***This is an electronic version of an article published in Vol 32 (2011) pp 616-633 in the International Journal of Primatology. The published version of this article is available at: http://link.springer.com/article/10.1007/s10764-011-9491-1**

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

52 to be affected by preparedness of the animal and release site suitability (Rijksen & Meijaard
53 1999). Reported survival rates vary widely between reintroduction attempts, but a survey of
54 data sourced from all existing rehabilitation centres (Russon 2009a) suggests a range of 20-
55 80% with a realistic average of 40%. The main aspects of the rehabilitation that are likely to
56 affect post-release success are post-release support, animal preparation and site choice
57 (Yeager 1997; Russon 2009a). Providing opportunities to develop survival skills during short-
58 term forest excursions is therefore expected to increase survival, but this has not been
59 systematically evaluated. The critical skills for successful orangutan rehabilitation are
60 considered to be food location and recognition, food processing techniques, arboreal
61 locomotion and safe resting postures, nest building, and appropriate behaviour with
62 conspecifics and other species (Orangutan Conservation and Reintroduction Workshop 2002;
63 Grundmann 2006).
64
65 Foraging techniques for procurement of complex foods require a level of cognitive
66 development and orangutans may require two or more years post-release before they are
67 sufficiently advanced, with continuing skill development through to adulthood (Russon 1998;
68 2006). The orangutan diet varies considerably across its range due to natural habitat
69 variations, seasonal fluctuations and habitat disturbance by external factors e.g. logging
70 (Russon 2009b). In turn, habitat quality affects feeding behaviour and population density.
71 Feeding behaviour can also be affected by animal factors such as sex, with some evidence
72 that adult orangutan males feed for longer, use larger home ranges, travel greater distances
73 and are more efficient feeders than females (Utami et al. 1997; Bean 1999). Sexual
74 dimorphism and feeding requirements are probably responsible for these sex differences
75 (Bean 1999; Key & Ross 1999; van Schaik et al. 2009), however Harrison (2009) reported no
76 sex differences in feeding behaviour in the population at Sebanggau, Central Kalimantan.
77 Additionally, body size can influence the ability to obtain or eat some specialised food

78 species (e.g. Neesia fruit) or food parts (Bean 1999; van Schaik & Knott 2001). Food
79 recognition skills appear to be attained slowly in ex-captive orangutans, and the acquisition of
80 novel foods may be facilitated through observation of conspecifics (Russon 2002). Released
81 rehabilitant orangutans in Sumatra have been shown to spend less time feeding and more time
82 travelling than their wild counterparts, which may be related to food provisioning (Russon
83 2009a). Age and relevant experience are important in determining suitability for release, since
84 juvenile primates usually display lower foraging success than adults (Janson & van Schaik
85 2002).
86
87 Arboreal locomotion is an important skill necessary for survival in the wild and includes
88 quadrumanous scrambling, brachiation, walking, vertical and angle climbing and vine
89 swinging and tree swaying (to facilitate movement between trees) (Sugardjito & van Hooff
90 1986; Thorpe & Crompton 2006). As orangutans get heavier they use more tree-swaying and
91 less brachiation and occupy lower forest zones more frequently (Sugardjito et al. 1996; Bean
92 1999). Body position during resting and locomotion is affected by the behavioural context,
93 such as whether the animal is feeding or not (Thorpe & Crompton 2006). Despite their
94 difference in size, both males and females climb to a similar extent, which comprises about
95 25% of all locomotion (Isler & Thorpe 2003). The duration of the journey may also influence
96 locomotion method, since in Borneo it has been reported that adult males travelling for long
97 periods prefer ground over arboreal travel (Galdikas 1978).
98
99 Nest building is an important skill to allow opportunities for safe resting, in which orangutans
100 display hanging, standing, sitting and lying down postures (Sugardjito et al. 1986). Wild
101 Sumatran orangutans may be proficient nest builders by three years of age (Van Noordwijk &
102 Van Schaik 2005), but most orphaned orangutans are separated early from their mother and
103 have few nesting skills. Both male and female wild orangutans build nests equally well,

