Locomotor Development and Gap Crossing Behaviour in Bornean Orangutans (*Pongo pygmaeus*)

By

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ABSTRACT

Orangutans are the largest predominantly arboreal primate and consequently have a diverse repertoire of positional behaviour. Problems associated with travel on thin flexible supports worsen as body size increases; therefore locomotion should vary with body size. The aim of this thesis was to explore how orangutans solve problems related to life in wild and captive environments and how this changes with growth and development. A cross-sectional sample of wild orangutans (*Pongo pygmaeus wurmbii*) was studied at Tuanan Field Station in Central Borneo with subjects ranging from infant to adult. Results from wild orangutans showed that locomotion varied according to body size with larger orangutans using larger supports and gaining stability by bearing their weight in suspension. In contrast captivity promoted higher frequencies of terrestrial behaviours and these increased with age. Wild orangutans crossed large gaps in the canopy by oscillating compliant trunks. However I found that these skills are not fully mastered until 6 years old. Mothers were found to provide assistance during gap crossing according to the needs of their offspring. This thesis has shown that complex locomotor behaviour develops slowly during ontogeny and this may have implications for orangutan life history in different types of habitat.

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1. GENERAL INTRODUCTION

Orangutans (*Pongo pygmaeus* and *Pongo abelii*) are the only Asian great apes and they live on the islands of Borneo and Sumatra, respectively. Unlike the African apes, orangutans live a predominantly arboreal lifestyle, travelling and feeding within the forest canopy. Orangutans are primarily frugivorous (MacKinnon 1974; Rijksen 1978) but they also feed on leaves, flowers, bark, insects and occasionally small mammals (Utami and van Hooff 1997). The forests of Southeast Asia have low productivity compared to those in Africa (van Schaik and Pfannes 2005) and this is suggested to have restricted orangutans from forming permanent social aggregations (Wrangham 1979; van Schaik and van Hooff 1983; Galdikas 1988; van Schaik 1999). Unlike the other great apes - chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and gorillas (*Gorilla gorilla*) - orangutans do not live in large family groups and the only permanent association is that of the mother with her single dependent infant. In orangutans the exclusive association between mother and offspring lasts for an average of 8 years until the bond is broken by the birth of a new infant. This represents the longest inter-birth interval of any mammal species (Galdikas and Wood 1990; Wich et al. 2004; van Noordwijk and van Schaik 2005). This is also considerably longer than found in gorillas and chimpanzees, which have average birth intervals of 4 and 6 years, respectively (Watts 1991; Boesch and Boesch-Achermann 2000). Reasons for the extended inter-birth interval in orangutans remain unclear.

1.1 Taxonomy

Sumatran and Bornean orangutans were only recently classified as separate species after marked genetic divergence was found in their DNA (Groves 2001; Warren et al. 2001; Zhang et al. 2001). The Sumatran species is classified as critically endangered (IUCN 2011); they are restricted to Northern Sumatra and the majority of the population, estimated at just 7,300 (Singleton et al. 2004) is located within the

Gunung Leuser National Park (Fox et al. 2004). Bornean orangutans are also endangered from widespread forest clearance and poaching (Nellemann et al. 2007). Fragmented populations of Bornean orangutans are distributed across Indonesian Borneo (Kalimantan) and the Malaysian states of Sabah and Sarawak with the population estimated to be between 40,000 and 50,000 (Meijaard and Wich 2007). The Bornean orangutan has been divided into three distinct sub-species: *P. p. pygmaeus* found in the Northwest (Sarawak and Northwest Kalimantan); *P. p. wurmbii* found in Central and Southwest Kalimantan; and *P. p. morio* found in the Northeast (Sabah and East Kalamantan) (Groves 1999) (see Figure 1.1).

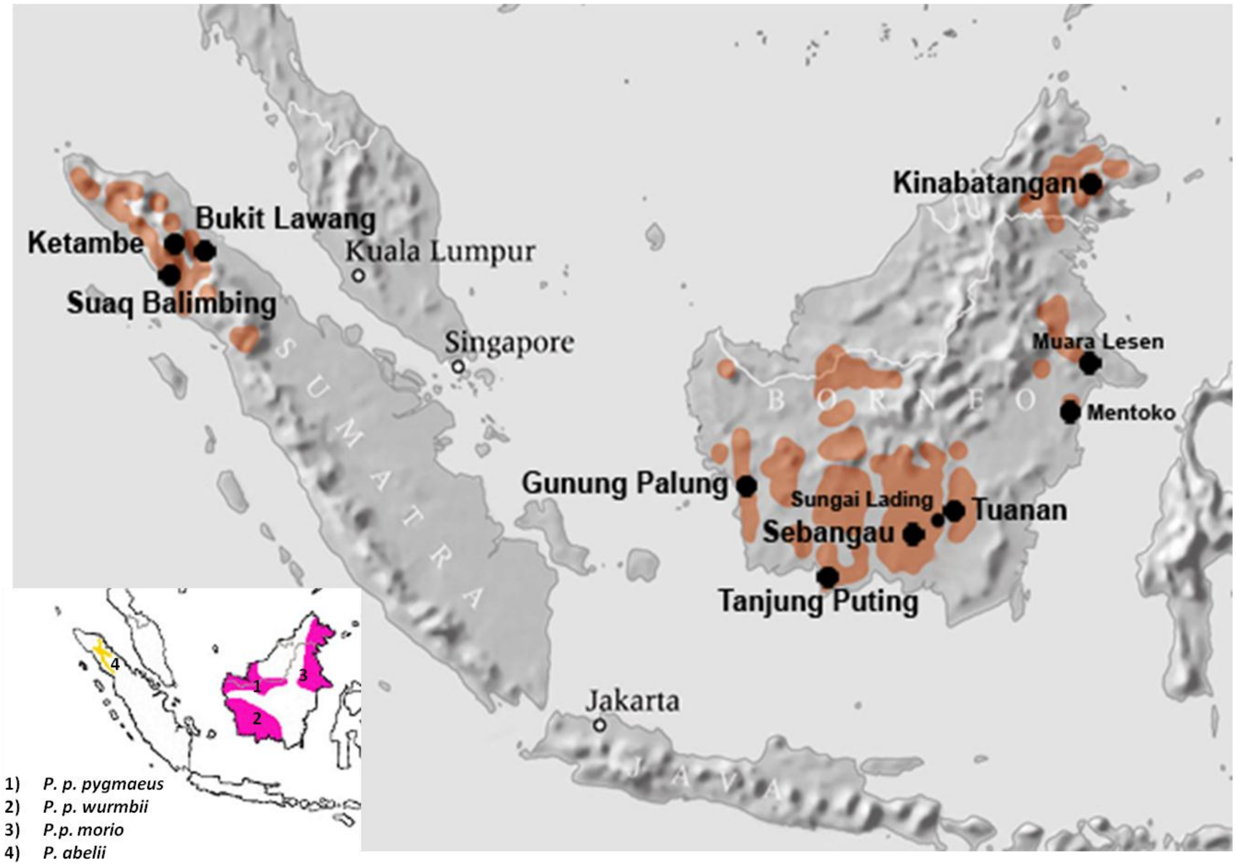

Figure 1.1 The distribution of orangutans in Borneo and Sumatra. Orangutan field sites are shown in bold and the smaller map indicates the distribution of the separate species and sub-species (taken from Orangutan Network 2010)

1.2 Species differences

As well as being genetically distinct populations there are also many morphological and behavioural differences between these taxa. Sumatran orangutans have longer, denser body hair that is lighter in colour than that of Bornean orangutans (Delgado and van Schaik 2000). The adult males have cheek flanges which point forwards in Borneo and large throat sacs for emitting long calls whereas the flanges of the Sumatran males are flat and they have smaller throat sacs (Delgado and van Schaik 2000). To date, investigations of available body mass data have not found any overall size differences between the genetically distinct populations (Markham and Groves 1990; Smith and Jungers 1997). However, there is very limited data available for wild orangutans and it may not be appropriate to compare the weights of captive orangutans because they are known to have different growth trajectories, with captive adults weighing on average 45% more than their wild counterparts (Fooden and Izor 1983). Craniofacial morphology in orangutans has been found to vary across the different populations of orangutans (Taylor 2006; Taylor and van Schaik 2007). Bornean orangutans were found to have smaller brains (Taylor and van Schaik 2007), and this correlated with increased load resistance in their mandible (Taylor 2006). Evidence suggests that these traits vary with forest productivity with orangutans from less productive forests having smaller brains and stronger mandibles (Taylor 2006; Taylor and van Schaik 2007). Sumatran forests generally have higher productivity owing to their young, nutrient-rich volcanic soils (Marshall et al. 2009a). In contrast the forests in Borneo grow on older, more weathered soils which are less productive than those in Sumatra (Marshall et al. 2009a). Within Borneo there is a trend in soil productivity running from West to East with the least productive soils found in East Kalimantan and Sabah (Wich et al. 2011). Thus, the craniofacial morphology of orangutans also follows the same pattern with the sub-species *P. p. morio* having the smallest brains and most load-resistant mandibles, *P.p. wurmbii* are intermediate and *P.p. pygmaeus* have the most similar craniofacial morphology to Sumatran orangutans *P. p. abelii* (Taylor 2006; Taylor and van Schaik 2007). Brains are composed of metabolically expensive tissue and when food is scare the costs of having a large brain may outweigh the benefits (Aiello and Wheeler 1995).When fruit is not available, Bornean orangutans rely on fall back foods such as bark (Knott 1998; Marshall et al. 2009b; Harrison et al. 2010), which is less energetically rewarding and can leave them in negative energy balance (Knott 1998). The higher load resistance in the Bornean mandibles has, therefore, been suggested to be an adaptation for eating tough fall back foods like bark, which are stripped from the tree with the teeth (Taylor 2006). Fruit availability also affects gregariousness in orangutans; in Sumatran forest where fruit is available all year (Delgado and Knott 2007), orangutans often congregate in large fruiting trees (van Schaik 1999). Therefore, habitat differences influence morphology and behaviour in orangutans.

1.3 Orangutan field sites

The majority of research on Sumatran and Bornean orangutans comes from a few dedicated long-term field sites (see Figure. 1). In Sumatra, Ketambe is the longest running field site, established in 1971 (Rijksen 1978). Ketambe is surrounded by primary dryland forest (van Schaik and Mirmanto 1985). To the south of Ketambe is Suaq Balimbing, located in primary swamp forest; this site is home to the highest known densities of orangutans (van Schaik 1999). The most famous field station in Borneo is Camp Leakey, which was established by Birute Galdikas in Tanjung Puting Reserve in 1971. The forests of Central Kalimantan are home to the orangutan sub-species *P. p. wurmbii*. These forests are characterised by seasonal peat-swamp forest with Tanjung Puting, Sabangau, Tuanan and Sungai Lading fields sites all located in this area (Marshall et al. 2009a). Both Gunung Palung in West Kalimantan and Kinabatangan in Sabah are situated in areas that contain both swamp and dryland forest. Kinabatangan is the only active Bornean site, where the sub-species *P. p. morio* is studied. Research has also been carried on *P. p.*

morio at Mentoko field site in Kutai National Park, but this site is no longer active. Relatively little is known about *P. p. pygmaeus* as there are no major field sites within the range of this sub-species.

1.4 Compliance in the arboreal habitat

Orangutans are the largest animals to live a predominantly arboreal lifestyle, and as problems associated with travelling on thin flexible (compliant) supports worsen with increased body size (Grand 1972; Cartmill and Milton 1977), dealing with compliant supports is likely to be one of the greatest challenges faced by orangutans. Primate positional strategies for dealing with compliant branches in the arboreal habitat were first examined by Grand (1972). As the thinnest branches are located at the periphery of trees where the majority of fruit is located (Grand 1972), positional strategies for dealing with thin branches are particularly important for feeding and crossing between trees. Whilst most primates are thought to lose energy when travelling on flexible branches (Alexander 1991), due to branch deformation and failing to utilise elastic recoil (Demes et al. 1995), orangutans are known to utilise compliant supports to cross gaps in the canopy and this has been found to be an order of magnitude less costly in terms of energy expenditure than descending to the forest floor and climbing up again (Thorpe et al. 2007a).

1.5 Primate positional behaviour

Primate positional behaviour has received considerable interest because the majority of primates live in the forest canopy and show diverse positional strategies for navigating this complex habitat (Garber 2007). Positional behaviour is made up of posture and locomotion. By definition, posture is a state where the centre of mass of the animal remains broadly static relative to the surroundings although the limbs may move, whereas locomotion is the action of moving from one place to another involving a gross mass displacement (Prost 1965). In general, primates spend the majority of their time in posture (Rose 1974;

McGraw 1998) e.g. eastern black and white colobus monkeys (*Colobus guereza*) spend around 85% of their time in posture (Morbeck 1977). For orangutans the proportion of time spent in posture is even higher at 90% (Thorpe and Crompton 2006). In terms of impact on the musculoskeletal system, forces generated during posture and locomotion can be relatively similar with, for example quadrupedal standing similar to quadrupedal walking. However, locomotion may also involve much higher forces such as those exerted when taking off from a leap (Warren and Crompton 1997; Demes et al. 1999) and vertical climbing, where the animal must oppose gravity to attain a change in height (Isler and Thorpe 2003). Although they are less frequent, the higher forces generated during locomotion are likely to have a greater influence on the musculoskeletal system than those associated with more passive types of posture (Hunt 1991). Over long periods of time, the behaviours that put the locomotor system under the most stress and exert high stresses regularly are expected to result in morphological changes (Preuschoft 1979; Hunt 1991). Therefore, this demonstrates that the study of positional behaviour is vital in understanding the morphology and behaviour of a species.

Although primate positional behaviour has been a topic of interest for many decades, the first studies tended to be rather descriptive and lacked standardisation (e.g. Avis 1962; Rijksen 1978). Despite early criticisms by Prost (1965) and Ripley (1967), it was not until 1996 when Hunt and colleagues wrote standard definitions of primate positional behaviour that comparisons between different studies were possible. Hunt et al. (1996) defined biomechanically distinct modes and submodes of locomotion and posture based on the body orientation: either orthograde (upright) or pronograde (horizontal); the main weight bearing body parts; method of weight bearing (e.g. suspension or compression); and gait pattern for modes of locomotion. By providing a standardised method of recording primate positional behaviour, Hunt et al. (1996) facilitated cross comparisons of positional behaviour between study sites and species.

1.6 The influence of body size on positional behaviour

One of the most fundamental questions in the study of primate positional behaviour is how body size impacts on a specie's, and an individual's, ability to traverse the complex arboreal environment. As the largest of the primates, the great apes are a particularly interesting taxon to examine this relationship. In a seminal paper Cartmill and Milton (1977) predicted that: 1) as body size increases primates should engage in more 'slow four-limbed climbing', and less leaping; and 2) that larger primates should use more suspensory forms of positional behaviour when dealing with thin branches because these are more stable when compared to above branch positions because the primate has, in effect, already fallen off the branch. They also predicted that larger primates would either utilise larger supports or spread their weight over multiple supports. Several studies have examined the influence of body size on positional behaviour in African apes (e.g. Hunt 1992b; Doran 1993; Hunt 1994; Remis 1995, 1999), and have found little support for predictions of Cartmill and Milton (1977). Hunt (1992b, 1994) examined male chimpanzees and found that larger males did not suspend more often or use larger supports and they climbed less than smaller males. Instead, Hunt (1992b, 1994) found that social rank was more important in determining positional behaviour of male chimpanzees and this was supported by a study of gorillas (Remis 1995), which found that lower ranking group males were forced to feed in the peripheries of trees where supports were smaller. However, social-rank effects may be limited to apes with multi-male societies, which does not apply to orangutans. Remis (1995) also found that larger male gorillas suspended and climbed less than the smaller female gorillas. However, Remis (1995) did find that male gorillas used larger supports than females. These differences were attributed to habitat use as the male foraged in the core of the tree where supports were larger and the females were more likely to forage in the peripheries of trees using multiple, thin terminal branches (Remis 1995). While these species do use arboreal supports they show a large proportion of terrestrial behaviour and, therefore, predictions that relate to arboreal support use may be better addressed through studies of predominantly arboreal species.

As the largest arboreal primates, orangutans have also been studied to investigate the influence of body size on positional behaviour (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005, 2006; Myatt and Thorpe 2011). Contrary to predictions, these studies did not find evidence to support the theory that larger orangutans gain stability by suspending more frequently than smaller orangutans, and during posture the opposite trend was observed with larger orangutans more likely to bear their weight in compression (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2006). However, larger orangutans may be able to use more compressive postures if they select larger more stable supports to use. In support of this theory, previous studies have found that the diameter of the support used increases with body size (Sugardjito and van Hooff 1986; Cant 1987a). These studies found that the larger adult males used larger supports than smaller adult females and adolescents. However, a more recent study of Sumatran orangutans at Ketambe (the same field site as Sugardjito and van Hooff 1986; Cant 1987a) found that adult females used larger supports than adult males and adolescents, reflecting their more cautious nature (Thorpe and Crompton 2005). This was even true of females that did not travel with infants. Therefore, Thorpe and Crompton, (2005) attributed this to a change in behaviour that occurred after becoming pregnant with their first offspring. Overall, the effect of body size on the locomotion of orangutans remains unclear and this may be in part because previous studies did not include data on infants and juveniles; therefore, the full range of orangutan body sizes has not yet been examined.

Very few studies of positional behaviour have examined the changes that occur with growth and development. Doran (1992b, 1997) was the first to examine how ontogenetic growth-related differences in body size influenced positional behaviour in the African apes. Doran (1992b) compared chimpanzee and bonobo development because adult bonobos are paedomorphic, in that they are similar in size and limb proportions to juvenile chimpanzees. Doran (1992b) found that younger chimpanzees and all bonobos engaged in more suspensory locomotion and less quadrupedalism compared with adult chimpanzees. She also found that the positional behaviour of adult bonobos most closely resembled that of immature chimpanzees, which indicates that body size rather than maturity determines positional behaviour in these species. Similarly, Doran (1997) also compared the development of positional behaviour of chimpanzees with their much larger relatives the mountain gorillas (*Gorilla gorilla beringei*) and again she observed that adult chimpanzee locomotion was most similar to immature gorillas of roughly the same body size. However, gorillas of all ages used less suspensory locomotion than chimpanzee adults, which suggests that subtle differences in morphology and habitat usage also influence the positional behaviour of these species. For example, gorillas eat more terrestrial herbaceous plants than chimpanzees, and, therefore, foraging requires that they spend more time on the ground (Malenky et al. 1994). Their morphology shows adaptations to terrestrial positional behaviour (Napier 1967; Roberts 1974; Susman 1979), which includes broader scapulae, shorter phalanges and metacarpals when compared to chimpanzees (Susman 1979; Jungers and Susman 1984; Inouye 1992). Overall, the positional behaviour data from the African apes provide limited support for the predictions of Cartmill and Milton (1977). As orangutans are the most arboreal of the great apes, changes related to growth and development may better reflect their need to gain stability on thin compliant supports.

1.7 Measuring body size

One of the primary problems that has hampered quantitative analysis of the relationship between body size and positional behaviour is an inability to obtain precise measurements of live wild animals without capturing them. Previous studies of orangutans have estimated body size by classing individuals into broad age-sex categories (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005;

Manduell et al. 2011; Myatt and Thorpe 2011). However, this method is not suitable for examining the subtle changes in body size that occur during growth. It is not usually feasible or ethical to measure large wild animals directly (Breuer et al. 2007). However, recent advances in photography have enabled measurements to be taken remotely, causing minimal disturbance to animals. These photographic techniques have been used successfully in studies of body length and fin characteristics in marine mammals (Perryman and Lynn 1993; Perryman and Westlake 1998; Durban and Parsons 2006). The use of parallel lasers in combination with photography enables a single photographer to take pictures that allow detailed measurements to be calculated (Durban and Parsons 2006) (see Figure 1.2).

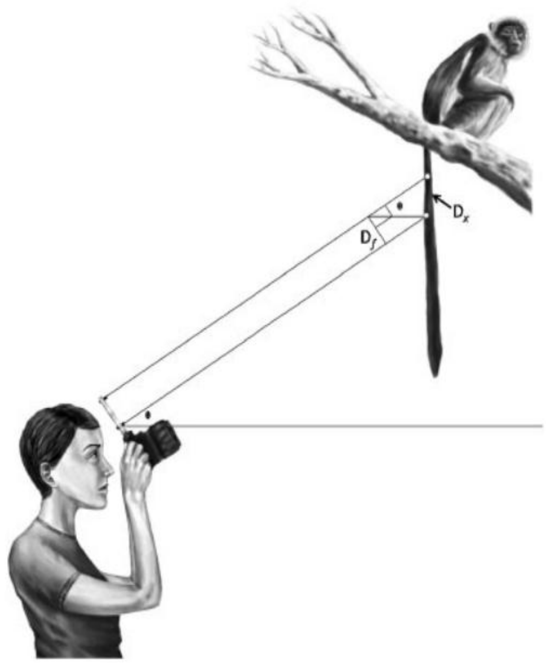

Figure 1.2 Using parallel laser photography to measure the tail of a red colubus monkey. The laser beams provide visible markers on the photograph, which are used as a scale bar (taken from Rothman et al., 2008).

This process uses visible marks on the photograph created by the laser beams as a scale bar to calculate actual measurements (Rothman et al. 2008). This technique has been successfully used on aquatic, terrestrial and arboreal species including elephants (*Loxodonta Africana*), orca whales (*Orcinus orca)* , ibex (*Capra ibex*), gorillas (*Gorilla gorilla*)and red colubus monkeys (*Procolobus rufomitratus*) (Durban and Parsons 2006; Shrader et al. 2006; Bergeron 2007; Breuer et al. 2007; Rothman et al. 2008). Laser photography allows field studies to collect both behavioural and morphometric data for wild subjects without substantially altering their behaviour. This has potential to further our understanding of how small changes in body size and proportions influence the positional behaviour of arboreal animals.

