Locomotor behaviour of wild orang-utans *(P. p. wurmbii)* in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia.

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PREFACE

I hereby declare that this thesis is the result of my own work. Where the work of other persons is either used or quoted, it is specifically stated in the text.

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Abstract

Field study of the locomotor behaviour of wild Bornean orang-utans (*Pongo pygmaeus wurmbii*) in a disturbed peat swamp forest revealed that orthograde suspensory locomotion dominated orang-utan locomotion. Comparison with other studies showed that whilst the overall locomotor repertoire of orang-utans did not substantially differ between species, the relative frequencies did. The subjects of the current study were found to exhibit substantially higher frequencies of tree-sway than found at other sites, suggesting that this energetically efficient mode of locomotion is an important aspect of traversing the arboreal environment of a disturbed peat swamp forest. Pronograde suspensory locomotion was observed at a substantially lower frequency in the Borenean *P. p. wurmbii* and *P. p. morio* than in the Sumatran *P. abelii,* suggesting that Bornean orang-utans exhibit pronograde behaviour at lower levels than their Sumatran counterparts. Log-linear modelling was used to identify key associations between orang-utan locomotion, body size, height in the canopy, and support use. Support type and support diameter were found to have the strongest associations with locomotor repertoire. This supports the suggestion by Thorpe and Crompton (2005) that orang-utans have evolved specific modes of locomotion in order to solve problems associated with traversing a complex arboreal environment. Height in the canopy was not found to have a direct influence on the locomotion of orang-utans when considered together with the variables support type and support diameter, although it was found to have a direct influence when considered with age-sex and number of supports. Age-sex class was found to have a limited influence on locomotion, concurring with Thorpe and Crompton's (2005) study on *P. abelii*. This suggests that orang-utans follow arboreal pathways selecting travel routes which are based on preferred locomotor-support combinations. Further research is needed to investigate the extent differences in orang-utan locomotion both between species and between habitat types.

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1. INTRODUCTION

Studies of positional behaviour in the wild provide a critical link between ecology, behaviour, and morphology (Stafford *et al.*, 2003). The Asian apes, more than any other, are restricted to an arboreal habitat (Thorpe and Crompton, 2006). As the world's largest arboreal primate species (Cant, 1987a), orang-utans (*Pongo* spp.) possess postcranial traits that facilitate their arboreal lifestyle, such as long forelimbs with hook-like hands, short hindlimbs with hand-like feet, and highly flexible hip and shoulder joints (Fleagle, 1988; MacLatchy, 1996; Delgado and van Schaik, 2000). Their locomotor behaviour is predominantly orthograde suspension whereby the body is orthograde with the head superior, and various combinations of all four appendages grasping supports in different ways, with suspension by the forelimbs from above (Cant, 1987b; Thorpe and Crompton, 2005).

Traditional classifications of orang-utans recognised only one species, with Bornean and Sumatran orang-utans being classed as separate sub-species. However, as a result of more recent genetic studies, the Sumatran (*Pongo abelii*) and Bornean (*P. pygmaeus*) orang-utans are now recognised as separate species (Xu and Arnason, 1996; Zhi *et al.,* 1996; Groves, 2001; Goossens *et al.,* in press). It is now generally accepted that there are three sub-species of Bornean orang-utan: *P. pygmaeus pygmaeus* from north-west Kalimantan to Sarawak, *P. p. morio* from north-west Kalimantan to Sabah and *P. p. wurmbii*, the subject of this study, in south-west and central Kalimantan (Groves, 2001; Singleton *et al.,* 2004; Goossens *et al.,* in press).

Peat swamp forests cover large areas of Kalimantan (approximately 6.8 Mha) (Rieley et. al., 1996) and are important habitats for remaining populations of wild orang-utans (Meijaard, 1997; Singleton et. al., 2004). There are two major categories of peatland in Kalimantan – topogenous and ombrogenous. The latter is the dominant habitat type in the Sabangau Ecosystem, the area in which this study was conducted. Ombrogenous peatland is gently-domed and for the main, receives all its water and nutrients from aerial precipitation. It comprises four distinct vegetation sub-types which have been described in detail elsewhere (Page *et al.,* 1997; 1999; Shepherd *et al.*, 1997; Morrogh-Bernard *et al.*, 2003). This study was restricted to mixed peat swamp forest where the forest canopy has three strata reaching a maximum height of 35m (Page *et. al.,* 1999). Trees grow on large hummocks formed by root plates, interspersed with hollows that fill with water during the rainy season and many have stilt or buttress roots and pneumatophores are common (Page *et. al.,* 1999, pers. obs.). The estimated 1996 orang-utan density of 1.9 - 2.4 individuals per square kilometre suggests that this habitat sub-type supports over 50% of the total population in the western catchment of the Sabangau Ecosystem (Husson *et. al.,* submitted). The Sabangau orang-utan population is now estimated at around 6,900 individuals (Singleton *et. al.* 2004; Husson *et. al.,* submitted), making it the largest contiguous population in the world.

Locomotion and feeding in an arboreal environment requires both the muscular strength able to counter gravity as well as the coordination between limbs to maintain balance on branches of variable diameter, flexibility, distance and orientation (Peters and Rogers, 2007). The principal stable elements in a forest are vertical tree trunks, which do not interconnect (Grand, 1972, 1984). Tree branches are tapered, and as a branch stretches outwards towards its periphery, it becomes weaker and less stable. As difficulties associated with balance, substrate strength, stability, and deformation increase with increasing weight, the large body mass of orang-utans strongly influences every solution to problems of habitat structure (Cant, 1987b; Cartmill, 1985). Weight may act as a constraint, prohibiting certain solutions. For example orang-utans cannot cross gaps by leaping in the same way that many other primate species can. Yet it may also facilitate some solutions such as tree-swaying, where their large body mass can be used to oscillate trees in order to cross a gap (Cant, 1992).

Orang-utans typically spend most of their time feeding, with the rest of their time being divided between resting, travelling, socialising and nest building (e.g. Galdikas, 1988; Mitani, 1989; Knott, 1999a). Orang-utans spend around 13.5% of their active period travelling (based on summaries of data collected from several sites) (Delgado and van Schaik, 2000; Knott, 1999a; Rodman, 1988) in which they expend a considerable amount of energy (Rodman, 1979; Wheatley, 1982; Knott, 1999b). Efficient travel through the rainforest canopy, in terms of minimising deviations from direct travel between two points, is constrained by the ability to use available structures as well as the ability to cross canopy discontinuities (Temerin and Cant, 1983; Cant 1988). The ability to cross gaps between trees is probably the single most important determinant of path length, which is important because reduced path length will lower energy expenditure on locomotion (Cant, 1992). Logging activity increases both the number and size of gaps in the canopy and could therefore decrease the travelling efficiency of orang-utans through the loss of continuous arboreal pathways (Rao and van Schaik, 1997). Consequently, individuals may be forced to travel longer distances around a gap, or to descend from the canopy and cross the gap on the ground (Felton *et al.*, 2003), resulting in increased energy expenditure (van Schaik, *et al.*, 2001). In a study by Thorpe *et al.* (2007a) in which orang-utan (*Pongo abelii*) energy costs were quantified, orang-utans used substrate compliance (flexibility) in order to decrease the energetic cost of locomotion by tree-swaying, which was found to be less than half as energetically costly as jumping or coming to the ground to cross the gap.

The type, size, and orientation of supports within the canopy has a considerable potential influence on the expressed locomotor repertoire of arboreal animals (Thorpe and Crompton, 2005). The diameters of the terminal branches are relatively small and orang-utans frequently need to move to these thin peripheral branches in order to travel from one tree to another (Grand, 1984). Thorpe and Crompton (2005) found support type and diameter to have the strongest associations with orang-utan locomotor repertoire suggesting that orang-utans solve a variety of complex habitat problems through the accurate assessment of flexibility, strength, position and distance of the support structures (Russon, 1998, Peters and Rogers, 2007).

Whilst orang-utans spend almost all of their time in the canopy, they do sometimes travel on the ground. This behaviour is more commonly observed in Bornean orang-utans where adult males, in particular, can travel for long periods on the ground (Mackinnon, 1974; Galdikas, 1979; Rodman, 1979; Tuttle, 1986; Rodman and Mitani, 1987; pers. obs.) although both juvenile and females are also known to travel on the ground over short periods (MacKinnon, 1974, pers. obs). Cant (1987b) attributes this major difference in habitat use between Bornean and Sumatran orang-utans to the presence of tigers in Sumatra, whereas in Borneo there are no predators sufficiently large to threaten adult orang-utans.

Subsequent to the standardised descriptions of primate locomotor and postural modes by Hunt *et al.*, 1996, the only comprehensive study on the locomotor behaviour of orang-utans is by Thorpe and Crompton (2005). Prior to this, orang-utan locomotion was only broadly described. Sugardjito (1982) was the first to quantify the locomotor behaviour of Sumatran orang-utans. This was followed by a more detailed study at the same site (Sugardjito and van Hoof, 1986). Cant (1987b) was the first to undertake a study of the locomotor behaviour of Bornean orang-utans (*P. p. morio*). However, this study only involved two adult females and took place during an "el nino" year, which may have influenced the ranging and foraging patterns of his subjects (Thorpe and Crompton, 2006).

Given the importance of peat swamp forests as wild orang-utan habitats, the aim of this study is to examine the locomotor behaviour of a population of wild Bornean orang-utans (*P. p. wurmbii*) in an area of disturbed peat swamp forest, in an attempt to:

1. Identify key associations between orang-utan locomotion and support use.
2. Identify any major differences in locomotor behavioural repertoires between species.

The sample size is small, not allowing a direct comparison with the results of the analysis by Thorpe and Crompton (2005). However, it is the first study to include detailed information on support use by *P. p. wurmbii* and only the second report of locomotion on wild orang-utans following the standardised descriptions of Hunt *et al.* 1996. As such, it builds on current knowledge of the relationships between locomotion and support use in orang-utans. In addition, it provides an insight into the locomotor behaviour of orang-utans in what is a very important habitat for wild orang-utan populations.

2. METHODS

2.1 Study Area

The field study took place within the Natural Laboratory for Peat Swamp Forest (NLPSF), a 500km^2 area of forest in which the Setia Alam Basecamp (02°19'S, 113°54'E) is situated. The area is located at the northern end of the Sabangau National Park (SNP), Central Kalimantan, Indonesia (Figure 1). The Sabangau catchment ranges from pristine to disturbed peat-swamp forest and comprises 6,000km^2 of the 22,000km^2 of tropical peat swamp found in this region. The area was described in detail by Page *et al.,* (1999), but see also Morrogh-Bernard *et al.,* (2003) and Buckley *et al.,* (2006). Orangutans in the NLPSF have been studied continuously since 2003, thus are known and habituated to observers.

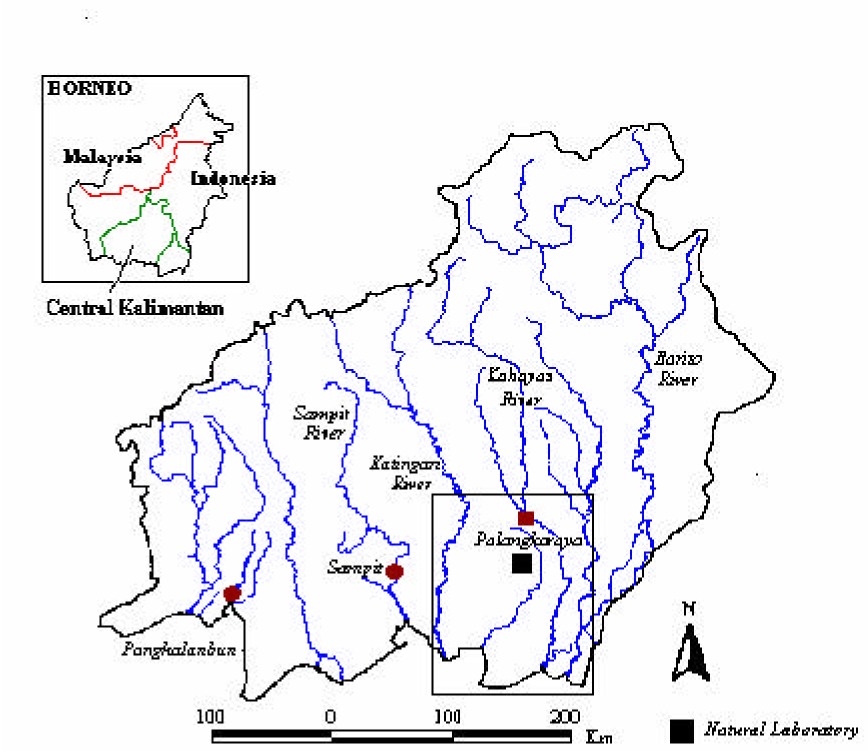


Figure 1. *Map Showing the Location of the Natural Laboratory (NLPSF) in Borneo.* The entire Sabangau forest stretches from just south of Palangka Raya in the north to the coast in the south, and from the River Kahayan in the east to the River Katingan to the west. Map courtesy of OuTrop.

The study site was a logging concession from 1966 to 1996 and almost as soon as the logging concession expired, illegal loggers moved in (Husson *et al.*, submitted). Currently, illegal logging has been stamped out within the NLPSF. However, many gaps in the forest canopy remain as a result of sustained disturbance and logging continues unabated in other areas of the Sabangau (Husson and Morrogh-Bernard, submitted). Logging not only creates gaps in the canopy through the direct removal of trees, but also through the creation of canals and skids in order to transport logs out of the forest. In addition, gaps in the forest canopy are created naturally (e.g. tree falls), through fire damage, and by bat hunters clearing areas in order to trap bats (Struebig *et al.*, in prep). The techniques used by illegal loggers in the Sabangau (where canals are dug in the peat, along which logs are floated out) are also having devastating affects on forest structure, as peat drainage leads to decreased stability of the peat, resulting in high levels of tree falls and an increased risk of susceptibility to fire (Watson *et al.,* 2000; D'Arcy and Page, 2002; Husson *et al.*, submitted).

2.2 Field Study

The study was conducted in a $4km^2$ area of disturbed peat swamp forest from the period March to September, 2007. All observations were made by a single observer (KLM) in order to ensure consistency. A grid system of trails cut by other researchers facilitates searching for orang-utans in the study area (Figure 2). Once an orang-utan was located it was followed until it made its night nest (15h00 – 19h00). The nest was returned to the following morning (04h30), before dawn. Once the animal arose from its nest it was then followed from nest-to-nest for a period of three days, a rest day would be taken where the focal orang-utan was followed by other observers, and then the orang-utan was followed again for three days to collect data for this study. Orang-utans were followed up to a maximum of 10 consecutive days, however, more frequently, the orang-utan had to be abandoned when it travelled too far out of the research area to allow observers to return to the nest the following day.