104 although males are more likely than females to reuse them (Ancrenaz et al. 2004). Although
105 all wild orangutans build night nests, the rate of day nest building varies between sites and
106 may be dependent on feed availability and habitat quality, and consequently whether the time
107 and energy are available to engage in this activity (Felton et al. 2003; Morrogh-Bernard et al.
108 2003; Johnson et al. 2005). Studies of other skills, such as nest-building and social
109 competence, are still required for rehabilitant or released orangutans, even though these are
110 highly likely to affect post-release survival rates.
111
112 The orangutan's solitary nature is due primarily to low food density in the forest, however
113 during periods of peak fruiting many animals may feed in close proximity (Sugardjito et al.
114 1987; Russon 1999). Social interaction with peers is especially important during the rearing
115 of orphaned orangutans due to the absence of learning opportunities from the mother-infant
116 bond (Grundmann 2006). Human-reared orphaned orangutans show a greater incidence of
117 stereotyped behaviour patterns than mother-reared infants (Cocks 2007a). Release
118 programmes usually involve simultaneous supervised release of several animals from one
119 location, although in the wild individuals are widely dispersed and mostly comprise just a
120 mother and her offspring or a small travel band (Galdikas 1985a; van Schaik 1999; Delgado
121 Jr. & van Schaik 2000). The release of multiple animals provides more opportunity for social
122 interaction, including play which is normal in the wild in juveniles, facilitating important
123 developmental functions (Zucker et al. 1986). In the wild orangutans have a long period of
124 dependence on their mother (van Noordwijk & van Schaik 2005), and it is unclear to what
125 extent a lack of maternal care would impact on the development of skills required for survival
126 (Yeager 1997). The intensive nature of rehabilitation is likely to increase abnormal and
127 stereotyped behaviours, especially as a result of greater social pressures of living in a large
128 group.
129

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

156 hut was situated at the centre of the each excursion area. Six to eight care givers accompanied
157 each group to ensure that the animals stayed close to their excursion site and to provide a
158 midday feed of rice or fruit. We recorded behavioural observations during each five hour
159 excursion period (0830 to 1330 h), however, if the weather was inclement the duration of the
160 excursion was reduced by up to two hours. Excursions that prematurely ended within the first
161 three hours were considered invalid and rescheduled for a different day. Two observers
162 followed different orangutans. We verified inter-observer reliability three times, by both
163 independently observing the behaviour of one individual and comparing data with 94.3%;
164 93.2%; 93.5% agreement between observers. We recorded behaviours known to be common
165 and important to survival: feeding behaviour, nest building, play, solitary and social
166 behaviour, locomotion and resting (Maple 1980; Zucker et al. 1986; Morrogh-Bernard et al.
167 2002). We also recorded stereotypic behaviours, predominantly sucking, because of their
168 common display in captivity (Table 1). Behaviours were not mutually exclusive and we
169 recorded duration in seconds. Orangutan behaviour is often recorded using mutually
170 exclusive categories (Morrogh-Bernard et al. 2002), however in this study orangutans
171 commonly performed two or more important behaviours simultaneously. We therefore
172 recorded combinations where two or three behaviours were i) unrelated (i.e. the performance
173 of one behaviour was not reliant on the performance of another behaviour) and ii) considered
174 important for analysis. Examples include 'drinking/tool use', 'eating/nest use',
175 'grooming/human interaction' and 'grooming/sucking'. We recorded 73 different
176 combinations through the course of this study. Each behavioural activity was accompanied
177 with a height classification, with the categories being ground level (including using the hut)
178 and an estimated height above ground level to the nearest 5 m (i.e. >0 m - <5 m, 5 m - <10 m,
179 10 m -<15 m, 15 - <20 m and >20 m). We recorded behaviour for each individual on three
180 separate days, giving one hundred and twenty observation days in total. We minimised
181 possible observer influences by wearing dark clothing, using binoculars, carrying minimal on-

person 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.

234 The most popular foods were leaves and fruit, but considerable time was also devoted to
235 eating bark and invertebrates. In total 72 different forest species were consumed. Feeding
236 time was affected by orangutan health, and health effects over the observation period (Table
237 2; Figure 1). Animals in good health (26.1% (21.7-31.4)) fed more than those in moderate
238 health (18.5% (15.0-22.9))($t_{2,33} = 2.6$, $p = 0.01$) and also increased the time they spent feeding
239 over the duration of the excursion (Figure 1), while those with health problems did not. Males
240 and females differed in leaf eating patterns over time with females reducing leaf consumption
241 in the middle of the excursion and males showing no hourly pattern (Figure 2). Heavier
242 animals ate for longer overall, but ate less bark and leaves and more insects than lighter
243 animals (Table 3)
244
245 Quadrupedal arboreal travel was the most common locomotion technique and showed
246 significant differences between health categories (Table 2). Animals in good health (n = 22)
247 spent 14.7% (9.1 – 23.9) of each hour in this form of locomotion. This was reduced to 5-8%
248 respectively for animals in Moderate (n = 12) ($t_{2,33} = 2.8$, $p < 0.01$) or Poor health (n = 6) ($t_{2,33}$
249 = 1.4, $p = 0.18$). Resting was also affected by health with orangutans in good health spending
250 significantly less time resting (9.8%, 7.7 - 12.6) than those in moderate (15.2%, 11.4 –
251 20.1)($t_{2,33} = -2.4$, $p = 0.02$) or poor health (17.9%, 11.7 – 27.4) ($t_{2,33} = -2.3$, $p = 0.027$).
252
253 Sex differences occurred for height use over the observation period. Female orangutans
254 significantly decreased ground activity mid-period, and decreased activity between 10 and
255 15m over time (Figure 2). Males showed no hourly differences in ground activity but
256 significantly decreased activity between 10 and 15m after the first hour (Figure 2).
257
258 Observation hour affected locomotion and resting activities with brachiation, climbing,
259 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