1.8 Orangutan positional behaviour

The positional behaviour of orangutans is a topic of considerable interest because they are the largest predominantly arboreal mammal, considerably more arboreal than the African apes, and problems associated with travel in a fragile, discontinuous habitat worsen as body size increases (Cartmill and Milton 1977). Orangutan locomotion was first described by Alfred Russel Wallace in 1869. Since then several studies have offered descriptive accounts of orangutan positional behaviour (Schaller 1961; Davenport 1967; MacKinnon 1971, 1974; Rodman 1977; Rijksen 1978; Galdikas 1979), but the first quantitative study was made by Sugardjito (1982) at Ketambe Research Station in Sumatra. However, the first quantitative studies lacked standardisation; Sugardjito (1982) and Sugardjito and van Hooff (1986) examined the positional behaviour of Sumatran orangutans using very broad categories, only four postures and five modes of locomotion. They also used the term ‘quadrumanous scrambling’ which included all locomotion that used fore- and hindlimbs in an irregular sequence for horizontal progression, which comprised about 50% of locomotor behaviour. Since this category did not provide information about the orientation of the body or whether body weight was primarily borne in suspension or compression, it is difficult to make accurate comparisons with subsequent studies or to understand the real dynamic between orangutans and their habitat. Cant (1987a) collected more detailed observations of positional behaviour and support use for Bornean orangutans at Mentoko field site in Kutai National Park, East Kalimantan including information on body orientation and direction of movement. However, he was only able to observe two female subjects as the males at Mentoko frequently travelled on the ground and were, therefore, difficult to follow. Cant (1987b) also recorded the postural behaviour and support use of Sumatran orangutans at Ketambe, for both male and female subjects feeding in two different species of fig tree (*Ficus virens* and *F*. *drupacea*). These early studies recorded positional behaviour within particular contexts; Sugardjito and van Hooff (1986) only recorded during travel and resting whereas Cant (1987a) recorded during travelling and feeding. This also makes cross comparisons difficult as positional behaviour has been found to vary according to context (Thorpe and Crompton 2005). Overall, these early studies did not have sufficient detail or sample sizes to provide a comprehensive analysis of positional behaviour and support use across age-sex categories.

The publication of the standardised classification system for primate positional behaviour by Hunt et al. (1996) paved the way for more detailed studies of orangutan positional behaviour. Thorpe and Crompton (2006) further refined the classification system for orangutan positional behaviour in their extensive study of the positional behaviour of Sumatran orangutans at Ketambe (See Appendix A for full list and definitions). The locomotor data were analysed using log-linear modelling to examine the multivariate relationships between locomotion, support use, age-sex category, height and contextual behaviour (Thorpe and Crompton 2005). Their results showed that the type, diameter and number of supports used had the greatest influence on locomotor behaviour. This led Thorpe et al. (2009) to examine the strategies used by orangutans to travel on the thin flexible branches. They found that orangutans typically used all four limbs in an un-patterned gait, grasping multiple supports when travelling on the thinnest supports. These studies based on standardised classification systems have revealed a great deal about the relationship between locomotor repertoire and associated ecological and behavioural variables. However, they are more limited in their ability to describe the subtle changes in positional behaviour that are involved in complex locomotion, such as during gap crossing. Myatt et al. (2011b) addressed this by carrying out a study at Ketambe that sought to develop a new and more precise technique for recording the detail of complex locomotor behaviour in orangutans by using annotated diagrams to examine how orangutans distributed their weight and aided their balance when oscillating trees to cross gaps (Figure 1.3).

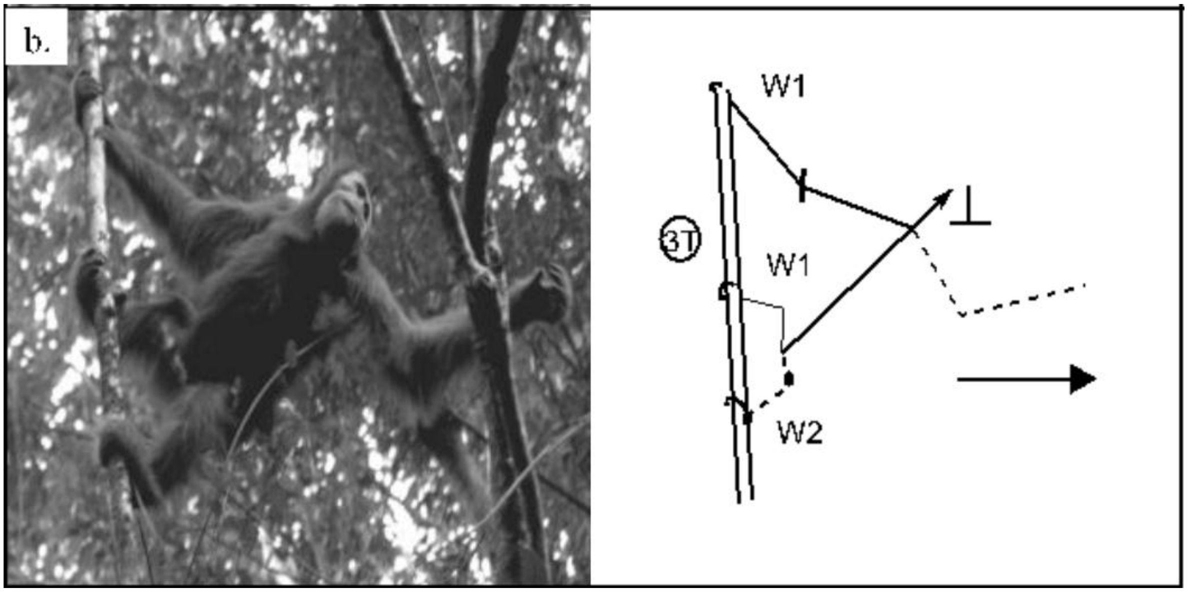

Figure 1.3 A Sutton Movement Writing figure diagram used to represent an orangutan swaying on a tree trunk. The diagram shows the position of the body and how the weight is distributed. For a full explanation see Myatt et al. (2011a).

Although this technique does allow very detailed data to be obtained, the amount of information required for each observation greatly limits the amount of data that can be collected in a day. Therefore, while it is useful for addressing specific questions regarding the mechanics of complex behaviours like tree sway, it is not a suitable technique for obtaining sufficient data to allow an understanding of the full scope of orangutan positional behaviour. Overall, these studies have provided detailed information on the positional behaviour of adult and adolescent orangutans, but there is still very little known about the positional behaviour of younger orangutans.

1.9 Positional behaviour differences

Some differences have been identified in the positional behaviour of Bornean and Sumatran orangutans. The most striking difference is that the large flanged males in Borneo often travel on the ground (Cant 1987b; Galdikas 1988; Manduell et al. 2011), while Sumatran males are not known to travel in this way (Thorpe and Crompton 2009), and this has been attributed to the absence of tigers (*Panthera tigris*) on the island of Borneo (Sugardjito and van Hooff 1986). A recent study of Bornean orangutans living in degraded peat-swamp forest was carried out to examine the species and habitat differences that exist between the two islands (Manduell et al. 2011).The results revealed subtle differences in the positional behaviour of Sumatran and Bornean orangutans; Bornean orangutans were found to exhibit lower frequencies of torso pronograde (horizontal trunked) types of locomotion when compared to their Sumatran counterparts. Manduell et al. (2011) attributed this to differences in forest structure and availability of supports in the site where studies had taken place. There were also differences in the incidence of tree swaying locomotor behaviour, which were found to be more common in the Bornean orangutans studied by Manduell et al. (2011). This difference was associated with the abundance of small flexible trees found in the disturbed peat-swamp forest where the study took place.

1.10 Life history differences

Primates have relatively slow life histories when compared with other mammals (Read and Harvey 1989). Both long inter-birth intervals and long immature phases characterize primate life histories (Harvey and Clutton-Brock 1985). Averaging 8 years, orangutan inter-birth intervals are the longest of any mammal (Wich et al. 2004; van Noordwijk and van Schaik 2005). This is considerably longer than found in gorillas and chimpanzees, which have average birth intervals of 4 and 6 years, respectively (Watts 1991; Boesch and Boesch-Achermann 2000). The growing body of long term data on orangutan life history suggests that there may also be inter-island differences in inter-birth intervals (Wich et al. 2009). The most accurate data come from the longest running field site Ketambe (see Figure 1.1 for locations), where the average birth interval is 9.3 years (Wich et al. 2004). The other Sumatran site for which data are available, Suaq Balimbing, has an average birth interval of 8.2 years (van Noordwijk and van Schaik 2005). In contrast, the data emerging from Bornean sites suggest that birth intervals are lower for this species. Two field sites provide data on Central Bornean orangutans (*P.p. wurmbii*); at Tanjung Puting the average birth interval was 7.7 years (Galdikas and Wood 1990) and at Gunung Palung it is 7 years (Knott 2001). Inter-birth intervals in East Kalimantan where the sub-species *P. p. morio* is found were found to be significantly shorter than both Sumatran and Central Bornean orangutans (Wich et al. 2009); at Kutai the average birth interval was 6.1 years (Suzuki unpublished data) and at Kinabatangan it was 6.5 years (Ancrenaz unpublished data). The length of birth interval at each site appears to increase with forest productivity and fruit availability (Wich et al. 2009). When fruit is scarce, orangutans rely on fall back food such as inner bark, which is less energetically rewarding (Knott 1998). The composition of inner bark in the diets of orangutans from different field sites was found to correlate negatively with forest productivity and inter-birth intervals (Anderson et al. 2008; Wich et al. 2009). Although mortality rates for wild orangutans are largely unknown, Knott (1998) has suggested that increases in the proportion of inner bark consumed could potentially increase mortality in Bornean orangutans. Studies have shown that when extrinsic mortality increases, intrinsic mortality also increases (Reznick et al. 1990; Stearns 2000) and Wich et al. (2009) suggested that the trend in inter-birth intervals is reflective of intrinsic life history differences caused by increased mortality. Therefore, Wich et al. (2009) predicted that in captivity, when resources were plentiful, Sumatran orangutans would still have the longer inter-birth intervals and Bornean orangutans would have higher mortality. However, data on captive orangutans did not support this hypothesis. This was further confirmed by a large study of captive orangutans by Anderson et al. (2008), which found the opposite to what they had expected; Sumatran orangutans had shorter inter-birth intervals and higher mortality in captivity. Anderson et al. (2008) suggested that phenotypic flexibility was more likely to explain the differences in birth intervals than intrinsic differences between the species. This is also supported by the fact that inter-birth intervals for both species are substantially lower in captivity (mean 5 years) (Anderson et al. 2008), when compared with wild orangutans. This suggests that orangutans may be able to adapt their reproductive behaviour in response to environmental change.

1.11 The development of skills hypothesis

Studies of orangutan development have examined the development of skills hypothesis (van Noordwijk and van Schaik 2005; van Adrichem et al. 2006), which proposes that young orangutans need to spend a long time in exclusive association with their mothers in order to learn all the foraging, travelling and nest building skills they need to survive. However, these studies did not find significant differences in the ages that orangutans acquire skills related to foraging, travelling or nest building in comparison to other species of great ape (van Noordwijk and van Schaik 2005; van Adrichem et al. 2006). Nest building skills were practised from the age of 1 and acquired by around 3 years old, which is long before the infants began to sleep in a separate nest from their mothers (van Noordwijk and van Schaik 2005). Infants were able to process most food items by the time they were 3 years old (van Noordwijk et al. 2009). Some foods did require more complex skills; for example, Sumatran orangutans extract the seeds of *Neesia* fruits from between stinging hairs using small stick tools and young orangutans were not observed to use these tools successfully until around 7 years old. However, these are not likely to be essential to their survival. The results also showed that mothers were more tolerant of begging for difficult or rare food items, and were even observed to share food with already weaned offspring (Jaeggi et al. 2008; van

Noordwijk et al. 2009). Thus, the skills hypothesis does not appear to account for the extended inter-birth interval in orangutans.

1.12 Gap crossing behaviour

Arboreal animals must travel on compliant supports in order to cross gaps in the canopy. Cant (1994) proposed three ways of dealing with compliant supports when crossing gaps: (1) ignore support compliance; (2) adjust for support compliance; and (3) utilise support compliance. Most arboreal animals either ignore compliance by carrying on regardless of support deformation or adjust their behaviour to compensate for support deformation by increasing their height or pausing to allow branch oscillations to stop (Alexander 1991; Cant 1994). These behaviours are costly for arboreal animals as they must regain height lost by branch deformation and also lose time and energy while waiting for oscillations to stop, these problems becoming increasingly worse as body size increases. In response to the problems associated with travel on compliant supports, orangutans are able to utilise support compliance in two ways: termed appendicular and mass deformation (Cant 1994). Appendicular deformation involves pulling in a compliant branch on an adjacent tree until a more stable support can be reached (Cant 1994). This technique is used to cross smaller gaps when terminal branches are within reach. However, as orangutans are too large to leap across gaps (Thorpe and Crompton 2006), they must cross larger gaps in the canopy by using their body mass to deform compliant supports, which has been found to lower the costs of travel by avoiding energetically expensive climbing (Thorpe et al. 2007a). This complex form of locomotion (Chevalier-Skolnikoff et al. 1982) involves bending or oscillating compliant trees or lianas until the next tree is within reach (Cant 1994; Thorpe and Crompton 2006; Thorpe et al. 2007a; Thorpe et al. 2009) (see Figure 1.4).

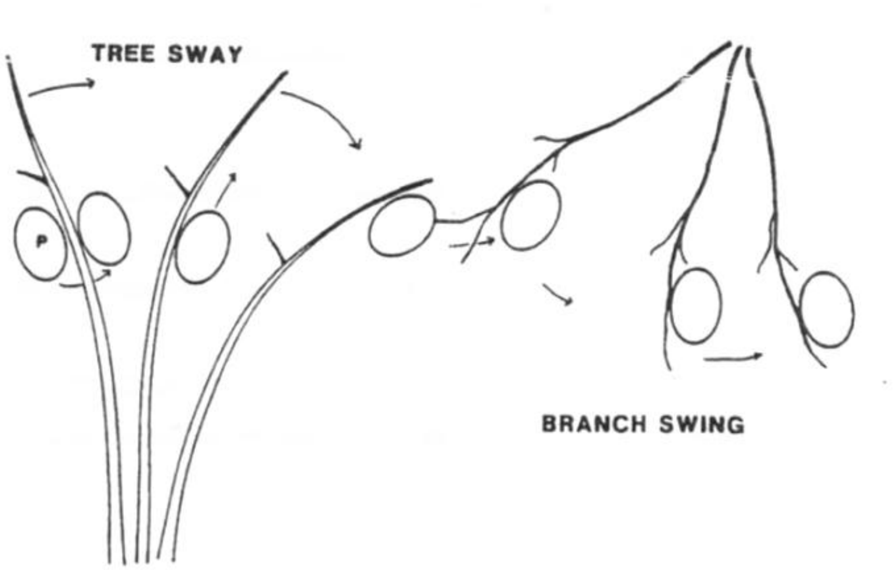

Figure 1.4 Forms of sway used by orangutans. The body of the animal is represented by an oval shape with arrows showing their direction of movement and the direction of movement of the support they are using (either tree or liana) (taken from Cant, 1994).

These skills are thought to be both physically and cognitively demanding to acquire (Chevalier-Skolnikoff et al. 1982; Bard 1995) and young orangutans are reliant on their mothers assistance during gap crossing until these skills are fully mastered (van Noordwijk et al. 2009). Recent studies of orangutan development have examined the development of independent travel in Sumatran orangutans by recording the amount of time when infants are carried by their mother (van Noordwijk and van Schaik 2005; van Adrichem et al. 2006). However, only one study has addressed the development of skills related to the manipulation of compliant vegetation for arboreal travel (Bard 1995).

1.13 The role of the mother

Orangutans lead semi-solitary lives (Delgado and van Schaik 2000) and therefore, offspring receive all their parental care and the majority of their social learning opportunities from their mothers. It is thought that wild infant orangutans learn technical skills such as nest building and food processing through observation of their mothers (van Noordwijk et al. 2009). This is supported by a study of Bornean orangutans at Tuanan field station, which found that infant orangutans paid closer attention when their mother was processing rare or difficult food items (Jaeggi et al. 2008). Orangutan mothers also appear to play an important role in the development of their offspring's arboreal skills (Bard 1995; van Noordwijk et al. 2009). The first study to examine maternal assistance during travel in orangutans was carried out by Bard (1995) at Tanjung Puting National Park, Borneo. Bard (1995) found that gap crossing skills developed slowly during ontogeny and offspring received substantial maternal assistance during travel. Orangutan mothers provided a variety of different types of assistance: the youngest offspring were carried across gaps and as they got older they progressed to travelling across their mothers' body while she held the trees together, and then to travelling on the same tree while their mother oscillated it or catching a tree their mother had already used on the backswing and riding it back again (Bard 1995). Young orangutans frequently solicited their mothers' assistance by making crying vocalisations when a gap in the canopy separated them from their mother (Bard 1995). By ignoring and refusing to provide assistance, Bard (1995) suggested that mother orangutans were encouraging independent behaviour in their offspring. This can be structured in a manner that is conducive to learning, by withdrawing assistance gradually so that infants are constantly challenged but are not presented with problems that are beyond their capability, a technique known as scaffolding (Wood et al. 1976). By systematically reducing carrying and other assistance during gap crossing, Bard (1995) proposed that orangutan mothers were scaffolding the development of independent locomotor behaviour in their offspring.

Maternal encouragement of independent locomotion has also been observed in other primate species including rhesus (*Macaca mulatta*) and pigtail (*M. nemestrina*) macaques (Maestripieri 1995, 1996) and gorillas (Maestripieri et al. 2002). In both macaque species Maestripieri (1995, 1996) found mothers left their infants and proceeded to encourage their independent locomotion by means of gestures and facial expressions. Such behaviour was also observed in a captive mother and infant gorilla. Maestripieri (1995) found that macaque infants that were encouraged in this way learned independent locomotor skills earlier than those that were not. The studies indicate that primate mothers can advance the learning of locomotor skills in their offspring using a combination of encouragement and refusing to provide assistance during travel.

1.14 Behavioural flexibility and play

In comparison to small bodied arboreal primates, orangutans show considerable behavioural flexibility in their locomotion adapting their limb movements to use diversely orientated combinations of supports (Povinelli and Cant 1995). Povinelli and Cant (1995) compared the locomotor behaviour of sympatric Sumatran primates: long-tailed macaques (*Macaca fascicularis*), siamang (*Symphalangus syndactylus*) and Sumatran orangutans. They found that the larger primates solved problems associated with habitat compliance by using increasingly less stereotyped and more flexible locomotor behaviours. Behavioural flexibility is thought to develop through vigorous locomotor play during ontogeny (Pellegrini et al. 2007). In 2001 Spinka and colleagues put forward the hypothesis that mammalian play was training for the unexpected. They suggested that playful movements with no immediate goal may have evolved to prepare young animals for a sudden loss of control where a fast flexible response would be required to save them from a life threatening situation. As orangutans are the largest arboreal primates with the most flexible locomotor patterns, locomotor play is likely to be especially important for their development. Yet little is known about the role of play in the development of locomotion in these species. Locomotor play in young animals may have additional developmental functions. Byers and Walker (1995) found that the peak in play behaviour coincided with the short period of time when it is possible to modify skeletal muscle fibre type and Gunter et al. (2008) found that bone mineral content in humans could be increased by exercise during childhood but not later on in life. This evidence suggests that locomotor play may play an essential role in musculoskeletal development. Healthy musculoskeletal development is essential for arboreal travel as behaviours such as climbing and suspensory locomotion require muscles that can generate greater stresses in order to oppose gravity (Isler and Thorpe 2003).

1.15 Captivity

In order to understand completely the positional behaviour potential of a species Prost (1965) recommended that thorough field studies be accompanied by laboratory or zoo-based studies in order to examine the total potential positional repertoire of a species that he termed totipotentiality. For arboreal animals captivity presents a far less varied and challenging environment in terms of support availability in comparison to natural forest. The diverse repertoire of positional behaviour exhibited by wild orangutans was found to be most influenced by support use variables (Thorpe and Crompton 2005), primarily by a combination of the number and diameter of supports used and secondarily by the number and type of supports used, e.g. tree or liana. This suggests that captive environments may elicit different kinds of positional behaviour in orangutans. However, there are very few studies of the positional behaviour of orangutans in captivity (Isler and Thorpe 2003; Hanson et al. unpublished data). Isler and Thorpe (2003) found that captive orangutans were less cautious than their wild counterparts when climbing in their enclosure, which they attributed to over familiarity with supports. A recent unpublished study of captive Sumatran orangutans by Hanson and colleagues found that high levels of ground use in captivity were associated with increased frequencies of quadrupedal walking. Arboreal behaviours such as vertical climbing and suspensory locomotion require muscles to generate greater stresses when compared to terrestrial behaviours like quadrupedal walking (Isler and Thorpe 2003). Therefore, elevated levels of terrestrial behaviour in captivity may have detrimental effects on bone and muscle development in captive orangutans. In order to investigate long-term consequences of life in captivity, developmental studies of captive and wild orangutan positional behaviour are required to establish whether captivity can provide an environment that allows for natural development.

1.16 Main objectives of the thesis

The main objective of this thesis is to examine how orangutan positional behaviour changes during ontogeny as body size increases and new skills are acquired. These questions are particularly interesting because orangutans have a wide range of body sizes and a diverse repertoire of positional behaviour (Thorpe and Crompton 2006). To date, studies of the influence of body size have divided orangutans into broad age-sex classes rather than actually quantifying body size. Therefore, I aim to sample individuals of all sizes and to develop a non-invasive measurement technique to assess body size variation quantitatively. The second aim of my study is to examine the gap crossing behaviour of orangutans at different developmental stages and for different body sizes, as skills related to gap crossing are among the most complex for young orangutans to acquire and require both cognitive and physical development. Studies of the ontogeny of locomotion may also reveal whether immature subjects do exhibit a wider range of more risky locomotor play behaviours that could contribute to the development of behavioural flexibility in the locomotion of adults. Orangutan mothers provide the majority of learning opportunities to their offspring (van Noordwijk et al. 2009); hence, this thesis further aims to discover if and how orangutan mothers facilitate learning of gap crossing skills in their offspring. Documenting the development of gap crossing skills during ontogeny may also help to establish whether learning these skills could contribute to the incredibly long period of maternal dependence found in this species. The final focus of the thesis is to compare orangutan positional behaviour across wild and captive environments. As captivity presents a greatly simplified environment, this thesis aims to find out whether orangutans in captivity exhibit natural positional behaviour and how captivity affects orangutan development of positional skills. Overall, this thesis will explore how orangutans solve problems related to life in a complex fragile environment and how this changes with growth and development. It is hoped that an improved understanding of orangutan positional development will help to improve orangutan captive management and rehabilitation.

1.17 Thesis structure

The chapters of this thesis are written in paper formats and will be submitted for publication. The thesis is structured as follows: **Chapters 2 and 3** examine the development of locomotion and posture in Bornean orangutans (*P. p. wurmbii*) ranging from infant to adult by classifying subjects according to their body size. The results are discussed in terms of growth and development. **Chapters 4 and 5** focus on gap crossing behaviour in Bornean orangutans. **Chapter 4** examines the development of gap crossing behaviours with increasing body size using a modelling approach to examine how body size, locomotor behaviour and support use influence the distance orangutans cross. **Chapter 5** examines the role of the mother in the development of independent gap crossing behaviour in young orangutans, and specifically addresses how maternal assistance varies with offspring age, gap size and support type. **Chapter 6** compares the positional behaviour of captive and wild Bornean orangutans focussing on development and how the captive environment influences positional development in this species. Finally, **Chapter 7** discusses the development of positional behaviour in orangutans with respect to body size, maternal assistance and environment and the implications for orangutans in captivity. In light of this, suggestions for future research are provided.

