of their common display in captivity (Table 1). Behaviours were not mutually exclusive and we recorded duration in seconds. Orangutan behaviour is often recorded using mutually exclusive categories (Morrogh-Bernard et al. 2002), however in this study orangutans commonly performed two or more important behaviours simultaneously. We therefore recorded combinations where two or three behaviours were i) unrelated (i.e. the performance of one behaviour was not reliant on the performance of another behaviour) and ii) considered important for analysis. Examples include ‘drinking/tool use’, ‘eating/nest use’, ‘grooming/human interaction’ and ‘grooming/sucking’. We recorded 73 different combinations through the course of this study. Each behavioural activity was accompanied with a height classification, with the categories being ground level (including using the hut) and an estimated height above ground level to the nearest 5 m (i.e. >0 m - <5 m, 5 m - <10 m, 10 m -<15 m, 15 - <20 m and >20 m). We recorded behaviour for each individual on three separate days, giving one hundred and twenty observation days in total. We minimised possible observer influences by wearing dark clothing, using binoculars, carrying minimal onperson equipment, avoiding interactions with study animals and maintaining a distance of at least 5-10 m.

As the variety of housing facilities differed in cage size, the number of animals per cage, keeper experience, degree of bonding, husbandry routines and food quality and quantity, we did not record the behaviour of the study orangutans while they were in their cages. Although the behaviour shown by the orangutans whilst not in the forest is important, we were focused on the behaviours shown in the forest excursions that might be useful post-release.

Statistical Analysis

In preparation for further investigation, we converted data from each orangutan (seconds per observational hour for each recorded behaviour) to the natural logarithm to achieve a normal distribution, after adding one second to all behaviours because of the large number of zero recordings. Infrequent behaviour variables (mean $< 2\%$ of the time) were excluded from further analysis. We analysed the variable subset (20 individual behaviours and 4 aggregated behavioural groups) using a Mixed Model Analysis of Variance procedure (Table 2). Each individual could not be considered independent of other animals due to the inter-group relationships as well as sequential observation hours within each day. Therefore, we used a nested sampling design. The 5 hours were considered repeated measurements, with the 3 observation days assumed to be independent of each other due to an interval of 3-4 weeks between observations. In this analysis, we included the effects of ‘sex’, ‘health’ and ‘observation hour’, as well as interactions between ‘observational hour’ and the other two variables. We generated paired comparisons only where a significant effect was indicated by the ANOVA, to reduce the possibility of Type 1 errors, and negate the need for a correction for multiple comparisons.

We calculated the mean percentage time spent engaged in each behavioural variable over all excursions, with a 95% confidence interval by back-transforming from the mean of the log values. A 95% confidence interval was derived from the least squared means and standard errors on the log scale with the mean, upper and lower limits then converted back to the original scale. This provided an overview of the behaviours that the OCQC orangutan population engaged in during forest excursions.

We tested for associations between predictor variables using a Generalised Linear Model (SAS) (between categorical and continuous variables) and Pearson's correlations (between continuous variables). Two variables, weight and the duration of time at the centre, confounded with each other and therefore could not be analysed using ANOVA. We used Pearson's correlations to test the relationship between these two variables and each observed behaviour.

Results

There was a strong relationship between orangutan weight and time spent in the centre ($r_{38} = 0.747$, $p < 0.0001$), but no association between sex and duration of time in the centre ($F_{1,29} = 0.07$, $p = 0.41$), sex and weight ($F_{1,29} = 0.7$, $p = 0.79$), health status and duration of time in the centre ($F_{2,29} = 0.06$, $p = 0.94$) or health and weight ($F_{2,29} = 0.04$, $p = 0.94$). Because of confounding effect between weight and the time spent in the centre, which was caused by many animals entering the centre at a young age, correlations with behaviour tended to occur together for these two factors (Table 3).

The most commonly observed behaviours were locomotion, feeding, resting, and social play (Table 1). Tool use was observed, but only rarely to access termite nests.

The most popular foods were leaves and fruit, but considerable time was also devoted to eating bark and invertebrates. In total 72 different forest species were consumed. Feeding time was affected by orangutan health, and health effects over the observation period (Table 2; Figure 1). Animals in good health (26.1% (21.7-31.4)) fed more than those in moderate health (18.5% (15.0-22.9))($t_{2,33} = 2.6$, $p = 0.01$) and also increased the time they spent feeding over the duration of the excursion (Figure 1), while those with health problems did not. Males and females differed in leaf eating patterns over time with females reducing leaf consumption in the middle of the excursion and males showing no hourly pattern (Figure 2). Heavier animals ate for longer overall, but ate less bark and leaves and more insects than lighter animals (Table 3)

Quadrupedal arboreal travel was the most common locomotion technique and showed significant differences between health categories (Table 2). Animals in good health (n = 22) spent 14.7% (9.1 – 23.9) of each hour in this form of locomotion. This was reduced to 5-8% respectively for animals in Moderate (n = 12) ($t_{2,33} = 2.8$, $p < 0.01$) or Poor health (n = 6) ($t_{2,33} = 1.4$, $p = 0.18$). Resting was also affected by health with orangutans in good health spending significantly less time resting (9.8%, 7.7 - 12.6) than those in moderate (15.2%, 11.4 – 20.1)($t_{2,33} = -2.4$, $p = 0.02$) or poor health (17.9%, 11.7 – 27.4) ($t_{2,33} = -2.3$, $p = 0.027$).