311 forage and feed in the forest, or orangutans with better foraging skills experiencing better
312 health.
313
314 Total feeding time was similar in male and female subjects. Adult orangutans are strongly
315 sexually dimorphic, however the study population was adolescent with body sizes
316 comparable between sexes, therefore nutritional requirements are also likely to be comparable
317 (Bean 1999).
318
319 Total feeding behaviour showed no differences between observation hours despite subjects
320 being given mid-day feeds by centre assistants, indicating that fatigue did not reduce feeding
321 behaviour towards the end of the excursion, and the orangutans were not dependent on care-
322 giver provisions.
323
324 The heavier orangutans spent more time engaged in feeding behaviour and insect eating than
325 lighter orangutans. This is probably desirable, although these orangutans appeared to have a
326 fatter body condition than wild orangutans of the same age. A lack of data on juvenile
327 weights of wild orangutans prevents accurate comparison. Excessive body condition could
328 reduce appetite during excursions and discourage the development of food searching skills,
329 although good condition upon eventual release is likely to sustain them in the event of food
330 shortages, thus assisting in the transition to the wild. Despite increased time spent feeding
331 overall, the heavier animals spent less time eating bark and leaves, but no greater time eating
332 fruit, all important foods for wild orangutans. The amount of time spent at the Centre did not
333 impact on any feeding categories so orangutans that had been there the longest did not feed
334 for longer than those there only a short time. As orangutans in care need to develop foraging
335 skills in preparation for release, this indicates an area of potential concern as to whether they
336 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

363 arboreal locomotion, locomotion overall and more likely to stand. Those that had been at the
364 Centre longest spent more time at ground level, which could indicate a reliance on food easily
365 obtained at ground level. Hanging decreased as weight increased. As arboreality is important
366 for post-release survival of rehabilitated orangutans, this provides some reason for concern
367 that larger (e.g. older) orangutans and those closer to release show less arboreality than lighter
368 orangutans or those at the centre for less time.
369
370 **Nesting**
371 Another critical skill for rehabilitated orangutans is proficiency in nest building. Not only
372 does this provide protection during sleep, it also minimises the risk of acquiring parasitic
373 infection, which is significant during ground sleeping (Grundmann 2006). Orangutans in the
374 OCQC population spent a mean of 2.5% of their excursion period nesting which is
375 approximately half the time spent by wild Tanjung Puting orangutans when adjusted for
376 observation time (Galdikas 1988). Nesting behaviour was not significantly affected by any of
377 the investigated factors including weight and the time spent at the Centre. This potentially
378 indicates lack of development of nesting skills with time, or an increase in efficiency in nest
379 building. Nesting behaviour in this population should be investigated further as much of the
380 nesting behaviour in this study was observed to be on the ground. It is also important to
381 investigate nesting behaviour for rehabilitating orangutans over full day excursions to
382 determine whether released orangutans will show adequate nesting behaviour for night and
383 midday rests.
384
385 **Social Interaction**
386 Orangutan rehabilitation centres are intensive facilities due to the large amount of animals
387 residing in them. Rehabilitant orangutans have more access to potential playmates than their
388 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.

Acknowledgements:

The authors are grateful to the Australian Orangutan Project and the Orangutan Foundation International, Orangutan Care and Quarantine Centre in Pangkalan Bun, Kalimantan for financial and in-kind support of the project. Additionally, the Indonesian Forestry Department, LIPI, Indonesian Police, Herry Roustaman, and Professor Hadi Alikodra from Institut Pertanian Bogor provided permit and visa support. Professional support was generously given by assistant Nelly Oktorina, Leif Cocks (Australian Orangutan Project), Professor Colin Groves (Australian National University), Stephen Brend (Orangutan Foundation UK), Ibu Waliyati (Orangutan Foundation Indonesia) and Yeti and the team at the OCQC. Additionally the editor in chief, Dr Joanna Setchell, and reviewers from the International Journal of Primatology provided valuable advice on the writing of this paper.