2. THE ONTOGENY OF LOCOMOTION IN BORNEAN ORANGUTANS: ASSESSING THE EFFECTS OF BODY SIZE ON LOCOMOTOR BEHAVIOUR

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Abstract

Orangutans (*Pongo* sp.) are the largest predominantly arboreal mammal and have a diverse repertoire of locomotor behaviour which allows them to travel within the complex and fragile forest canopy. As the problems associated with travel in an unstable environment worsen with increased body size, both locomotor behaviour and support use have been hypothesised to relate to body size. Previous studies have sampled the locomotor behaviour of four age-sex categories, omitting data collection on pre-adolescent orangutans. This is the first study to sample the locomotor behaviour across the full range of orangutan body sizes. Data collection was carried out at Tuanan field station, Central Kalimantan and the study subjects were 17 wild Bornean orangutans. A non-invasive laser photography technique was used to take measurements of study subjects, which provided a continuous independent variable that enabled regression analysis to be performed. Multivariate log-linear analysis of grouped data was also used to find the relationships which best explained the observed variation in locomotor behaviour. In contrast to previous studies, locomotion was found to be strongly associated with body size. Both support diameter and suspensory locomotion were found to increase with increasing body size in

accordance with classic predictions of body size and positional behaviour. Locomotor behaviour had the strongest association with the support variables diameter and number of supports, which indicates that stability is the most important factor in determining the type of locomotion used. These results suggest that orangutans adapt their locomotor behaviour as they grow in order to travel on compliant arboreal supports.

2.1 Introduction

The positional behaviour of orangutans is a topic of considerable interest because they are the largest predominantly arboreal mammal, and because problems associated with travel in a fragile, discontinuous habitat worsen as body size increases (Cartmill and Milton 1977). To overcome the challenge of travel in the forest canopy, orangutans have evolved a diverse repertoire of locomotor behaviour (Thorpe and Crompton 2006) using their fore-and hindlimbs in different combinations of suspension and compression and with a range of body orientations. Orangutans show considerable variation in body size, ranging from an average of 1.9 kg at birth (Cocks 2001) to up to 90 kg for an adult male, with adult females reaching approximately half the body weight of adult males (Markham and Groves 1990). Hence, both age and sex determine body size. Orangutans are, therefore, a good model to examine how body size influences the positional behaviour of arboreal primates (Sugardjito and van Hooff 1986; Cant 1987a). So far studies have investigated the effects of body size on the locomotor behaviour of orangutans using age-sex categories to study body size differences (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005; Manduell et al. 2011). Some notable differences were found: adult females were found to be the most cautious age-sex group using the most stable support combinations (Thorpe and Crompton 2005; Thorpe et al. 2009), which suggests that sex is more important in determining support use than body size. However, several studies have found some correlation between locomotor behaviour and support use with body size (Sugardjito and van Hooff

1986; Cant 1987a). Overall, the effect of body size on the locomotion of orangutans is unclear; the limitations associated with low sample sizes may cause subtle differences in locomotor behaviour to remain undetected by statistical analysis. To date, no study has examined the positional behaviour of pre-adolescent orangutans and therefore the full range of orangutan body sizes has not been fully represented in previous studies. A full investigation of orangutans ranging in body size from infant to adult is required to understand fully the relationship between body size and locomotor behaviour.

When investigating locomotor ecology, it is important to take a representative sample of the population (Ripley 1967). Therefore, it is important to sample all of the age classes that engage in independent locomotor behaviour. As soon as infant orangutans begin to move off their mother's body, in their first year of life, they must be able to navigate their arboreal habitat in order to survive. Yet, infants and adults face different challenges related to arboreal locomotion. As the deformation of arboreal supports is proportional to the mass of the animal that uses them, orangutans of different sizes experience different levels of stability and must adjust their locomotor behaviour accordingly. Therefore, orangutans are predicted to alter their locomotor behaviour as they grow in response to the effect that their mass has on their habitat. Inter-specific comparisons of African apes provide evidence to support this theory: Doran (1992; 1997) found that juvenile apes of larger species (gorillas and chimpanzees) had similar locomotor behaviour to adults of smaller species, chimpanzees and bonobos, respectively. These studies suggest that it is body size rather than maturity that is influencing the locomotor behaviour of these species.

As branches taper towards their ends, the shortest gaps between trees are usually separated by the thinnest supports. These peripheral branches are also where the most fruit is located (Grand 1972) and therefore, arboreal animals must use thin, unstable supports during feeding and travel. Larger animals should experience more stability on thin supports when body weight is borne by suspension beneath the support compared with compression above the support (Cartmill and Milton 1977; Cant 1992). Hence, the prediction is made that larger animals should engage in higher frequencies of suspensory positional behaviours than smaller animals. This prediction has not been borne out by the findings of previous studies of orangutans (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005; Manduell et al. 2011). In fact, Cant (1987a) found that the smaller adult females used more suspensory postures than a large adult male who used more above branch postures during feeding, however, with a sample size of just three individuals, this evidence is not conclusive. Furthermore, locomotion represents a greater challenge as movement must be coordinated and supports used for locomotion are subject to greater stress than during posture and, therefore, body size may have more influence on locomotion than on posture. Although previous studies of orangutan locomotion have not found size-related differences in the frequency of suspensory locomotion, classifications of behaviour have not been consistent. The locomotor mode ‘quadrumanous scrambling’ used by Sugardjito and van Hooff (1986) does not distinguish between locomotion that is primarily suspensory and assisted bipedalism. Also, the oscillatory behaviours of ride (support moves in direction of travel) and sway (support moves back and forth) have been presented previously without positional distinctions (Sugardjito 1982; Thorpe and Crompton 2005; Manduell et al. 2011) grouping compressive and suspensory behaviours together. Overall frequencies of suspensory locomotion for different sized orangutans are required to investigate fully the theory of Cartmill and Milton (1977) on the relationship between body size and suspension.

Since stability decreases on smaller supports, and since this problem worsens as body size increases (Grand 1972), there has been considerable interest in whether larger animals use larger supports (Crompton 1983; Cant 1987a, 1992; Hunt 1992b; Remis 1995; Thorpe and Crompton 2005). Intra-specific studies of galagos (*G. crassicaudatus*) (Crompton 1983) and Sumatran orangutans (Cant 1987a) found that support diameter was related to body size with larger animals more likely to use larger supports. Conversely, a study of chimpanzees did not find size-related differences in support use, but, instead support use was associated with social rank (Hunt 1992b). Remis (1995) also found that in gorillas support use was influenced by social rank and changed with party composition, although female gorillas did use smaller support types than males. Orangutan social structure has been described as semi-solitary (Delgado and van Schaik 2000) and, therefore, social rank is unlikely to have a strong influence on overall support use because the majority of daily activities occur while orangutans are alone or in the company of their own dependent offspring. However, a more recent study of Sumatran orangutans by Thorpe and Crompton (2005) did not find that support use was related to body size, but found that adult females used larger supports than adult males. These findings have been attributed to the onset of more cautious locomotor behaviour in adult females after the birth of their first offspring (Thorpe and Crompton 2005). A comparison of different sized orangutans prior to adolescence is required to avoid sex-related differences seen in adult orangutans.

The complex relationships between arboreal animals and their habitat can be examined by constructing models that best explain the observed behaviour. During extensive log-linear analysis of data on Sumatran orangutans by Thorpe and Crompton (2005) and Bornean orangutans by Manduell et al. (2011) the age-sex category was not found in any of the most important relationships between variables, whereas the variables ‘support type’ and ‘support diameter’ were most strongly associated with locomotor behaviour. The homogeneity in locomotor behaviour across age-sex categories in Sumatran orangutans was attributed to ‘arboreal pathways’ which all age-sex categories were observed to follow (Thorpe and Crompton 2005). The existence of favoured routes between feeding trees means that different individuals tend to use the same supports for travel and are, therefore, more likely to use similar locomotor behaviours (Thorpe and Crompton 2005). The use of arboreal pathways has not been observed in Bornean orangutans inhabiting disturbed peat swamp forest (Manduell et al., 2011; pers.

obs.) and habitat differences are likely to account for this. Selective logging increases the size of gaps between emergent trees and causes the lower canopy to become more dense (Vogel et al. 2009) which forces orangutans in disturbed forests to travel lower in the canopy (Manduell et al. 2011). When travelling in dense vegetation there are different travel options available to orangutans. For example, they may clamber using handfuls of foliage to bear their weight or they may oscillate thin, compliant trees of which there are many in a selectively logged forest (Manduell et al. 2011). Therefore, in the absence of arboreal pathways we might expect age-sex category to have a greater influence on locomotor behaviour but Manduell et al. (2011) did not find evidence to support this theory.

This study examines the relationship between body size and locomotor behaviour in the largest predominantly arboreal animal by sampling the locomotor behaviour of subjects ranging from infant to adult. We hypothesise that locomotion will show distinct associations with body size with respect to both type of locomotion and the supports that are used for it. More specifically, we hypothesise that: 1) the level of suspensory locomotion will increase with increasing body size; 2) larger orangutans will use larger diameter supports to bear their weight; and 3) lianas are expected to be used more by smaller orangutans because they are more easily oscillated than trees.

2.2 Methods

This study was conducted at Tuanan field station (2°09'S, 114°26'E) within the Mawas Reserve, Central Kalimantan, Indonesia. The study area consists of around 725 ha of lowland peat-swamp forest with an orangutan density of 4.25/km^2 (van Schaik et al. 2005). This area has been subjected to selective logging and as a result the forest is dominated by young, small trees. Prior to the onset of continuous research at Tuanan in 2003, a grid-based trail system was cut and orangutans in the area were identified and habituated to human observers. This study was carried out from June-October 2009 and January-July

2010. The study subjects were 17 wild Bornean orangutans (*Pongo pygmaeus wurmbii*) including individuals of all age-sex categories (Table 2.1). The immature subjects ranged in age from 1 to 11 years.

Table 2.1 Focal orangutans observed at Tuanan Research Station, Central Kalimantan between July 2009 and July 2010. Body size category refers to the categories used in the log-linear analysis which were based on forearm length and 'focal days' refers to the number of whole days of observation.

Name	Age-sex category	Forearm length (cm)	Body size category	Focal days
Mawas	Infant female	12.8	1	10
Kino	Infant male	17.4	1	10
Jip	Juvenile male	20.7	2	10
Deri	Juvenile male	23.5	2	7
Jerry	Immature male	27.3	3	10
Streisel	Immature female	29.9	3	9
Milo	Immature female	31.3	3	7
Ido	Immature male	-	3	6
Kondor	Immature female	33.2	3	10
Juni	Adult female	35.4	3	5
Kerry	Adult female	38.0	3	5
Mindy	Adult female	-	3	4
Budhi	Sub-adult male	-	3	1
Ekko	Sub-adult male	-	3	2
Gismo	Sub-adult male	45.6	3	4
Preman	Adult male	50.9	3	3
Isidor	Adult male	-	3	2

Data collection employed focal animal sampling (Altman 1974) by following an individual until it made a night nest (between 15:00 and 19:00) and arriving before it awoke the next day at approximately 04:45. Subjects were followed for a maximum of 10 days per month and effort was made to sample each individual in more than one month to minimise the effect of any bias related to temporarily available food sources (Thorpe and Crompton 2005). Instantaneous sampling at the 1-minute mark was used to sample locomotor behaviour and support use. A digital watch with an auto-repeat countdown vibration alarm function was used to ensure that instantaneous sampling was accurate without disturbing the orangutans. Locomotor behaviour was classified according to the descriptions of orangutan positional behaviour given by Thorpe and Crompton (2006), which are based on the standardised classification system of Hunt et al. (1996). Where necessary, additional modes of positional behaviour observed in the study subjects but not represented in the classification of Thorpe and Crompton (2006) were described according to the principles proposed by Hunt et al. (1996). Thus, modes of locomotion were assigned based on the orientation of the body, which limbs were bearing weight and whether they were bearing weight in suspension or compression. Locomotor modes were further differentiated into sub-modes according to the gait pattern (regular or scramble) and whether limbs were flexed or extended (Hunt et al. 1996). The number of weight bearing supports and the type and diameter of each support were recorded for locomotion involving up to four supports (Thorpe and Crompton 2005). If more than four supports were used only the type and diameter of the main weight-bearing support was recorded (Cant 1987b). All data were collected by a single observer (ACP) and periods of self-training in classifying behaviour and estimating support diameters were undertaken prior to and during data collection to ensure consistency and accuracy.

In order to gauge the body sizes of the individuals, a non-invasive laser photography technique (Rothman et al. 2008) was used whereby parallel lasers were attached to a camera (Canon EOS 400D) with a specifically designed aluminium frame. The lasers were positioned exactly 4cm apart and provided visible marks on the photograph, which were used as a scale bar (see Figure 2.1).

Figure 2.1 A photograph of a juvenile orangutan taken at Tuanan Research Station in February 2010 using parallel lasers, which provide a scale bar to quantify linear measurements taken from the subject.

The lasers were used to measure the subject's limbs, which were photographed when they were perpendicular to the field of view of the camera to avoid errors associated with foreshortening. The photographs were measured using Image J version 1.43 (Bethesda, MD) to estimate the length of subject's forearms from the elbow to the wrist, using the prominent olecranon process of the ulna and the radio-carpal joint as landmarks. For each subject a minimum of three photographs where landmarks were visible and limbs appeared to be perpendicular to the camera were used to get a forearm measurement. The largest value was taken as the forearm measurement because foreshortening can only cause underestimation of the true distance. This yielded measurements for 12 of the 17 subjects. The subjects in Table 2.1 are listed in order of size with the positions of the five unmeasured subjects estimated by comparing them to measured individuals when they were observed together.

As the relationship between body size and locomotor behaviour was the primary focus of this study, subjects were grouped into six size groups according to their forearm length: infants (<20cm), juveniles (20-25cm), small adolescents (25-30cm), large adolescents (30-35cm), adult females (35-40cm) and adult males (>40cm). However, it was necessary to conflate the categories further to obtain large enough cell frequencies (over 5) for log-linear analysis. The method of conflating size groups was experimented with to find the categories which best described the variation in locomotor behaviour seen. The conflations, which produced models with the highest significance (i.e. *P* values), were those that kept infants and juveniles separate and grouped adolescents and adults. Therefore, the size categories used in this analysis were: 1 (forearm length <20cm), 2 (forearm length 20-25cm) and 3 (forearm length >25cm). The boundary between sizes 2 and 3 corresponds with the size at which mothers cease to assist their offspring during gap crossing (see chapter 4 and 5).

During data collection 57 biomechanically distinct sub-modes of locomotion were observed. However, for the purposes of this chapter, these were divided into five broad categories: pronograde compression (quadrupedal and tripedal locomotion), pronograde suspension (inverted quadrupedal and pronograde bridge), orthograde compression (bipedal walk), orthograde suspension (brachiation, clamber) and vertical climb/descent. The oscillatory behaviours ride and tree sway were recorded according to the orientation of the body and whether weight was borne in suspension or compression. As a result, they are distributed between all of the five locomotion categories and are not analysed separately. Frequencies of oscillatory behaviour at different ages are reported in Chapter 4 and the overall frequency of oscillatory behaviour in wild orangutans is reported in Chapter 6.

Due to the constraints of the sample size, only two categories could be used for each of the support use variables. In the field, the arboreal support types: trunk, bough, branch and liana were distinguished, and these were analysed in two categories, tree and liana. The diameter categories were recorded using the following categories of Cant (1987a) with the addition of one smaller category: <2, ≥2-<4, ≥4-<10, ≥10-<20, ≥20-<40 and ≥40cm but for the categorical analysis only two diameter categories were used: <10 and >10cm. Similarly, the number of supports was conflated into two categories: 1 support and >1 support. The conflation decisions were made on the basis of the best fitting model with sufficiently high cell frequencies.

2.2.1 Statistical analysis

This study combined multiple statistical approaches to investigate the relationships between continuous and categorical variables. Linear regression was used to investigate correlation between the independent continuous variable forearm length and locomotor behaviour variables: frequency of suspension and the average support diameter. The relationships between categorical variables were explored using chi-square contingency tables and log-linear modelling for multiple categorical variables. Log-linear analysis was carried out using SPSS (Version 18, Chicago, IL) to find a model which best explained the distribution of the data. Log-linear has several advantages for the analysis of positional behaviour data; it allows multiple hypotheses to be explored within the same model providing estimates of significance (*P* values) so that different relationships can be directly compared. The whole model is also given a goodness of fit statistic called the likelihood ratio chi-square. This has an associated degrees of freedom and *P* value, which are calculated by comparing the observed frequencies with those generated by the model. In log-linear high *P*-values indicate a good fit with a perfect fit (*P*=1) obtained when observed frequencies are identical to those predicted by the model (Agresti 1990; Thorpe and Crompton 2005). Individual terms in the final model can be investigated further using contingency tables (for 2-way interactions) and by log-linear modelling of the residual for higher order interactions. This study used adjusted standardised residuals (ASRs) to explore the relationships between the variables at the cell level. Adjusted residuals were used because unlike standardised residuals, they take into account the overall sample size and, therefore, quantify how far the observed frequency differs from the expected more accurately (Haberman 1973). Absolute values of the ASR greater than 2 indicate that the observed is significantly different from the expected (Bewick et al. 2004).

There are a few assumptions of the analysis that must be adhered to in order to preserve the power of the test: expected cell frequencies must not be zero and no more than 20% can be less than 5 (Tabachnick and Fidell 1996). If the data are clustered and the sample size is not large enough to accommodate this, low cell frequencies are a problem. For these reasons it was necessary to conflate categories within variables to increase cell frequencies. This meant that some of the initial detail that was collected was lost and rare behaviour combinations tended to be ignored (Thorpe and Crompton 2005). On the other hand it can be useful to conflate categories in alternative ways to find out where the most biologically important distinctions are (Thorpe and Crompton 2005; Manduell et al. 2011).

A further benefit of log-linear is that it is possible to define structural zeros (i.e. combinations of variable categories that cannot possibly occur), so that they do not affect the accuracy of the model. For example, orangutans cannot walk bipedally on a thin liana without using another support to bear weight in suspension. However, it is not possible to carry out hierarchical log-linear model selection automatically in SPSS whilst specifying structural zeros. Therefore, this study used the general log-linear function to carry out a manual backwards elimination. Terms were eliminated one at a time starting with the highest order interactions, and the partial χ^2 and degrees of freedom were used to obtain corresponding *P*-values. In each round the term with the highest *P*-value was eliminated and the process was repeated until only the most significant terms ($P<0.1$) were left in the model.

2.3 Results

This study produced 4913 instantaneous observations of locomotion and support use from 17 individuals collected over 105 whole observation days. Orthograde suspension was the most common type of locomotion accounting for 52% of all observations. The remaining 48% was made up of vertical climb/descent (19%), pronograde suspend (13%), orthograde compression (10%) and pronograde compression (6%). Locomotion on lianas was less frequent than locomotion on trees; lianas were used in only 7% of observations. The majority of locomotion occurred on supports of less than 10cm diameter (87%) and multiple supports were used more often than single supports (60% and 40%, respectively).

The relationship between body size and locomotion was initially examined using a simple chi-squared test to assess the association between the two variables. The results of the chi-squared test indicate that there is a strong association between body size and locomotion (χ^2= 139.6, DF= 8 and P<0.001). The chi-squared contingency table (Table 2.2) was used to determine the nature of the relationship between the two variables through patterns in the row percentages and the adjusted standardised residuals (ASRs).

Table 2.2 Contingency table for the association: size * locomotion. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Size group	Prono Compress	Prono Suspend	Ortho compress	Ortho suspend	Vertical climb/descent	Total
1	8.5 (31.6) *4.5*	11.5 (18.2) *-1.9*	11.8 (24.2) *1.9*	41.9 (16.7) *-7.5*	26.4 (29.5) *7.1*	(20.9)
2	5.8 (21.5) *0.4*	15.4 (24.0) *2.3*	7.1 (14.4) *-3.6*	49.3 (19.4) *-2.1*	22.3 (24.5) *3.3*	(20.6)
3	4.5 (46.9) *-4.0*	13.1 (57.8) *-0.4*	10.7 (61.5) *1.4*	57.0 (63.9) *7.9*	14.7 (46.0) *-8.5*	(58.5)
Total	5.6	13.2	10.2	52.3	18.7	100

Each cell contains the row %, (column %) and the adjusted standardised residual (ASR), shown in italics. For example, 8.5% of the locomotion of orangutans in size group 1 was pronograde compression and 31.6% of all pronograde compression observations were made when sampling size 1 orangutans.

The residuals show that pronograde compression is used more than expected by smaller orangutans and less than expected by larger orangutans. The opposite pattern is seen in orthograde suspension which increases in frequency as body size increases. Vertical climb and descend are most associated with the smaller body size categories, with the largest orangutans using this locomotion less than expected.

To investigate the hypothesis that suspensory behaviour increases with body size a linear regression was performed by plotting the subjects individually by the length of their forearm and their overall percentage of suspensory locomotion (Figure 2.2).