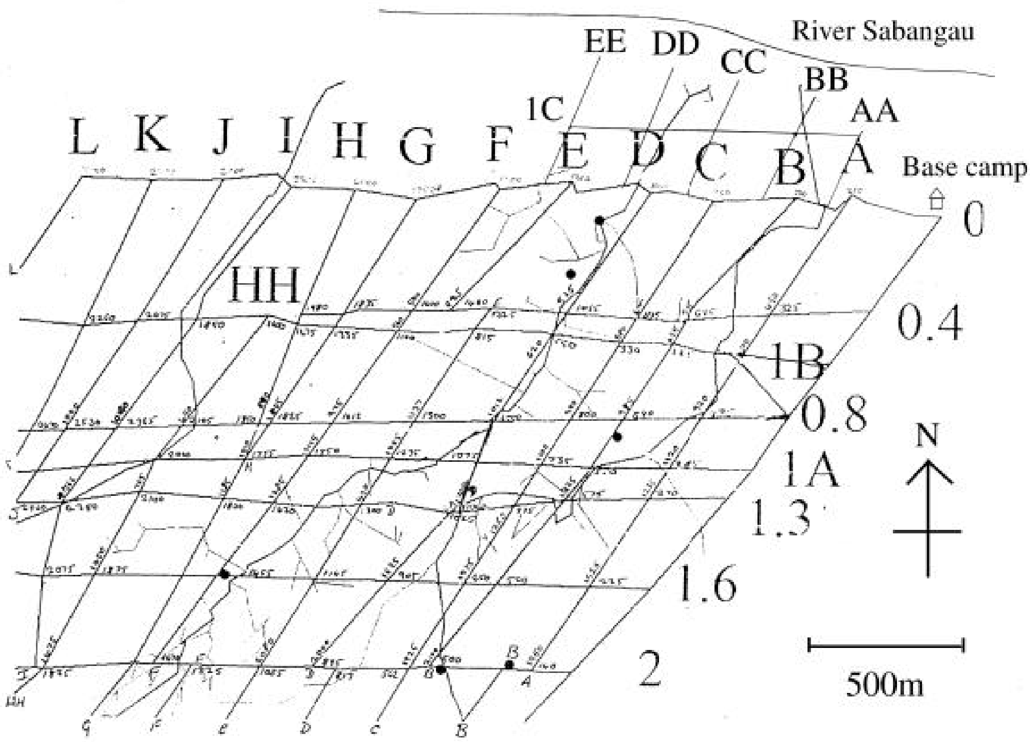


Figure 2. *The Grid System for Orang-utan Follows in the Natural Laboratory (NLPSF).* The lettered transects are 250m apart along Transect 0, and the numbered transects are numbered according to their approximate distance in kilometres from Transect 0. Map courtesy of OuTrop.

Whilst data were being collected on one orang-utan, wherever possible, local field assistants continued searching other parts of the research area for another orang-utan. This was done in order to incorporate as many different individuals into the study, as the majority of data being collected in the initial months tended to be on one adolescent female, the only orang-utan that could be found. During the first three months of data collection in particular, it was especially difficult to find orang-utans, as there was very little fruiting in the research area. This is likely to cause orang-utans to move to other areas within their home ranges in order to find food. In addition, a large part of the fieldwork took place during the wet season, where rain and wind made it very difficult to see or hear orang-utans and thus extremely difficult to locate.

The other main obstacle encountered during the course of data collection was the poor visibility of orang-utans in the wild. As the study took place in disturbed peat swamp forest, the undergrowth was often very dense as a result of past disturbance, making it difficult to walk through. In addition, as orang-utans tended to travel low down in the canopy, it was necessary to maintain a sufficient distance so as not to impinge on the focal animals natural behaviour whilst trying to remain sufficiently close to observe their positional behaviour with a fine degree of detail. As a consequence, it was not always possible to decipher the locomotor mode and support use, even with the aid of binoculars. This substantially reduced the number of observed sample points obtained during each follow.

Self-training in the estimation of positional modes, heights and support diameters was undertaken prior to the collection of data and throughout the data collection period in order to ensure accuracy. The classification of positional behaviour follows that detailed by Hunt *et al.* (1996) but also includes additional positional modes described by Thorpe and Crompton (2006). Whilst 34 biomechanically distinct locomotor submodes were identified during the course of the data collection period (Appendix A), for the purposes of the present study they are conflated into the seven submodes detailed in Table 1, following Thorpe and Crompton (2005).

Instantaneous sampling and locomotor bout sampling are currently the most commonly used methods in studies of locomotor behaviour (Doran, 1992). In this study, data were collected using focal instantaneous sampling on the 1-min mark, using a digital watch with a countdown-return beeper function. Given the desired detail on appendage use and support characteristics, instantaneous sampling proved to be more appropriate as these details could be easily recorded at the time of the signal. Details of data collected at each sample point are presented in Table 1.

TABLE 1. Positional Behaviour Observations[1]

1. **Date**
2. **Individual**
3. **Time**
4. **Positional mode**[2]

   1.Quadrupedal walk: Locomotion on top of supports angled at <45º; typically all the four limbs contact the support in a particular sequence. The torso is pronograde (—) or roughly parallel to the support (Hunt *et al.,* 1996). Includes tripedal walk, quadrupedal run, and tripedal run.

   2. Bipedal walk: Hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. Includes flexed and extended bipedalism, and hand-assisted bipedalism in which hindlimbs bear more than 50% of body mass, but one or both forelimbs are used to assist, either in suspension or compression, and bear more than their own weight.

   3. Climb/descent: Ascent and descent on supports angled at ≥45º.

   4. Torso-orthograde suspension: Includes brachiation and orthograde clamber which is a forelimb suspensory torso-orthograde mode (|), but with hindlimbs assisting. All the four limbs act as propulsors, with most body weight borne by the abducted forelimbs. Also includes the mode drop, in which all pre-drop postures were orthograde in nature.

   5. Torso-pronograde suspension[3]***:*** All the four limbs are used in some combination; the torso is pronograde, and limbs are in tension.

   6. Bridge: A torso-pronograde gap-closing movement where the hands reach out to grasp a support on one side of a gap and cautiously pull the body across the open space with the feet retaining their grips until a secure position is established on the other side (Youlatos, 1993)

   7. Oscillation: Combines modes tree sway and ride. Tree sway is a gap crossing movement used between trees where either body weight or oscillation are used to deform branches, and often the pre-gap closing posture resembles clinging more than suspension. Ride is similar to tree sway, but is used from tree to ground, it can also be used to move from a higher to a lower level in the canopy as in Thorpe and Crompton (2005). A vertical, small diameter support is grasped in a clinging posture and a movement or oscillation overbalances the support. The weight of the individual's body pulls the support from a vertical orientation toward horizontal. As the support approaches horizontal a suspensory posture may result, after or during which the grip with the hindlimb is released and the feet contact the ground/support(s) at a lower level in the canopy.
5. **Height:** 5m intervals up to 30m, >30m (measured as the vertical distance from the animal to the ground).
6. **Number of supports:** 1, 2, 3, 4, >4
7. **Support type:** branch, bough, trunk, liana, other (aerial roots, nest)
8. **Support diameter:** <2cm; ≥2-<4cm; ≥4-<10cm; ≥10-<20cm; ≥20-<40cm; ≥40cm
9. **Behaviour:** feeding (acquiring, processing, and eating); travel

[1] Data collection followed Thorpe and Crompton (2005)
[2]All follow those of Hunt *et al.* (1996) and include all submodes as detailed in their study, with additional postures of Thorpe and Crompton (2005) also included.
[3] For analysis, pronograde suspension and bridge were conflated, as both had very small frequencies.

Thirteen individuals were observed, including all age-sex categories (Table 2). Adult males are defined as those exhibiting secondary sexual characteristics such as cheek flanges, throat pouches and increased body mass, adult females are those females that have given birth. Sub-adult males are those which are sexually active but lack secondary sexual characteristics, and immature males and females as those showing no sexual activity (Rijksen, 1978).

Although data were collected on locomotion during both travel and feeding, the latter only contributed <5% of all observed bouts. Although focal animals moved in order to change position while feeding, this rarely took place on the time cues. As a result, insufficient data was collected on locomotion during feeding to allow it to be incorporated in the log-linear analysis, or be meaningful in the comparison with previous studies.

TABLE 2. Study Subjects

Age-sex category	Name	No. focal days	No. focal hours	Notes
Adult Male	Beethoven	3	21	Dominant Male
	Jupiter	9	89	Dominant Male
	Leonardo	1	8	Newly flanged Male (not habituated)
	Mozart	2	13.5	Young Adult Male (not dominant)
Adult Female	Indah	11	88	Travels with Isabella (18 months)
	Juliet	1	4	Travels with Julius (2-3 yrs)
Subadult Male	Archimedes	1	7	
	Orson	4	26	
	Romeo	1	11	
	Zeus	1	10.5	
Adolescent Female	Feb	19	170	Independent
	Indy	3	17	Independent daughter of Indah
Adolescent Male	Bengy	3	28	Independent

2.3 Statistical Analysis

A total of 6,599 instantaneous observations of position behaviour were obtained, 5,525 of postural behaviour and 1,074 of locomotion. Of the 1,074 instantaneous samples of locomotor behaviour only 623 included detailed specifics of support use, due to poor visibility. Consequently, for the log-linear analysis, the data are analysed in two parts. The relationships between locomotion, age-sex category, height and number of supports are analysed for all observations (n=1,074, "basic analysis"), then a more detailed analysis of support use is presented for the observations which include data on support type and support diameter (n=623).

The interdependence of observations is a particular problem in the analysis of positional behaviour (i.e. locomotion and posture), as sequential observations using a small time interval are thought to be highly dependent thus complicating statistical analysis (Mendel, 1976; Janson, 1984, 1990; Hunt, 1992; Dagosto, 1994; Hunt, 1994; McGraw, 1996; Warren and Crompton, 1997; Cant *et al.,* 2001; Thorpe and Crompton, 2006). Whilst some studies have chosen to omit statistical tests of significance, instead only presenting frequencies (e.g. Cant, 1987b), others have employed a variety of procedures in order to deal with the violation of independence (e.g. Janson, 1984; Hunt, 1992; Dagosto, 1994; Gebo and Chapman, 1995; McGraw, 1996; Cant et al, 2001). However, when observing orang-utans in the wild visibility is severely impeded by the dense foliage, especially when trying to collect the type of detailed data required in this study. Orang-utans also tend to rest frequently during travel bouts (Thorpe and Crompton, 2005; pers obs). These factors meant that sequential observations of locomotor behaviour were rarely obtained and it is therefore felt that the dependence between data points is minimal. Thorpe and Crompton (2005) also noted these factors meant that the dependence between data points was of minimal concern. Therefore, following Thorpe and Crompton (2005), all locomotor observations in this study are analysed.

Forty four percent of all observed locomotor bouts sampled behaviour of adolescent males and females (3 individuals), 27% that of adult males (4 individuals), 11% that of sub-adult males (4 individuals) and 18% that of adult females (2 individuals). It is acknowledged that there is a degree of under-sampling in the case of both adult females and sub-adult males. In addition, a large amount of the data collected on adolescents was on one individual as she was the only orang-utan that could be found for much of the duration of the field study. Consequently, a large proportion of the observed locomotor bouts on adolescents were from one female. However, the Friedman test revealed that the adolescents showed a significant correspondence ($\chi^2 = 11.8$, $P < 0.05$) and could therefore be grouped together. Locomotion on the ground was often difficult to observe due to poor visibility and was rarely obtained. Consequently, observations were solely obtained for arboreal locomotion.

Categorical data of the sort collected in this study are typically summarised in contingency tables and tested by chi-square or log likelihood (G-test) procedures (Cant *et. al.,* 2001). However, while valid for two-dimensional analyses, analysis of multidimensional contingency tables using a series of all possible combinations of two-dimensional tables is not an appropriate technique as it may lead to misleading conclusions being drawn (Gilbert, 1981; Agresti, 1990; Everitt, 1992). Therefore, log-linear modelling was used to analyse multiple relationships between locomotion, age-sex, height and substrate variables. Log-linear analysis is a technique for analysing categorical or frequency data and can be thought of as the frequency equivalent of multifactorial ANOVA because, like multifactorial ANOVA, it analyses the separate and combined effects of several factors on a dependant variable.

Log-linear models represent an expression of how the observed data are affected by variables or combinations of variables and its strength lies in its ability to be extended to quite complicated contingency tables involving several variables. There are a number of advantages in using log-linear analysis for data of the type collected in positional behaviour studies. Firstly, log-linear analysis is designed for categorical data. Secondly, it allows hypothesis to be tested concerning the interactions between variables. Third, different interactions between variables a able to be ranked in order of their relative importance and finally, it does not require the data to come from a normally distributed population.

Thorpe and Crompton (2005) note that, like any type of multivariate analysis, log-linear analysis should primarily be considered as a means of exploring the data. Like χ^2, log-linear analysis compares the actual cell counts in a contingency table to the values predicted by the model (the expected values). In log-linear analysis tables are formed that contain one-way, two-way and higher order associations. The procedure aims to construct a model where the cell frequencies in a contingency table are accounted for by the minimum number of terms. This is done through a process of backward elimination. The final model includes only the associations necessary to reproduce the observed frequencies. A significance value of 1 for the χ^2 likelihood ratio indicates a perfect fit of the model's predicted cell counts to the observed cell counts, although a P value of >0.05 is considered significant (Thorpe and Crompton, 2005; Thorpe *et al.,* 2007b). A good-fitting model provides a basis for describing and making inferences about associations among categorical responses (Agresti, 1990).

The variable interactions (i.e. model expressions) produced by log-linear models can be analysed in more detail in order to investigate the nature of associations between variables. A useful method of exploring relationships between those variable associations is through contingency tables containing row and column percentages and standardised cell residuals (SCRs). Standardised cell residuals indicate by their sign whether an interaction is more (positive values) or less (negative values) common than predicted by the model and, by their size, to what degree. Standardised cell residuals greater than ±2.0 indicate a substantial variation from the model predictions and, therefore may be of particular interest (Thorpe *et. al.,* 2007a).

Odds ratios represent ratios of probabilities. They are used to establish correlations which underlie significant associations (Crook, 1997). For example, for the interaction height * locomotion, of the 218 of observations of oscillation, 194 were in the "preferred" height category. Therefore, the probability that oscillation will take place in the "preferred" height category is 194/219 (0.9), and the probability that oscillation will take place in the "not preferred" height category is 24/218 (0.1). The odds ratio of these probabilities is 9 (0.9/0.1) which establishes a correlation between height and oscillation with oscillation being 9 times more likely to take place in the "preferred" height category than in the "not preferred" height category.