References:

Ancrenaz, M, Calaque, R & Lackman-Ancrenaz, I 2004, 'Orangutan Nesting Behaviour in Disturbed Forest in Sabah, Malaysia: Implications for Nest Census' *International Journal of Primatology,* vol. 25, no. 5, pp. 983-1000.

Bean, A 1999, 'Ecology of Sex Differences in Great Ape Foraging', in PC Lee (ed), *Comparative Primate Socioecology,* Cambridge University Press, Cambridge, UK, pp. 339-362.

441 Becker, C 1984, *Orang-utans und Bonobos im Spiel,* Profil-Verlag, Munich.
442 Buckland, H 2005, *The oil for ape scandal: How palm oil is threatening the orangutan,*
443 Friends of the Earth Trust, viewed 28 February 2010,
444 http://www.foe.co.uk/resource/reports/oil_for_ape_full.pdf
445 Cocks, L 1998, *Captive Orang utans (Pongo pygmaeus and Pongo abelii): Factors Affecting*
446 *Mortality in Relation to the Different Sexes,* viewed 22 February 2009,
447 http://www.orangutan.org.au/assets/images/publicdocs/SexDifferences.doc.
448 Cocks, L (a) 2007, 'Factors Influencing the Well-being and Longevity of Captive Female
449 Orangutans (*Pongo pygmaeus*)' *International Journal of Primatology,* vol. 28, no. 2, pp. 429-
450 440.
451 Cocks, L (b) 2007, 'Factors Affecting Mortality, Fertility and Well Being in Relation to
452 Species Differences in Captive Orangutans', *International Journal of Primatology,* vol. 28,
453 no. 2, pp. 421-428.
454 Delgado Jr., R & van Schaik, CP 2000, 'The behavioral ecology and conservation of the
455 orangutan (*Pongo pygmaeus*): A tale of two islands', *Evolutionary Anthropology,* vol. 9, no.
456 5, pp. 201-218.
457 Fagen, R 2002, 'Primate juveniles and primate play', in ME Pereira & LA Fairbanks (eds),
458 *Juvenile primates: life history, development, and behavior,* University of Chicago Press,
459 Chicago, pp. 182-196.
460 Felton, AM, Engstron, LM, Felton, A & Knott, CD 2003, 'Orangutan population density,
461 forest structure and fruit availability in hand-logged and unlogged peat swamp forests in
462 West Kalimantan, Indonesia', *Biological Conservation,* vol. 114, no. 1, pp. 91-101.
463 Galdikas, B (a) 1978, 'Orangutan Adaptation at Tanjung Puting Reserve: Mating and Ecology',
464 in DA Hamburg & ER McCown (eds), *The Great Apes: Perspectives on Human Evolution,*
465 Benjamin/Cummings Pub. Co., Menlo Park, California, pp. 195-233.
466 Galdikas, B (b) 1978, *Tanjung Puting Orangutan Age-Sex Classes,* viewed 10 October 2005,

http://www.orangutan.org/facts/agesex.php

Galdikas, B (a) 1985, 'Adult male sociality and reproductive tactics among orangutans at Tanjung Puting Borneo Indonesia', *Folia Primatologica,* vol. 45, no. 1, pp. 9-24.

Galdikas, B (b) 1985, 'Sub-adult male orangutan sociality and reproductive behaviour at Tanjung Puting', *American Journal of Primatology,* vol. 8, no. 2, pp. 87-99.

Galdikas, B 1988, 'Orangutan diet, range, and activity at Tanjung Puting, Central Borneo', *International Journal of Primatology,* vol. 9, pp. 1-35.

Grundmann, E 2006, 'Back to the wild: will re-introduction and rehabilitation help the long-term conservation of orangutans in Indonesia?', *Social Sciences Information,* vol. 45, no. 2, pp. 265-284.

Hamilton, R & Galdikas, B 1994, 'A preliminary study of food selection by the orangutan in relation to plant quality', *Primates* vol. 35, no. 3, pp. 255-263.

Harrison, M 2009, 'Orang-utan feeding behaviour in Sabangau, Central Kalimantan', PhD thesis, University of Cambridge, UK.

Isler, K & Thorpe, S 2003, 'Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (Pongo.pygmaeus.abelii)', *Journal of Experimental Biology,* vol. 206, pp. 4081-4096.