Sex differences occurred for height use over the observation period. Female orangutans significantly decreased ground activity mid-period, and decreased activity between 10 and 15m over time (Figure 2). Males showed no hourly differences in ground activity but significantly decreased activity between 10 and 15m after the first hour (Figure 2).

Observation hour affected locomotion and resting activities with brachiation, climbing, standing and activity between 5m and <15m all declining over time, and ground activity decreasing mid-period (Table 2; Figure 3). Forest hut use increased significantly from hour one (0.1%, 0.0 - 0.2) to hour four (0.2%, 0.1-0.4) ($t_{4,428}$ = -2.6, p = 0.009) and five (0.2%, 0.1 - 0.4) ($t_{4,428}$ = -2.3, p = 0.02).

Heavier animals performed less brachiation, climbing, quadrupedal arboreal travel, vine swinging, hanging and locomotion in total, and more standing (Table 3). Animals that had been at the Centre the longest performed less brachiation, climbing, vine swinging, but more standing and spent more time on the ground (Table 3).

Nesting occupied 2.5% (1.53 – 3.46) of the total excursion time. There were no significant effects of 'sex', 'health', 'hour', 'sex and hour', or 'health and hour' (Table 2). Additionally, no correlation was seen for nest building with orangutan weight or the time spent in captivity (Table 3).

The main form of social behaviour was play between conspecifics (Table 1). The only individual behaviour significantly affected by sex was social play (Table 2) with males playing more (2.1%, 1.3 - 3.5) than females (0.9%, 0.5 - 1.6)($t_{1,33}$ = 2.6, p = 0.02). Social playing was less common in heavier animals and those in the centre the longest. Human interaction significantly increased over time (Figure 3).

Discussion

We found that more than 30% of the observation period was spent in locomotion, with many active behaviours, such as climbing and brachiation, decreasing over the observation period. Human interaction and forest hut use increased with time. Health affected feeding and locomotion behaviour, as did body weight and the duration of time spent at the centre.

Feeding

The rehabilitant orangutans consumed 72 different forest species during the course of the study. This is low compared to wild orangutans such as those at Tanjung Puting National Park, who consume more than 300 different foods, however extensive post-release studies of orangutans show that food knowledge expands considerably after release (Peters 1995; Riedler 2007 in Russon 2009; Russon 2002, 2009). Rehabilitants fed mainly on leaves, fruit, bark and invertebrates, which again differs from the diet of wild orangutans in nearby Tanjung Puting, where fruit comprised approximately 70% of all food eaten, followed by bark and leaves (20% and 15% respectively) (Hamilton & Galdikas 1994). Both studies were conducted during the wet season and in similar habitats, although the forest at the OCQC is much smaller and more degraded than that in Tanjung Puting. The OCQC orangutans only had access to the forest for five hours every two to four days, compared with the permanent access of the Tanjung Puting orangutans (Hamilton & Galdikas 1994). Fruit has a higher energetic content than leaves, however it was less readily available, and access is likely to be affected by competition due to the high density of rehabilitant orangutans. Although the time cost may not be so important with permanent access, if access is infrequent it may be more cost effective to consume more leaves due to their ready availability. Fruit procurement may also result in separation from the group and/or competition from conspecifics in rehabilitant orangutans, again leading to greater relative attractiveness of more available foods. In addition the necessary skills for fruit procurement may not have been as well developed as in wild orangutans.

Health impacted on feeding behaviour with orangutans in good health feeding more overall and increasing over time, compared to orangutans with moderate or poor health. This could indicate a causal relationship in either direction, with good health assisting the ability to forage and feed in the forest, or orangutans with better foraging skills experiencing better health.

Total feeding time was similar in male and female subjects. Adult orangutans are strongly sexually dimorphic, however the study population was adolescent with body sizes comparable between sexes, therefore nutritional requirements are also likely to be comparable (Bean 1999).

Total feeding behaviour showed no differences between observation hours despite subjects being given mid-day feeds by centre assistants, indicating that fatigue did not reduce feeding behaviour towards the end of the excursion, and the orangutans were not dependent on care-giver provisions.

The heavier orangutans spent more time engaged in feeding behaviour and insect eating than lighter orangutans. This is probably desirable, although these orangutans appeared to have a fatter body condition than wild orangutans of the same age. A lack of data on juvenile weights of wild orangutans prevents accurate comparison. Excessive body condition could reduce appetite during excursions and discourage the development of food searching skills, although good condition upon eventual release is likely to sustain them in the event of food shortages, thus assisting in the transition to the wild. Despite increased time spent feeding overall, the heavier animals spent less time eating bark and leaves, but no greater time eating fruit, all important foods for wild orangutans. The amount of time spent at the Centre did not impact on any feeding categories so orangutans that had been there the longest did not feed for longer than those there only a short time. As orangutans in care need to develop foraging skills in preparation for release, this indicates an area of potential concern as to whether they have learnt sufficient feeding skills to be able to energetically support themselves on release.