The analysis was performed using SPSS version 15.0.

2.4 Data Preparation

The power of log-linear analysis is weakened if more than 20% of cells within a multiway contingency table have an expected value of less than 5 (Tabachnick and Fidell, 1996). Consequently, it was necessary to conflate variables in order to meet these criteria. In order to ascertain the most suitable substitute variables, categories were reclassified in alternative ways (Tables 3 and 4) and all possible combinations were tested. The way in which variables were classified initially followed Thorpe and Crompton (2005) in order to allow a comparison between the two studies with locomotor modes being combined on a basis of broad biomechanical similarities. For example, in some variable classifications, bipedalism and orthograde suspension were combined as they body is held in an orthograde position (e.g. LOCOc, LOCOf) whereas in others bipedalism was combined with quadrupedalism as both are compressive postures (e.g. LOCOd, LOCOe). However, the small data set in this study meant that some categories had to be conflated to a greater extent than in Thorpe and Crompton (2005). The choice of categories for variables such as height and support diameter were established by testing all possible combinations in order to establish which variable classifications led to better fitting models. For example, height was reclassified in a number of different ways (Table 3). However, sequential categories did not produce good fitting models. It was noted that majority of travel, 77%, took place between 5 and 15m so and it was therefore assumed that orang-utans favoured these levels for travel. Consequently the category, "*Height-4"* was created which comprised "preferred" (≥5-<15m) and "not preferred" (all other height categories), which led to better fitting models than the other height substitute variables in the basic, support type and support diameter analysis. Similarly, "*no. of supports-3",* which differentiated between the use of single and multiple supports was selected on the basis that it resulted in better fitting models. However, whilst "*age-sex-3"* resulted in better fitting models in the basic analysis it resulted in high levels of sampling zeros and expected values <5 in both the support type and support diameter analysis. Consequently, "*age*" was selected as the substitute variable in the support analysis, as it consistently produced better results by way of sought after features (i.e. a high significance value, a low percentage of sampling zeros, and simple interactions) than the other categories.

As the sample size in this study is small, the substitute categories were often selected on the basis that they did not result in high levels of sampling zeros and had the sample size been larger it is possible that other substitute categories may have produced better fitting models.

TABLE 3. Substitute classifications tested in log-linear analysis

Original variable	Substitute classification	Categories
1. Age-sex	Sex	male; female
	Age	adult; adolescent
	Age-sex-1	adult female; adult male; subadult male; adolescent
	Age-sex-2	adult female; adult male + subadult male; adolescent
	Age-sex-3	adult female + subadult male; adult male; adolescent
2. No. of supports	No. of supports-1	1; 2; 3; 4; >4
	No. of supports-2	1; 2-4; >4
	No. of supports-3	1; >1
3. Height	Height-1	<10 m; 10-15 m; >15 m
	Height-2	<10 m; >10 m
	Height-3	<15 m; >15 m
	Height-4	≥5-15 m (preferred); <5 m + >15m (not preferred)
4. Support type	Type-1	branch/bough, trunk; other; multiple branch/bough; multiple trunk; mix tree; multiple other
	Type-2	branch/bough; multiple branch/bough; trunk; multiple trunk; mix
	Type-3	branch/bough; trunk; mix
5. Support diameter	Diam-1	<10 cm; >10 cm; multiple <10 cm; multiple >10 cm; mixed <10, >10 cm
	Diam-2	<4 cm; >4 cm; multiple <4 cm; multiple >4cm; mixed <4, >4 cm
	Diam-3	<10 cm; >10 cm; mixed <10, >10 cm
	Diam-4	<4 cm; 4-10 cm; >10 cm; mixed <4, 4-10, >10 cm
	Diam-5	<4 cm; >4 cm; mixed <4, >4cm
	Diam-6	<10 cm; >10 cm; multiple <10 cm; mixed <10, >10 cm

TABLE 4. Substitute locomotor classifications tested in log-linear analysis

Locomotor Classification	Categories
LOCO-a	1) quadrupedal, 2) bipedal, 3) orthograde suspend, 4) pronograde suspend, 5) climb/descent, 6) oscillation
LOCO-b	1) quadrupedal, 2) orthograde suspend + bipedal walk, 3) pronograde suspend, 4) climb/descent, 5) oscillation
LOCO-c	1) quadrupedal + pronograde suspend, 2) bipedal + orthograde suspend, 3) climb/descent, 4) oscillation
LOCO-d	1) quadrupedal + bipedal, 2) orthograde suspend + pronograde suspend, 3) climb/descent, 4) oscillation
LOCO-e	1) quadrupedal + bipedal, 2) orthograde suspend + pronograde suspend, 3) climb/descent + oscillation
LOCO-f	1) quadrupedal + pronograde suspend, 2) bipedal + orthograde suspend, 3) climb/descent + oscillation
LOCO-g	1) quadrupedal + bipedal + pronograde suspend, 2) orthograde suspend, 3) climb/descent, 4) oscillation
LOCO-h	1) quadrupedal + pronograde suspend, 2) orthograde suspend, 3) bipedal + climb/descent, 4) oscillation
LOCO-i	1) suspension, 2) compression, 3) mix
LOCO-j	1) pronograde, 2) orthograde, 3) oscillation

3. RESULTS

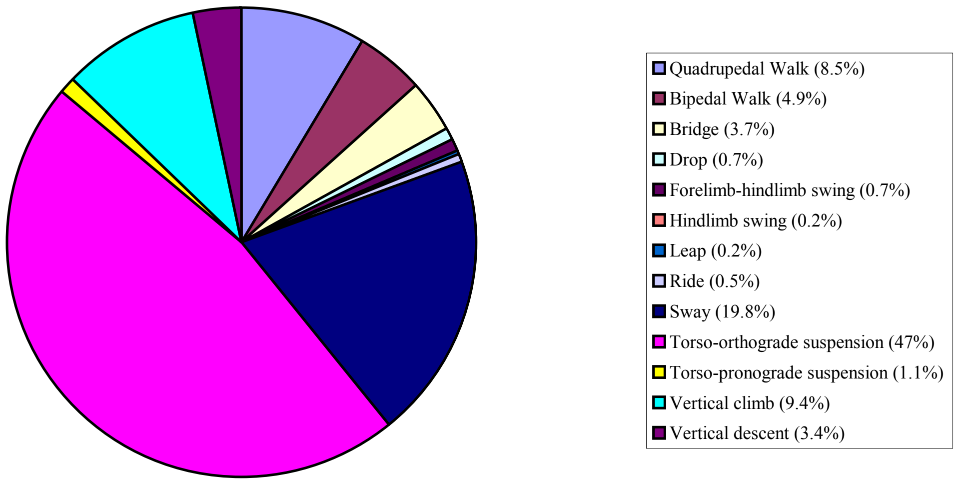
The results are divided into four main sections.

1. The descriptive data from the entire data set (see Appendix A).
2. The Basic Analysis - log-linear analysis using the larger data set (incorporating variables locomotion, age-sex, height and number of supports).
3. The Support Analysis - log-linear analysis for the smaller data set (incorporating variables locomotion, age-sex, height, support type and support diameter).

3.1 Descriptive Data

The frequency of locomotor modes is displayed in Figure 3. Locomotor behaviour definitions and frequencies for all locomotor modes and submodes are detailed in Appendix A. Thirteen different modes were recorded in which thirty-four different submodes were identified (Fig. 3). In summary of the main results, torso-orthograde suspension, which includes the submodes orthograde clamber, orthograde transfer and brachiation, dominated the locomotor repertoire of the study subjects accounting for 47% of all observed locomotion. Sway was the next most commonly observed mode accounting for nearly 20% of observed locomotion. Torso-orthograde suspension is 3.6 times more common than vertical climb/descent, over 5 times more common than quadrupedalism and over 9 times more common than torso-pronograde suspension.

Fig 3. Percentage of bouts for each locomotor mode



With regard to age-sex category, 43.5% of observed locomotor bouts sampled behaviour of adolescents and 56.5% sampled behaviour of adults. Study subjects tended to travel low in the canopy with over 90% of travel taking place below 15m. Seventy five percent of travel took place in the "preferred" height category (≥5-15m) and 54% of travel took place in trees of height >10,≤15m. Finally, in 58% of all observed locomotion more than one support was used for weight bearing. (See Appendix B for detailed frequencies of environmental variables)

3.2. Basic Analysis

This section uses the entire locomotion data set (n=1,074) in order to assess the variables age-sex, height and the number of supports in respect to their relationship with locomotion in wild orang-utans.

3.2.1 Model Selection for the Basic Analysis

The five statistically best fitting models in the basic analysis, for all combinations of variables are detailed in Table 5. *LOCO-a* and *LOCO-b* (Table 4) contained very high levels of sampling zeros and expected frequency values of less than 5 and therefore were not considered in the analysis.

TABLE 5. The five best-fitting models in the basic analysis

Model Variables	χ^2	Degrees of freedom	Significance level (P)[1]	Model expressions (variable relationships)
LOCO-j * Age-Sex-3 * Height-4 * No. of Supports-3	7.222	13	0.890	age-sex * locomotion * no. supports age-sex * height height * locomotion
LOCO-h * Age-Sex-3 * Height-4 * No. of Supports-3	10.421	16	0.844	age-sex * locomotion * no. supports height * locomotion * no. supports
LOCO-c * Age-Sex-3 * Height-4 * No. of Supports-3	12.710	18	0.808	age-sex * locomotion * no. supports age-sex * height height * locomotion
LOCO-h * Age-Sex-1 * Height-4 * No. of Supports-3	11.307	16	0.790	age-sex * locomotion * no. supports height * locomotion * no. supports
LOCO-h * Age * Height-4 * No. of Supports-3	8.116	11	0.703	height * locomotion * no. supports age-sex * no. supports locomotion * age-sex

[1] A significance value of P = 1 for the likelihood ratio χ^2 indicates a perfect fit of the model's predicted cell counts to the observed cell counts, but values >0.05 are significant.

The variable combination LOCO-h (quadrupedalism & pronograde suspension, orthograde suspension, bipedalism & climb/descent, and oscillation) was the locomotor mode combination which consistently resulted in the best fitting models (Table 5). Similarly, the combination Age-Sex-3 (adult males, adult females & sub-adult males, and adolescents) consistently resulted in better fitting models than other age-sex categories.

LOCOj produced the bets model overall, which means that locomotion can be best explained in terms of orthograde, pronograde and oscillatory locomotion. However, as this model only contained a few categories it was felt that much of the detail was lost. LOCOh had more complex three-way associations and was therefore rejected as a suitable model. In light of this, the model selected was LOCOc * Age-Sex-3 * Height-4 * No. supports-3 (Table 5). The results of this model are detailed in Table 6. LOCOc was selected as it retained more detail in terms of distinctions between locomotor modes and was one of the statistically best fitting modes. I addition, it was the most similar to LOCOf (the variable combination that produced the best fitting models in the support analysis), with the exception that climb/descent are conflated into one category.

The variable combination LOCOc combines locomotor modes into "quadrupedalism + pronograde suspension", "bipedalism + orthograde suspension", "climb/descent" and "oscillation" (Table 4). "Bipedalism + orthograde suspension" dominated locomotion, accounting for 53% of all bouts, followed by "oscillation" which accounted for 20% of all bouts. "quadrupedalism + pronograde suspension" and "vertical climb/descent" were observed at similar levels, around 13%.

TABLE 6. Model of best-fit in the basic analysis and associated standardised χ^2 values

Model Variables	χ^2	Degrees of freedom	Significance level (P)
LOCO-c[a] * Age-Sex-3[b] * Height-4[c] * No. of Supports-3[d]	12.710	18	0.808
Model Expressions	**Partial χ^2**	**Degrees of freedom**	**Standardised χ^2 (χ^2/degrees of freedom)**
a) locomotion * height	33.319	3	11.11
b) locomotion * age-sex * no. of supports	25.184	6	4.2
c) height * age-sex	7.050	2	3.53

[a] LOCO-c: orthograde suspension + bipedalism; pronograde suspension + quadrupedalism; vertical climb/descent; oscillation
[b] Age-Sex-3: adult males; adult females + sub-adult males; adolescents
[c] Height-4: "preferred" (5-15m); "not preferred" (<5m; >15m)
[d] No. of Supports-3: 1; >1

3.2.2 Model of best-fit in the basic analysis

In log-linear modelling, the standardised χ^2 values associated with the interactions of the different variables can be ranked in order of relative importance (Table 6). The variable relationships from the backward-elimination log-linear analysis indicate that height has the most important influence on locomotion. This interaction is nearly three times as important as the next interaction, locomotion * age-sex * no. of supports and over three times as important as the final interaction, height * age-sex. The three-way association, locomotion * age-sex * no. of supports, implies that number of supports used for locomotor modes varies with age-sex, and the variable interaction, age-sex * height indicates that there is a difference in the heights used by the different age-sex categories during travel, however, these relationships are rather weak as indicated by the low standardised χ^2 values (Table 6).

3.2.3 Variable Associations in the Basic Analysis

The contingency tables for the variable associations found in the basic analysis namely, locomotion * height; locomotion * age-sex * no. of supports; and height * age-sex (Table 6) are presented in Tables 7, 8 and 9.

*i) Basic Model Interaction: locomotion * height*

In the basic model, height had the most important influence on locomotion. 77% of all observed locomotion took place in the "preferred" height category. Looking at the contingency table, we can see that bipedalism + orthograde suspension is the predominant form of locomotion in the "preferred" height category where it was more than twice as likely to be observed than the next most commonly observed mode namely, oscillation (Table 7, column percentages). In addition, bipedalism + orthograde suspension was also the predominant form of locomotion in the "not preferred" height category where it was more than three times as likely to be exhibited than the next most commonly observed mode namely, vertical climb/descent.

***TABLE 7. Contingency table for basic model interaction: locomotion * height*[1]**

	Height		
Locomotor Mode	"Preferred"	"Not Preferred"	Total
Quadrupedalism + Pronograde suspension	76.9 (13.4) 0.0*	23.1 (13.6) 0.1*	13.4
Bipedalism + Orthograde suspension	74.5 (51.3) -0.7*	25.5 (59.3) 1.3*	53.1
Climb/descent	69.6 (11.7) -1.0*	30.4 (17.3) 1.9*	13.0
Oscillation	89.0 (23.6) 2.0*	11.0 (9.9) -3.7*	20.5
Total	77.2	22.8	100.0

[1] Entries are in row % and (column %) for each locomotion * type unit, e.g. for quadrupedalism + pronograde suspend at the preferred height: 76.9% of all quadrupedalism + pronograde suspend was at the preferred height, and 13.4% of all locomotion at the preferred height was quadrupedalism + pronograde suspend. Asterisks denote standardised cell residuals (negative values indicate frequency is lower than expected).