Janson, C & van Schaik, C 2002, 'Ecological Risk Aversion in Juvenile Primates: Slow and Steady Wins the Race', in M Pereira (ed), *Juvenile Primates: Life History, Development and Behaviour,* University of Chicago Press, Chicago, pp. 57-74.

Johnson, AE, Knott, CD, Pamungkas, B, Pasaribu, M & Marshall, AJ 2005, 'A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts', *Biological Conservation,* vol. 121, pp. 492-507.

Key, C & Ross, C 1999, 'Sex Differences in the Energy Expenditure in Non-human Primates', *Proceedings from the Royal Society of London B.* vol. 266, no. 1437, pp. 2479-2485.

493 Knott, C 1998, 'Changes in Orangutan Caloric Intake, Energy Balance and Ketones in
494 Response to Fluctuating Fruit Availability', *International Journal of Primatology,* vol. 19,
495 no. 6, pp.1061-1079.
496 Maple, T 1980, *Orangutan Behaviour*, Van Nostrand Reinhold Co., New York.
497 Markham, RJ 1990, 'The behavioural and environmental requirements of orang-utans under
498 long-term captive conditions', PhD Thesis, Department of Anatomy and Human Biology,
499 University of Western Australia, Crawley.
500 Morrogh-Bernard, H, Husson, S & Mclardy, C 2002, 'Orangutan Data Collection
501 Standardization', in *Orang-utan Culture Workshop,* San Anselmo, USA, viewed 4 December
502 2005, www.orangutannetwork.net/data_collection.htm
503 Morrogh-Bernard, H, Husson, S., Page, SE & Rieley, JO 2003, 'Population status of the
504 Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central
505 Kalimantan, Indonesia', *Biological Conservation,* vol. 110, no. 1, pp. 141-152.
506 Orangutan Conservation and Reintroduction Workshop 2002, *Final Report,* viewed 7 January
507 2010
508 http://www.cbsg.org/cbsg/workshopreports/26/orangutan_conservation_and_reintroduction_
509 workshop_final_report_2002.pdf
510 Rijksen, H D & Meijaard, E 1999, *Our Vanishing Relative : The Status of Wild Orang-utans*
511 *at the Close of the Twentieth Century*, Kluwer Academic Publishers, Dordrecht.
512 Russon, A 1998, 'Forest cognition in Rehabilitant Orangutans', *Seventeenth Congress of*
513 *International Primatological Society, 10-14 August 1998,* International Primatological
514 Society, Antananarivo, Madagascar.
515 Russon, A 1999, *Orangutans – Wizards of the Rainforest*, Robert Hale Ltd. London.
516 Russon, A 2002, 'Return of the native: Cognition and site-specific expertise in orangutan
517 rehabilitation', *International Journal of Primatology,* vol. 23, no. 3, pp. 461-478.

518 Russon, A 2006, 'Acqusition of complex foraging skills in juvenile and adolescent orangutans
519 (*Pongo pygmaeus)*: Developmental Influences', *Aquatic Mammals,* vol. 32, no. 4, pp. 500-
520 510.
521 Russon, A (a) 2009, 'Orangutan rehabilitation and reintroduction', in SA Wich, SS Utami
522 Atmoko, T Mitra Setia & CP van Schaik (eds), *Orangutans: Geographic variation in*
523 *behavioral ecology and conservation,* Oxford University Press, New York, pp. 327-350.
524 Russon, A (b) 2009, 'Geographic variation in orangutan diets', in SA Wich, SS Utami
525 Atmoko, T Mitra Setia & CP van Schaik (eds), *Orangutans: Geographic variation in*
526 *behavioral ecology and conservation,* Oxford University Press, New York, pp. 135-156.
527 Sugardjito, J & van Hooff, J 1986, 'Age-sex class differences in the positional behaviour of
528 the Sumatran orang-utan, in the Gunung Leuser National Park, Indonesia', *Folia*
529 *Primatologica,* vol. 47, pp. 14-25
530 Sugardjito, J, te Boekhorst, IJA & van Hooff, JARAM 1987, 'Ecological constraints on the
531 grouping of wild orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park,
532 Sumatra, Indonesia', *International Journal of Primatology,* vol. 8, no. 1, pp. 17-41.
533 Sugardjito, J 1995, 'Conservation of Orangutans, Threats and Prospects', in R Nadler, B
534 Galdikas, L Sheeran, & N Rosen (eds), *The Neglected Ape*, Plenum Press, New York, pp. 45-
535 49.
536 Thorpe, SKS & Crompton, RH 2006, 'Orangutan positional behavior and the nature of
537 arboreal locomotion in Hominoidea', *American Journal of Physical Anthropology,* vol. 131,
538 no. 3, pp. 384-401.
539 Utami, S, Wich, S, Sterck, E, & van Hooff, J 1997, 'Food Competition Between Wild
540 Orangutans in Large Fig Trees', *International Journal of Primatology,* vol. 18, no. 6, pp.
541 909-927.