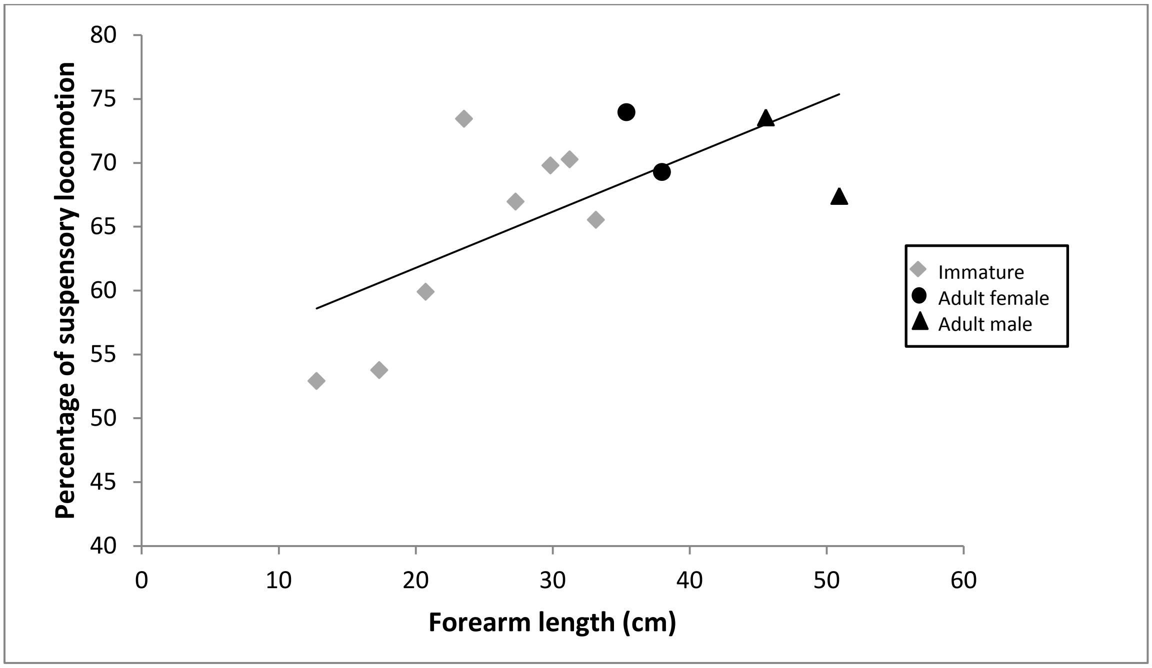

Figure 2.2 Total percentage of arboreal locomotion where the majority of body weight was borne in suspension (either orthograde or pronograde) plotted against subjects' forearm length. Data from 17 wild Bornean orangutans of different ages collected from July 2009- July 2010 at Tuanan Research Station.

A positive relationship between forearm length and suspensory behaviour was found (y=0.44x + 53) but the correlation is relatively weak (R^2= 0.46).

After finding a significant relationship between size and locomotion, we went on to examine these variables in relation to the habitat variables, which were used by orangutans for locomotion: the type and diameter of the main weight bearing support and the number of weight-bearing supports. Three different combinations of variables (Table 2.3) were tested to establish which variables were required to produce a well-fitting model.

Table 2.3 Comparing three log-linear models produced from different variable combinations. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Variable combination	**Likelihood ratio χ^2**	**DF**	**Sig level (*P*)**	**Model expressions (variable relationships)**
1. SIZE, TYPE, DIAMETER, NUMBER OF SUPPORTS	2.57	2	0.28	Size* type Type*diameter*no of sup Size*diameter*no of sup
2. LOCOMOTION, TYPE, DIAMETER, NUMBER OF SUPPORTS	3.46	2	0.18	Loco*diameter*no of sup Type*diameter*no of sup Loco*type
3. SIZE, LOCOMOTION, TYPE, DIAMETER, NUMBER OF SUPPORTS	21.31	26	0.73	Size*diameter Loco*diameter*no of sup Type*no of sup Size*loco*no of sup Size*loco*type

Table 2.3 shows that although models, which only included either size or locomotion and habitat variables (1 and 2) did produce a significant model, (*P*-values >0.05 are considered significant), the model, which includes all of the variables explains the data considerably better (*P*= 0.73). We, therefore, only examined the variable relationships found in this best-fitting model in further detail.

The hierarchical model of best fit (model 3 in Table 2.3) has five interaction terms and all lower order and main effects are subsumed under these terms. The terms in the model are ranked in order of their relative importance in the model, which was assessed by dividing the partial χ^2 by the degrees of freedom (Crook 1997) (Table 2.4). The most important terms in the model were size*diameter and locomotion*diameter*number of supports, as these have more than three times as much influence on the model than the next most important term, type*number of supports.

Table 2.4 Log-linear model of best fit including size, locomotion and habitat variables. DF, degrees of freedom. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Log-linear model expressions (variable relationships)	**Partial χ^2**	**DF**	***P***	**Standarised χ^2 (χ^2/DF)**
Size*diameter	61.29	2	<0.001	30.65
Locomotion* diameter* number of supports	116.18	4	<0.001	29.05
Type* number of supports	8.59	1	0.003	8.59
Size* locomotion*number of supports	18.17	8	0.02	2.27
Size* locomotion* type	14.64	8	0.07	1.83

As large contingency tables are notoriously difficult to disentangle, the individual terms in the model are presented here in separate charts and tables to ease interpretation. The interaction between size and support diameter (Figure 2.3) shows that smaller orangutans use small supports more, and large supports less, than larger orangutans. The grouped data support the hypothesis that larger orangutans use larger supports. To examine the strength of this relationship, a linear regression was carried out by plotting subjects individually according to their forearm length and the mean diameter of the main support they used in locomotion (Figure 2.4). The regression shows a positive linear relationship between forearm length and average support diameter ($y = 0.13x + 3.04$) with a strong correlation coefficient ($R^2 = 0.8$). The proximity of the adult subjects to the line of best fit indicates that they fit the trend very well.

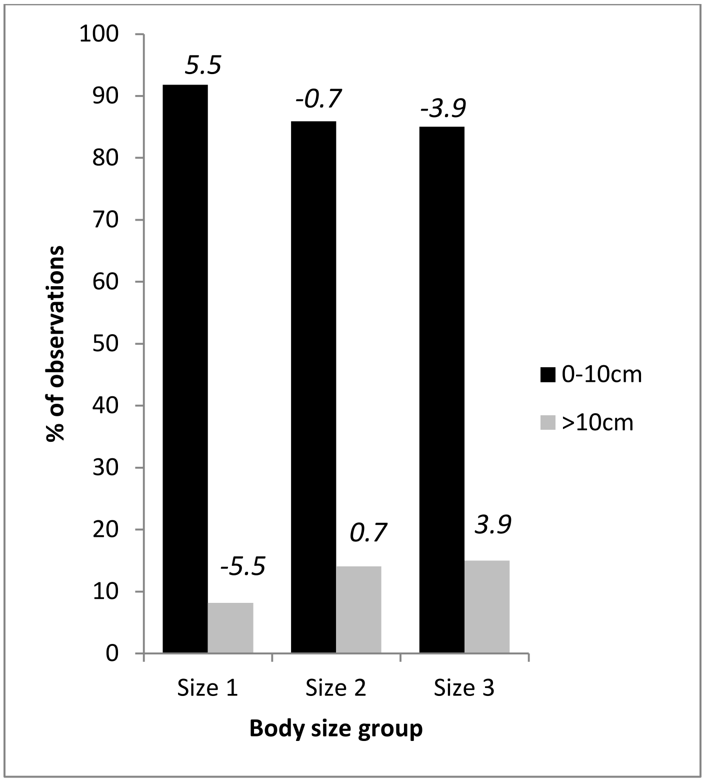

Figure 2.3 The log-linear model association: size * diameter. Size categories are based on forearm length. Black bars show % of small supports (<10cm) used and grey bars show % of large supports (>10cm) used. Values above bars are adjusted standardised residuals. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

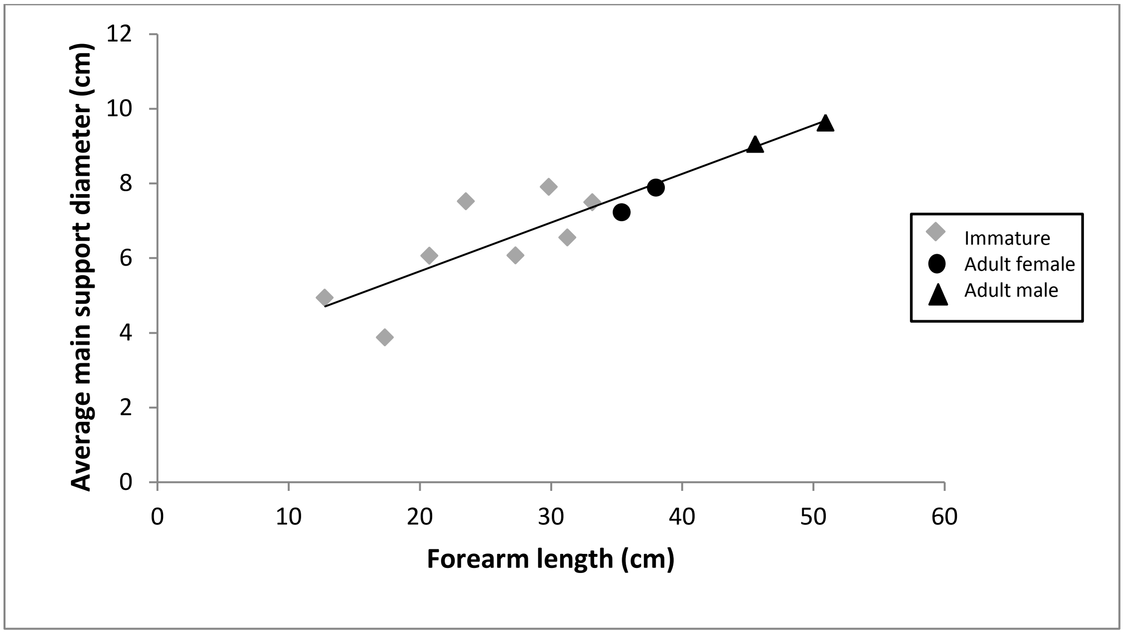

Figure 2.4 Mean main weight bearing support diameter used by each subject (calculated using the midpoint of each diameter class) plotted against subjects' forearm length. Immature orangutans plotted with diamond shaped points, adult females plotted with circular points and adult males plotted with triangular points. Data collected at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

The second most important interaction in Table 2.4 suggests that locomotion is strongly associated with the habitat variables diameter and number of supports used. Table 2.5 was constructed from a log-linear model of the variables locomotion, diameter and number of supports, the 3-way interaction was removed from the saturated model so that the residuals generated represent the 3-way interaction. These adjusted residuals indicate by their size and sign (+/-) the strength and direction of the relationship, respectively, between the type of locomotion and the corresponding support variable combination. Residuals with an absolute value greater than 2 indicate a significant association; therefore, all locomotion excluding orthograde compression has significant support associations. The residuals show that locomotion can be divided into two groups according its support variable associations, which are separated by a bold vertical line in Table 2.5. Locomotion where weight is borne in compression, and vertical climb and descent are associated with two distinct combinations: large single supports and multiple small supports, whereas suspensory locomotion is most strongly associated with small single supports and multiple large supports.

Table 2.5 Table for log-linear model interaction: locomotion * diameter * number of supports. Shaded boxes represent behaviour combinations that were observed more than expected. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Locomotion	**Orthograde compression**				**Pronograde compression**				**Vertical climb/descent**				**Orthograde suspension**				**Pronograde suspension**			
Diameter (cm)	0-10		>10		0-10		>10		0-10		>10		0-10		>10		0-10		>10	
Number of supports	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1
Frequency (%)	0.4	8.8	0.1	0.9	1.8	2.7	0.8	0.3	6.8	6.2	4.4	1.3	18.8	29.1	0.8	3.5	5.5	6.6	0.3	0.9
Adjusted residual	-1.5	**1.5**	**1.5**	-1.5	-4.5	**4.5**	**4.5**	-4.5	-7.7	**7.7**	**7.7**	-7.7	**8.5**	-8.5	-8.5	**8.5**	**3.4**	-3.4	-3.4	**3.4**

The interaction between habitat variables type and number of supports (Table 2.6) shows that orangutan locomotion is most associated with the support combinations: single liana and multiple tree supports.

Table 2.6 Contingency table for the log-linear model association: type * number of supports. Data from the locomotor behaviour of 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

	Number of supports		
Type	**1**	**>1**	**Total**
tree	39.2 (91.7) *-3.4*	60.8 (94.2) *3.4*	(93.2)
liana	48.5 (8.3) *3.4*	51.5 (5.8) *-3.4*	(6.8)

Each cell contains the row %, (column %) and the adjusted standardised residual (ASR), shown in italics. For example, 39.2% of locomotion on trees used single supports and 91.7% of all single support use observations were on trees.

The final two terms in the model, size*locomotion*number of supports and size*locomotion*type have the least influence on the model (standardised χ^2s of 2.27 and 1.83 and *P* values of 0.02 and 0.07, respectively) and there are fewer significant 3-way associations between the categories of the interacting variables (Table 2.7 andTable 2.8). Table 2.7 shows the relationship between size, locomotion and number of supports. Pronograde compression on multiple supports is more associated with size 1 (containing infant subjects) than the larger size categories. All size categories use multiple supports more frequently for orthograde compression yet only the largest orangutans use single supports, shown by the large positive residual (2.2). Orthograde suspension also occurs more on multiple supports and this type of locomotion is used more by larger orangutans. Single supports are favoured for climbing and multiple supports for pronograde suspension and the residuals show that these relationships are most pronounced at size 2 (containing juvenile subjects).

Table 2.8 shows the relationship between size, locomotion and support type. Pronograde compression is used more by smaller orangutans and only size 1 were observed to use this type of locomotion on lianas. Smaller orangutans climb and descend more than larger orangutans and size 1 orangutans are more likely to use lianas for this type of locomotion than larger orangutans. Larger orangutans use orthograde suspensory locomotion more than smaller orangutans and they are more likely to use lianas for this type of locomotion than the other size categories. Size 2 orangutans are more likely to use lianas for pronograde suspensory locomotion than other size categories.

Table 2.7 Table for model interaction size * locomotion * number of supports

Locomotion	**Orthograde compression**						**Pronograde compression**						**Vertical climb/descent**						**Orthograde suspension**						**Pronograde suspension**					
Size group	Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3	
Number of supports	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1	1	>1
Frequency %	0.1	2.4	0.0	1.4	0.4	5.9	0.7	1.1	0.7	0.5	1.3	1.4	3.2	2.3	3.2	1.4	4.9	3.7	3.2	5.6	4.5	5.6	11.9	21.5	1.1	1.3	1.3	1.9	3.4	4.3
Adjusted residual	-0.8	**0.8**	-1.9	**1.9**	**2.2**	-2.2	-1.5	**1.5**	**0.8**	-0.8	**0.7**	-0.7	-0.2	**0.2**	**1.5**	-1.5	-1.1	**1.1**	**0.4**	-0.4	**0.9**	-0.9	-1.1	**1.1**	**1.2**	-1.2	-2.7	**2.7**	**1.4**	-1.4

Table 2.8 Table for model association size * locomotion * type

Locomotion	**Orthograde compression**						**Pronograde compression**						**Vertical climb/descent**						**Orthograde suspension**						**Pronograde suspension**					
Size group	Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3		Size 1		Size 2		Size 3	
Type	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana	Tree	Liana
Frequency %	2.3	0.1	1.4	0.0	6.1	0.2	1.7	0.1	1.2	0.0	2.6	0.0	4.9	0.7	4.2	0.4	8.3	0.3	7.9	0.8	9.1	1.1	31.4	2.0	2.2	0.2	2.6	0.6	7.2	0.4
Adjusted residual	-0.1	**0.1**	**1.1**	-1.1	-0.8	**0.8**	-2.1	**2.1**	**1.1**	-1.1	**1.1**	-1.1	-2.4	**2.4**	**0.4**	-0.4	**1.9**	-1.9	**1.4**	-1.4	**0.7**	-0.7	-2.0	**2.0**	**1.4**	-1.4	-2.2	**2.2**	**0.9**	-0.9

2.4 Discussion

The aim of this study was to take a cross-sectional sample of orangutan locomotion from its onset during infancy through to adulthood to examine the changes that take place with growth and development. This study shows distinct size-related trends in three key types of locomotor behaviour: pronograde compression, orthograde suspension and vertical climb/descent. Pronograde compression (quadrupedalism) on arboreal supports was negatively correlated with body size and this is likely to be due to the constraints of large body size in the arboreal habitat. Larger animals used quadrupedal locomotion, but this was mainly during terrestrial travel which was not included in this analysis. Arboreal quadrupedalism is associated with single large supports and multiple small supports (i.e. support combinations with a large continuous horizontal surface area). Smaller orangutans were able to walk quadrupedally on a larger proportion of their habitat because more of the available supports were large relative to their body size.

This study found that orthograde suspension was the most common type of locomotion accounting for 52% of all locomotor behaviour and this is comparable with the results of previous studies, which also found that suspensory locomotion makes up approximately half of all locomotion observations (Cant 1987b; Thorpe and Crompton 2005; Manduell et al. 2011). This study found that the proportion of orthograde suspension was greater in the locomotor repertoires of larger orangutans, which supports the body size suspension theory of Cartmill and Milton (1977). The disturbed forest at Tuanan has an abundance of small supports making it an ideal place to test the hypothesis that larger animals suspend more because thin supports are more stable when weight is borne by suspension below the support rather than in compression from above it (Cartmill and Milton 1977). Eighty-seven percent of orangutan locomotion at Tuanan occurred on small supports (<10cm in diameter) compared with 59% at Ketambe

(Thorpe and Crompton 2005) and locomotion on single small supports was strongly associated with both pronograde and orthograde suspensory behaviour. Although pronograde suspension was strongly associated with single small supports, there was no clear size-related trend. However, this category included both inverted quadrupedal locomotion and pronograde bridging and bridging is used by all orangutans to cross gaps in the canopy (see Chapter 4).

Vertical climb and descent are negatively correlated with body size: they make up on average 19% of orangutan locomotion but size 1 orangutans (infants) are almost twice as likely to climb and descend as larger orangutans. Climbing is energetically costly, particularly for larger animals (Thorpe et al. 2007a) and, therefore, it is advantageous for orangutans to make as few vertical deviations as possible. However, horizontal travel may be disrupted by gaps in the canopy. Larger animals have a longer reach and a greater mass, which facilitates gap crossing methods that utilise compliant supports: appendicular and mass deformation (Cant 1994; Chapter 4). This allows larger animals to cross more of the gaps that they encounter without making vertical deviations whereas smaller orangutans may find it easier to climb or descend to a level where the gap in the canopy is narrower.

The results of this study support the prediction that larger orangutans use larger supports. The degraded habitat around the research area may have contributed to this finding. Small supports dominate disturbed forests and smaller orangutans experience more stability on smaller supports so they are able to use a greater proportion of the supports that are available whereas larger orangutans may need to take routes where larger supports are available. A positive relationship between body size and support diameter was also found by Cant (1987) and Remis (1995) when looking at the difference between adult male and female orangutans and gorillas, respectively. Interestingly, Thorpe and Crompton (2005) did not find that support diameter correlated with body size while observing orangutans at the same site as Cant (1987), but, instead, they found that the smaller adult females opted for larger supports than adult males and they attributed this to the females adopting a more cautious approach to locomotion after first parturition regardless of whether they were accompanied by dependent offspring. In our study we found no apparent effect of sex on adult orangutan support use. Adult females used smaller supports than adult males, which correlated with their respective body sizes. The adult female subjects we sampled all had young offspring and all were observed carrying their offspring during this study so their apparent lack of more cautious locomotor behaviour is somewhat surprising. Habitat differences may explain the different results of these studies, since orangutans in disturbed forest travel lower in the canopy than those in pristine forest and there are less large supports at lower levels of the forest (Manduell et al., 2011; pers. obs.). If an orangutan were to fall from low in the canopy the chance that it would result in serious injury is much lower, especially for a small orangutan. Hence, there may be less motivation for mothers with infants to be more cautious.

The combination of support diameter and number of supports are found together in the most important model interaction to involve locomotion (Table 2.5). This makes sense biologically because as large arboreal animals, orangutans must find support combinations that bear their weight and several small supports may be used as the equivalent to one large support. Different types of locomotion require different levels of stability and continuity. For example, locomotion where limbs are held at right angles to the body such as quadrupedal walk and vertical climb were found to be associated with the continuous large support combinations: either one large support or multiple small supports (often entwined together to form a continuous mesh). Sumatran orangutans were also found to prefer single large supports for quadrupedal locomotion (Thorpe and Crompton 2005; Thorpe et al. 2007b) but these authors did not find an association with multiple small supports. Habitat differences may account for this, as there are a greater proportion of large supports in the pristine forest where the study of Sumatran orangutans was carried out. Quadrupedal scrambling over meshes of interwoven small supports may be an adaptation to locomotion in a degraded forest. In contrast, suspensory locomotion was found to be a more flexible behaviour, associated with travel on single thin supports, allowing orangutans to gain access to the terminal branches where the majority of the fruit is located. Suspensory locomotion is also associated with multiple large supports, which are typically spaced further apart; the abducted limbs allow orangutans greater reach which enables them to cross discontinuous canopy.

We found that body size and locomotion were strongly associated when examined in a 2-way contingency table (Table 2.2), and these variables were also in two of the terms in the final log-linear model of size, locomotion and habitat variables (Table 2.4). The type and number of supports used were both in separate interactions with size and locomotion, which indicates that the association between size and locomotor behaviour is modified by the habitat variables type and number of supports. However, these terms were the least influential in the model so the relationships between the variables were more difficult to interpret than those with higher standardised chi-squared values. The ranked model interactions indicated that locomotion is more strongly tied to habitat variables than body size but body size is also present in the most important model interaction, the 2-way interaction with diameter. This indicates that support use is strongly influenced by body size and as locomotion is most strongly related to support use, so trends in the availability of different sized supports are likely to contribute to the size-related differences seen in locomotion.

Almost all lianas in the forest around Tuanan were in the small diameter category (<10cm) and, hence, we needed to define structural zeros (combinations of variables that could not possibly occur). Lianas were used more by smaller orangutans, which could simply be an artefact of their small diameter. However, lianas have different properties from tree supports: vertical lianas hang from trees, allowing them to be easily oscillated and they are, therefore, ideal supports for small orangutans to use to cross gaps. Lianas are strongly associated with suspensory locomotion in all orangutan size categories but smaller orangutans show more variation in their liana locomotion often using them for vertical climb/descent. Our study could not ascertain whether smaller orangutans use lianas for more types of locomotor behaviour simply because they are more able to use supports with small diameters than larger orangutans or whether other physical properties of lianas facilitate their use by smaller orangutans. To investigate fully the relationship between body size and support type, we would need to compare the use of liana and tree supports across different diameter categories and this would require a study site with a greater density of large lianas such as those in more pristine forests.

The aim of our study was to investigate the effect of body size on locomotor behaviour, however we acknowledge that by sampling individuals ranging from infant to adult, differences in observed locomotor behaviour may have been due to both size and locomotor ability, which have both physical and cognitive components. For example, analysis of the gap crossing behaviour of Tuanan orangutans (Chapter 5) has shown that orangutans progress in their ability to utilise compliant supports for gap crossing between the ages of 1 and 6 which correspond to the first two size groups in this study. As skills like oscillating a tree back and forth require both cognitive and physical development, differences between the gap crossing behaviour of infants and adults are likely to be due to the combined influence of body size and skill acquisition. For the purpose of the present analysis, we categorised locomotion according to the orientation of the trunk and whether weight was borne in suspension or compression in order to minimise any effect of skill acquisition, and specifically the ability to manipulate compliant supports. For example, rather than grouping oscillatory behaviours together as have previous studies (Thorpe and Crompton 2005; Manduell et al. 2011) our study assigned them to different categories according to the position of their body.