Oscillation was particularly associated with travel in the "preferred" height category (89%, SCR = 2.0), and negatively associated with travel in the "not preferred" height category (11%, SCR = -3.7), with oscillation being 9 times more likely to take place in the "preferred" height category. Quadrupedalism + pronograde suspension did not deviate far from the values predicted by the model in either of the height categories, as indicated by the very low standardised cell residual values. However, odds ratios calculated indicate the quadrupedalism + pronograde suspension are 4 times more likely to be observed in the "preferred" height category. Both bipedalism + orthograde suspension and climb/descent are over twice as likely to be observed in the "preferred" height category.

*ii) Basic Model Interaction: locomotion * age-sex * no. of supports*

The number of supports used for different locomotor modes varies with age-sex category, although this relationship is rather weak, as indicated by the low standardised χ^2 value (Table 6). During travel, study subjects are 1.5 times more likely to use multiple supports for weight bearing. Adult males are strongly associated with oscillation on single supports (65.5%, SCR = 3.6, Table 8) and are over 7 times more likely to use a single support than a multiple support. In contrast, adolescents are negatively associated with oscillation on single supports (22.7%, SCR = -3.2) and adult females + sub-adult males lie in between the two and do not deviate far from the values predicted by the model (44.3%, SCR = 0.5, Table 8, column percentages). Adult males are negatively associated with bipedal walk & orthograde suspension on single supports (4.8 %, SCR = -2.9) and with quadrupedalism & pronograde suspension on multiple supports (3.7%, SCR = -3.1).

TABLE 8. Contingency table for basic model association: locomotion * age-sex * no. of supports [1]

No. of Supports	Locomotor Mode	Age-Sex Category: Adult female + subadult male	Adult male	Adolescent	*Total*
One Support	Quadrupedalism + Pronograde suspension	19.0 (5.7) -0.5*	14.3 (3.6) -1.3*	66.7 (10.6) 1.4*	*7.3*
	Bipedalism + Orthograde suspension	34.0 (25.7) 1.4*	7.5 (4.8) -2.9*	58.5 (23.5) 1.3*	*18.5*
	Climb/descent	17.7 (24.3) -1.3*	22.9 (26.2) -1.2*	59.4 (43.2) 1.9*	*33.6*
	Oscillation	26.7 (44.3) 0.5*	47.4 (65.5) 3.6*	25.9 (22.7) -3.2*	*40.6*
	Total	*24.5*	*29.4*	*46.2*	*100.0*
> One Support	Quadrupedalism + Pronograde suspension	40.3 (21.4) 1.5*	6.5 (3.7) -3.1*	53.2 (19.6) 1.2*	*15.8*
	Bipedalism + Orthograde suspension	25.5 (59.8) -1.3*	33.1 (85.0) 1.8*	41.5 (67.9) -0.4*	*70.2*
	Climb/descent	31.8 (6.0) 0.2*	18.2 (3.7) -0.8*	50.0 (6.5) 0.5*	*5.6*
	Oscillation	45.5 (12.8) 1.6*	24.2 (7.5) -0.3*	30.3 (6.0) -1.1*	*8.4*
	Total	*29.8*	*27.3*	*42.9*	*100*

[1] Entries are row % and column (%) for no. supports * locomotion * age-sex. e.g., for oscillation on one support in adult males: 65.5 of all adult male locomotion on one support was oscillation and 47.4% of all oscillation on one support was by adult males. Asterisks denote standardised cell residuals (negative values indicate frequency is lower than expected).

In "adult females + subadult males", oscillation was the most commonly observed mode of locomotion on single supports where it was nearly twice as likely to be exhibited than both "bipedalism + orthograde suspension" and "vertical climb/descent" and nearly eight times as likely to be observed than "quadrupedalism + pronograde suspension. On multiple supports "bipedalism + orthograde suspension" was the prevalent form of locomotion in "adult females + subadult males" where it was nearly 3, 4.6 and 10 times more common than "quadrupedalism + pronograde suspension", "oscillation" and "vertical climb/descent", respectively (odds ratios).

In adolescents, vertical climb/descent is the most commonly observed form of locomotion on single supports where it is nearly twice as likely to be observed than "bipedalism + orthograde suspension" and oscillation, and seven times as likely to be observed than "quadrupedalism + pronograde suspension", whereas on multiple supports "bipedalism + orthograde suspension" is the prevalent mode of locomotion in adolescents. It is 3.5, 10 and 11.6 times more likely to be exhibited on multiple supports than "quadrupedalism + pronograde suspension", vertical climb/descent and oscillation, respectively (odds ratios).

In adult males, oscillation is the prevalent form of locomotion on single supports. It is 2.5 times more likely to be observed than vertical climb/descent and 13 and 21 times more likely to be exhibited than "bipedalism + orthograde suspension" and "quadrupedalism + pronograde suspension", respectively. On multiple supports, as with the other age-sex categories, "bipedalism + orthograde suspension" is the predominant form of locomotion. It is 12 times more likely to be observed than oscillation, and 21 times more likely to be observed than "quadrupedalism + pronograde suspension" and vertical climb/descent (odds ratios).

*iii) Basic Model Interaction: height * age-sex*

TABLE 9. Contingency table for support model association: height * age-sex [1]

Height	Age-Sex Category			Total
	Adult female + subadult male	Adult male	Adolescent	
"Preferred"	31.0 (81.8)	23.8 (67.7)	45.2 (79.8)	77.1
	1.0*	-1.8*	0.7*	
"Not Preferred"	23.2 (18.2)	38.2 (32.3)	38.6 (20.2)	22.9
	-1.8*	3.4*	-1.2*	
Total	29.2	27.1	43.7	100.0

[1] For explanation of table, see Table 7.

The variable interaction height * age-sex in the basic model indicates that there is a difference in the heights used for travel between the different age-sex categories, although the low standardised χ^2 value indicates that this relationship is relatively weak (Table 6).

Just over 32% of adult male travel took place in the "not preferred" height category. This is higher than expected (SCR = 3.4, Table 9). Adult males were 2.3 times more likely to travel in the "preferred" height category, whereas this figure was much higher in "adult females + subadult males" and adolescents who were both 4 times more likely to travel in the "preferred" height category (odds ratios)

3.2.4 Summary of the Basic Analysis

The model expressions in the basic model show that all variables included in the model influence locomotion in some form. However, the magnitude of these relationships varies. Height had the strongest association with locomotion whereas the relationship between age-sex and locomotion varied according to single or multiple support use. Age-sex was not found to have a direct association with locomotion, but there was a direct association between age-sex and height, indicating that the heights at which orang-utans travel in the canopy varies according to age-sex class.

In summary, "bipedalism + orthograde suspension was the prevalent form of locomotion in both the "preferred" and "not preferred" height categories. Oscillation was strongly associated with travel in the "preferred" height category and negatively associated with travel in the "not preferred" height category. Adult males used single supports for oscillation more than expected, whereas adolescents used single supports for oscillation less than expected. Adult males used single supports for "bipedalism + orthograde suspension" less than expected. In adult males and adult females + subadult males, oscillation was the most commonly observed mode of locomotion on single supports whereas in adolescents the most commonly observed mode utilising single supports was vertical climb/descent. On multiple supports, "bipedalism + orthograde suspension" was the prevalent mode across all age-sex classes. Adult males used multiple supports for "quadrupedalism + pronograde suspension" less than expected. Adult males travelled in the "not preferred" height category more than expected.

3.3 Support Analysis

This section examines a sub-set of the data (n=623), which includes detailed information on support type and support diameter.

3.3.1 Model Selection for Support Analysis

For the support analysis models, in order to identify which substitute variables were the most desirable in terms of a high significance level, P, but a low percentage of sampling zeros, all possible combinations were assayed. In the support analysis, "Age" (Table 3) and "LOCO-f" (Table 4) were selected as the substitute variables as they consistently produced models with a relatively high significance level, no or few sampling zeros, and a low percentage of expected values <5. Whilst it is not ideal to conflate locomotor categories to such a large extent as much of the detail is lost, if the dataset is small (as is the case in this study) then it is a necessity.

In the "support" analysis it was impossible to include support type and support diameter in the same model as it resulted in unacceptable levels of sampling zeros. Consequently, models of best fit were found for variable subsets which looked at the relationship between support type, locomotion and (a) age; and (b) height, and between support diameter, locomotion and (a) age; and (b) height. The use of liana's, either as a single substrate, multiple substrates or mixed with tree substrates accounted for only 4.4% of the total observed locomotor bouts and therefore caused a large number of sampling zeros in the substrate type models. For this reason, lianas were excluded from the log-linear analysis.

3.3.2 Models of Best Fit in Support Analysis

Given the small data set, the support analysis was undertaken using subsets containing different variable categories. The support type analysis contained two subsets namely, Locomotion*Type*Height and Locomotion*Type*Age, and the support diameter analysis contained two subsets namely, Locomotion*Diameter*Height and Locomotion*Diameter*Age. The models of best fit are presented in Table 10.

TABLE 10. Model of best-fit in the Support Analysis and associated standardised χ^2 values[1]

A. Support Type Analysis

Subset (a) – Age-Sex			
Model Variables	χ^2	**Degrees of freedom**	**Significance level (P)**
LOCO-f[a] * Age[b] * Support Type-2[e]	15.809	10	0.105
Model Expressions	*Partial* χ^2	*Degrees of freedom*	*Standardised* χ^2 *(χ^2/degrees of freedom)*
locomotion * type	536.531	8	67.07
type * age	14.811	4	3.703
Subset (b) – Height			
Model Variables	χ^2	**Degrees of freedom**	**Significance level (P)**
LOCO-f[a] * Height-4[c] * Support Type-2[e]	8.038	10	0.625
Model Expressions	*Partial* χ^2	*Degrees of freedom*	*Standardised* χ^2 *(χ^2/degrees of freedom)*
locomotion * type	536.531	8	67.07
type * height	79.816	4	19.954

B. Support Diameter Analysis

(a) Subset – Age-Sex			
Model Variables	χ^2	**Degrees of freedom**	**Significance level (P)**
LOCO-f[a] * Age[b] * Support Diameter-2[f]	3.618	8	0.890
Model Expressions	*Partial* χ^2	*Degrees of freedom*	*Standardised* χ^2 *(χ^2/degrees of freedom)*
Locomotion * diameter	357.884	8	44.735
age * locomotion	8.450	2	4.225
age * diameter	15.921	4	3.98
(b) Subset – Height			
Model Variables	χ^2	**Degrees of freedom**	**Significance level (P)**
LOCO-f[a] * Height-4[c] * Support Diameter-2[f]	6.170	10	0.801
Model Expressions	*Partial* χ^2	*Degrees of freedom*	*Standardised* χ^2 *(χ^2/degrees of freedom)*
locomotion * diameter	356.732	8	44.59
height * diameter	35.979	4	8.99

[1] Large standardized χ^2 values correspond to most important interactions and are ranked for each model accordingly.
[a] LOCO-f: orthograde suspension + bipedalism; pronograde suspension + quadrupedalism; vertical climb/descent; oscillation
[b] Age: adults; adolescents
[c] Height-4: “preferred” (5-15m); “not preferred” (<5m; >15m)
[d] No. of Supports-3: 1; >1
[e] Support Type-2: branch/bough, multiple branch/bough, trunk, multiple trunk, mix
[f] Support Diameter: <4cm; >4cm; multiple <4cm; multiple >4cm; mix (<4cm; >4cm)

3.3.3 Variable Associations in the Support Analysis

A. Support Type Analysis (locomotion * support type * age/height)

The variable interactions for the support type models are locomotion * support type; support type *age; and support type * height. Interaction effects for the support models show that all tested variables do influence locomotion in some form (Table 10, B). Comparison of the standardised χ^2 values associated with variable interactions shows that in the support type models the association "locomotion * type" is substantially stronger in both the age sub-set where it has over 18 times more influence than the interaction between age and support type, and height sub-set where it has over 3 times more influence than the interaction between height and support type (Table 10, B). This indicates that support type has a stronger influence on locomotor mode than the other variables included in the model. Each interaction is highlighted in turn in the following section using contingency tables and figures displaying standardised cell residuals (SCRs).

*i) locomotion * support type*

The model revealed that support type has the strongest influence on locomotion (Table 10, B). The most commonly observed locomotor mode on all support types is "bipedalism + orthograde suspension" with the exception of single trunks (Table 11, column percentages). Single trunks show a strong relationship with "climb/descent + oscillation" (92.3%, SCR = 11.9) whereas "bipedalism + orthograde suspension" constitutes by far the most common locomotor mode used on multiple trunks (97.2%, Table 11) a figure that was greater than expected (SCR = 8.7). "Bipedalism + orthograde suspend" is negatively associated with the use of single trunks (SCR=-9.2)

"Quadrupedalism + pronograde suspend" is more strongly associated with "multiple branch/bough" (SCR=6.5) and "single branch/bough" (SCR=3.1) whilst this mode is negatively associated with both single and multiple trunks, as indicated by negative SCR values. The study subjects show a strong affinity for "climb/descent + oscillation" on single trunks than any of the other modes (SCR = 11.9) and exhibit comparatively less vertical climbing on other substrates than expected by the model (Table 11). When exhibiting "climb/descent + oscillation", the study subjects were 80 times more likely to use a single trunk than a single branch/bough or multiple trunk and 11 and 7 times more likely to use a single trunk than multiple branch/bough or mixed tree support, respectively (odds ratios).

TABLE 11. Contingency table for support model association: locomotion * type

Locomotion	Support type					Total
	Branch/bough	Trunk	Multiple branch/bough	Multiple trunk	Mix tree	
Quadrupedalism + Pronograde suspend	19.4 (25.9)	9.7 (3.2)	51.4 (32.2)	2.8 (1.4)	16.7 (13.3)	(11.6)
	3.1*	-3.7*	6.5*	-3.6*	0.5*	
Bipedalism + Orthograde suspend	12.5 (68.5)	3.4 (4.5)	20.3 (52.2)	47.3 (97.2)	16.6 (54.4)	(47.5)
	2.2*	-9.2*	0.7*	8.7*	1.0*	
Vertical climb/descent + Oscillation	1.2 (5.6)	79.6 (92.3)	7.1 (15.7)	0.8 (1.4)	11.4 (32.2)	(40.9)
	-4.1*	11.9*	-4.2*	-7.4*	-1.3	
Total	9.2	35.1	18.3	22.9	14.5	100.0

[1] Entries are in row % and (column %) for each locomotion * type unit, e.g. for quadrupedalism + pronograde suspend on a single branch/bough: 19.4% of all quadrupedalism + pronograde suspend was on single branch/bough, and 25.9% of all locomotion using a single branch/bough was quadrupedalism + pronograde suspend. Asterisks denote standardised cell residuals (negative values indicate frequency is lower than expected.