van Noordwijk, M & van Schaik, C 2005, 'Development of Ecological Competance in Sumatran Orangutans', *American Journal of Physical Anthropology,* vol. 127, no.1, pp. 79-94.

van Schaik, C 1999, 'The socioecology of fission-fusion sociality in orangutans', *Primates,* vol. 40, no. 1, pp. 69-86.

van Schaik, C & Knott, C 2001, 'Geographic variation in tool use on *Neesia* fruits in Orangutans', *American Journal of Physical Anthropology,* vol. 11, pp. 331-342.

van Schaik, CP, van Noordwijk, MA & Vogel, ER 2009, 'Ecological sex differences in wild orangutans', in SA Wich, SS Utami Atmoko, T Mitra Setia & CP van Schaik (eds), *Orangutans: Geographic variation in behavioral ecology and conservation,* Oxford University Press, New York, pp. 255-268.

Wich, SA, Utami Atmoko, SS, Mitra Setia, T & van Schaik, CP (eds), *Orangutans: Geographic variation in behavioral ecology and conservation,* Oxford University Press, New York.

Yeager, C 1997, 'Orangutan Rehabilitation in Tanjung Puting National Park, Indonesia', *Conservation Biology,* vol. 11, no. 3, pp. 802-805.

Zucker, E, Dennon, M & Maple, T 1986, 'Play Profiles of Captive Adult Orangutans: A Developmental Perspective', *Developmental Psychobiology,* vol. 19, no. 4, pp. 315-326.

561 **Table 1. Ethogram for juvenile, Bornean orangutans during forest excursions with**

562 **mean percentage (and CI 95%) of time engaged in behaviour per excursion**

563

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)

564

565 Sexual activity, aggressive interactions, sliding, crawling and social grooming all took less

566 than 0.1 % of time and therefore were not analysed. Abnormal behaviours commonly

567 reported in laboratory primates were not observed (e.g. pacing, rocking, clinging).

568

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	$F_{1,33} = 0.4$ $p = 0.56$	$F_{1,33} = 4.5$ $p = 0.02$	$F_{4,428} = 0.5$ $p = 0.73$	$F_{4,428} = 1.6$ $p = 0.17$	$F_{8,428} = 1.0$ $p = 0.40$

571 **Table 3. Relationships between behaviour and orangutan weight and duration of time**

572 **spent at the Centre (n = 40)**

573

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

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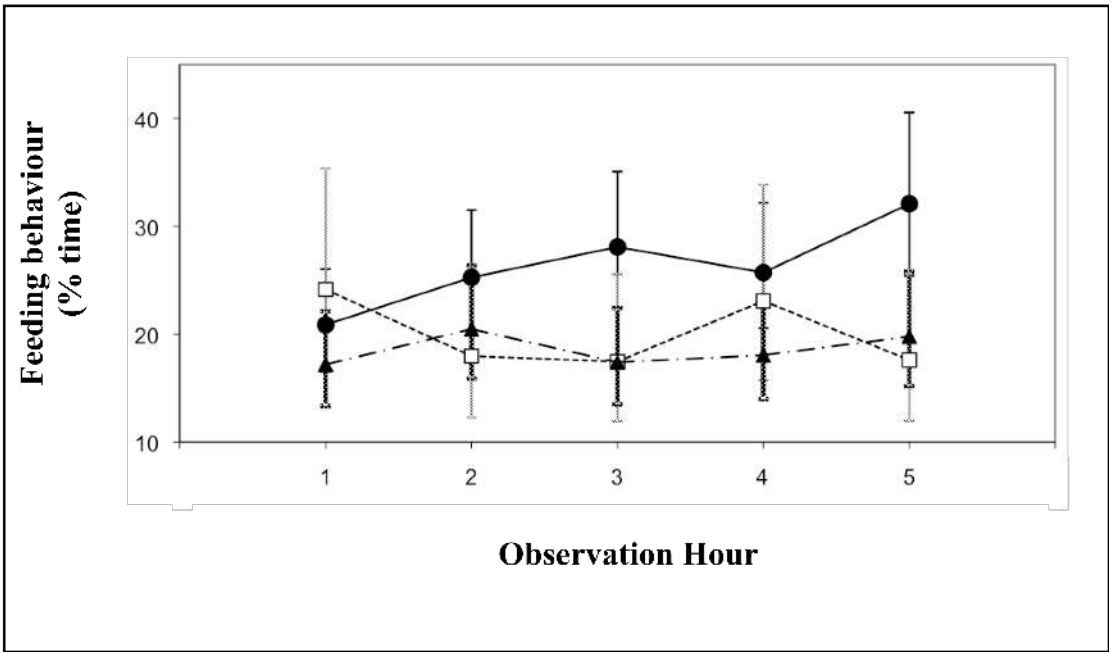