Locomotion

A key requirement for reintroduction is good locomotion skills, especially in the high parts of the forest, where proficiency will increase safety and food items may be procured that cannot be reached by other species. In this study quadrupedal arboreal travel was the most common form of locomotion (approximately 14%). This form of travel is similar to the combined categories of ‘quadrumanous scrambling’ in the study by Sugardjito and van Hooff (1986), which indicated that ‘quadrumanous scrambling’ is the most common form of locomotion across all sex-age orangutan classes in Sumatra with juveniles using this form of locomotion for approximately 50% of the time. Quadrupedal arboreal travel was reduced, and resting increased in animals with health problems although total locomotion and other arboreal activities remained unaffected, suggesting that travel was still undertaken using alternative techniques.

Wild orangutans are continuously exposed to the forest, while rehabilitating orangutans have forest access for just a small proportion of their day, therefore activity budgets or diurnal patterns are not expected to mimic that of their wild counterparts. Hourly differences were seen, however, in the OCQC population over the five hour observation period which suggests accumulated animal fatigue over time. Climbing, brachiation, standing and activity at 5 - <15m all reduced over time, ground activity decline mid-period, and forest hut use increased over time.

Locomotion choices and resting position were strongly influenced by weight and time at the Centre. Heavier animals and those longer at the centre were less likely to participate in arboreal locomotion, locomotion overall and more likely to stand. Those that had been at the Centre longest spent more time at ground level, which could indicate a reliance on food easily obtained at ground level. Hanging decreased as weight increased. As arboreality is important for post-release survival of rehabilitated orangutans, this provides some reason for concern that larger (e.g. older) orangutans and those closer to release show less arboreality than lighter orangutans or those at the centre for less time.

Nesting

Another critical skill for rehabilitated orangutans is proficiency in nest building. Not only does this provide protection during sleep, it also minimises the risk of acquiring parasitic infection, which is significant during ground sleeping (Grundmann 2006). Orangutans in the OCQC population spent a mean of 2.5% of their excursion period nesting which is approximately half the time spent by wild Tanjung Puting orangutans when adjusted for observation time (Galdikas 1988). Nesting behaviour was not significantly affected by any of the investigated factors including weight and the time spent at the Centre. This potentially indicates lack of development of nesting skills with time, or an increase in efficiency in nest building. Nesting behaviour in this population should be investigated further as much of the nesting behaviour in this study was observed to be on the ground. It is also important to investigate nesting behaviour for rehabilitating orangutans over full day excursions to determine whether released orangutans will show adequate nesting behaviour for night and midday rests.

Social Interaction

Orangutan rehabilitation centres are intensive facilities due to the large amount of animals residing in them. Rehabilitant orangutans have more access to potential playmates than their wild counterparts and this may influence the amount of play behaviour seen however, we are not aware of any published data on the amount of play shown by wild juvenile orangutans, for comparison with our data. Further study needs to be conducted on social interactions with conspecifics and care-givers to determine their role in the success of rehabilitation. Social interaction may facilitate learning in orphaned orangutans, although little mimicry was observed. In contrast, human interaction, although sometimes a necessity in the absence of orangutan mothers, may also inhibit successful rehabilitation, contributing to reliance on humans and lack of social independence.

In this study, male subjects played socially more than female subjects but the time spent in auto-play was comparable between sexes. Previous studies found correlating sex differences in the duration of social play, and in the repertoire of play behaviour in captive orangutans (Maple 1980; Zucker et al. 1986; Becker, cited in Fagen 2002). These have been attributed to gender differences in adult behavioural repertoire. Alternatively, they may reflect differences in adaptation of males and females to the confinement and imposed social structure of captivity (Fagen 2002). Social play decreased with weight (age) and time in the centre, which is unsurprising as many species show a decline in play behaviour with age (Fagen 2002).

One social behaviour - human interaction – increased over the observation period. As human care-givers act as mother substitutes to orphaned orangutans, this is most likely due to fatigue, a corresponding need for security, or a desire for food.

Conclusions

Juvenile, rehabilitant orangutans display many behaviours considered important for survival in the wild. Orangutan weight and the amount of time spent at the centre were negatively correlated with time spent in arboreal locomotion and bark and leaf consumption. This indicates there may be detrimental effects of keeping orangutans in captivity for long periods before release. Fatigue over the observation period affected many behaviours especially arboreal locomotion and resting. Persistent health problems could adversely affect survival potential through reductions in quadrupedal locomotion and an increased need for resting. On-going monitoring of the rehabilitation process and release programs, especially in post-release monitoring is critical to improving current techniques for raising orphaned orangutans, especially as the true survival rate for released orangutans is still unknown.