*ii) age * support type*

The support type model (subset - age, Table 11, B) showed that there was a direct association between age and support type, although this relationship is weaker than between locomotion and support type. Both adults and adolescents had a high frequency of travel using single trunks as supports. Adolescents showed a strong association with the use of single branches/boughs (SCR = 2.2, Fig. 7) whereas adults showed a negative association with this support type (SCR = -2.0).

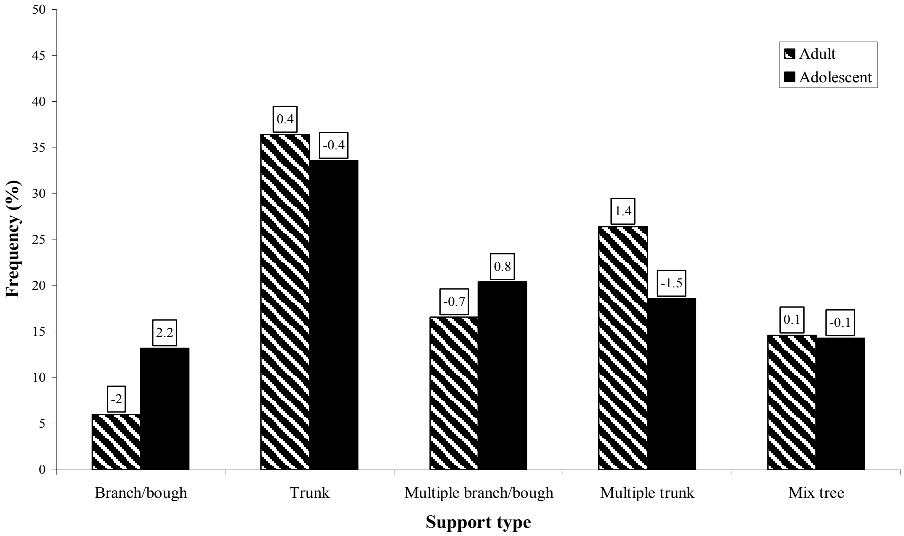


FIGURE 4. *Support type model interaction: age * type. Values in boxes are standardised cell residuals.*

*iii) height * support type*

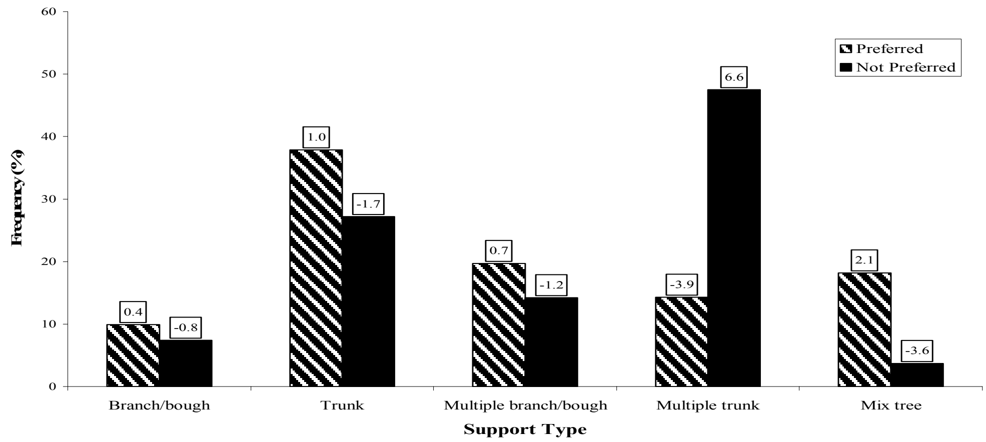


FIGURE 5. *Support type model interaction: height * type. Values in boxes are standardised cell residuals.*

The support type model (subset – height, Table 10, B) revealed that height has a direct association with support type, although this relationship is not as strong as between locomotion and support type. Multiple trunks were the most dominant support type used in the "not preferred" height category whereas in the "preferred" height category, single trunks were the most commonly used support (Fig. 8). Mixed tree supports had a strong association with travel in the "preferred" height category (SCR = 2.1, Fig. 8), whereas travel in the "not preferred" height category showed a negative association with this support type (SCR = -3.6). Travel in the "not preferred height category had a strong association with travel on multiple trunks (SCR = 6.6) whereas travel in the " preferred" height category was negatively associated with this support type (SCR = -3.9).

B. Support Diameter Analysis (locomotion * support diameter * age/height)

Interactions for the support diameter models are: locomotion * support diameter; age * locomotion; support diameter *age; and support diameter * height (Table 10, C). In the support diameter models the association "locomotion * diameter" is stronger in both the age and height sub-sets. In the age subset it is over 10 times more important than the association between age and locomotion and 11 times more important than the association between age and diameter. In the height sub-set the association "locomotion * diameter" has nearly 5 times more influence than the association between height and diameter (Table 10, C, standardised χ^2 values). Each of the interactions for the models are highlighted in turn using contingency tables and figures, with the exception of age-sex * locomotion which was included in Section A (Basic Analysis).

*i) locomotion * support diameter*

The model showed that support diameter has the strongest influence on locomotion (Table 10, C). Looking at the contingency table “bipedalism + orthograde suspension” is the predominant locomotor mode for all diameter categories with the exception of single supports “>4 cm”, where levels are substantially reduced and “climb/descent + oscillation” is 6 times as likely to be exhibited (odds ratios). “Bipedalism + orthograde suspend” is particularly associated with multiple supports of >4 cm diameter (90.5%, SCR = 7.4), and is 90 and 11 times more likely to be exhibited in this support diameter category than “quadrupedalism + pronograde supend” and “climb/descent + oscillation” respectively (odds ratios). “Quadrupedalism + prongrade suspension” is more strongly associated with multiple supports of <4 cm (SCR=6.7) where it is nearly 1.5 times more likely to be exhibited than on single supports of >4 cm and mixed supports and 13 times more likely to be exhibited than on multiple supports >4cm. This mode was not observed on single supports of <4 cm diameter (odds ratios)

TABLE 12. Contingency table for support model association: locomotion * diameter

	Support diameter					
Locomotion	<4 cm	>4 cm	Multiple <4 cm	Multiple >4 cm	Mix (<4,>4 cm)	Total
Quadrupedalism +	0 (0)	28.8 (8.2)	41.1 (37.5)	2.7 (1.5)	27.4 (15.4)	(11.6)
Pronograde suspend	-1.5*	-1.7*	6.7*	-3.5*	1.2*	
Bipedalism + Orthograde	4.8 (73.7)	11.6 (13.3)	12.9 (47.5)	42.2 (90.5)	28.6 (64.6)	(47.5)
suspend	1.7*	-7.9*	0.0*	7.4*	2.9*	
Vertical climb/descent +	2.0 (26.3)	78.8 (78.5)	4.7 (15.0)	4.3 (8.0)	10.2 (20.0)	(40.9)
Oscillation	-1.0*	9.4*	-3.6*	-6.0*	-3.7*	
Total	3.0	41.5	12.9	21.9	20.7	100.0

[1] For explanation of table, see Table 11.

Study subjects show a strong affinity for “climb/descent + oscillation” on single supports >4 cm in diameter than any of the other modes (SCR = 9.4). They are 6 and 10 times as likely to exhibit “climb/descent + oscillation” on this support diameter category than “bipedalism + orthograde suspend” and “quadrupedalism + pronograde suspend”, respectively (odds ratios). When exhibiting “climb/descent + oscillation”, study subjects are 8 times as likely to exhibit “climb/descent + oscillation” on a single support >4 cm in diameter than on mixed supports (<4, >4 cm) and 39, 19 and 15 times as likely to use a single support >4 cm in diameter than a single support <4cm in diameter, multiple supports <4 cm in diameter and multiple supports >4 cm in diameter, respectively (odds ratios).

*ii) age * support diameter*

The support diameter model (subset – age, Table 10, C) showed that there was a direct association between age and support diameter, although this relationship is weaker than the relationship between locomotion and support diameter. Locomotion using single supports (>4 cm diameter) is the most commonly used support diameter for both age classes, followed by multiple supports (>4cm diameter). Single supports (<4cm diameter) was the least commonly used support diameter classification for both adults and adolescents (Fig 9).

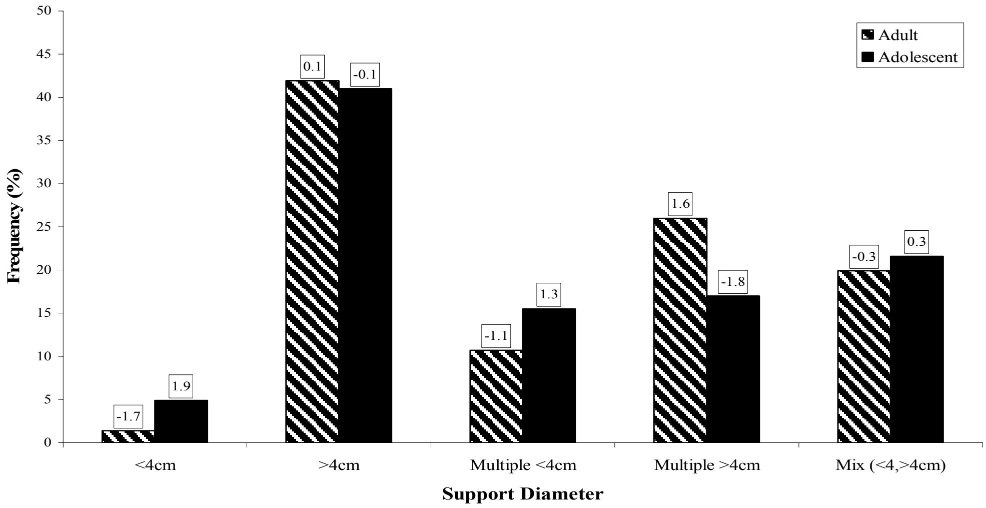


FIGURE 6. *Support diameter model interaction: age * diameter. Values in boxes are standardised cell residuals.*

*iii) height * support diameter*

The support diameter model (subset – height, Table 10, C) showed that there was a direct association between height and support diameter, although this relationship is not as strong as the relationship between locomotion and support diameter. The majority of travel in the "preferred" height category is on single supports (>4 cm diameter) whereas in the "not preferred" height category the majority of travel took place on multiple supports (>4 cm diameter). Travel on multiple supports (>4cm diameter) in the "preferred" height category is less than predicted by the model (SCR = -2.7) whilst at "not preferred" heights it is greater (SCR = 4.6) (Fig. 7).

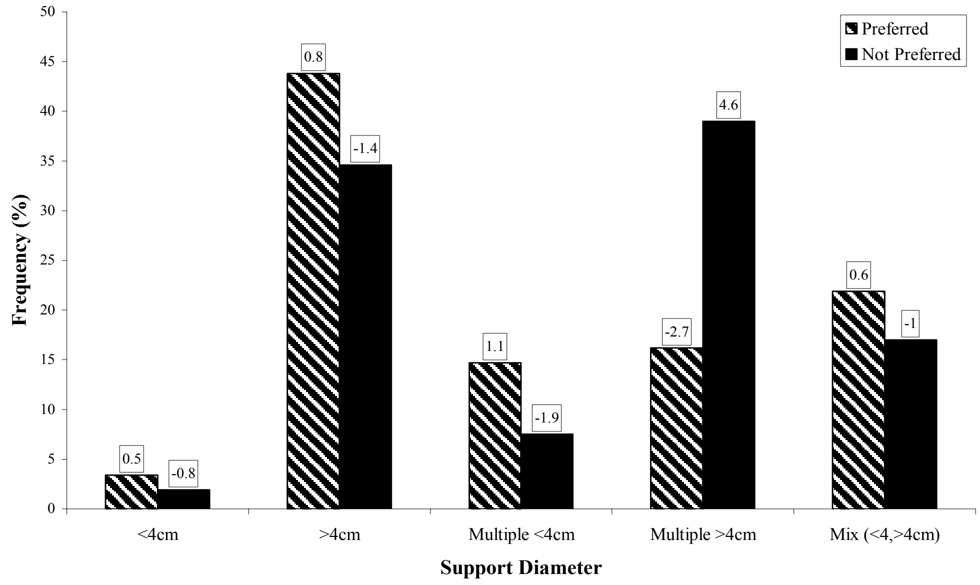


FIGURE 7. *Support diameter model interaction: height * diameter. Values in boxes are standardised cell residuals.*

3.3.4. Summary of the Support Analysis

In the support type sub-set model, support type had the strongest influence on locomotion. "Bipedalism + orthograde suspension" were strongly associated with travel on multiple trunks, accounting for 97% of all observed travel using multiple trunks as supports. "Vertical climb/descent + oscillation" was strongly associated with travel on single trunks accounting for 92% of all travel using single trunks as supports. "Quadrupedalism + pronograde suspension" was strongly associated with both single and multiple branches and boughs. Adolescents used single branches or boughs more than adults whilst adults used multiple trunks as supports more than adolescents. All other support types included in the model were similarly used by both adults and adolescents. Multiple trunks were more commonly utilised in the "not preferred" height category, whereas mixed tree supports and single trunks were more associated with travel in the "preferred" height category.

In the support diameter sub-set model, support diameter had the strongest influence on locomotion. The majority of "quadrupedalism + pronograde suspension" took place on multiple small supports (<4cm), whereas the majority of "bipedalism + orthograde suspension" was on multiple larger supports (>4cm). In contrast, "vertical climb/descent + oscillation" was most often exhibited on single larger supports (>4cm).

Adults and adolescents similarly used single larger supports and mixed supports but adolescents used both single and multiple small supports more than adults whilst adults used multiple larger supports more than adolescents. Multiple larger supports were used more often in the "not preferred" height category whereas multiple small supports were used more often in the "preferred" height category.