Although it is not possible to interpret the effects of growth and skill acquisition separately as they are highly correlated, it is possible to identify the specific results, which may have been influenced by skill acquisition. The variables, which showed correlation with body size were support diameter and type of locomotion. It is possible to conceive that locomotor ability could influence the choice of support diameter in two ways: firstly, it is more difficult to balance on a smaller support and this could cause less skilled individuals to use larger supports. Secondly, individuals that are not as skilled in support manipulation may not be able to manipulate larger, less compliant supports and this would cause less skilled individuals to use smaller supports. Overall, it is unlikely that locomotor ability substantially influenced the relationship between body size and support diameter. Of the three types of locomotion that were found to correlate with body size, pronograde compression and orthograde suspension are strongly associated with large and small supports, respectively. Therefore, variation in use is likely to be related to the constraints of the habitat, which vary with body size rather than skill. However, the higher frequencies of vertical climb and descent in smaller orangutans may have been related to their ability to cross gaps in the canopy, a combination of both body size and cognitive ability.

In conclusion, log-linear analysis has proved to be a useful technique for establishing relationships between multiple categorical variables. It has allowed us to examine multiple hypotheses within the same model and provided values with which to assess the importance of different variable relationships. Our study has found that the locomotor behaviour of Bornean orangutans was most strongly associated with the habitat variables diameter and number of supports and that body size was most strongly associated with support diameter. Although not present in the most important model interactions, our study has found a relationship between body size and locomotor behaviour, specifically in the frequencies of pronograde compression, orthograde suspension and vertical climb/descent. It is unfortunate that we were not able to analyse the data using the full detail in which it was collected. As the data were clustered around variable combinations that were very common, it was not possible to use log-linear analysis to investigate the rarest behaviour combinations. Consequently, rare behaviours that were associated with particular body size groups did not contribute to this model and, therefore, we may have under-estimated the effect of body size on locomotor behaviour. Yet, our study has found a relationship between body size and the locomotor behaviour of Bornean orangutans in disturbed peat-swamp forest. As habitat type is also likely to influence positional behaviour, more data are required on the positional behaviour of young orangutans in less disturbed forests. Moreover, much larger datasets are needed in order to model locomotion data using the fine-scale categories with which it is recorded. Long-term studies of orangutan locomotion in different habitat types are essential to understand fully the development of locomotor behaviour in these species.

2.4.1 Next step

After finding body size related differences in positional behaviour and support use during orangutan locomotion the aim of chapter 3 was to establish whether the same relationships existed during static behaviour. As predicted by Cartmill and Milton (1977) orangutan suspensory behaviour was found to increase with increasing body size during arboreal locomotion, effectively increasing their stability on thin, flexible branches. During posture orangutans also use thin branches in the periphery of trees in order to access the fruit which grows there. Therefore, larger orangutans may need to use more suspensory posture during feeding behaviour. However, unlike locomotion, postures often occurs for long durations and support stability may have a greater influence on orangutan support selection than it does during locomotion where support contact time is usually very short. Chapter 3 investigates the positional strategies of different sized orangutans during static behaviour.

3. THE INFLUENCE OF BODY SIZE ON THE POSTURAL BEHAVIOUR OF BORNEAN ORANGUTANS (*Pongo pygmaeus wurmbii*)

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Abstract

Arboreal habitats are complex environments where vegetation is abundant but stable supports are in short supply. As branches taper towards their ends, the peripheries of trees offer the least stable supports but this is where the majority of the fruit is located. Orangutans are the largest predominantly arboreal primates and, therefore, dealing with compliant branches is a problem which they are expected to be well adapted to cope with. Orangutans have a diverse repertoire of postural behaviour that allows them to carry out all of their daily activities in the forest canopy. The aim of this study was to examine the influence of body size on arboreal postural behaviour and support use. We recorded the postural behaviour and support use of wild Bornean orangutans ranging from infants to adults. We were able to quantify body size variation using a non-invasive, photographic measurement technique, which allowed us to model the relationships between body size, posture and support use variables. This study found that suspensory posture decreased as body size increased, which challenges the theory that larger animals should suspend more to gain stability on compliant supports. Instead, larger animals were found to gain stability by using larger supports to bear their weight and by spreading their weight over multiple supports when using small supports. In contrast, small orangutans used single small supports more often, particularly favouring lianas. More risky forms of posture such as suspension from one limb were

most associated with the infant and juvenile subjects. This study has highlighted the need to sample all ages within a population to understand fully the influence of growth and development on the postural behaviour of orangutans.

3.1 Introduction

Orangutans are the largest predominantly arboreal primates, which makes their positional behaviour a subject of great interest because travelling and feeding in a complex, fragile environment is challenging for large bodied animals. Positional behaviour is comprised of locomotion and posture; posture describes behaviour where the centre of mass remains stable and locomotion involves displacement of body mass (Prost 1965). To date, most studies of orangutan positional behaviour have focused on locomotion (Sugardjito 1982; Thorpe and Crompton 2005; Thorpe et al. 2007a; Thorpe et al. 2007b; Thorpe et al. 2009; Manduell et al. 2011), but posture accounts for approximately 90% of an orangutan's daily activity (Thorpe and Crompton 2006). Orangutans have a diverse repertoire of postural behaviour (Thorpe and Crompton 2006) which allows them to feed and travel within the forest canopy. Orangutans are primarily frugivorous and the majority of fruit is located in the terminal branches of trees. As branches taper towards their ends (Grand 1972), feeding on thin supports is a particular problem that orangutan posture has adapted to cope with.

For large bodied animals using small supports, positions where body weight is borne in suspension are thought to be more stable than positions where weight is borne in compression (Cartmill and Milton 1977). This has led to the hypothesis that suspensory behaviour should increase with increasing body size. Previous studies of orangutan positional behaviour have found limited evidence to support this theory when the influence of body size on positional behaviour was examined by using broad age-sex categories as a correlate for body size (Sugardjito and van Hooff 1986; Thorpe and Crompton 2005, 2006; Manduell et al. 2011). These studies compared the locomotor behaviour of adult males, adult females and adolescents and did not find size-related variation in suspensory behaviour. However, an analysis of a large sample of Bornean orangutans ranging from infant to adult (see Chapter 2) found that suspensory locomotion increased with increased body size in accordance with the theory of Cartmill and Milton (1977). When the influence of body size on postural behaviour was examined, previous studies have found that as size increased, the frequency of suspensory posture also decreased (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2006), which contradicts the body size suspension hypothesis (Cartmill and Milton 1977). However, the only immature subjects included in these studies were already adolescent, with the youngest subjects sampled by Sugardjito and van Hooff (1986) and Thorpe and Crompton (2006) being 6 and 7 years old, respectively, and Cant (1987a) only included adults. Therefore the effect of body size on posture during ontogeny remains unclear.

Arboreal supports decrease in stability as diameter decreases and load increases (Grand 1972) and, therefore, larger animals have been predicted to use larger supports (Cant 1992) or distribute their weight over a greater number of supports (Cartmill and Milton 1977). Previous studies of orangutan posture have found evidence that larger orangutans use larger supports (Cant 1987a; Myatt and Thorpe 2011). In addition Myatt and Thorpe (2011) found that when orangutans used smaller supports they were likely to use a greater number of supports than when they used larger supports, although they were not able determine how this relationship changed with body size. In order to interpret the complex interactions between body size, postural behaviour and support use variables, samples are required of the full range of orangutan body sizes.

Previous studies have also identified differences in the positional behaviour of the two species of orangutan. Sumatran orangutans were found to exhibit more pronograde positional behaviour compared to Bornean orangutans that used more orthograde behaviour (Thorpe and Crompton 2009;

Manduell et al. 2011). It is unclear whether this is a difference between the orangutan species or an adaptation to the habitat where the studies were conducted. Studies of Sumatran orangutans were conducted in pristine dry land forest (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2006; Myatt and Thorpe 2011) whereas the Bornean orangutan studies have been carried out in degraded forest in both dry land forest (Cant 1987b) and swamp forest (Manduell et al. 2011). Orthograde positional behaviour is suggested to be an adaptation that enables orangutans to use thin terminal branches (Grand 1972; Hunt 1996; Crompton et al. 2008) and, therefore, Sumatran orangutans may have exhibited higher levels of pronograde suspension because there are more large supports in the pristine rain forest.

There are also methodological considerations when making comparisons between different studies. Studies of primate positional behaviour use one of two methods of sampling- instantaneous time sampling (ITS) or bout sampling. These are used to address different questions with bout sampling used for questions related to the number of occurrences of a behaviour and ITS used for questions about the proportion of time for which a behaviour persisted (Dagosto 1994). However, Doran (1992a) found that ITS and bout sampling methods can provide comparable results when sample sizes are large. Both suffer from non-independence of data points (Dagosto 1994; Gebo and Chapman 1995; Warren and Crompton 1997) as successive observations may not be independent of the last. This is a particular problem for ITS sampling of postural behaviour because a single posture often lasts longer than the sample interval. Myatt and Thorpe (2011) avoided the problem of non-independence by taking only one posture data point between each bout of locomotion. However, this method of sampling is likely to under-represent postures which tend to occur for long periods of time when animals are feeding and resting and over-represent postures that occur when animals pause briefly during travel. This is likely to have a homogenising effect on postural datasets. Therefore, a measure which takes account of posture duration is important to examine the subtle differences in positional behaviour between animals of the same species with different body sizes.

In wild orangutans, the immature phase typically lasts a minimum of 10 years (Wich et al. 2004) and this comprises a wide range of body sizes. To date no study has compared the positional behaviour of immature orangutans at different stages of development. Although previous studies have included immature subjects, for the purpose of analysis they have been grouped within a single category (Sugardjito and van Hooff 1986; Thorpe and Crompton 2005; Manduell et al. 2011; Myatt and Thorpe 2011). Therefore changes that take place during ontogeny have not been properly addressed. During ontogeny young primates experience both physical and cognitive development. These changes may influence both postural behaviour and habitat use. In particular the prevalence of play behaviour during ontogeny is likely to influence the types of postures exhibited and the supports which are used. Mammalian play has been described as training for the unexpected (Spinka et al. 2001) and often involves more risky behaviours. Postures that are more risky may involve suspending from only one limb or using thin, flexible supports. In particular, the use of lianas is expected to be more common in the postural behaviour of smaller orangutans because these supports are readily oscillated, which is a key orangutan play behaviour (MacKinnon 1974). By using body size rather than age it is possible to assess the impact of both ontogenetic and sex-related variation in body size on the postural behaviour of orangutans.

The main aim of this study was to determine how the changes in body size that occur throughout life influence the postural behaviour and support use of orangutans. We will examine the following hypotheses: 1) Larger orangutans use more suspensory postures to increase stability on thin supports (Cartmill and Milton 1977); 2) Larger orangutans use larger supports to bear their body weight; 3) When using smaller supports, larger orangutans distribute their weight over multiple supports more often than smaller orangutans (Cartmill and Milton 1977); and 4) Smaller orangutans utilise lianas more than larger orangutans, which is likely to correspond with the age range when play behaviour is most frequent.

3.2 Methods

This study was conducted at Tuanan field station (2°09'S, 114°26'E) within the Mawas Reserve, Central Kalimantan, Indonesia. The study area consists of approximately 725 ha of lowland peat-swamp forest with an orangutan density of 4.25/km^2 (van Schaik et al. 2005). This area has been subjected to selective logging and as a result the forest is dominated by young, small trees. Prior to the onset of continuous research at Tuanan in 2003, a grid-based trail system was cut and orangutans in the area were identified and habituated to human observers. This study was carried out in June-October 2009 and January-July 2010. The study subjects were 17 wild Bornean orangutans including individuals of all age-sex categories (Table 3.1). The immature subjects ranged in age from 1 to 11 years.

Table 3.1 Orangutans observed at Tuanan Research Station, Central Kalimantan between July 2009 and July 2010. Age-sex category incorporates subject's sex and maturity, forearm length was measured from photographs taken during observation and focal days is the number of whole days of observation.

Subject	Age-sex category	Forearm length (cm)	Focal days
Mawas	Infant female	12.8	10
Kino	Infant male	17.4	10
Jip	Juvenile male	20.7	10
Deri	Juvenile male	23.5	7
Jerry	Immature male	27.3	10
Streisel	Immature female	29.9	9
Milo	Immature female	31.3	7
Ido	Immature male	~32	6
Kondor	Immature female	33.2	10
Juni	Adult female	35.4	5
Kerry	Adult female	38.0	5
Mindy	Adult female	~40	4
Budhi	Sub-adult male	~42	1
Ekko	Sub-adult male	~45	2
Gismo	Sub-adult male	45.6	4
Preman	Adult male	50.9	3
Isidor	Adult male	~50	2

Data collection employed focal animal sampling (Altman 1974) by following an individual until it made a night nest (between 15:00 and 19:00) and arriving before it awoke the next day at approximately 04:45. Subjects were followed for a maximum of 10 days per month and effort was made to sample each individual in more than one month to minimise the effect of any bias related to temporarily available food sources such as seasonally fruiting trees (Thorpe and Crompton 2005). Instantaneous sampling at the 1-minute mark was used to sample postural behaviour and support use. A digital watch with an auto-repeat countdown vibration alarm function was used to ensure that instantaneous sampling was accurate without disturbing the orangutans. Postural behaviour was defined according to the classifications of orangutan positional behaviour by Thorpe and Crompton (2006) which was based on the standardised classification system of Hunt et al. (1996). Where necessary, additional modes of positional behaviour observed in the study subjects but not represented in the classification of Thorpe and Crompton (2006) were described according to the principles proposed by Hunt et al. (1996). Thus modes of posture were assigned based on the orientation of the body, which limbs were bearing weight, whether they were bearing weight in suspension or compression, and whether the limbs were flexed or extended (Hunt et al. 1996). The number of weight-bearing supports and the type and diameter of each support were recorded for postures involving up to four supports (Thorpe and Crompton 2005). If more than four supports were used only the type and diameter of the main weight-bearing support was recorded (Cant 1987b). All data were collected by a single observer (ACP) and periods of self-training in classifying behaviour and estimating support diameters were undertaken prior to and during data collection to ensure consistency and accuracy.

To quantify the body size of each individual a non-invasive laser photography technique (Rothman et al. 2008, Chapter 2- Figure 2.1) was used whereby parallel green lasers were attached to a camera (Canon EOS 400D) using a specifically designed aluminium frame. The lasers were held in the frame exactly 4cm apart and provided visible marks on the photograph which were used as a scale bar. The lasers were used to measure the subject’s limbs, which were photographed when they were perpendicular to the field of view of the camera to avoid errors associated with foreshortening. The photographs were measured using Image J version 1.43 (Bethesda, MD). As orangutans have a high intermembral index (the ratio of forelimb to hindlimb length) their forelimbs show greater variation in length than their hindlimbs. In practise it was easier to measure the forearm than the upper arm in photographs because locating the shoulder joint was more difficult than locating the wrist. We, therefore, chose to use forearm length as a proxy for overall body size.

Forearms were measured from the elbow to the wrist, using the prominent olecranon process of the ulna and the radio-carpal joint to locate these points. For each subject at least five suitable photographs were measured and the largest value was taken to be the closest to the true length because foreshortening can only cause underestimation. Sufficient photographs were obtained for 12 of the 17 subjects listed in Table 3.1, and forearm lengths of the remaining five unmeasured subjects were estimated by comparing them to measured individuals when they were observed together in the field.

During data collection 135 biomechanically distinct sub-modes of posture were observed. However, for the purposes of this chapter posture was divided into 11 positional modes: hindlimb suspend, forelimb-hindlimb suspend, orthograde forelimb suspend, orthograde quadrumanous suspend, pronograde suspend, cling, orthograde stand, pronograde stand, squat, sit and lie. These were the same categories used by Myatt and Thorpe (2011) with the addition of lie which was not present in their study of feeding posture.

Due to the constraints of the sample size only two categories could be used for each of the support use variables. In the field, the arboreal support types- trunk, bough, branch and liana were distinguished, and were analysed in two categories, tree and liana. The diameter categories were recorded using the following categories also used by previous studies (Cant 1987a; Thorpe and Crompton 2006; Thorpe et al. 2009; Myatt and Thorpe 2011): <2, ≥2-<4, ≥4-<10, ≥10-<20, ≥20-<40 and ≥40cm but for the categorical analysis only two diameter categories were used: <10 and >10cm. Similarly, the number of supports was conflated into two categories: 1 support and >1 support. The conflation decisions were made on the basis of the best fitting model with sufficiently high cell frequencies.

3.2.1 Statistical analysis

Instantaneous sampling of postural behaviour causes non-independence of data points because each mode of posture may span multiple sample intervals. However, methods that discard non-independent data points (Hunt 1992a; Myatt and Thorpe 2011) under-represent postures that tend to occur for a long time and over-represent behaviours with short durations (Doran 1992a). Another method of dealing with dependent data points is to take a random sample of 25% of the dataset (Warren and Crompton 1997; Thorpe and Crompton 2006) to reduce the likelihood that dependent data points will be included. Our study compared percentages of postural behaviour in a 25% random sample with those calculated using all the data to examine whether dependent data affected the frequencies and we found that frequencies of postures were approximately the same in both samples (see Table 3.7).

A combination of methods was used to analyse the relationships between the categorical variables: type of posture, support type, support diameter and number of supports and the continuous body size variable forearm length. Firstly, regression analysis was used to establish the relationships between forearm length and the amount of suspensory posture and the average support diameter. Next log-linear analysis was used to obtain a model which contained the most significant variable interactions (see Thorpe and Crompton 2005; Thorpe et al. 2007b; Manduell et al. 2011; Chapter 2). The significant model terms were examined individually by looking at the residual patterns using chi squared contingency tables (for categorical variables) and by further regression analysis for interactions that involved the continuous covariate forearm length.

3.3 Results

Overall, 30031 instantaneous observations of orangutan postures were made from 17 individuals. ‘Sit’ was the most frequently observed orangutan posture comprising 51% of the observations. Suspensory postures accounted for 35% of observations and the most frequently observed types were orthograde forelimb suspend (12%) and forelimb-hindlimb suspend (11%). The majority of orangutan posture (90%) used supports with diameters of less than 10cm as the main weight-bearing support. Only 4% of postural behaviour used lianas as the main support, and the remaining 96% occurred on tree supports. Orangutans used single and multiple supports in approximately equal proportions: 48% and 52%, respectively.

Linear regression was carried out to look at the relationship between postural behaviour and body size. To examine the hypothesis of Cartmill and Milton (1977) the overall percentage of suspensory posture was plotted against forearm length for each subject (Figure 3.1). A significant negative correlation (R^2=0.78, <0.0001) between forearm length and percentage of suspensory posture was found (Figure 3.1). This indicates that larger orangutans are more likely to use postures where weight is borne in compression whereas smaller orangutans are more likely to use suspensory positions during static behaviour. The relationship between body size and suspensory posture has been fitted with a logarithmic line of best fit as the data points most closely fitted this curve. The logarithmic relationship indicates that the rate of change in suspensory posture slows as the animal gets larger. Therefore, the Ln (forearm length) has a direct relationship with the percentage of suspensory behaviour.

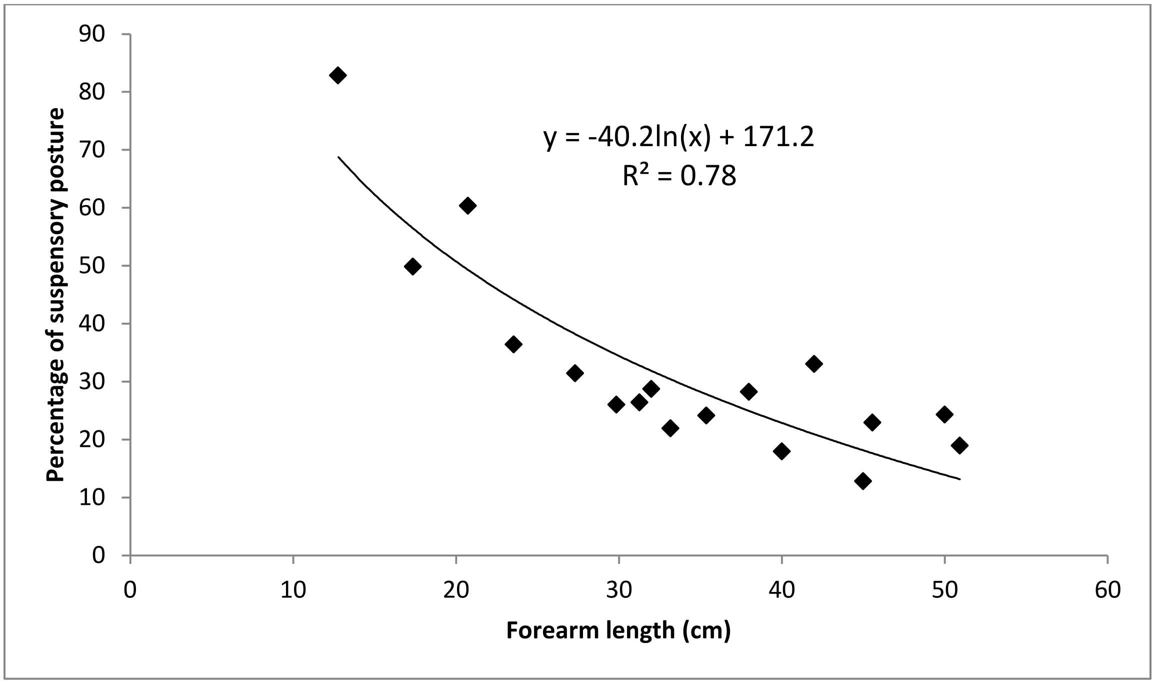

Figure 3.1 Relationship between total percentage of arboreal posture where the majority of body weight was borne in suspension (either orthograde or pronograde) plotted and forearm length. The data are fitted with a logarithmic line of best fit. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

As larger orangutans did not appear to be gaining stability by using more suspensory types of posture (Figure 3.1), another regression was carried out to investigate how the average support diameter used in posture changed with forearm length (Figure 3.2). A positive linear relationship was found between forearm length and average support diameter. This shows that larger orangutans use larger supports to bear their weight during static behaviour.