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Table 1. Ethogram for juvenile, Bornean orangutans during forest excursions with mean percentage (and CI 95%) of time engaged in behaviour per excursion

BEHAVIOUR	DESCRIPTION	DURATION Mean % (95% confidence interval)
FEEDING BEHAVIOUR		
a) FEEDING		
Eating	Process of placing food in mouth, chewing and swallowing without tools	22.0 (19.1 - 24.9)
Patch Travel	Travelling within a patch (single tree or two conjoined food trees)	1.3 (0.6 – 2.0)
Drinking	Drinking of a liquid, using mouth only, a cupped hand, or a utensil (e.g. Spout)	0.9 (0.7 – 1.1)
Food Searching	Actively searching for food. May be indicated by visible searching or investigation	0.9 (0.6 – 1.3)
Food Processing	Preparing a food for eating, such as 'lathering', 'biting', 'peeling'	0.8 (-0.04 – 1.5)
b) FOOD CHOICE		
Leaves		6.3 (4.8 – 7.7)
Fruit		5.5 (3.1 – 7.9)
Bark		2.6 (1.9 – 3.3)
Invertebrates		2.4 (0.2 – 4.6)
Non-forest food from care-giver		1.7 (0.9 – 2.5)
Pith		1.2 (0.6 – 1.8)
Sticks		1.1 (0.8 – 1.3)
Flowers		0.4 (0.1 – 0.7)
Forest food from care-giver		0.2 (-0.4 – 0.8)
NESTING BEHAVIOUR		
Nest Building, Re-using and Re-building	Construction of a new nest, or re-using or re-building of an old nest	2.5 (1.5 - 3.5)
SOLITARY BEHAVIOUR		
Auto-play	Play behaviour involving focal animal only.	3.0 (2.1 - 3.9)
Grooming	Grooming parts of the body	1.7 (1.1 - 2.4)
Non-Food Tool Use	Using tools for other than eating	0.2 (-0.3 – 0.7)

SOCIAL BEHAVIOURS		
a) INTERACTION		
Social Play	Play behaviour with conspecifics, accompanied by a 'play face'	5.9 (4.8 – 6.9)
Other Human Interact	Any interaction with a human not included elsewhere (e.g. aggression)	4.0 (2.4 – 5.7)
Friendly Interaction	Two or more orangutans in friendly interaction that is not sexual or play	0.8 (0.6 – 1.1)
Clinging to a care-giver	Clinging to a human care-giver	0.2 (0.01 - 0.3)
Food interaction	Interaction between focal another other over food, (e.g. giving, stealing, begging)	0.4 (0.3 – 0.6)
Observing Eating	Focal animal observes a conspecific eating	0.1 (0.04 – 0.2)
LOCOMOTION		
a) SOLITARY		
Quadrupedal Arboreal Travel	Move across a ceiling using all four limbs	13.6 (11.0 – 16.2)
Walk	Walk using both feet and hands	8.2 (6.4 – 10.0)
Climb	Climb vertically up an item or tree	6.8 (6.1 – 7.6)
Vine Swing	Swing on a vine to reach the next vine or tree	4.1 (3.1 – 5.1)
Brachiate	Move through trees using arms only	2.5 (1.5 – 3.4)
Tree Sway	Sway tree to get from one tree to another	1.7 (1.2 – 2.1)
Bipedal Walk	Walk upright on feet only	1.4 (1.0 – 1.8)
Travel on Human	Being carried by human care-giver	0.3 (0.2 – 0.4)
Focal Following	Focal animal following another	0.2 (0.1 – 0.3)
RESTING		
Hanging	Hanging below an item using hands and/or legs	9.7 (8.6 – 10.9)
Bipedal Standing	Standing upright on feet only on horizontal substrate	2.2 (1.4 – 2.9)
Squat	Body hunched with feet on ground and weight supported by legs	1.8 (0.6 – 3.0)
Sit	Body upright with weight on bottom and legs together	1.7 (0.9 – 2.4)
Standing	Standing on feet and hands whilst on horizontal substrate	1.1 (0.5 – 1.8)
Lying	Body lying horizontal but not asleep	0.8 (0.6 – 1.0)
Sleeping	Lying or sitting with eyes closed, and exhibiting little movement, necked relaxed	0.1 (0.0 – 0.2)

STEREOTYPIES AND OTHER ABNORMAL BEHAVIOURS		
Sucking	Sucking without a nutritional basis, often on a thumb or toe	0.6 (0.1 – 1.1)
Other	Any other abnormal behaviour	0.5 (0.2 – 0.8)
HEIGHT CATEGORIES		
Forest Hut	Using the care-givers' forest shelter	7.1 (3.0 – 11.2)
Ground		28.1 (22.0 – 34.2)
>0-<5m		39.1 (35.2 – 43.1)
5-<10m		13.0 (9.6 – 16.4)
10-<15m		8.8 (5.6 – 12.0)
15-<20m		3.6 (1.6 – 5.7)
20-<25m		0.4 (-0.2 – 1.0)

Sexual activity, aggressive interactions, sliding, crawling and social grooming all took less than 0.1 % of time and therefore were not analysed. Abnormal behaviours commonly reported in laboratory primates were not observed (e.g. pacing, rocking, clinging).