4. Discussion

Recording Methods

The main obstacle when recording the behaviour of wild orang-utans is locating them. Aside from the long-call of adult males, orang-utans are not particularly noisy animals, and they tend to be found by hearing them travelling (the crashing of trees), or sometimes eating (some fruits make a distinct "popping" sound when being processed). As much of the study was conducted during the wet season, rain and wind made it very difficult to locate individual orang-utans. In addition, for a large proportion of the study period there were few trees fruiting in the study area which may have caused individuals to move to different parts of the forest in search of food. As the study area is peat swamp forest, during the wet season the forest is flooded. As a result, when searching for orang-utans it was necessary to wade slowly and quietly through the water, in order to locate them. This reduced the amount of forest that could be covered each search day. In contrast, during the dry season it is much easier to walk around whilst still being quite enough to hear orang-utans travelling or eating, thus allowing for greater areas to be covered in comparison to the wet season. These aforementioned factors severely hindered the location of individuals for study and days fruitlessly spent searching for orang-utans soon turned into weeks. For a while Feb, an adolescent female, was the only orang-utan that could be found and as a consequence, much of the data collected is on her. Thus the data collected in this study is skewed towards one individual. This is an unfortunate reality of researching wild apes. However, as highlighted in the methods, the result of the Friedman test showed that the frequencies observed in Feb had a significant correspondence to the other adolescent orang-utans observed in the study and could therefore be grouped together. It is therefore felt that although the data is skewed, it is not of enormous concern. In addition, age-sex (large data set) and age (small data set) only appeared to have a limited influence on the locomotor repertoire of orang-utans when other variables were considered, such as height, number of supports, support type and support diameter.

In recording the locomotor behaviour of each focal animal, instantaneous recording was used. A timer provided an audio cue every 1minute sample interval and if it was not possible to see what the focal animal was doing then nothing was recorded. Whilst this is an ideal way to record orang-utan locomotor behaviour in the wild, it could be a potential source of bias. It is possible that certain locomotor modes could be more conspicuous than others. Thus increasing the frequency of more clearly visible modes of locomotion, whilst under-recording those locomotor modes which are more likely to be obscured from view. However, wherever possible modes together with variables such as height were noted down, even if support use was not clearly visible, and these were included in all but the support type and support diameter analyses.

Locomotion

In order to understand the relationship between orang-utan locomotor behaviour in the context of the habitat in which they live, very detailed observations of positional behaviour are required. As a result of the difficulties experienced in monitoring the behaviour of these arboreal apes in the wild (visibility is severely impeded by the very dense foliage in the study area) the number of observations is overall quite low. However, when data are collected with a large amount of detail, as in this study, it allows for finely delineated categories to be combined, whereas it is not possible to divide initially broad categories into more refined ones (Cant *et al.,* 2001). Consequently, it was possible to conflate categories in order to analyse the data through log-linear modelling. Experimenting with combinations of variables in the log-linear models revealed that the way in which they are categorised influences the nature of the relationships found between them. By experimenting with different variable classifications it was possible to identify main trends with regard to the locomotor behaviour of wild orang-utans in the Sabangau forest. Although the sample size was too small to allow a direct comparison with the results from log-linear modelling of locomotion in Sumatran orang-utans (*P. abelii*) by Thorpe and Crompton (2005), some similarities and differences can still be highlighted.

In the log-linear model from the larger data set (Section 3.2), which included the variables locomotion, height, age-sex and the number of supports, height was found to have the strongest association with locomotion. This contrasts with the model containing the same variables, but with different classifications, in the support analysis (Section 3.3) where height was not found to have a direct association with locomotion but was instead modified by the number of supports. In the larger data set, oscillation and climb/descent were separate categories with oscillation being strongly associated with travel in the “preferred” height category (i.e. ≥10-15m) whereas climb/descent had a positive association with travel in the “not preferred” height category. In the smaller data set (support analysis) it was necessary to further conflate categories (as a result of large numbers of expected values <5) and better fitting models were produced when oscillation and climb/descent were combined, where they showed a positive association with travel using a single support in both height categories.

The variable age-sex was also classified differently in the two analyses (Sections 3.2. and 3.3). In the analysis using the larger data set (Section 3.2) the category age-sex comprised adult males, adult females + sub-adult males, and adolescents. In the support analysis (Section 3.3) this category was differentiated merely by age into adults and adolescents. In the smaller data set, age was found to have the strongest association with locomotion whereas in the larger data set, the influence of age-sex on locomotion was modified by the number of supports used. This highlights the fact that the variable relationships produced in log-linear models differs depending on the way in which the variables in the models are classified.

Classifying the locomotor modes into suspension, compression, mix (LOCO-i) and orthograde, pronograde, oscillation (LOCO-j) both produced significant P values in the log-linear models. However, differentiating between orthograde and pronograde postures generally produced better fitting models than differentiating between suspensory and compressive postures. In fact, when different combinations of variables were being assayed, the model *age-sex-3 * no. of supports-3 * Height5 * Loco-j* (Tables 3,4) produced the best fitting model overall (P = 0.89). This would suggest that the distinction between orthograde and pronograde positional behaviour is more important than the distinction between suspensory and compressive behaviour when factors such as age-sex, height and number of supports are considered.

In the basic analysis (models which included the variables age-sex, locomotion, height and number of supports), log-linear models that combined sub-adult males with adult females generally resulted in better-fitting models than those which combined sub-adult males with adult males. This contrasts with the findings of Thorpe and Crompton (2005), who found better fitting models when sub-adult males were combined with adult males thereby suggesting that adult male locomotor patterns develop prior to the onset of secondary sexual characteristics. However, this disparity should be interpreted with caution as in this study, the overall sample size is very small and sub-adult males and adult females are, in particular, under represented. Nevertheless, it is possible that body weight could play a more significant role in a disturbed forest habitat than found in unlogged dipterocarp forest. Large amounts of tree sway were observed in this study, more than found in other sites (Sugardjito, 1982; Sugardjito and van Hoof, 1986; Cant, 1987; Thorpe and Crompton, 2006). Body weight plays a large role in the oscillation of compliant supports and adult males were observed to oscillate supports more frequently than other age-sex classes, with oscillation comprising a lower frequency in the smaller adolescents. Thus, better fitting models when the larger, heavier adult males are separated from the similar sized sub-adult males and adult females could be a result of the influence of greater body weight facilitating and thereby increasing the frequency of tree-sway in adult male orang-utans. However, the potential for inter-specific differences between orang-utans cannot be discounted. This is the first study to include all age-sex categories on Bornean orang-utans, as Cant's (1987) study of the Bornean sub-species *P. p. morio* was restricted to two females, although levels of tree sway in adult females were higher in this study (22%, Appendix B) than observed in *P.p. morio* (7%). However, these differences whether inter-specific or as a consequence of habitat variation is merely speculation, and more research is necessary in order to investigate the true extent of this difference between studies.

Results from the log-linear models showed that height in the canopy was best described when categories were conflated into "preferred" and "not preferred". The "preferred" height category comprised heights >5; ≤15m, whilst the "not preferred" height category comprised heights ≤5m and >15m with 77% of all observed locomotion taking place in the "preferred" height category. Thorpe and Crompton (2005) found that the majority of travel took place below 20m; and Cant (1987b) found that the majority of travel took place in the understorey and lower main canopy. It would therefore appear that orang-utans prefer to traverse the arboreal environment at relatively low levels in both mixed peat swamp forest as well as mixed dipterocarp forest. However, ideally the relative canopy type for these heights would be required for a better comparison.

The model from the larger data set (Section 3.2.3) revealed that oscillation is strongly associated with travel in the "preferred" height category (>5; ≤15m). Cant (1987b) found the majority of tree sway occurred in the understorey and Thorpe and Crompton (2005) also noted that oscillation was predominantly associated with travel below 20m. This is expected as oscillation is reliant on support compliance and at lower levels there are greater numbers of younger trees which are more flexible than the taller larger trees. In the study site there is a high density of smaller trees ≤15m, which can easily be oscillated given the large body mass of orang-utans in order to facilitate travel between trees. In contrast, vertical climb and descent was more associated with travel in the "not preferred" height category. It accounted for the majority of travel recorded at >15; ≤20m (34.2%, Appendix B, Table ii). Adult males had a greater association with travel in the "not preferred" height category and looking at this in more detail (Appendix B, Table iii) it would appear that adult males tended to travel below 5m more than the other age-sex classes, with travel at this level accounting for 21% of their observed travel bouts, whereas above 15m the frequencies for adult males are comparable with other age-sex classes. However, it must be noted that these observations are based on frequencies only and have not been subjected to statistical testing and therefore must be interpreted with caution.

Of the previous studies of orang-utan locomotor behaviour, only Thorpe and Crompton (2005) and Cant (1987a) recorded support characteristics. This study followed the methods of Thorpe and Crompton (2005) and recorded the diameter and type of all supports used whereas Cant (1987a) only recorded the main weight bearing support. Consequently, the results of this study, with regard to support use during locomotion are mainly compared to the results of Thorpe and Crompton (2005).

Results from the "basic analysis" (models including age-sex, height, locomotion and number of supports) show that the number of supports used for locomotion is comparable to that of Thorpe and Crompton's (2005) study, as better fitting models were found when multiple supports were combined into a single category. This substantiates the suggestion by Thorpe and Crompton (2005) that while orang-utans adopt a different approach to locomotion on single supports than on multiple supports, it does not change whether they are moving on two relatively large supports or handfuls of foliage. However, the number of supports used during travel was not found to have a direct association with locomotion but was instead in a three-way association with age-sex (Section 3.2) and direct association with age (Section 3.3).

Although the data set was too small to allow support type and support diameter to be included in the same model, all subset models (Table 10) show that support type and support diameter had a greater influence on locomotor repertoire than other variables included in the models namely, age and height. The results of the log linear analysis for support type and support diameter thus indicate that both these environmental variables have strong associations with the locomotor repertoire of wild orang-utans. This concurs with the findings of Thorpe and Crompton (2005) thereby supporting their suggestion that orang-utans have evolved particular locomotor modes in order to solve a variety of complex habitat problems. For example, when exhibiting climb/descent or oscillation, orang-utans tended to use single trunks as supports which were >4cm in diameter. Both quadrupedalism and pronograde suspension tended to involve the use of multiple smaller or mixed sized branches or boughs as supports. Bipedalism and orthograde suspend was strongly associated with the use of multiple trunks which were >4cm in diameter. However, as the submode *orthograde clamber* accounted for a large proportion of the observations in this category, the support use for this locomotor mode skewed the results as when traversing the understorey the study subjects tended to clamber using the multiple, closely spaced, trunks of trees as support types.

Theoretical predictions of the relationship between positional behaviour and body mass, which imply that larger animals should suspend more than smaller ones (Cartmill and Milton, 1977), do not appear to be borne out for orthograde and pronograde suspensory locomotion in this study. Whilst the different age-sex classes exhibited similar levels of orthograde suspension (Appendix B, Table i), pronograde suspension contributed less to the overall locomotor repertoire of adult males than was the case in other age-sex classes. With regard to compressive locomotor modes, adolescents tended to exhibit quadrupedalism more frequently than other age-sex classes whereas adult females tended to exhibit higher levels of bipedalism than other age-sex classes. Cant (1987a) found no difference in the frequency of suspensory postures between adult males and adult females and Thorpe and Crompton (2005) also found that adult males did not use suspensory locomotion more than sub-adult males and adult females which are half the body weight or than adolescents which are perhaps three times smaller.

In order to perform the log-linear analysis, it was necessary to conflate locomotor modes which are biomechanically distinct. For example, "quadrupedalism + pronograde suspension" which are both pronograde postures but quadrupedalism is a compressive mode of locomotion whereas pronograde suspension is a suspensory form of locomotion. Whilst individual modes are referred to in the text, it must be noted that these are qualitative and therefore any comments are merely speculative and must therefore be interpreted with caution, as they were not subjected to rigorous statistical testing.

In this study the conflated category of "bipedalism + orthograde suspend" was the most commonly observed form of locomotion where it showed a strong association with multiple supports. "Bipedalism + orthograde suspend" is particularly associated with travel on multiple trunks and on multiple supports (>4 cm) or mixed supports and is similarly observed in both adults and adolescents. Thorpe and Crompton (2005) found that orthograde suspension was associated with the use of multiple lianas (below 20m) and Cant (1987b) found that horizontal clambering was exhibited at high levels on lianas (<4cm) but on larger supports (>4cm) it was more commonly exhibited on tree supports. In this study the use of lianas was too infrequent to allow it to be included as a support type. However, it appears that the association with multiple trunks found in this study implies that vertical supports are an important aspect of orthograde suspensory locomotion. Thorpe *et al.,* (2007) note that locomotion on flexible branches is safer if supported from above as well as from below and the advantage of hand assisted bipedalism is that it maximises safety on small, flexible supports such as those found on peripheral branches which are necessary to negotiate when obtaining food sources or crossing between the crowns of trees. As orthograde suspsension and bipedalism are combined in this analysis it is not possible to confirm whether bipedalism is associated with small branches, however, it is clear that both of these modes are associated with multiple supports.

"Oscillation" is strongly associated with single supports in the "preferred" height categories. In the support analysis the combined category "oscillation + vertical climb/descent) is very strongly associated with single trunks and single supports >4cm. Thorpe and Crompton (2005) found that orang-utans tended to favour multiple tree supports for oscillatory locomotion. However, in this study, orang-utans tended to use single supports, mainly the trunks of smaller trees, for oscillatory locomotion. This is likely to be due to the nature of the habitat in the study area where there is a high density of small trees, thus orang-utans are able to oscillate smaller trees (<10cm diameter) about the trunk. Over 90% of oscillations took place in trees of height <15m. Oscillation was observed at a high frequency in adult males where it accounted for nearly 30% of their locomotor repertoire. It was observed at much lower levels in adolescents where it only accounted for 13% of locomotion and was similarly observed in adult females and sub-adult males where it accounted for about 22%. This disparity between age-sex classes would suggest that the frequency of oscillatory locomotion increases with increasing body weight. Sugardjito and van Hooff (1986) also found levels of oscillation to be higher in adult males than in other age-sex classes. Orang-utans exhibit extreme sexual dimorphism in body size (Rodman and Mitani, 1987), with the average body mass of adult males (78kg) being more than twice that of adult females (36kg) (Delgado and van Schaik, 2000). Therefore, the larger body mass of adult males would be expected to facilitate tree sway as they can achieve the large swaying amplitudes required more easily, or use their weight to cause the tree to bend laterally, moving the passenger with it as described by Cant (1987).