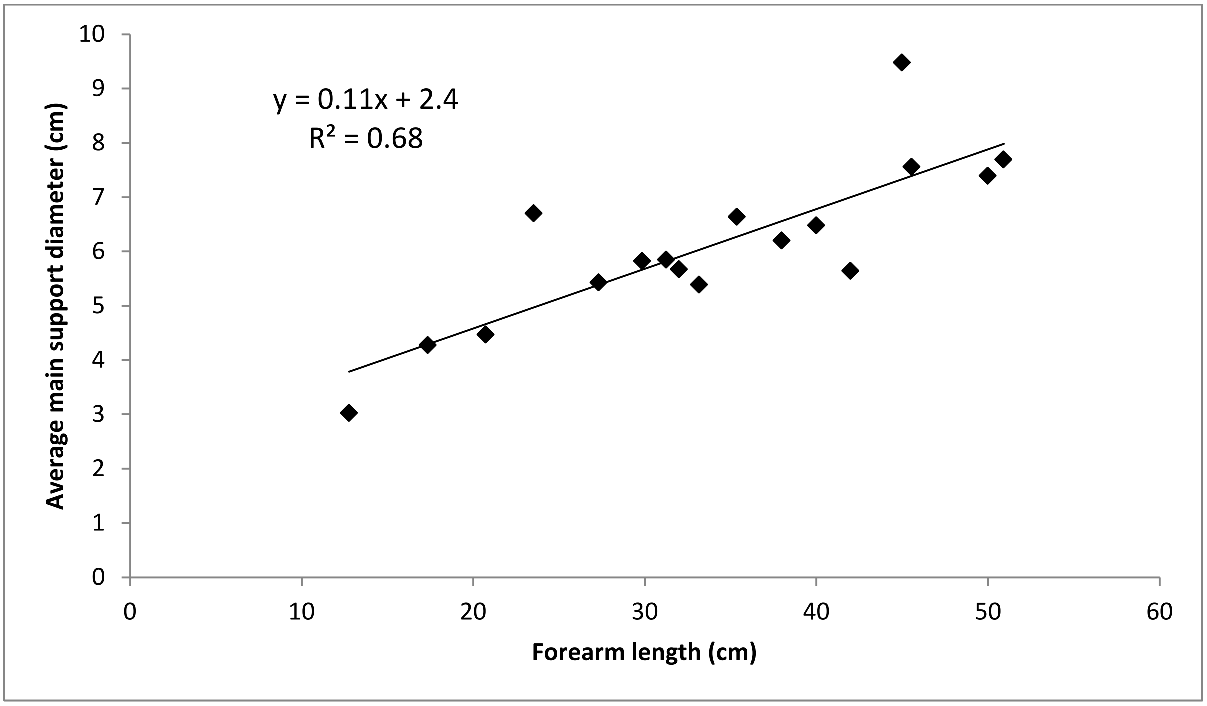

Figure 3.2 Mean main weight bearing support diameter used by each orangutan (calculated using the midpoint of each diameter class) plotted against forearm length. Posture data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

To examine the multivariate relationships between body size, posture and the habitat variables of support diameter, type and number of supports, log-linear analysis was carried out using a continuous covariate (forearm length) with the remaining categorical variables treated as factors. Following backwards elimination of all terms with *P*-values >0.05, the hierarchical model of best fit (*P*=0.76, 5 degrees of freedom) contained six variable relationships listed in Table 3.2. The model contains one 3-way and five 2-way terms and all lower order and main effects are subsumed under these terms. The terms are listed in order of their importance in the model which was calculated by dividing the partial χ^2 values by their degrees of freedom (Crook 1997). All of the significant model interactions were examined in further detail to determine the nature of the relationship between the variables.

Table 3.2 Log-linear model of best fit for the variables: forearm length, posture, support type, diameter and number of supports. DF, degrees of freedom. Posture data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Log-linear model expressions (variable relationships)	**Partial χ^2**	**DF**	***P***	**Standarised χ^2 (χ^2/DF)**
Posture*number of supports	288.37	10	<0.0001	28.84
Forearm length * diameter* number of supports	13.68	1	<0.001	13. 68
Posture*diameter	103.61	10	<0.0001	10.36
Forearm length * posture	79.95	10	<0.0001	8.00
Posture* type	69.40	10	<0.0001	6.94
Forearm length* type	4.80	1	<0.05	4.80

Likelihood ratio $\chi^2 = 2.59$, DF = 5, $P = 0.76$, $n = 30031$ observations. $p<0.0001$

The most important interaction in the model is posture * number of supports. This indicates that orangutan postural behavior differs according to whether they are using single or multiple supports. Relationships involving two categorical variables can be examined using χ^2 contingency tables. The adjusted residuals (ASRs), as shown in Table 3.3, indicate by their size and sign, the strength and direction of the relationship between each posture and the use of single or multiple supports. Adjusted residuals with absolute values greater than 2 indicate a significant relationship. The results show that orthograde quadrumanous suspend, forelimb-hindlimb suspend, pronograde suspend, orthograde stand, pronograde stand and squat are all strongly associated with multiple supports whereas sit, lie, cling and hindlimb suspend are strongly associated with single supports. Orthograde forelimb suspend does not show a significant association with either single or multiple supports.

Table 3.3 Contingency table for the association: Posture * number of supports. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Postural behaviour	**Number of supports**		
	1	**>1**	**Total**
Hindlimb suspend	3.9 (81.3) *17.9*	0.8 (18.7) *-17.9*	2.3
Forelimb-hindlimb suspend	8.3 (34.7) *-16.2*	14.3 (65.3) *16.2*	11.4
Orthograde forelimb suspend	12.2 (46.9) *-1.1*	12.6 (53.1) *1.1*	12.4
Orthograde quadrumanous suspend	0.9 (8.3) *-32.4*	9.3 (91.7) *32.4*	5.3
Pronograde suspend	1.3 (19.4) *-17.8*	4.9 (80.6) *17.8*	3.2
Cling	0.8 (89.5) *9.6*	0.1 (10.5) *-9.6*	0.4
Orthograde stand	1.4 (11.2) *-32.4*	10.4 (88.8) *32.4*	6.1
Pronograde stand	0.9 (21.5) *-12.7*	2.9 (78.5) *12.7*	1.9
Squat	0.2 (26.7) *-4.6*	0.6 (73.3) *4.6*	0.4
Sit	63.3 (59.2) *40.5*	39.9 (40.8) *-40.5*	51.1
Lie	6.8 (59.2) *9.5*	4.3 (40.8) *-9.5*	5.5
Total	47.8	52.2	100

Each cell contains the row %, (column %) and the adjusted standardised residual (ASR), shown in italics. For example, 3.9% of the locomotion on 1 support was hindlimb suspension and 81.3% of all hindlimb suspension was observed on one support. Pearson $\chi^2 = 3992$, DF=10 and P<0.0001

The second most important term in the model is the 3-way interaction: forearm length * diameter * number of supports. The presence of a 3-way interaction including the covariate forearm length indicates that the relationship between the number of supports and the main diameter of support used differs according to the size of the animal. This was examined through multiple regressions of support use combinations plotted against the individual's forearm length. When using a single support, smaller orangutans use small diameter supports more than larger orangutans (Figure 3.3A & E), and larger orangutans use large diameter supports more than smaller orangutans (Figure 3.3B & E). All orangutans use multiple small diameter supports regularly and there is no body size-related trend in this (Figure 3.3C). However, larger orangutans tend to use multiple large diameter supports more than smaller orangutans (Figure 3.3D, but not significant at P=0.11). When orangutans use small diameter supports, smaller orangutans tend to use single supports more than larger orangutans and larger orangutans tend to use multiple supports more than smaller orangutans (Figure 3.3F), although this also falls short of significance at P=0.14.

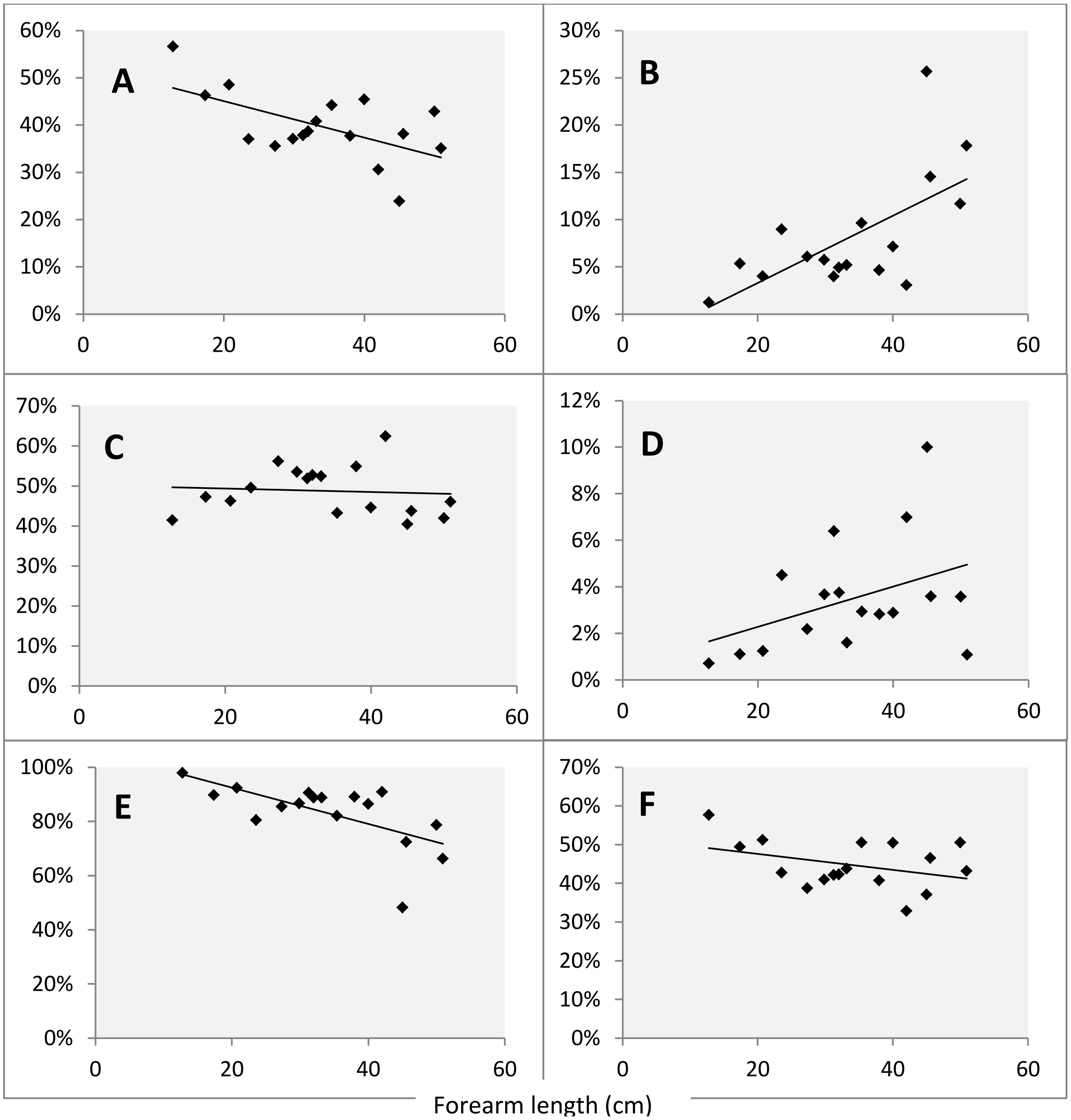

Chart	Dependent variable	Gradient	Intercept	R^2	*P*
A	Percentage of single small support use	-0.39	52.82	0.34	0.013*
B	Percentage of single large support use	0.36	-3.83	0.41	0.005*
C	Percentage of multiple small support use	-0.04	50.22	0.01	0.761
D	Percentage of multiple large support use	0.086	0.55	0.16	0.114
E	If single support used: percentage small	-0.67	105.91	0.40	0.006*
F	If small support used: percentage single	-0.21	51.77	0.14	0.141

Figure 3.3 Linear regressions using forearm length as the independent variable and the percentage of each given support use combinations (A-F) as the dependent variable. The table contains the parameters- gradient, intercept, r^2 and *P* value (*P<0.05) for each of the regression lines.

The model interaction between posture and support diameter was examined by a χ^2 contingency table. The results of the χ^2 test (χ^2 = 1696.5, DF=10 P<0.0001) indicate that there is a strong relationship between these variables. As expected, orangutans appear to be adjusting their postural behavior according to the diameter of the support they are using to bear their weight. High positive ASRs in Table 3.4 show that suspensory postures are most associated with small supports, particularly forelimb-hindlimb suspend and orthograde forelimb suspend.

Table 3.4 Contingency table for the association: Posture * diameter. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Postural behaviour	**Diameter**		
	<10cm	**>10cm**	**Total**
Hindlimb suspend	2.5 (99.3) *8.2*	0.2 (0.7) *-8.2*	2.3
Forelimb-hindlimb suspend	12.4 (97.8) *16.3*	2.5 (2.2) *-16.3*	11.4
Orthograde forelimb suspend	13.3 (96.4) *13.9*	4.5 (3.6) *-13.9*	12.4
Orthograde quadrumanous suspend	5.6 (95.5) *7.5*	2.4 (4.5) *-7.5*	5.3
Pronograde suspend	3.4 (96.2) *6.5*	1.2 (3.8) *-6.5*	3.2
Cling	0.2 (40.6) *-19.0*	2.6 (59.4) *19.0*	0.4
Orthograde stand	6.1 (90.2) *0.3*	6.0 (9.8) *-0.3*	6.1
Pronograde stand	1.7 (82.0) *-6.4*	3.4 (18.0) *6.4*	1.9
Squat	0.4 (80.8) *-3.3*	0.8 (19.2) *3.3*	0.4
Sit	50.0 (88.1) *-11.1*	60.6 (11.9) *11.1*	51.1
Lie	4.3 (70.9) *-26.4*	15.8 (29.1) *26.4*	5.5
Total	90	10	100

Each cell contains the row %, (column %) and the adjusted standardised residual (ASR), shown in italics. Pearson χ^2 = 1696.5, DF=10 and P<0.0001.

Cling and the compressive postures are strongly associated with large supports. The only posture that did not show a significant association with support diameter was orthograde stand.

The model interaction between type of posture and the continuous covariate forearm length was examined by comparing the results of linear regressions between each type of posture and forearm length. Each posture variable was calculated by taking the number of observations of that posture as a percentage of all posture observations. The results in Table 3.5 are arranged in ascending order of their gradient. Postures at the top of the table were used more by smaller orangutans and postures at the bottom of the table were used more by larger orangutans. Suspensory postures were used more frequently by smaller orangutans, particularly orthograde forelimb suspend and hindlimb suspend. The compressive postures, sit, orthograde stand and lie were used more frequently by larger orangutans.

Table 3.5 Linear regression parameters for the interactions between types of posture (dependent variable) and forearm length (independent variable). Asterisks denote significant relationships: **<0.05, *<0.1. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Dependent variable	**Gradient**	**Intercept**	**R^2**	***P***
Orthograde forelimb suspend	-0.80	38.7	0.61	<0.001**
Hindlimb suspend	-0.21	9.2	0.58	<0.001**
Forelimb-hindlimb suspend	-0.14	15.7	0.19	0.078*
Pronograde suspend	-0.08	5.8	0.32	0.018**
Cling	-0.05	2.0	0.64	<0.001**
Pronograde stand	-0.02	2.4	0.04	0.424
Orthograde quadrumanous suspend	-0.01	6.0	0.01	0.736
Squat	-0.01	0.8	0.26	0.038**
Lie	0.08	2.7	0.03	0.482
Orthograde stand	0.13	2.5	0.24	0.046**
Sit	1.12	14.3	0.58	<0.001**

The model interaction between posture and type of support was examined by a χ^2 contingency table. The ASRs in Table 3.6 show that suspensory postures are more associated with lianas whereas the compressive postures are more associated with trees. These results are similar to those for the interaction posture * diameter, which suggests that lianas are associated with certain postures because they are small.

Table 3.6 Contingency table for the association: Posture * type. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Postural behaviour	**Type**		
	Tree	**Liana**	**Total**
Hindlimb suspend	2.2 (90.1) *-8.1*	5.7 (9.9) *8.1*	2.3
Forelimb-hindlimb suspend	10.9 (91.4) *-14.6*	24.5 (8.6) *14.6*	11.4
Orthograde forelimb suspend	11.6 (90.1) *-19.6*	30.6 (9.9) *19.6*	12.4
Orthograde quadrumanous suspend	5.0 (90.0) *-12.5*	13.2 (10.0) *12.5*	5.3
Pronograde suspend	3.1 (94.6) *-2.1*	4.2 (5.4) *2.1*	3.2
Cling	0.5 (98.5) *1.5*	0.2 (1.5) *-1.5*	0.4
Orthograde stand	6.2 (97.3) *2.9*	4.1 (2.7) *-2.9*	6.1
Pronograde stand	2.0 (98.8) *3.4*	0.6 (1.2) *-3.4*	1.9
Squat	0.4 (94.2) *-1.0*	0.6 (5.8) *1.0*	0.4
Sit	52.5 (98.7) *24.7*	16.3 (1.3) *-24.7*	51.1
Lie	5.7 (100) *8.5*	0 (0) *-8.5*	5.5
Total	96	4	100

For explanation see Table 3.3. Pearson $\chi^2 = 1129$, DF=10 and $P<0.0001$

The final interaction in the log-linear model is the 2-way interaction between support type and the covariate forearm length. A regression was used to examine the relationship between support type and body size by plotting the percentage of liana use against forearm length. Liana use (4%) was far rarer than tree use (96%); therefore, changes in liana use were more interesting than changes in tree use. Figure 3.4 shows strong negative correlation (R^2=0.83) between these variables and as with the suspensory posture regression in Figure 3.1, the line of best followed a logistic curve rather than a straight line. The shape of the curve suggests that smaller orangutans use lianas to bear their weight during posture more than larger orangutans and that the strength of this relationship decreases as the size of the animal increases.

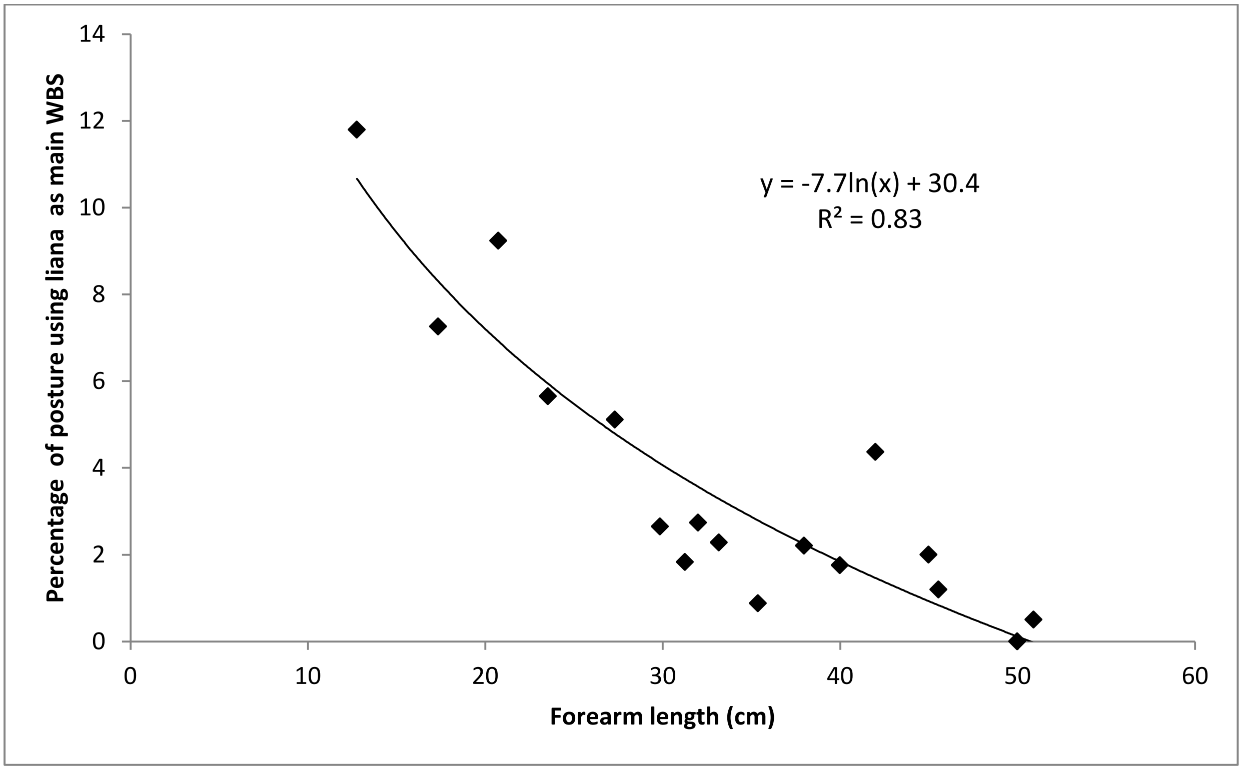

Figure 3.4 Total percentage of arboreal posture where a liana was used as the main weight-bearing support (WBS) plotted against subject's forearm length. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

In order to verify that non-independence of data points was not causing bias to the relative frequencies of postural behaviour, a random sample of 25% of the dataset was taken to check that frequencies were not substantially different. Table 3.7 shows that the percentages of postural behaviour in the random sample are approximately the same as those in the full dataset.

Table 3.7 Comparison of postural behaviour percentages from full dataset with 25% random sample. Data from 17 wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Postural behaviour	Full dataset	25 % random sample
Hindlimb suspend	2.1	2.3
Forelimb-hindlimb suspend	11.2	11.4
Orthograde forelimb suspend	12.9	12.4
Orthograde quadrumanous suspend	5.4	5.3
Pronograde suspend	3.2	3.2
Squat	0.3	0.4
Orthograde stand	5.9	6.1
Sit	51.1	51.1
Cling	0.5	0.4
Pronograde stand	1.9	1.9
Lie	5.4	5.5
Total	100.0	100.0

3.4 Discussion

3.4.1 Comparisons with other studies

Overall, the postural repertoire of orangutans in this study was dominated by sit. This has also been found by previous studies of Sumatran and Bornean orangutans (Sugardjito and van Hooff 1986; Cant 1987b; Thorpe and Crompton 2006). Sit is also the most common posture in all other ape species apart from siamangs (*Symphalangus syndactylus*) (Hunt 1991), which use orthograde forelimb suspension more often (Fleagle 1976). Frequencies of other postural modes observed in Sumatran orangutans

(Thorpe and Crompton 2006) are generally similar with a few notable exceptions. Hindlimb suspend and orthograde forelimb suspend are substantially higher in the current study. This is likely to be a result of the inclusion of younger subjects in this study, since this study found these postures were more associated with the behaviour of smaller orangutans. The frequency of orthograde quadrumanous suspend was also higher than in the Sumatran study. This posture was often used by larger orangutans on multiple small supports. Therefore, habitat structure may account for the differences between the two studies as the disturbed forest at Tuanan had an abundance of small supports. Percentages of the pronograde postures of pronograde suspend (3.2%) and pronograde compression (1.9%) were lower than previously observed in Sumatran orangutans by Thorpe and Crompton (2006) at 3.7% and 3.6%, respectively. These results are in agreement with other comparative studies of orangutan locomotion, which have found that Sumatran orangutans exhibit higher frequencies of pronograde behaviours such as pronograde walking and pronograde suspensory locomotion (Thorpe and Crompton 2006) than Bornean orangutans (Cant 1987b; Manduell et al. 2011). It is unclear whether these differences are primarily species or habitat differences. The positional behaviour studies of Sumatran and Bornean orangutans to date have been carried out in contrasting habitat types: Sumatran orangutans in tall pristine forest and Bornean orangutans in low, degraded forest. This study found that pronograde behaviours such as pronograde stand and pronograde suspend were more associated with larger supports than orthograde stand and orthograde suspensory postures in the disturbed forest. As less disturbed forests have a greater abundance of large trees, which have larger branches, habitat differences, rather than species differences may be responsible for the differences in observed positional behaviour.