Table 2. Results (F values, df, and *p* values) of ANOVA test on log transformed behaviour durations and 'sex', 'health', 'hour', 'sex X hour', and 'health X hour'

Behaviour	Sex	Health	Hour	Sex x Hr	Health x Hr
Feeding (total)	$F_{1,33} = 0.5$ $p = 0.47$	$F_{2,33} = 3.7$ $p = 0.04$	$F_{4,428} = 0.6$ $p = 0.70$	$F_{4,428} = 0.2$ $p = 0.92$	$F_{8,428} = 2.2$ $p = 0.03$
Eat fruit	$F_{1,33} = 0.3$ $p = 0.60$	$F_{2,33} = 3.0$ $p = 0.06$	$F_{4,428} = 1.6$ $p = 0.17$	$F_{4,428} = 1.2$ $p = 0.32$	$F_{8,428} = 1.1$ $p = 0.40$
Eat bark	$F_{1,33} = 0.1$ $p = 0.81$	$F_{2,33} = 0.4$ $p = 0.64$	$F_{4,428} = 1.5$ $p = 0.19$	$F_{4,428} = 1.3$ $p = 0.29$	$F_{8,428} = 1.9$ $p = 0.06$
Eat leaves	$F_{1,33} = 1.2$ $p = 0.28$	$F_{2,33} = 0.4$ $p = 0.69$	$F_{4,428} = 0.5$ $p = 0.72$	$F_{4,428} = 2.5$ $p = 0.04$	$F_{8,428} = 1.0$ $p = 0.41$
Eat insects	$F_{1,33} = 0.01$ $p = 0.92$	$F_{1,33} = 2.3$ $p = 0.12$	$F_{4,428} = 1.4$ $p = 0.23$	$F_{4,428} = 1.1$ $p = 0.38$	$F_{8,428} = 1.0$ $p = 0.43$
Nesting (total)	$F_{1,33} = 1.9$ $p = 0.18$	$F_{1,33} = 1.5$ $p = 0.23$	$F_{4,428} = 1.0$ $p = 0.41$	$F_{4,428} = 0.7$ $p = 0.57$	$F_{8,428} = 1.1$ $p = 0.36$
Auto-play	$F_{1,33} = 0.3$ $p = 0.57$	$F_{2,33} = 2.2$ $p = 0.13$	$F_{4,428} = 1.4$ $p = 0.23$	$F_{4,428} = 1.5$ $p = 0.21$	$F_{8,428} = 1.5$ $p = 0.16$
Human interaction	$F_{1,33} = 0.02$ $p = 0.88$	$F_{2,33} = 1.9$ $p = 0.17$	$F_{4,428} = 4.0$ $p < 0.01$	$F_{4,428} = 1.6$ $p = 0.19$	$F_{8,428} = 0.7$ $p = 0.68$
Social play	$F_{1,33} = 6.5$ $p = 0.02$	$F_{2,33} = 0.7$ $p = 0.51$	$F_{4,428} = 1.1$ $p = 0.38$	$F_{4,428} = 1.9$ $p = 0.11$	$F_{8,428} = 1.7$ $p = 0.10$
Walk (bipedal + quadrupedal)	$F_{1,33} = 0.2$ $p = 0.65$	$F_{2,33} = 0.6$ $p = 0.55$	$F_{4,428} = 1.3$ $p = 0.27$	$F_{4,428} = 1.8$ $p = 0.13$	$F_{8,428} = 0.6$ $p = 0.81$
Brachiate	$F_{1,33} = 0.4$ $p = 0.54$	$F_{2,33} = 0.4$ $p = 0.66$	$F_{4,428} = 3.7$ $p < 0.01$	$F_{4,428} = 0.8$ $p = 0.51$	$F_{8,428} = 1.5$ $p = 0.15$
Climb	$F_{1,33} = 0.0$ $p = 0.99$	$F_{2,33} = 0.01$ $p = 0.99$	$F_{4,428} = 6.1$ $p < 0.001$	$F_{4,428} = 0.5$ $p = 0.71$	$F_{8,428} = 0.9$ $p = 0.51$
Arboreal quad. travel	$F_{1,33} = 0.5$ $p = 0.50$	$F_{2,33} = 4.2$ $p = 0.02$	$F_{4,428} = 1.0$ $p = 0.40$	$F_{4,428} = 0.4$ $p = 0.79$	$F_{8,428} = 1.2$ $p = 0.31$
Vine-swing	$F_{1,33} = 2.8$ $p = 0.11$	$F_{2,33} = 0.3$ $p = 0.72$	$F_{4,428} = 2.0$ $p = 0.09$	$F_{4,428} = 2.2$ $p = 0.07$	$F_{8,428} = 0.8$ $p = 0.58$
Stand (bipedal + quadrupedal)	$F_{1,33} = 0.3$ $p = 0.58$	$F_{2,33} = 1.1$ $p = 0.36$	$F_{4,428} = 2.5$ $p = 0.04$	$F_{4,428} = 1.2$ $p = 0.31$	$F_{8,428} = 0.2$ $p = 0.98$
Hang	$F_{1,33} = 1.7$ $p = 0.20$	$F_{2,33} = 0.5$ $p = 0.59$	$F_{4,428} = 1.1$ $p = 0.36$	$F_{4,428} = 0.8$ $p = 0.53$	$F_{8,428} = 1.0$ $p = 0.46$
Activity in forest hut	$F_{1,33} = 1.2$ $p = 0.28$	$F_{1,33} = 0.5$ $p = 0.60$	$F_{4,428} = 2.5$ $p = 0.04$	$F_{4,428} = 0.5$ $p = 0.72$	$F_{8,428} = 1.5$ $p = 0.15$
Activity ground	$F_{1,33} = 0.1$ $p = 0.81$	$F_{2,33} = 0.2$ $p = 0.82$	$F_{4,428} = 2.7$ $p = 0.03$	$F_{4,428} = 2.6$ $p = 0.03$	$F_{8,428} = 0.5$ $p = 0.85$
Activity >0m - <5m	$F_{1,33} = 0.4$ $p = 0.56$	$F_{2,33} = 1.1$ $p = 0.35$	$F_{4,428} = 1.0$ $p = 0.39$	$F_{4,428} = 2.1$ $p = 0.08$	$F_{8,428} = 0.8$ $p = 0.60$
Activity 5m - <10m	$F_{1,33} = 1.1$ $p = 0.31$	$F_{2,33} = 1.7$ $p = 0.21$	$F_{4,428} = 6.3$ $p < 0.001$	$F_{4,428} = 0.5$ $p = 0.76$	$F_{8,428} = 0.8$ $p = 0.65$
Activity 10m - <15m	$F_{1,33} = 0.2$ $p = 0.69$	$F_{2,33} = 2.0$ $p = 0.16$	$F_{4,428} = 4.9$ $p = 0.01$	$F_{4,428} = 3.9$ $p < 0.01$	$F_{8,428} = 0.7$ $p = 0.73$
Activity 15m - <20m	$F_{1,33} = 0.5$ $p = 0.49$	$F_{2,33} = 0.5$ $p = 0.61$	$F_{4,428} = 2.0$ $p = 0.10$	$F_{4,428} = 1.6$ $p = 0.17$	$F_{8,428} = 1.9$ $p = 0.06$
Locomotion total	$F_{1,33} = 0.3$ $p = 0.62$	$F_{1,33} = 0.3$ $p = 0.74$	$F_{4,428} = 1.5$ $p = 0.22$	$F_{4,428} = 0.5$ $p = 0.77$	$F_{8,428} = 0.8$ $p = 0.65$
Rest activity total	$F_{1,33} = 0.4$ $p = 0.56$	$F_{1,33} = 4.5$ $p = 0.02$	$F_{4,428} = 0.5$ $p = 0.73$	$F_{4,428} = 1.6$ $p = 0.17$	$F_{8,428} = 1.0$ $p = 0.40$