Vertical climb/descent was strongly associated with single supports and, as mentioned above, the combined category "oscillation + vertical climb descent" was strongly associated with single trunks of >4cm in diameter. Vertical climb/descent was slightly more associated with travel in the "not preferred" height category than other locomotor modes. Vertical climb/descent was less commonly observed in adult females than in other age-sex classes (Appendix B, Table i) although the reasons for this are not clear. In addition to transferring between canopy layers, vertical climb/descent is commonly associated with entering and leaving larger fruiting trees, and also Jeletung trees (*Dyera Sp.)* in order to eat the pith of branches (pers. obs.). The diet of the study animals during the observation period comprised 36% leaves, 23% fruit, 17% bark, 15% invertebrates (ants and termites), 2% flowers and 6% other (including epiphytes, branch pith, pandan and fungi) (n=1084 observations). Adult females were observed eating substantially less fruit than other age sex classes during the course of data collection. This disparity between age-sex classes may be due to the differences in the diet of individuals during each nest-to-nest follow. However, past logging activity in the forest has resulted in areas of differing levels of disturbance. There are likely to be differences with the amount of vertical displacement required in different areas of the study site and differences in the levels of disturbance between home ranges may also impact on the locomotor behaviour at the individual level.

Quadrupedalism and torso-pronograde suspensory locomotion were conflated to form one category in order to perform the log-linear analysis and were found to be associated with multiple, small supports. In contrast, Thorpe and Crompton (2005) found a strong association with quadrupedalism and single supports of >10cm in diameter. However, frequencies for quadrupedalism at the submode level are markedly different between the two studies, with *symmetrical gait walking* being less frequently observed in the current study. *Pronograde scrambling* or *irregular gait walking* accounted for nearly 70% of all quadrupedalism observed in this study and, by definition, in *irregular gait walking* the supports are typically small, irregularly placed and variously angled (Hunt *et. al.,* 1996). Whilst the small data set would not permit statistical analysis, looking at supports used during symmetrical gait walking, individuals tended to used single supports >10cm. In a disturbed peat swamp forest, which naturally has a lower canopy and smaller trees, and where many of the larger trees have been logged, the availability of sufficiently large branches is likely to be lower than in a pristine dipterocarp forest. It is therefore suggested that the reduced levels of symmetrical gait walking found in this study could potentially be a consequence of the reduced availability of suitable supports. However, as no data is available on support availability it is not possible to say for certain whether there is a correlation between support availability and locomotion and therefore these comments are purely speculative.

Although some of the more infrequently observed modes were not able to be included in the log-linear analysis as they resulted in high levels of sampling zeros, they are listed in Appendix A. From this we can see that although orang-utans are generally regarded as slow, cautious climbers, they are capable of fast and acrobatic locomotion. 'Leap', 'drop' and 'rump-first cascade descents' involve increased speeds at the expense of safety (Thorpe and Crompton, 2006). Whilst these modes were only rarely observed, all incidences of 'leap' and all observations of 'drop' with the exception of one, in an adult female, were observed in immature individuals and all observations of 'rump-first cascade descent' were of one sub-adult male. Thorpe and Crompton (2006) noted that at Ketambe, many of the more risky locomotor strategies were exhibited by individuals fleeing an aggressive situation, or by adolescents. 'Lunging bridge' was only observed being exhibited by a mother and her independent daughter and 'descending bridge' was only observed once, by an adolescent. Thorpe and Crompton (2006) suggested that orang-utans could become more cautious in their locomotion as they age and/or increase body mass. However, they acknowledge that as these fast and risky locomotor modes are only rarely observed it would be extremely difficult to obtain enough field observations to quantify this. It must be noted, that although these observations were not recorded, adult-males were observed to exhibit powerful, acrobatic and potentially risky modes of locomotion on a number of occasions, particularly when trying to push over tree snags (branchless dead trees) in order to obtain termites held within, or prior to the vocalisation of long-calls (pers. obs.).

Behaviour

Although data were collected on locomotion during both travel and feeding, the latter only contributed <5% of all observed bouts. This is mainly due to orang-utans being reliant on “fall-back” foods such as leaves, bark and invertebrates during the study period. Feeding on leaves and bark often took place in small trees where focal animals tended to remain in a posture during feeding. Although focal animals moved in order to change position while feeding, this rarely took place on the time cues. For example, when eating bark an orang-utan would use a variety of postures to strip the bark from the tree but then sit and eat it, which would be the most time consuming part of the process (Thorpe and Crompton, 2006; pers. obs.), and when eating invertebrates such as termites from a rotten log, they would frequently remain sitting on the ground, or alternatively carry the log up a tree where they would sit on a branch or bough and suck out the termites, which could take a long time (pers. obs.). As a result, insufficient data was collected on locomotion during feeding to allow it to be incorporated in the log-linear analysis, or be meaningful in the comparison with previous studies.

Comparison with Previous Field Studies

Table 13 shows frequencies for the most commonly occurring locomotor modes observed during travel in comparison to the previous studies of Thorpe and Crompton (2006); Cant (1987a) and Sugardjito and van Hooff (1986). Table 13 contains figures extracted from Thorpe and Crompton (2006) with the addition of the results of the current study. Table 14 provides a summary of the sample size and site description of this and previous studies. Both this study and Thorpe and Crompton (2005, 2006) used instantaneous samples whilst the studies by Cant (1987a) and Sugardjito and van Hooff (1986) used bout sampling, the former weighted bout by distance, while the latter by time. However, where sample sizes are sufficiently large, locomotor bout sampling with distance should provide results comparable with instantaneous sampling (Doran, 1992, Thorpe and Crompton, in press). There were also differences in methodology with regard to locomotor classifications between the different studies. Only the current study and studies by Thorpe and Crompton (2005, 2006, in press) followed the standardised descriptions of locomotor behaviour by Hunt *et al.,* 1996. Therefore, some of the differences between studies could be attributable to differences in classification.

Frequencies for the most commonly occurring locomotor modes observed during travel in comparison to the previous studies of Thorpe and Crompton (2006), Cant (1987b), and Sugardjito and van Hooff (1986) are presented in Table 13. As already highlighted, data from the current study for locomotion during feeding were not sufficiently large to be included and therefore only frequencies for travel are presented.

As found in previous studies (Thorpe and Crompton, 2005, Cant, 1987b), torso-orthograde suspension dominates orang-utan locomotion. Frequencies of sway are much higher in this study than were found in previous studies (Table 13). Torso-pronograde suspensory locomotion was observed at a substantially lower frequency in *P. p. wurmbii* than in *P. abelii* but at similar levels to those observed in *P. p. morio*. However, quadrupedalism occurred at substantially lower levels in *P. p. wurmbii* than was observed in both *P. abelii* and *P. p. morio*. Brachiation and forelimb swing also occurred at much lower levels than was observed in all of the other studies. Mentoko and Ketambe are both unlogged, mixed dipterocarp forests whereas the Sabangau is a logged mixed peat swamp forest (Table 14). Therefore, it is likely that support availability will differ considerably between sites.

Only this study and the study by Thorpe and Crompton (2005, 2006) on *P. abelii* were subsequent to the standardised descriptions of primate positional behaviour (Hunt *et al.,* 1996). Consequently, there are differences in the classifications of locomotor behaviour between studies. Sugardjito and van Hooff (1986) only differentiated between five different locomotor modes and grouped a number of different modes together under the category “quadrumanous suspend” in their study of *P. abelii*. Cant (1987b) in his study of *P. morio* advanced the classification of orang-utan locomotion by distinguishing between modes according to the orientation of the body, the relationship with the substrate (above or below) and the direction of movement. Nevertheless, it is still possible to compare the findings of each of the different studies with some interesting results.

TABLE 13. Percentages of commonly observed locomotor modes during travel from the current study in comparison to previous studies (as in Thorpe and Crompton, 2006)[1,2]

Mode	Submode	Borneo		Sumatra	
		Present study	***Cant (1987b)***	***Thorpe and Crompton (2005)***	***Sugardjito and van Hoof (1986)***
		Travel	Travel	Travel	Travel
Quadrupedal and tripedal walk		**8**	**12**	**15**	**12**
	Walk	*2*	*12*	*7*	*?*
	Pronograde scramble	*6*	*?*	*8*	*?*
Torso-orthograde suspensory locomotion		**47**	**62**	**39**	**?**
	brachiation and forelimb swing	*4*	*11*	*16*	*19*
	orthograde clamber and transfer	*43*	*51*	*23*	
Torso-pronograde suspensory locomotion		**1**	**1**	**3**	
Forelimb/hindlimb swing		**1**	**?**	**0**	
Bipedal Walk		**5**	**#**	**7**	**46**
	Bipedal walk	*1*	*0*	*2*	
	Assisted bipedal walk	*4*	*#*	*5*	
Bridge		**4**	**?**	**4**	
Vertical climb		**9**	**12**	**14**	**11**
Vertical descent		**3**	**6**	**8**	
Drop		**1**	**?**	**2**	**?**
Sway		**20**	**7**	**7**	**12**
Ride		**1**	**?**	**1**	**?**

[1] Results for previous studies taken from Thorpe and Crompton (2006).
[2] Overall frequencies are shown for locomotor modes (**in bold**) and frequencies for submodes (*in italics*) to allow comparison where classification system of previous authors differs from the present study.
[3] ?, not clear if this mode was observed, or not, or if it was observed but combined with another mode (Thorpe and Crompton, 2006).
[4] #, Cant (1987b, p. 74) notes that assisted bipedalism was observed but was in all probability recorded as orthograde clamber, thus frequencies are not provided (Thorpe and Crompton, 2006).
[5] Quadrumanous suspend of Sugardjito and van Hooff's (1986) appears to include all these modes/submodes (Thorpe and Crompton, 2006).

TABLE 14. Site details and sample size of present and previous studies.

Study	*Site*	*Species*	*Sample Size*	*Habitat Type*[1]	*Disturbance*[1]
Present	Sabangau	*P. p. wurmbii*	1,075 (instantaneous)	Peat Swamp	Logged
Thorpe and Crompton (2005)	Ketambe	*P. abelii*	2,811 (instantaneous)	Mixed Dipterocarp	Unlogged
Cant (1987b)	Mentoko	*P. p. morio*	4,340m (distance)	Mixed Dipterocarp	Unlogged
Sugardjito and van Hoof (1986)	Ketambe	*P. abelii*	12,105 bouts (time)	Mixed Dipterocarp	Unlogged

[1] *Morrogh-Bernard* et. al.,(in press).

As found in previous studies (Thorpe and Crompton, 2005, Cant, 1987b), torso-orthograde suspensory locomotion dominates orang-utan locomotion. The results of this study compared to that of Thorpe and Crompton (2006) and Cant (1987b), suggest that *P. abelii, P.p. morio* and *P. p. wurmbii* have the capability to perform the same overall range of locomotor behaviours. However, the frequency of these behaviours appears to differ between species. Overall, *P. p. wurmbii* exhibited higher levels of sway than both *P.p. morio* and *P. abelii*. Torso-orthograde suspension was higher in *P.p. wurmbii* and *P.p. morio* than in *P. abelii*, and lower levels of pronograde compression were observed in *P.p. wurmbii* than in both *P. abelii* and *P.p. morio*.

Thorpe and Crompton (in press), in their comparison of *P. abelii* with *P. p. morio* (Cant, 1987b), found that *P. p. morio* exhibited lower levels of orthograde compression (bipedalism). However, there were substantial differences in methodology in Cant's (1987b) study, where only hand-assisted forms of bipedalism were observed, which were classified together with orthograde clamber. In this study, the frequency of orthograde compression in *P.p. wurmbii* was similar to that observed in Thorpe and Crompton's (2006) study of *P. abelii*, although in *P. p. wurmbii* this was predominantly hand-assisted. Nonetheless, hands-free bipedalism was observed thereby demonstrating that Bornean orang-utans do employ unassisted bipedality.

Frequencies of sway are much higher in this study than were found in previous studies (Thorpe and Crompton, 2005; Cant 1987b; Sugardjito and van Hoof, 1986). This may be in response to past disturbance in the study area, resulting in a high density of smaller trees (<10cm diameter). Gaps are also prevalent in this site due to past logging and associated skids and canals, as well as naturally occurring gaps as a consequence of tree falls, the incidence of which may be exacerbated by the drainage of peat by logging canals. It would therefore, not be unexpected to observe a high frequency of oscillatory locomotion as this mode facilitates gap grossing and has also been shown to lower the energetic cost of locomotion (Thorpe and Crompton, 2007). Another theory is that the trees could naturally be more compliant in the Sabangau due to the less solid peat base thus facilitating tree sway at this site. Tree sway in the study area tended to involve the orang-utan using its body weight to bend the tree laterally, moving the passenger with it as described by Cant (1987b) as well as the to-and-fro oscillations described by Sugardjito and van Hooff (1986). In this study, orang-utans were also observed to oscillate vertical lianas in a manner akin to that described by Thorpe and Crompton (2006), although this was rarely observed.

Orthograde suspension includes the submodes orthograde clamber and brachiation (Appendix A). Brachiation was observed at much lower levels in this study than found in previous studies (Sugardjito, 1982; Sugardjito and van Hoof, 1986; Cant, 1987; Thorpe and Crompton, 2006). Cant (1987b) found that brachiation accounted for 11% of observed locomotion during travel. This was higher in Ketambe accounting for 16% and 19% (Thorpe and Crompton, 2006; Sugardjito and van Hooff, 1986, respectively). In this study, brachiation accounted for a mere 4% of all observed locomotion. Cant (1987b) found that brachiation mostly occurred in the lower main canopy on substrates ≥4, <10cm in diameter, whereas Thorpe and Crompton (in press) found that substrates <4cm in diameter were commonly used for brachiation, although the range of support sizes was comparable between species. Looking at the support diameter used during brachiation and forelimb swing in this study, the findings are comparable with previous studies with branches or boughs, ≥4, <10cm in diameter being the most commonly utilised supports. Cant (1987b) noted that much brachiation must automatically become clamber because of the orang-utans capacity to reach substrates below with the hindlimbs due to their large body size. It is possible that the low levels of brachiation observed in this study could be a result of this, with the forest structure causing much brachiation to become orthograde clamber as support availability enables the hindlimbs to assist rather than the orang-utan relying on the forelimbs to bear most of the body weight. Given that orang-utans in this and previous studies tended to use smaller supports (<10 cm diameter) for brachiation, it is unlikely that a lack of substrate availability is responsible for the low levels of brachiation observed in this study. Therefore, there must be other factors causing orang-utans in this study to prefer other modes of locomotion. Looking at the data for brachiation it appears to be more commonly observed in adolescents and least commonly observed in adult males. This would support the suggestion by Cant (1987b) that in the larger orang-utans brachiation automatically becomes orthograde clamber, whereas in smaller orang-utans it remains as brachiation where hindlimbs are not able to reach suitable supports below.