In our study suspensory postures made up 35% of the observed postural behaviour. Thorpe and Crompton (2006) found that only 19% of the observed postural behaviour of Sumatran orangutans was suspensory which they noted was lower than a previous study by Sugardjito and van Hooff (1986) at the same site and also lower than reported for Bornean orangutans by Cant (1987b). Although there are no documented size differences between the species of orangutan (Anderson et al. 2008), this may have been influenced by inclusion of different sized subjects. Thorpe and Crompton (2006) included more adult and sub-adult male subjects in their study, which are larger than adult females and adolescents. Therefore, this may account for the particularly low levels of suspension found by our study. Posture also varies according to context but comparisons between the studies are problematic because Cant (1987a) only recorded posture during feeding and Sugardjito and van Hooff (1986) only took data during travel pauses and resting. Differences in sampling methods can also make comparisons between studies difficult. A recent study of Sumatran orangutans by Myatt and Thorpe (2011) found that 43% of postural behaviour was suspensory but postures occurring on consecutive sample intervals were only recorded when the orangutan had moved in between. Therefore, this sampling method is likely to have over-estimated suspensory postural behaviour because they frequently occur during pauses between locomotion whereas compressive postures like sit and lie occur most during long bouts of feeding and resting and would therefore have been recorded less.

3.4.2 Body size suspension hypothesis

The present study found that suspensory behaviour decreased as forearm length increased which was the opposite relationship to that found when the locomotor behaviour of these subjects was analysed (Chapter 2). The results of our posture study conflict with the body size suspension hypothesis of Cartmill and Milton (1977) which states that larger animals are expected to suspend more because suspensory positions are more stable on thin supports. The opposing trends seen in suspensory posture and locomotion are likely to reflect the different pressures that influence support use in different contexts. For example, during travel, support choice may be predominantly influenced by factors such as path length (minimising the distance travelled between feeding and resting sites) and canopy continuity (avoiding large gaps in the canopy) (Thorpe et al. 2007a). Therefore, orangutans may need to use smaller supports, which are most stable in suspensory positions (Cartmill and Milton 1977). Conversely, orangutans may select supports that are large enough to bear their weight in compression more frequently during posture where they intend to spend considerable time resting or processing food to avoid putting strain on their limbs. A study measuring the oxygen consumption of spider monkeys (*Ateles geoffrey*) and slow lorises (*Nycticebus coucang*) found that more energy was expended when resting in suspensory postures compared with above branch positions (Parsons and Taylor 1977) and the difference was greater for the larger spider monkeys indicating that these effects may be magnified with increasing body size. As both energy expenditure and muscle strain are likely to increase with body size, this may account for the negative relationship with suspensory posture. Larger orangutans also have longer arms which may allow them to reach fruit located in thin terminal branches whilst sitting on larger main branches (Cant 1987b), and they can also break off branches containing fruit and move to more stable supports to eat it (Myatt and Thorpe 2011). This is likely to reduce the need for suspensory posture during feeding in larger orangutans.

3.4.3 Body size diameter hypothesis

The results of our study confirmed that larger orangutans use larger supports in postural behaviour which was also found with locomotor behaviour (Chapter 2). This supports the results of previous work on the postural behaviour of Sumatran orangutans which also found that larger orangutans use larger, more stable supports (Myatt and Thorpe 2011). As previously discussed, during posture larger orangutans tend to use compression more than suspension and compressive postures require more stable supports. Therefore, we might expect to find a greater magnitude of difference in the support diameter use of different sized orangutans during posture in comparison to locomotion because larger orangutans further decrease their stability on small supports during posture by using positions where their weight in borne in compression more often than smaller orangutans. However, this was not observed since on average orangutans used larger supports for locomotion when compared with posture and the rate of increase in support diameter with forearm length was also greater for locomotor behaviour (Chapter 2). Orangutans may be able to use smaller supports when they are not moving because they are generating less force; forces generated by locomotor behaviour are likely to increase the stress on supports and, therefore, require orangutans to use larger supports. This has implications for feeding as the majority of fruit is located on thin terminal branches and this allows orangutans to feed on smaller supports than they travel on.

3.4.4 Log-linear model

The model of best fit was broken down into six significant interaction terms; five 2-ways and one 3-way. The support use variables type, diameter and number of supports were all included in the model and each was present in a 2-way interaction with postural behaviour. These results supplement the findings of previous studies of orangutan posture (Cant 1987b; Myatt and Thorpe 2011) and locomotion (Cant 1987b; Thorpe and Crompton 2005; Thorpe et al. 2009; Manduell et al. 2011; Chapter 2), which suggest that distinct positional behaviours have evolved to allow orangutans to utilise different aspects of their habitat. Whereas log-linear analysis of locomotor behaviour in Bornean orangutans found that locomotion had a significant 3-way relationship with diameter and number of supports (Chapter 2), the results of this chapter indicate that the relationships between posture and support use variables may be less complicated. Posture was most strongly associated with the support variable number of supports used. Suspensory postures that involved fore- and hindlimbs at the same time were all strongly associated with multiple supports whereas those that use either forelimbs or hindlimbs were more associated with single supports. Orthograde stand and squat were more associated with multiple supports, which may reflect a lack of stability in these positions, which requires additional support from above. Pronograde stand was also more associated with multiple supports in our study, which Thorpe and Crompton (2005) found to be more associated with single supports. This is likely to reflect habitat differences and, specifically, the lower abundance of large branches and greater amount of interwoven small supports at this study site.

The interaction between posture and support diameter divided the suspensory and compressive modes of posture. All suspensory modes of posture were more associated with small supports and compressive modes of posture and cling were associated with large supports. The results for the interaction between posture and type of support were similar to those of diameter in that lianas, which tended to be smaller and were more associated with suspensory postures and tree supports, which tended to be larger, were more associated with compressive forms of posture. These results are similar to the results for locomotor behaviour in Chapter 2 and indicate that support diameter has a greater influence on positional behaviour than support type, which was also found for the locomotor behaviour of Sumatran orangutans (Thorpe and Crompton 2005).

3.4.5 Body size number of small supports hypothesis

The most important interaction in the model to involve forearm length was the 3-way interaction: Forearm length * diameter * number of supports. As expected there was a negative relationship in the use of single small supports and a positive relationship in the use of single large supports with increasing forearm length. When using multiple supports the relationships were less clear: all of the study subjects used multiple small supports to bear their weight in similar frequency. The habitat around the study site may account for this as small supports were abundant and all orangutans frequently used interwoven meshes of small supports, which can be relatively stable. When using small supports larger orangutans were more likely to use multiple supports than single supports, which supports hypothesis 3 that larger animals gain stability on small supports by using multiple supports (Cartmill and Milton 1977). Previous studies have also found that orangutans spread their weight over multiple supports when using small supports, which has been suggested as an adaptation allowing them to feed in the terminal branches of trees (Thorpe and Crompton 2006; Thorpe et al. 2009; Myatt and Thorpe 2011). In our study multiple large supports were used much less frequently reflecting their lack of availability in the habitat. This combination was most associated with the postural behaviour of larger orangutans as small orangutans were unlikely to require extra stability on large supports.

3.4.6 Postural behaviour and ontogeny

We also found distinct relationships between forearm length and the majority of the types of posture analysed. As previously discussed, suspensory behaviours were more associated with the postural behaviour of smaller orangutans, and of the suspensory postures, orthograde forelimb suspend and hindlimb suspend showed the most negative relationship with forearm length. These behaviours often utilise only one limb. They, therefore, tend to be less stable than forms of quadrumanous suspension such as pronograde suspend and orthograde quadrumanous suspend, which allow body weight to be spread over multiple supports and are used more by larger orangutans. Postural behaviours that use one limb are more risky than postures that involve multiple limbs because if a support breaks they have a greater risk of falling. Suspension from one limb was particularly associated with play behaviour in younger orangutans. Play has been described as training for the unexpected (Spinka et al. 2001) and by using the most unstable postures, young orangutans enhance their agility which is likely to be beneficial if they encounter a sudden threat. Alternatively, postures that only use one limb may be associated with play because they allow young orangutans three free limbs to interact with play partners. Young orangutans spend a substantial amount of their time playing (van Noordwijk and van Schaik 2005), but in Tuanan orangutan mothers rarely associate with conspecifics. Therefore, opportunities for social play are rare and represent, on average, just 1% of daily activity (van Noordwijk et al. 2009).

Liana use was found to decrease with increasing forearm length (see Figure 3.4). Play behaviour may contribute to this relationship because play also decreases with increasing forearm length and lianas are associated with play. Liana use is particularly associated solitary play, which accounts for 15-45% of daily activity prior to weaning (~6 years old) (van Noordwijk et al. 2009). The initial steep decrease in the use of lianas from 1-6 years corresponds with the period when solitary play behaviour decreases to less than 2% of daily activity in weanling immature orangutans (van Noordwijk et al. 2009). These results suggest that ontogenetic differences in activity budget may influence the postural behaviour of orangutans.

3.4.7 Conclusion

Overall, this study has shown that there are significant relationships between body size and the postural behaviour of orangutans. These results agree with the findings of previous studies of orangutan posture (Cant 1987a; Myatt and Thorpe 2011); in that contrary to the body size suspension hypothesis (Cartmill and Milton 1977), suspensory postural behaviour decreases with increasing body size. Since analysis of the locomotor behaviour of these orangutans showed the opposite trend in suspensory behaviour (Chapter 2), this study suggests that different selection pressures may be involved in locomotion and static behaviour. By modelling postural behaviour using a continuous body size variable, this study was able to examine the postural behaviour changes that take place during growth and development in more detail than was previously possible. The results highlight the importance of including infants and juveniles in studies of positional behaviour as ontogenetic development is also likely to influence the positional behaviour of young primates.

3.4.8 Next step

So far I have examined the effect of body size on orangutan positional behaviour and support use. Broad size-related trends in support use and body position were identified during both locomotion and posture. However, these datasets were not able to provide information on when young orangutans developed the locomotor skills needed to travel independently in the canopy. To investigate this, I recorded locomotor behaviour in its most challenging context: crossing gaps between trees. By recording gap crossing locomotor behaviour along with the distance crossed, Chapter 4 focusses on how orangutan gap crossing strategies change during development with physical and cognitive maturation.

4. THE ONTOGENY OF GAP CROSSING BEHAVIOUR IN BORNEAN ORANGUTANS (*Pongo pygmaeus wurmbii*) INHABITING A DEGRADED PEAT SWAMP FOREST

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Abstract

For orangutans, the largest predominantly arboreal primates, gaps in the canopy present a particular challenge. The shortest gaps between trees lie between thin peripheral branches, which offer the least stability to large animals. Orangutans have developed a diverse range of locomotor behaviours to navigate thin branches and cross gaps between trees. The aim of this study was to examine the development of these behaviours with increasing body size and to determine which factors influence the distance orangutans cross in a disturbed swamp forest habitat. A non-invasive photographic technique was used to measure the body size of subjects. We recorded locomotor behaviour, support use and two estimates of distance: the distance between the trunks and the distance that was actually crossed every time a focal orangutan crossed between two trees. As body size increased, we found that orangutans used locomotor behaviours that involved bending and swaying compliant supports more frequently, and they also used trunks more often than branches and lianas. The distance that orangutans crossed increased with body size and larger orangutans took less continuous routes between trees. However, body size was not the only factor that influenced the distance crossed when travelling

between trees; the gap crossing technique was important too. More complex behaviours, which utilised compliant trunks and lianas, were used to cross the largest gaps. This study provides preliminary evidence for cognitive development in gap crossing techniques that involve bending and swaying compliant supports and indicates that these skills are not fully mastered until orangutans reach 6 years old.

4.1 Introduction

Efficient travel through the forest canopy which minimises deviations from direct travel between two points, is constrained by an animal's ability to use available supports to cross discontinuities in the forest canopy. Hence, the ability to cross gaps in the canopy is a key factor in determining path length (Temerin and Cant 1983), and thus the daily energetic cost of locomotion for orangutans (Cant 1992). In response to their complex habitat, orangutans, the largest arboreal apes, have developed a diverse repertoire of positional behaviour, which allows them to navigate their complex arboreal habitat (Cant 1987b; Thorpe and Crompton 2006). Crossing gaps between trees is likely to be one of the most challenging problems faced by orangutans because the narrowest gaps between trees are found between thin compliant (flexible) branches (Grand 1972), which will deflect further under the weight of the animal. Utilising compliant supports for gap crossing is both cognitively and physically demanding (Chevalier-Skolnikoff et al. 1982) and these skills have been found to develop slowly during ontogeny (Bard 1995). Therefore, gap crossing is a key area to examine when investigating the development of independent locomotor abilities in young orangutans.

Cant (1994) proposed a classification system to describe the interactions of arboreal animals with compliant vegetation, which recognised that some arboreal animals appear able to use compliant vegetation to their advantage during locomotion and feeding. Interactions which involve utilisation of habitat compliance fall into two categories: mass deformation, where a support is intentionally deformed using body mass; and appendicular deformation, where a limb is used to pull a compliant branch towards the body (Cant, 1994). While Cant (1994) proposed that larger arboreal animals, such as orangutans, could utilise compliant supports, other studies demonstrated that mass deformation and the oscillations of compliant terminal branches caused by animals moving along them increased the energetic expenditure of arboreal locomotion in monkeys (Alexander 1991) and lemurs (Demes et al. 1995). In agreement with Cant (1994), Thorpe et al. (2007a) found that orangutans could utilise the potential energy in compliant supports to aid arboreal travel during tree sway, which they showed was less than half as energetically costly as jumping and an order of magnitude less costly than crossing terrestrially for a similar sized gap. Thorpe et al. (2007a) also provided anecdotal evidence that orangutans may be able to obtain energy return from compliant supports in other forms of locomotion, but this has yet to be quantified.

Orangutans have a diverse repertoire of locomotor behaviour which allows them to travel exclusively on arboreal supports. Orangutan locomotion is characterised by upright-torso (orthograde) suspensory positions (Crompton et al. 2008), which requires greater limb mobility than pronograde locomotion (Povinelli and Cant 1995). Adaptations which allow considerable rotation of the shoulder joint are shared by all apes and these facilitate the highly abducted arm positions, which are required for orthograde suspension (Larson 1998). Orangutan muscles are also able to generate force at a range of joint angles, which allows them to utilise diversely orientated supports with variable compliance (Payne et al. 2006; Myatt et al. 2011a). Thus, orangutans are able to show considerable flexibility in their responses to discontinuous canopy. During gap crossing locomotion the position of the torso may be orthograde or pronograde (Thorpe et al. 2009; Myatt 2010). When the branches of an adjacent tree are within reach, orangutans can cross by pulling thin compliant branches towards their bodies until a more stable branch can be reached (Cant 1994). Cant (1994) termed this behaviour appendicular deformation and orangutans use it during orthograde transfer and pronograde bridging behaviour (Hunt et al. 1996; Thorpe and Crompton 2006). Orangutans rarely leap across gaps (Cant 1992); when crossing larger gaps in the canopy they use their body mass to deform compliant supports across the gap (Cant 1992, 1994; Thorpe and Crompton 2005, 2006; Thorpe et al. 2007a; Thorpe et al. 2009). Orangutans use their mass to deform and oscillate compliant trees and lianas, swaying them with increasing amplitude until a support on the opposite side of the gap can be reached (MacKinnon 1974; Sugardjito and van Hooff 1986; Cant 1992; Thorpe and Crompton 2005). This behaviour allows them to cross gaps in the canopy without descending to the forest floor, avoiding ground predators and energetically expensive climbing (Thorpe et al. 2007a).

The continuity of the forest canopy experienced by animals of different mass varies because larger animals deform branches downwards more readily (Grand 1972). Having a greater body mass can have both positive and negative implications for travel in the forest canopy. For example, an adult orangutan can use its body weight to facilitate gap crossing by exploiting compliant supports (as in tree sway), whilst a young orangutan may be too light to deform the supports sufficiently to cross the same gap and may have to take an alternative route. However, a smaller body mass can be beneficial because smaller animals are less likely to break thin branches at the peripheries of trees, which allows them to take more continuous travel routes (Cant, 1992). This is likely to have implications for orangutan support use during gap crossing; while adult orangutans can use the thin terminal branches when they grasp multiple branches and hold them in the line of their greatest strength (Thorpe et al. 2007a), they are less able to use thin horizontal branches for horizontal progression because they deform downward more readily. However, larger orangutans can avoid using thin terminal branches to bear their weight because their long limbs allow them to reach these branches whilst supporting their weight on more stable supports (Myatt and Thorpe 2011).

Since orangutans are highly sexually dimorphic and body mass varies with both age and sex, locomotor behaviour has been predicted to vary with age-sex category (Sugardjito and van Hooff 1986; Cant 1992; Thorpe and Crompton 2005; Manduell et al. 2011). However, previous studies of orangutan positional behaviour have found age-sex category to have limited influence on positional behaviour and support use (Thorpe and Crompton 2005, 2006; Manduell et al. 2011; Myatt and Thorpe 2011). Thorpe and Crompton (2005) proposed two reasons for the congruence in positional behaviour across the age-sex classes. Firstly, orangutans of all age-sex classes were found to follow the same travel routes or ‘arboreal pathways’ and, as they found a strong association between support type and positional behaviour, this may have minimised differences. Secondly, adult females were found to exhibit more cautious locomotor behaviour preferring large stable supports similar to the much heavier males, a likely consequence of having given birth (Thorpe and Crompton, 2005). Another factor that might influence age-sex differences in locomotion is habitat structure. A study of orangutan positional behaviour in the degraded swamp forests of Central Kalimantan (Manduell et al. 2011) did not observe orangutans using arboreal pathways like the orangutans that inhabit the pristine forests of Sumatra (Thorpe et al. 2005). Thus, orangutans inhabiting degraded forest may take travel routes that are more suited to their body size, which is expected to lead to size-related variation in locomotor behaviour and support use.

Gap crossing skills are cognitively challenging for young orangutans to learn (Chevalier-Skolnikoff et al. 1982; Bard 1995). Orangutans must be able to perceive the physical properties (affordances) of supports to utilise them successfully. Young orangutans discover the affordances of their environment through play and exploratory behaviour (Chevalier-Skolnikoff 1983) as do human infants (Gibson 1988; Palmer 1989; Adolph et al. 1993). While appendicular deformation of compliant supports appears to be reasonably intuitive, certain forms of mass deformation are likely to require more advanced cognitive abilities (Chevalier-Skolnikoff et al. 1982). For example, during tree sway orangutans often deform supports away from their intended travel direction in order to increase the magnitude of their sway. Chevalier-Skolnikoff et al. (1982) suggest that this behaviour indicates that orangutans cross gaps by forming mental representations of them prior to crossing, which they consider indicative of the most cognitively complex stage of Piaget's sensorimotor intelligence series, *insight*. As the extent to which a substrate deforms depends on the body mass of the deformer, orangutans must also adapt their locomotor behaviour as they grow. As young orangutans differ in both body mass and cognitive development, age-related differences in locomotor behaviour are expected to be more pronounced in immature orangutans. Previous studies have not collected data from both infant and juvenile age groups, which may account for the limited differences in locomotor behaviour found by these studies (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005, 2006; Manduell et al. 2011).

The aim of the present study was to investigate the development of gap crossing behaviour through observations of different aged orangutans ranging from infant to adult. Specifically we hypothesise that: 1) the use of compliance during gap crossing will increase as body size increases. In particular, mass deformation is expected to be more common in the gap crossing locomotion of heavier orangutans; 2) Smaller orangutans will use smaller support types (such as branches and lianas) for gap crossing whereas larger orangutans will use trunks more often; 3) The size of the gap crossed when animals move between trees will increase as body size increases; 4) Larger orangutans will cross a greater proportion of the distance between tree trunks without using continuous vegetation than smaller orangutans, which will take more continuous routes; and 5) The skills required to cross a gap using mass deformation will develop later than other gap crossing skills as they are both cognitively and physically challenging.

4.2 Methods

4.2.1 Study site and subjects

This study was carried out at Tuanan research station (2°09'S, 114°26'E) within the Mawas Reserve, Central Kalimantan, Indonesia. The study area consists of approximately 725 ha of lowland peat swamp forest with an orangutan density of 4.25/km^2 (van Schaik et al. 2005). The area is highly degraded and has been subject to selective logging in the early 1990s. Prior to the onset of continuous research at Tuanan in 2003, a grid-based trail system was cut and orangutans in the area were identified and habituated to human observers. The subjects were 17 wild Bornean orangutans ranging from infant to adult (Table 4.1). As this was a cross-sectional study of locomotor development, subjects of different ages, and therefore body sizes, were chosen, which represent different stages of development. Immature subjects ranged in age from 1 to 11 years and adults of both sexes were sampled. Subjects were divided into six size groups according to the actual measurements of their forearms as follows: 1) <20cm (infants); 2) 20-25cm (juveniles); 3) 25-30cm (small adolescents); 4) 30-35cm (large adolescents); 5) 35-40cm (adult females and a small adult male); and 6) >40cm (large adult males both flanged and unflanged).

4.2.2 Measurement technique

To quantify the body size of each individual a non-invasive laser photography technique (Rothman et al. 2008) was used whereby parallel green lasers were attached to a camera (Canon EOS 400D) using a specifically designed aluminium frame. The lasers were held in the frame exactly 4cm apart and provided visible marks on the photograph which were used as a scale bar. The lasers were used to measure the subjects' limbs, which were photographed when they were perpendicular to the field of view of the camera to avoid errors associated with foreshortening. The photographs were measured using Image J version 1.43 (Bethesda, MD). As orangutans have a high intermembral index their forelimbs show greater variation in length than their hindlimbs. In practise it was easier to measure the forearm than the upper arm in photographs because locating the shoulder joint was more difficult than locating the wrist. Forearm is also an important measure for gap crossing ability because it contributes to the distance an individual can reach to cross a gap. It was therefore chosen as a proxy for body size in this study.