Table 3. Relationships between behaviour and orangutan weight and duration of time spent at the Centre (n = 40)

Behaviour	**Orangutan weight**		**Time spent at Centre**	
	r correlation	*p* value	r correlation	*p* value
Feeding (total)	0.31	0.05	0.10	0.53
Eat fruit	0.073	0.66	0.04	0.79
Eat bark	-0.36	0.02	-0.05	0.76
Eat leaves	-0.44	<0.01	-0.15	0.35
Eat insects	0.51	<0.001	0.29	0.06
Nesting (total)	0.04	0.81	0.02	0.92
Auto-play	-0.26	0.10	-0.07	0.68
Human interaction	0.03	0.87	0.12	0.46
Social play	-0.55	<0.001	-0.58	<0.001
Walk (bi + quad)	0.18	0.27	0.27	0.10
Brachiate	-0.64	<0.001	-0.36	0.02
Climb	-0.63	<0.001	-0.47	<0.01
Arboreal quad. travel	-0.38	0.02	-0.30	0.06
Vine-swing	-0.48	<0.01	-0.37	0.02
Stand (bi + quad)	0.43	<0.005	0.56	<0.001
Hang	-0.45	<0.01	-0.24	0.13
Activity in forest hut	0.02	0.92	0.11	0.49
Activity ground	0.23	0.16	0.32	0.04
Activity >0m - <5m	-0.30	0.06	-0.14	0.40
Activity 5m - <10m	-0.12	0.46	-0.24	0.14
Activity 10m - <15m	0.03	0.88	-0.05	0.75
Activity 15m - <20m	0.14	0.38	0.08	0.61
Locomotion (total)	-0.40	0.01	-0.29	0.07
Rest activity (total)	<0.01	0.98	0.18	0.27