Given that the study site has been subjected to both legal and illegal logging activity resulting in an uneven canopy, there is potentially a greater expectation for vertical displacement than observed at other sites. However, this was not the case, with vertical climb/descent occurring at lower frequency than found in *P. abelii* and *P.p. morio.* Climbing is relatively more energetically costly for larger animals (Taylor *et al.,* 1972; Cartmill 1972, 1974; Cartmill and Milton, 1977). Energy expenditure on locomotion is of great importance particularly if energy budgets become negative to the point where reproduction is affected. Female orang-utan reproduction is suppressed during periods of negative energy balance (Knott 1998, 1999) and so any increases in energy expenditure during travel, particularly if combined with a reduction in food-energy availability in the forest (which is likely to be the case in an area suffering from logging disturbance) could have potentially devastating long-term effects on the population.

Torso-pronograde suspensory locomotion was observed at a lower frequency in *P. p. wurmbii* than in *P. abelii* (Thorpe and Crompton, 2006) but at similar levels to those observed in *P. p. morio* (Cant, 1987a). This may suggest that Bornean orang-utans exhibit pronograde behaviour at lower levels than their Sumatran counterparts. However, quadrupedalism occurred at substantially lower levels in *P. p. wurmbii* than was observed in both *P. abelii* and *P. p. morio.* These differences between orthograde and pronograde behaviour between studies may possibly reflect differences in support availability between sites. As mentioned, the study site used in the present study was subjected to both concession and illegal logging in the past, resulting in many of the large trees being lost. Thus, support availability is likely to differ considerably to both Mentoko (Cant, 1987a) and Ketambe (Thorpe and Crompton, 2005), which are both unlogged, mixed dipterocarp forests (Morrogh-Bernard *et. al.,* in press). However, none of the previous studies on locomotion and positional behaviour collected detailed data on support availability and therefore this suggestion cannot presently be tested.

Both Thorpe and Crompton (2005) and Cant (1987a) had a much higher frequency of liana use than was found in the current study. It is thought that past logging activity in the study site may have reduced the number of large lianas available. However, Cant *et. al.,* (1990) showed that single lianas as thin as 1.4cm in diameter can support 132 kg, which is 1.25 times adult male body mass (Thorpe and Crompton, 2005). Cant (1987a) described curtains of lianas at Mentoko, whereas Thorpe and Crompton (in press) noted that the distribution of lianas at Ketambe was highly varied. In the Sabangau, orang-utans were observed exhibiting various modes on lianas such as sway and vertical climb. However, the incidence of these observations was too low for it to be included as a support type in the log-linear analysis as it caused a high number of sampling zeros. Nevertheless, these observations do show that *P. p. wurmbii* do make use of lianas as a support type, albeit more rarely than at other sites. It is possible that the availability of lianas as exploitable support types may be reduced in this area as a result of past disturbance. However, as there is no data on the availability of supports it is impossible to say with any certainty whether the use of lianas as supports corresponds to the availability within the forest.

Thorpe and Crompton (2005) found that contrary to classic predictions, age-sex category had only a limited influence on orang-utan support use and locomotion and attributed this to the presence of arboreal pathways followed by individuals of all age-sex categories. In their study, individuals from different age-sex classes were observed to use the same travel routes when moving between distant areas, and when accessing major fig trees, which fruited for a substantial period of time. In this study orang-utans were seldom observed together and therefore it was difficult to assess whether they used the same travel routes. However, the same individuals were observed using the same routes. For example, an adult male which occasionally travelled very near to the research camp appeared to follow exactly the same route every time (pers. obs.). This implies that arboreal pathways are also used in the Sabangau. The presence of arboreal pathways indicate that many routes are planned in advance, based on preferred locomotor-support combinations (Thorpe and Crompton, *in press*). However, whether these locomotor-support preferences are selected in order to reduce energy expenditure (minimum horizontal and vertical displacement) or to provide the shortest, fastest, or safest route is less apparent. Vertical climb/descent, probably the most energetically costly mode, was observed at slightly lower levels lower in the current study whilst tree-sway, an energetically efficient mode of locomotion, was observed at much higher frequency in the current study, which could suggest that energy efficiency plays a strong role in the choice of locomotor-support preference when travel routes are planned in the Sabangau. However, it is possible that orang-utans are tree-swaying at higher levels in a habitat where this mode of locomotion is more easily exploitable (i.e. a high frequency of compliant supports), or that the presence of gaps in the canopy necessitates high frequencies of this mode. Further comparative research on the availability of compliant supports is necessary in order to investigate this suggestion.

The high incidence of large gaps that orang-utans encounter in the Sabangau, due to logging skids, canals and bat-hunting, means that individuals must factor these in when traversing the forest as they must either circumvent the gaps increasing path length or come down to the ground, both of which increase energy expenditure. When large gaps or clearings were encountered, orang-utans sometimes came to the ground in order to feed on termites in the rotten logs, or appeared to follow previously traversed routes as their locomotor behaviour did not seem to be impeded by the presence of such gaps, more that they knew where the gaps where and merely skirted round them. It was generally not the case of encountering a gap, trying to cross it but not being able to, and then having to circumnavigate said gap. However, on one occasion, an adult female oscillated a tree in order to cross a gap. Her immature but independent daughter tried a number of times to oscillate the same tree to no avail and she then climbed higher in the tree but was still unable to bridge the gap. She then took an alternative route and tried to oscillate another tree and was again unsuccessful. She eventually circumnavigated the gap and joined her mother (pers. obs.).

5. Conclusions

This analysis shows that, in concurrence with the study of Thorpe and Crompton (2005), of all the variables included in the analysis, both support type and support diameter were revealed to have the strongest associations with locomotor repertoire. This further demonstrates that orang-utans have evolved specific modes of locomotion in order to solve problems associated with traversing a complex arboreal environment. However, whether support-locomotor combinations are selected to provide the shortest, fastest, or safest route or whether they are selected to reduce path length or minimise vertical displacement is not clear.

Height in the canopy had a direct association with the observed locomotor repertoire of orang-utans when adult males and oscillation were considered separately. However, when combined with other categories height in the canopy did not directly influence the observed locomotor repertoire of orang-utans, but was instead modified by the number of supports, support type and support diameter. Whilst age-sex class did have an influence on locomotor repertoire this was more limited than the influence of support variables.

Comparison with previous studies revealed that although there was a lack of gross differences in locomotor behaviour between *P. p. wurmbii*, *P. p. morio* and *P. abelii*, there are differences in the frequency of observed modes. The most interesting difference between studies is the high levels of tree-sway observed in the Sabangau. However, the reasons for these differences are not clear. Are the largest differences at the species- or habitat- level? It would seem that many of the differences could be attributed to differences in habitat type between study sites, although these are merely hypothesised, as no comparative data are available for forest structure and support availability. Further research, which controls for habitat type, is therefore required in order to ascertain the extent of differences between orang-utan locomotor behaviour.

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APPENDIX A. Locomotor mode definitions

Locomotor mode, *submode*, description	**% bouts**
Quadrupedal Walk	
Symmetrical gait walk (L1a[1])	3.35
Irregular gait walk (scramble) (also called pronograde scramble) (L1c1)	5.7
Tripedal Walk	0
Tripedal walk (L2)	
Bipedal Walk	
Extended Bipedal Walk (L3a)	0
Flexed Bipedal Walk (L3b)	0.19
Hand-assisted Extended Bipedal Walk: bipedal walk in which hindlimbs bear more than 50% of body mass in full extension, but one or both forelimbs are used to assist, either in suspension or compression and bear more than their own weight.[2]	1.77
Hand-assisted Flexed Bipedal Walk: as for "hand-assisted extended bipedal walk", but with hindlimbs relatively more bent.[2]	0.84
Bipedal Scramble: body is orthograde and majority of body mass is borne by hindlimbs, but hindlimb kinematics are not characteristic of smooth bipedal gait. Typically, supports are small, irregularly placed, and variously angled. Hindlimbs may utilize both extension and flexion during gait cycle.[2]	0
Hand-assisted bipedal scramble: as above, but one or both forelimbs also bear more than their own weight, either in compression or suspension. Similar to "orthograde clamber", but majority of body mass is carried by hindlimbs	2.13
Vertical Climb	
Flexed-elbow Vertical Climb (L8a)	5.58
Ladder Climb (L8b)	0.84
Vertical Scramble (L8c)	0.56
Extended-elbow vertical climbing (L8d)	2.42
Bimanual pull-up (L8f)	0
Vertical Descent	
Rump-first symmetrical descent (L8g1)	2.14
Rump-first scramble descent (L8g2)	0.56
Rump-first cascade descent: equivalent to "head-first cascade descent", but rump-first.	0.1
Rump-first extended elbow descent: kinematically reverse of "vertical climb-extended elbow", with limbs moving in sequence, normally hand over hand, foot over foot.[2]	0.1
Head-first descent (scramble) (L8h2)	0.46
Head-first descent (cascade) (L8h3)	0

Torso-orthograde suspensory locomotion	
Brachiate (L9a)	2.42
Forelimb swing (L9d)	0.93
Flexed-elbow forelimb swing (L9e)	0.28
Orthograde transfer (L9f)	4.55
Orthograde clamber (L9g)	38.51
Arrested drop (L9h)	0.1
Torso-pronograde suspensory locomotion	
Inverted quadrupedal walk (L10a)	0.1
Inverted tripedal walk: as above, but with only three limbs.[2]	0.1
Inverted quadrupedal run (L10b)	0
Inverted pronograde scramble (L10c)	0.93
Hindlimb Swing: body is held upside-down, and animal swings on one or both hindlimbs. Often used as intermediary form of locomotion to reorient the body between two longer bouts of different locomotor modes.[2]	0.19
Forelimb-hindlimb swing: suspensory locomotion which may or may not follow regular limb sequence, utilising both forelimbs and hindlimbs in both orthograde and pronograde positions.[2]	
Cartwheel swing: sequence of suspensory locomotion on horizontal or negatively inclined support which resembles sequence of limb usage seen in human cartwheels.[2]	0
Ipsilateral swing: swinging from ipsilateral fore- and hindlimb. Exhibited as single swing to join two other modes of locomotion.[2]	0.65
Bridge	
Cautious pronograde bridge (L11a)	3.07
Inverted pronograde bridge: as above, except with body in inverted pronograde suspension.[2]	0.1
Lunging bridge (L11b)	0.46
Supinograde bridge (L11d)	0
Descending bridge (L11e)	0.1
Leap	
Pronograde leap (L12a)	0.19
Drop	
Unimanual suspensory drop (L13c): as described in Hunt *et al.,*(1996), but orang-utans often tended to use one limb to maintain contact with support throughout drop, although support does not bear any weight during fall.[2]	0.65
Bimanual suspensory drop (L13d)	0
Sway: based on tree sway (L16) of Hunt *et al.*'s (1996), but expanded to include any locomotion which relies on oscillation of supports to progress forward. Also includes locomotion where orang-utan swings on vertical branch/liana.[2]	19.8
Ride (L17): orang-utans use "ride" to move between different levels of the canopy as well as from tree to ground (Hunt *et al.,* 1996, Thorpe and Crompton, 2005, 2006)	0.46

[1] Where locomotor descriptions follow exact definition of Hunt *et al.,* (1996), the code for the definition in their paper is specified (e.g., L1a)

[2] Where locomotor descriptions follow those of Thorpe and Crompton (2006)

APPENDIX B: Locomotor Mode Tables

Table (i) Locomotor mode and age-sex class (n=1064)

	Age-sex class				
Locomotor Mode	Adult female	Adult male	Sub-adult male	Adolescent	Total
Quadrupedalism	14.3 (6.8)	22.0 (6.9)	9.9 (7.4)	53.8 (10.6)	8.6
Bipedalism	30.2 (8.4)	11.3 (2.1)	7.5 (3.3)	50.9 (5.8)	5.0
Orthograde suspension	19.3 (51.8)	27.7 (49.1)	10.5 (44.6)	42.4 (46.9)	48.1
Pronograde suspension	19.2 (5.2)	3.8 (0.7)	19.2 (8.3)	57.7 (6.5)	4.9
Vertical climb/descent	8.0 (5.8)	23.9 (11.4)	13.0 (14.9)	55.1 (16.4)	13.0
Oscillation	19.3 (22.0)	39.4 (29.8)	11.9 (21.5)	29.4 (13.8)	20.5
Total	18	27.2	11.4	43.5	100.0

[1] Entries are in row % and (column %) for each locomotion * type unit, e.g. for quadrupedalism in adult females: 14.3% of all observed quadrupedalism was by adult females, and 6.8% of all locomotion by an adult female was quadrupedalism.

[2] Discrepencies between overall locomotor percentages in the above table and those displayed in table 9 are due to the exclusion of rarely observed locomotor modes in the above table.

Table (ii) Locomotor mode and height in the canopy (n=1064)

	Height					
Locomotor Mode	<5m	≥5;<10m	≥10<15m	≥15,<20m	≥20m	Total
Quadrupedalism	4.9 (2.7)	25.9 (5.4)	56.8 (10.6)	8.6 (9.6)	3.7 (42.9)	8.6
Bipedalism	0.0 (0.0)	21.3 (2.6)	55.3 (6.0)	23.4 (15.1)	0.0 (0.0)	5.0
Orthograde suspension	21.5 (75.3)	41.2 (54.5)	34.0 (40.1)	3.1 (21.9)	0.2 (14.3)	48.1
Pronograde suspension	3.8 (1.4)	30.8 (4.1)	51.9 (6.2)	9.6 (6.8)	3.8 (28.6)	4.9
Vertical climb/descent	10.9 (10.3)	27.0 (9.6)	43.1 (13.6)	18.2 (34.2)	0.7 (14.3)	13.0
Oscillation	6.9 (10.3)	42.2 (23.8)	46.8 (23.5)	4.1 (12.3)	0.0 (0.0)	20.5
Total	13.9	37.0	41.5	7.0	0.7	100.0

[1] For explanation of table, see Table A.

Table (iii) Age-sex and height in the canopy (n= 1064)

	Age-sex class				
Height	Adult female	Adult male	Sub-adult male	Adolescent	Total
<5m	13.7 (10.5)	39.7 (20.8)	8.2 (9.9)	38.4 (12.0)	13.9
≥5;<10m	13.7 (27.9)	27.3 (38.0)	10.1 (32.2)	49.0 (40.6)	37.0
≥10<15m	24.0 (55.8)	20.6 (32.6)	13.4 (48.8)	39.5 (42.0)	41.5
≥15,<20m	14.5 (5.8)	27.6 (7.5)	11.8 (7.4)	46.1 (7.5)	7.0
≥20m	0.0 (0.0)	42.9 (1.1)	28.6 (1.7)	28.6 (0.4)	0.7
Total	18.0	27.2	11.4	43.5	100

[1] For explanation of table, see Table A.