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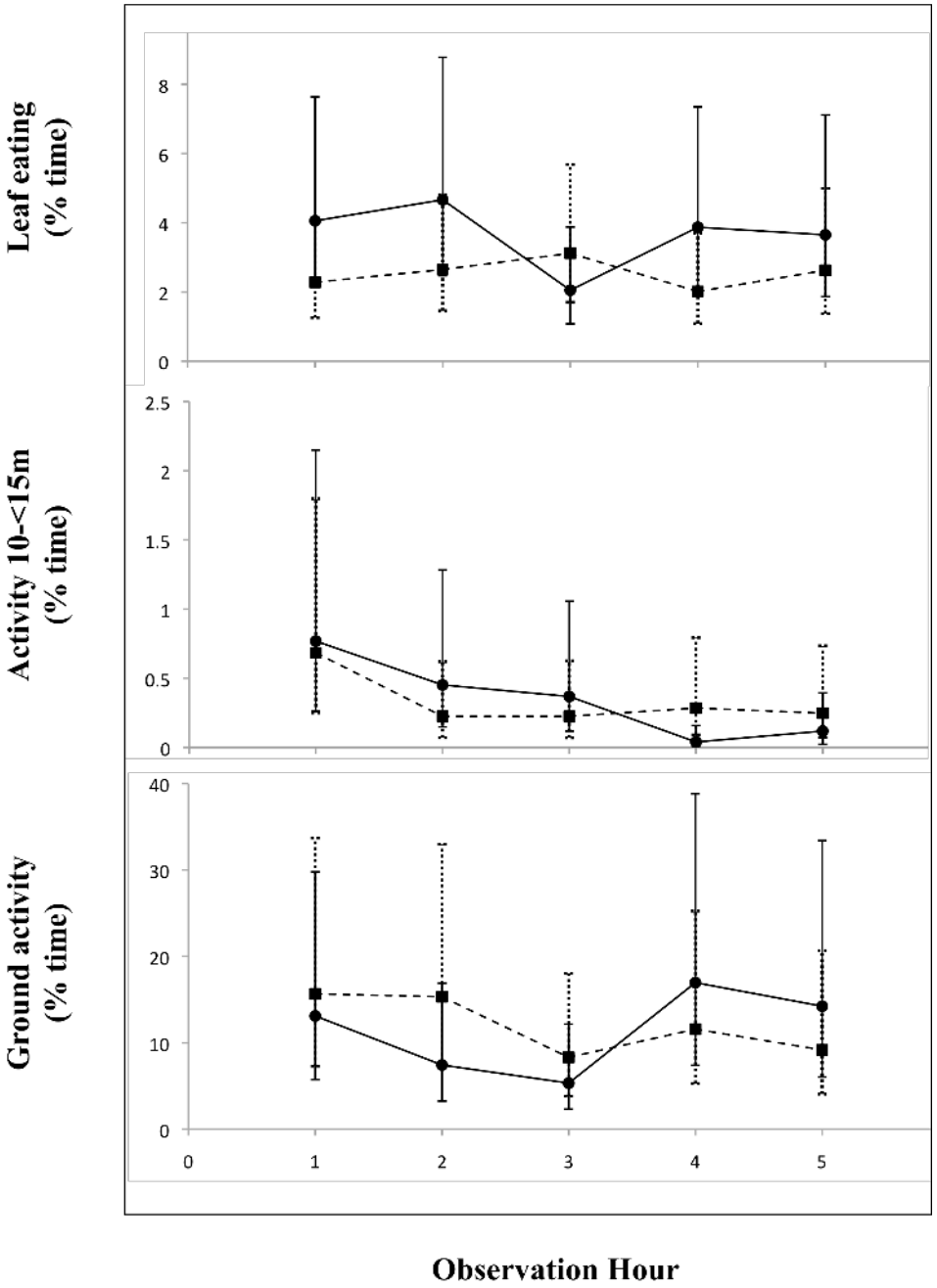
576