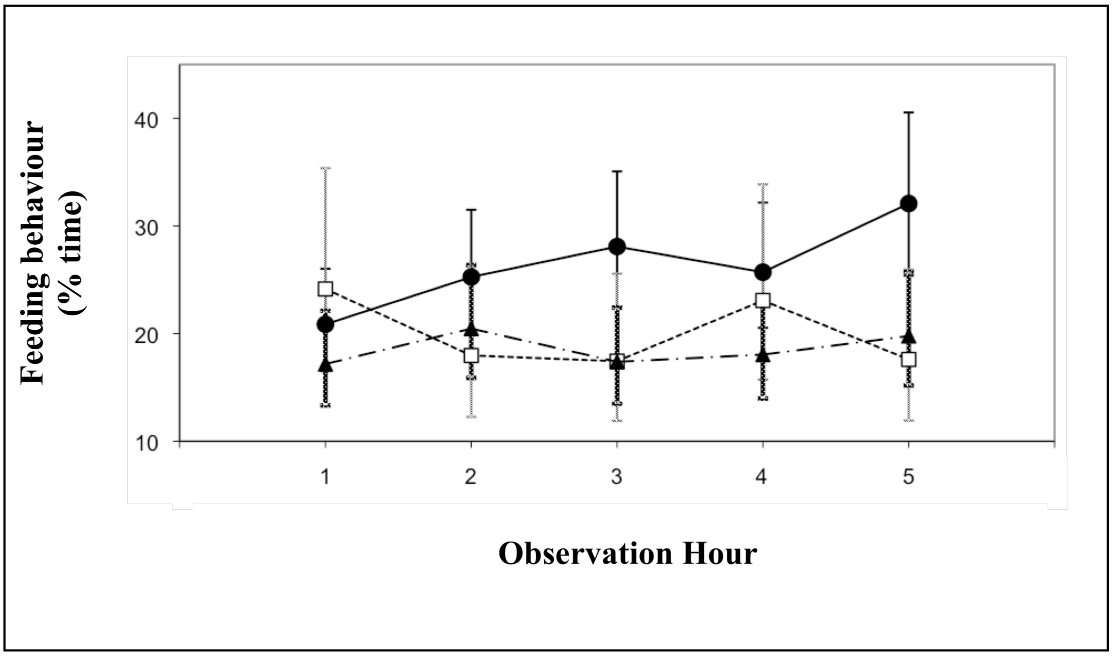

Figure 1. Feeding activity of three health groups (good —●—, moderate – –▲– – and poor ---□---) of juvenile orangutans over five observation hours (mean % time and 95% confidence interval)

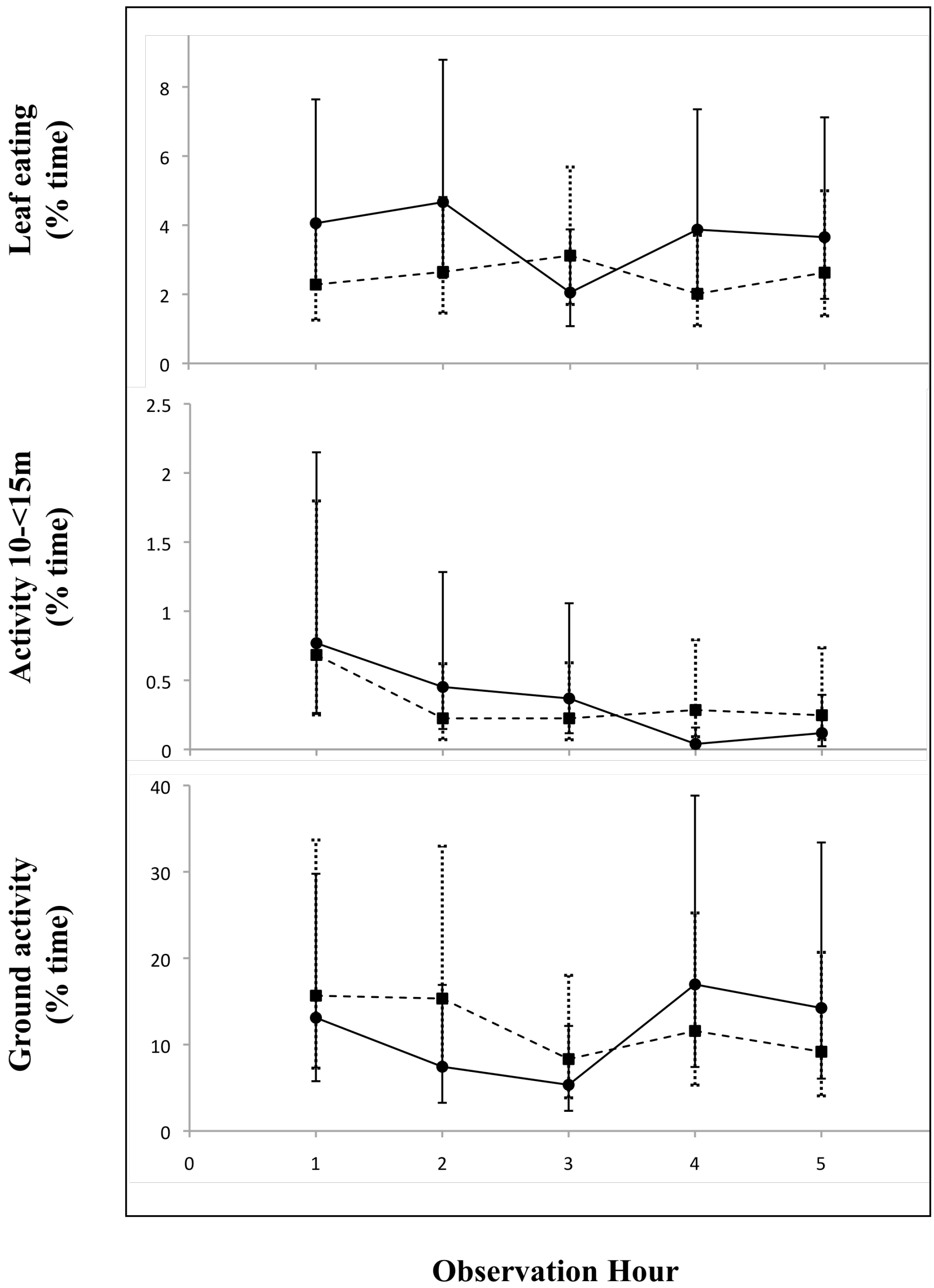

Figure 2. Patterns of activity (10 - <15m) of male (--■--) and female (─●─) juvenile orangutans over five observation hours (mean % time with 95% confidence intervals)

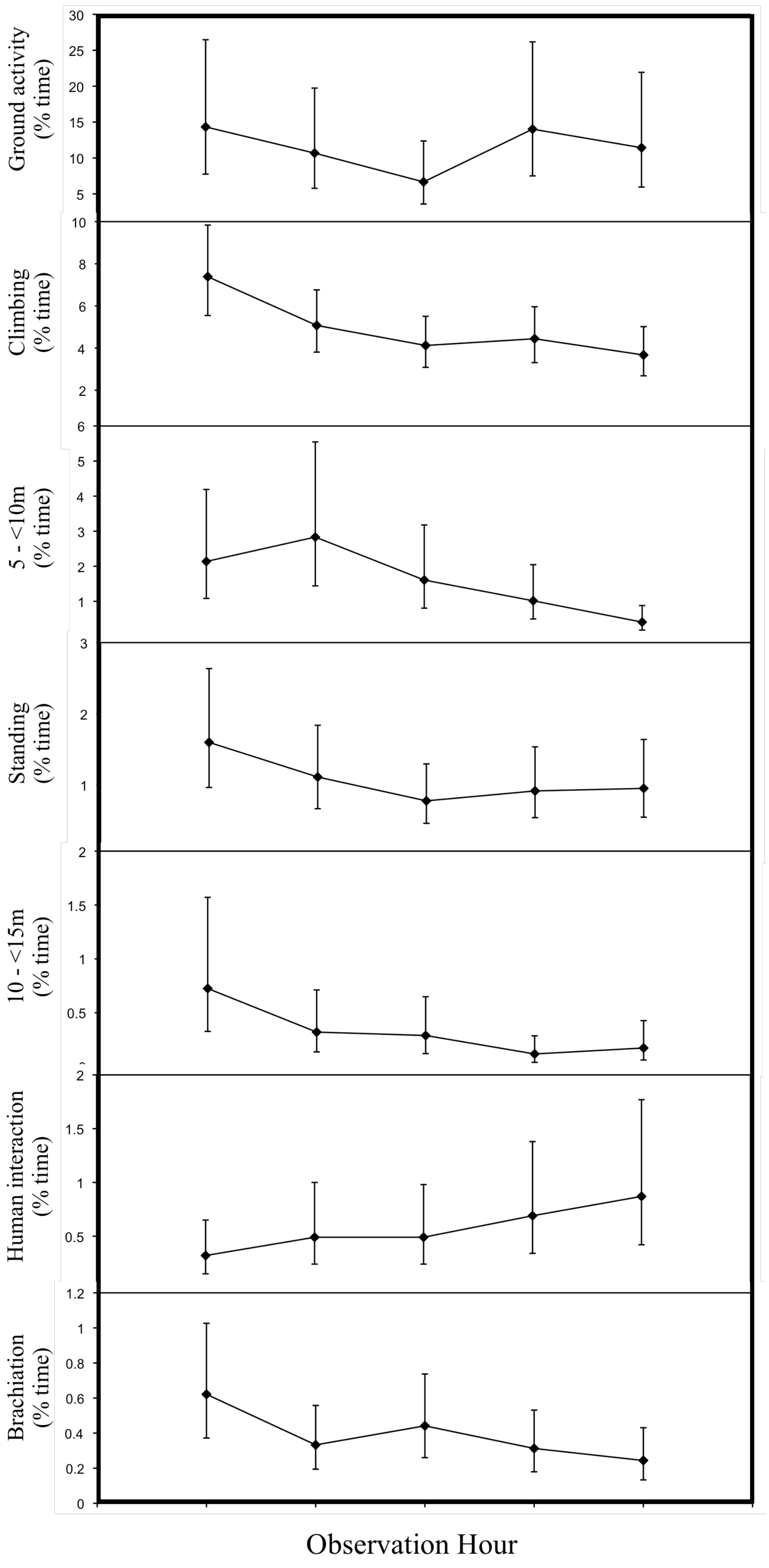

Figure 3. Activity shown by juvenile orangutans over five observation hours (mean % time with 95% confidence interval)