577 **Figure 1. Feeding activity of three health groups (good —●—, moderate – –▲– – and**

578 **poor ---□---) of juvenile orangutans over five observation hours (mean % time and 95%**

579 **confidence interval)**

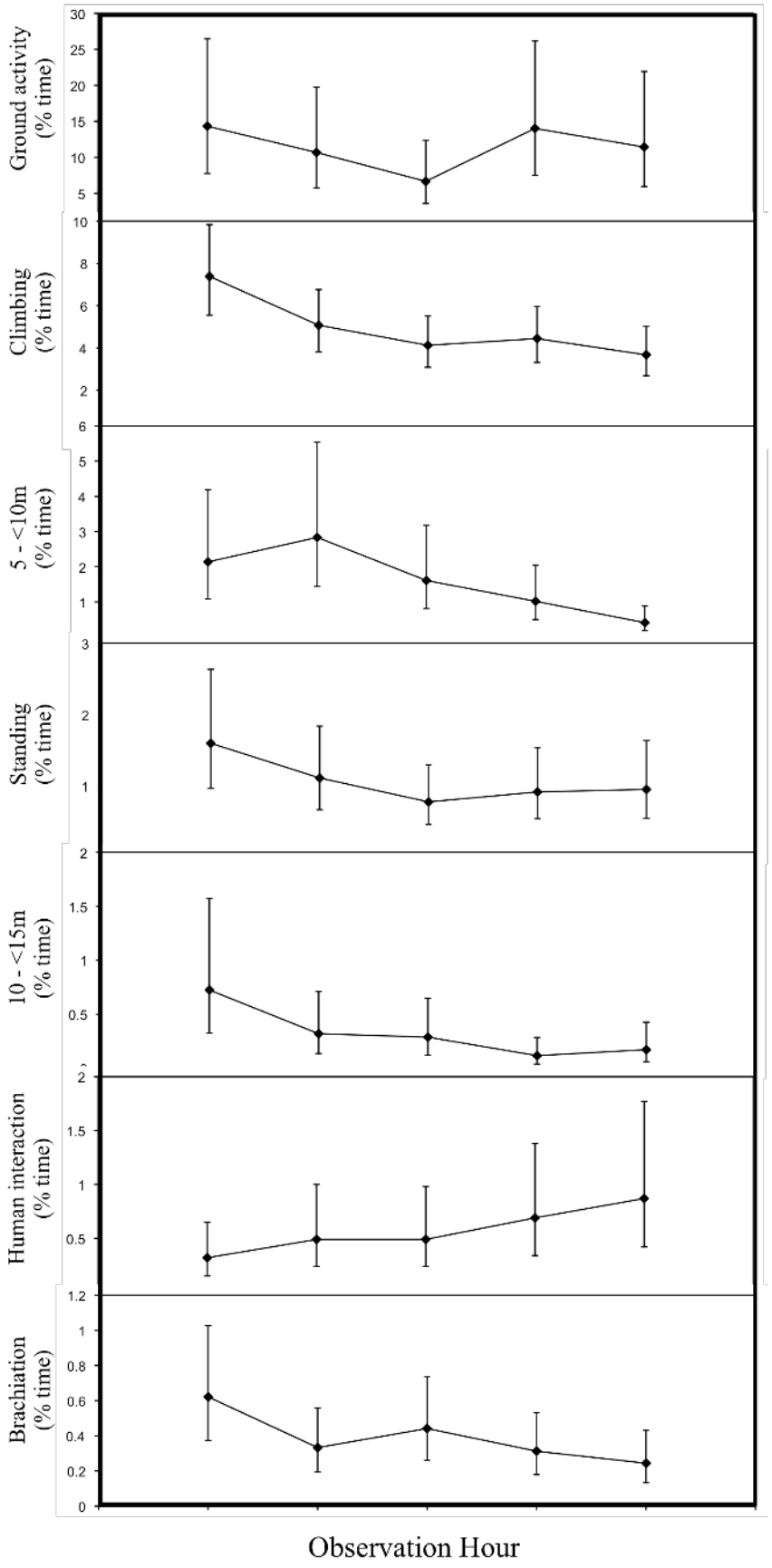


580

581 **Figure 2. Patterns of activity (10 - <15m) of male (--■--) and female (—●—) juvenile**

582 **orangutans over five observation hours (mean % time with 95% confidence intervals)**

583



584

585 **Figure 3. Activity shown by juvenile orangutans over five observation hours (mean %**

586 **time with 95% confidence interval)**