Forearms were measured from the elbow to the wrist, using the prominent olecranon process of the ulna and the radio-carpal joint to locate these points. Photographs of subjects were taken at the same time as focal sampling. At least five suitable photographs of each subject were measured and the largest value was taken to be the closest to the true length because foreshortening can only cause underestimation. Sufficient photographs were obtained for 12 of the 17 subjects listed in Table 4.1, forearm lengths of the remaining five unmeasured subjects were estimated by comparing them to measured individuals when they were observed together in the field.

Table 4.1 Focal orangutans observed at Tuanan Research Station, Central Kalimantan between July 2009 and July 2010. Size group refers to the categories used in the GLMM which were based on forearm length and focal days refers to the number of whole days of observation.

Focal	Age-sex category	Forearm length (cm)	Size group	Focal days
Mawas	Infant female	12.8	1	10
Kino	Infant male	17.4	1	10
Jip	Juvenile male	20.7	2	10
Deri	Juvenile male	23.5	2	7
Jerry	Immature male	27.3	3	10
Streisel	Immature female	29.9	3	9
Milo	Immature female	31.3	4	7
Ido	Immature male	~32	4	6
Kondor	Immature female	33.2	4	10
Juni	Adult female	35.4	5	5
Kerry	Adult female	38.0	5	5
Mindy	Adult female	~40	5	4
Budhi	Sub-adult male	~42	5	1
Ekko	Sub-adult male	~45	6	2
Gismo	Sub-adult male	45.6	6	4
Preman	Adult male	50.9	6	3
Isidor	Adult male	~50	6	2

4.2.3 Data collection

The study was carried out from June to November 2009 and January to July 2010. Continuous observations of focal subjects were carried out from when the subject awoke from their nest in the morning to when they rested in their evening nest, typically from 05:00 to 17:00. Subjects were followed for a maximum of 10 days over more than one month to minimise possible bias introduced by temporarily abundant food sources (Thorpe and Crompton 2005). The interval between observation periods varied but effort was made to keep it short especially for the younger subjects and the observation periods for an individual were no more than 6 months apart. Every time focal orangutans were observed crossing between trees locomotor behaviour, support use and estimates of the distance between the trunks and the size of the gap crossed were recorded using a digital voice recorder to enable the observer to watch and record simultaneously. Self-training in estimating horizontal distances in the forest was carried out at regular intervals to ensure estimations were accurate.

4.2.4 Locomotor behaviour

Gap crossing locomotion was recorded following the standard classification system for primate positional behaviour (Hunt et al. 1996; Thorpe and Crompton 2006) which classifies locomotor behaviour according to body orientation, weight-bearing limbs and whether weight is borne in suspension or compression (Table 4.2). Gap crossing locomotion can also be classified by the interaction with compliant vegetation, in which the compliance of supports can be utilised in one of two ways; by appendicular deformation whereby a support is pulled towards the body or mass deformation where the animal uses its mass to deform a support so that it allows them to cross a gap (Cant 1994). Conversely, locomotion that did not utilise a compliant support was termed non-compliance utilising (NCU).

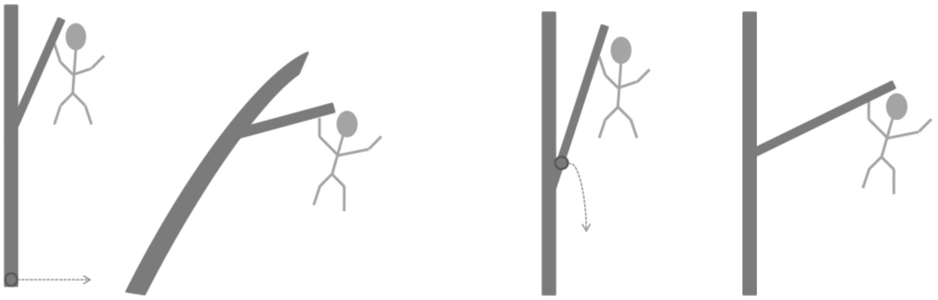
Table 4.2 Types of gap crossing locomotion divided by their interaction with compliance recorded during a study of Bornean orangutans carried out at Tuanan Research Station from July 2009 to July 2010.

Non-compliance utilising	**Definition**
Leap	A movement involving a period of free flight where the hindlimbs act as propulsors. Orangutans very rarely leap except when fleeing dangerous situations.
Drop	Take-off is initiated by falling. Orangutans often maintain contact with a support while they fall but without using it to bear weight.
Appendicular deformation	
Transfer	Orthograde suspensory locomotion where a support on the landing tree is pulled in by a hand or foot.
Cautious pronograde bridge	Pronograde locomotion where hands grasp and pull in branches from the landing tree. Foot holds are released once the position is secure.
Inverted pronograde bridge	As with cautious pronograde bridge except torso is inverted with head facing upwards.
Mass deformation	
Descending bridge	A lunge that results in hindlimb suspension, hands grasp a lower support on the landing tree and the progression is downwards at ≥135°
Lunging bridge	An incomplete leap where the feet retain hold of a compliant support on the take-off tree, and bend it by lunging. The hands grasp a distant support on the landing tree.
Supinograde bridge	As with lunging bridge but with body inverted.
Ride	A compliant support is deformed in the direction of travel.
Sway	A compliant support is oscillated back and forth with increasing amplitude until the adjacent tree can be reached.

Definitions follow the standardized classifications system of Hunt et al. (1996) and Thorpe and Crompton (2006).

4.2.5 Support use

Three types of support were distinguished: trunks, the primary members of trees; branches, all other tree elements including twigs and foliage and; lianas, vines with woody stems. This study recorded the support that was used to make the crossing. For modes that utilised support compliance the support that was deformed to make the crossing was recorded (see distinction in Figure 4.1 a and b) and for all other modes of locomotion, the last support that the subject made contact with on the take-off tree was recorded.



A)

B)

Figure 4.1 Illustrations of how support use was recorded during the orangutan gap crossing behaviour ride. A) Ride on trunk and B) ride on branch.

4.2.6 Distance estimates

This study recorded distance estimates to the nearest metre every time a subject moved between two trees (Figure 4.2). Firstly, the actual gap crossed (AGC) was an estimation of the horizontal distance travelled from the take-off point to the landing point. When the gap was crossed using mass deformation locomotion, the take-off point was estimated as the last location of the orangutan prior to support deformation (Figure 4.2a). For all other types of behaviour the take-off point was the last part of the take-off tree that the orangutan made contact with (Figure 4.2b). If this distance was estimated to be less than 0.5m the AGC was recorded as zero (Figure 4.2c). In cases where a subject crossed a gap to get to a liana and then used the liana to get to the next tree, details of both crossings were recorded (Figure 4.2d). In addition, we estimated the distance between the trunks of the take-off and landing tree. This enabled us to quantify the AGC in relation to the distance between the trunks to examine the extent to which orangutans use continuous vegetation to cross between trees.

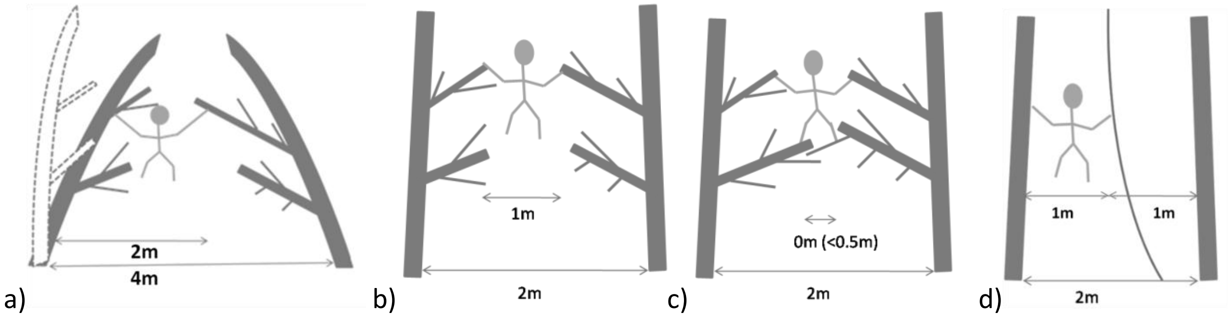


Figure 4.2 Illustrations of how the actual gap crossed by orangutans (upper dimension lines) and the distance between the trunks (lower dimension lines) were estimated during different types of gap crossing a) to d).

4.2.7 Statistical analysis

This study used a combination of different types of analysis to examine the development of gap crossing behaviour. Frequencies of locomotor behaviour and support use were used to establish broad changes in gap crossing behaviour of orangutans during ontogeny. Linear regression was used to examine the effect of body size on the distance an orangutan could cross by plotting forearm length against AGC. We extended this principle to examine the effects of physical and cognitive development. Thus, we expected a linear relationship between forearm length and AGC if body size were the only factor influencing the AGC. However, if skill acquisition also influenced the distance an individual could cross we would expect to find a regression line with a steeper slope while learning and growth were taking place, with the slope becoming less steep once full skills competence was reached and only growth was affecting the AGC. Finally we examined which factors and combinations of factors influenced the size of gap an orangutan could cross by fitting a generalized linear mixed model (GLMM) using AGC as the response variable and size group, gap crossing behaviour and support type as predictors. The GLMM was carried out using R 2.13 (LME4 package, R Development Core Team 2010). GLMMs allow both fixed and random effects to be modelled, which was particularly important for the study because the data consisted of many observations collected from each individual. Individual identity was included as a random effect on the intercept. Another benefit of GLMMs is that they can accommodate non-normal error structures. For this analysis a Poisson distribution with a log link was required to fit the distribution of the response variable AGC, since the response variable took discrete values (AGC was measured to the nearest 1m), and was skewed toward smaller values.

4.3 Results

In total 10699 independent crossing events were recorded for nine immature orangutans and eight adult orangutans. Figure 4.3 shows that modes of gap crossing behaviour that utilised compliance by mass deformation increased with body size. The amount of appendicular deformation increased slightly between groups 1 (infants) and 2 (juveniles), but remains at a similar level in the other size groups. Smaller subjects had higher frequencies of gap crossing behaviour that did not utilise compliance (Figure 4.3). Support use varied with size group and type of locomotor behaviour (Figure 4.4). Larger orangutans used trunks more and smaller orangutans used branches more. When type of locomotion was also considered it is clear that orangutans of different sizes used different types of support for behaviours that employed mass deformation: the smaller orangutans used lianas and branches more frequently than larger orangutans (except for the smallest that rarely used mass deformation). There is a clear relationship between size and tendency to utilise compliant trunks for gap crossing locomotion (Figure 4.4).

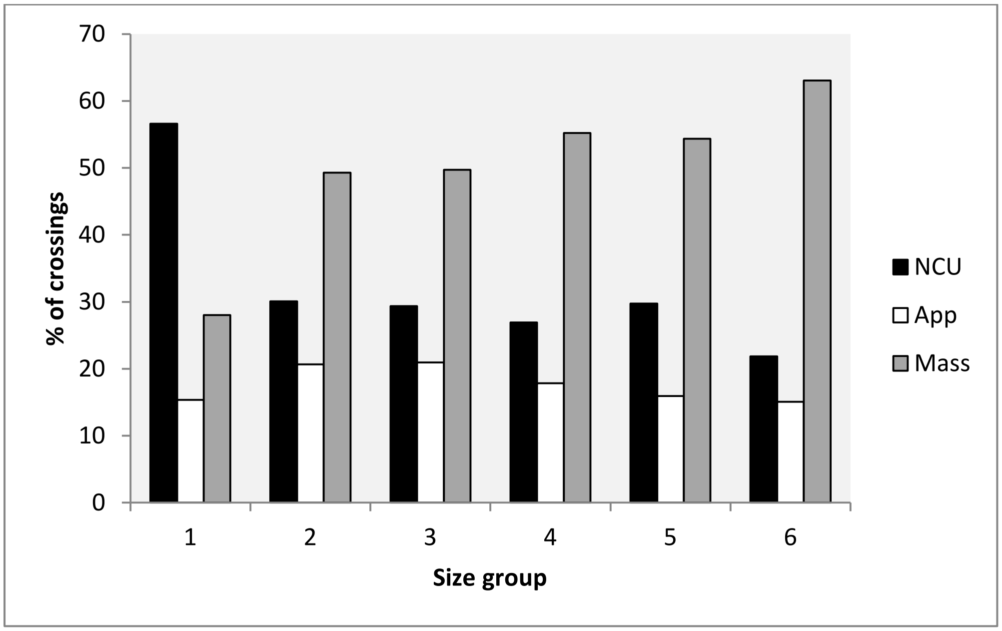


Figure 4.3 The percentage composition of three different types of locomotor behaviour: NCU; non-compliance utilising; App- appendicular deformation; and Mass- mass deformation for six size groups of orangutan based on forearm length. Data collected at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

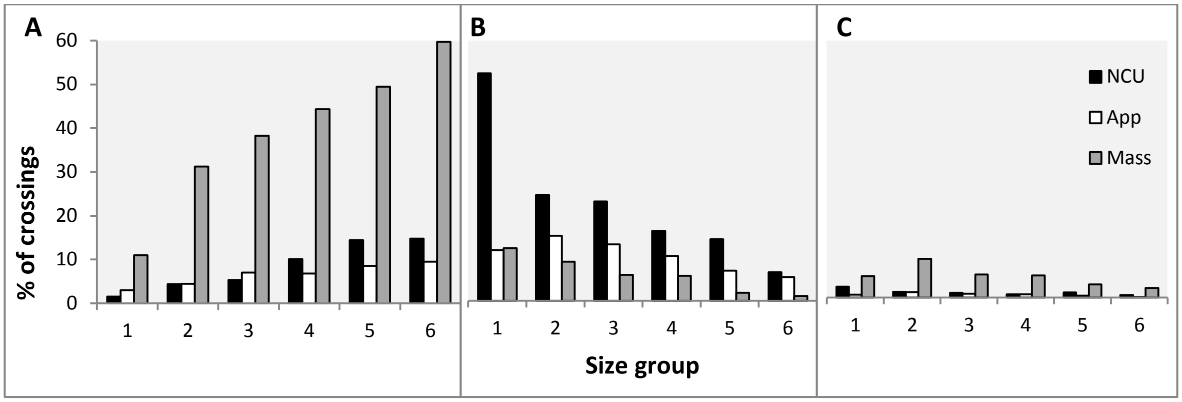


Figure 4.4 The percentage composition of support used during gap crossing (A- trunk, B- branch and C- liana) for different types of locomotor behaviour: NCU; non-compliance utilising; App- appendicular deformation; and Mass- mass deformation for six size groups of orangutan based on forearm length. Data collected at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

The mean AGC distance increased with forearm length although the largest subject was a major outlier (Figure 4.). The largest subject was an adult male that predominantly traveled near to the ground, in areas where the trees were closer together. As the locomotor behavior of the largest subject differed from the other subjects, two regression lines were plotted to include and exclude this data point. When this data point was excluded the line of best fit was steeper and fitted the other points better R^2= 0.89 (Figure 4.). The percentage of the gap crossed was calculated by dividing the AGC by the distance between the two trunks *100 (see Figure 4.2). These values were also plotted against individual forearm length (Figure 4.6). In this relationship the adult male was no longer an outlier. There is strong positive relationship between forearm length and the percentage of the gap crossed ($y = 2.16x - 18.37$, R^2=0.90), which shows that smaller orangutans use the vegetation located between the trunks to travel between trees more than larger orangutans (Figure 4.6). These results suggest that body size is the primary determinant of AGC.

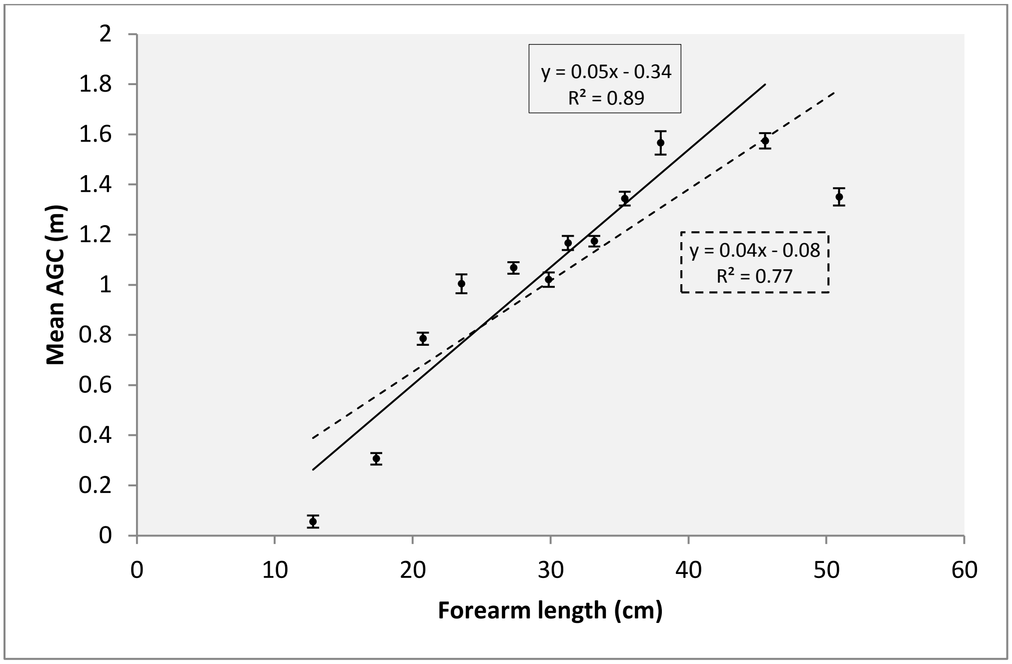


Figure 4.5 The relationship between mean actual gap crossed (AGC) and forearm length for the 12 measured orangutans. The solid line shows a linear regression between AGC and forearm length excluding the most extreme outlier and the broken line shows the linear regression when all data points are included. The error bars show the standard error about the mean. Data collected at Tuanan Research Station from July 2009- July 2010.

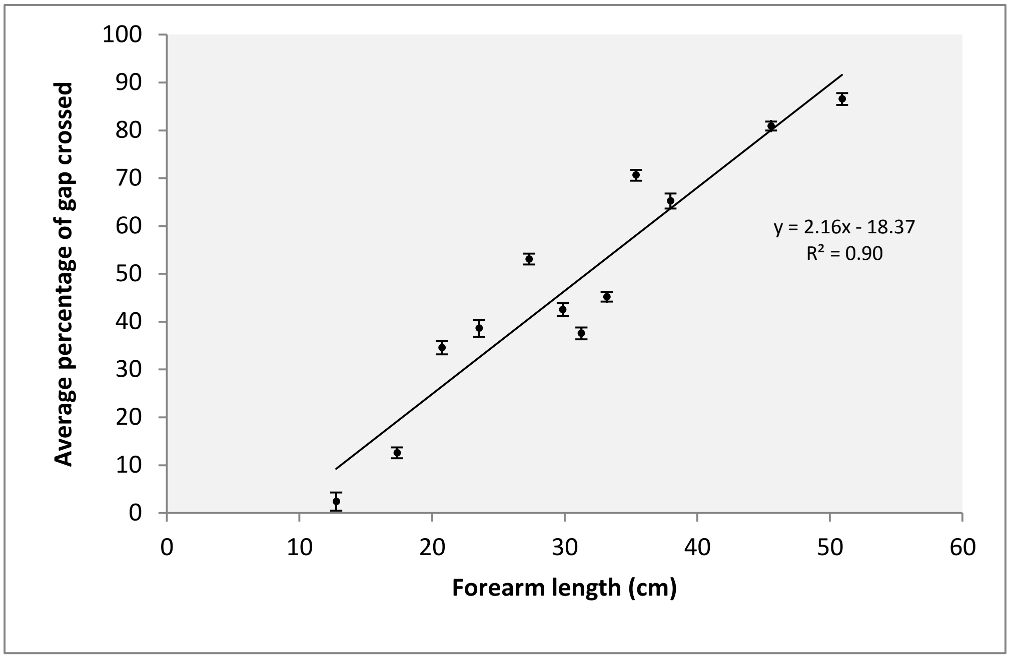


Figure 4.6 The mean relationship between the percentage of gap crossed (calculated by dividing the AGC by the distance between the trunks of the two trees *100) and forearm length. Data collected on Bornean orangutans at Tuanan Research Station from July 2009- July 2010.

The GLMM tested fixed effects: size group (based on forearm measurements), type of locomotion and take-off support. The response variable (AGC) was not normally distributed. A chi-squared test in which the binned response variable was compared to a randomly generated Poisson distribution of the same mean and sample size revealed that the original distribution was consistent with a Poisson distribution, so the GLMM was specified with a Poisson distribution family and a log link. After an iterative model fitting and criticism process, this final model of best fit was:

AGC ~ Size group * type of locomotion + type of locomotion * take-off support + (1 | Individual)

The final model was selected based on the value of the AIC and the significance (*P* value) of the interactions contained within it. The distribution of the residuals was checked, but there were no obvious patterns of over or under-dispersion, non-homogeneity of variance, or other features that might invalidate the model. The model of best fit includes two 2-way interactions and three main effects. All main effects were found to be significant ($P<0.05$) (Table 4.3) and the 2-way interactions each showed significant interactions among the levels (see Appendix B). These results show that the distance an orangutan crossed when it moved between trees was influenced by three factors: the size of the orangutan, the type of locomotor behaviour it used and the type of support it used in the take-off tree. Additionally the effect of body size is modified by the type of locomotor behaviour and the effect of locomotor behaviour is modified by the type of support used.

The parameter estimates shown in Table 4.3 indicate the effect of the factor levels on the AGC. For each factor the first category is taken as a baseline from which other values are calculated. For example, for the type of locomotor behaviour category, non-compliance utilising behaviour is taken as the baseline and other types of locomotion are listed in order of increasing complexity in terms of their use of compliance. The parameter estimates indicate that orangutans use increasingly more complex locomotor behaviours that involve both appendicular and mass deformation to cross larger gaps. The same pattern is seen with body size group: as body size increases so do the parameter estimates for the effect on AGC, which shows that larger orangutans cross larger gaps. The take-off support estimates indicate by their negative values that orangutans use branches and lianas to cross smaller gaps when compared to trunks, which was used as the baseline for this variable.

Table 4.3. Generalized linear mixed model- fixed effects that influenced the gap crossed by orangutans when moving between trees. Data collected at Tuanan Research Station from July 2009- July 2010.

Main effects	**Estimate**	**Std. Error**	**z value**	***P***
Intercept	-3.32	0.46	-7.21	<0.001
Type of locomotion				
Appendicular	1.44	0.52	2.77	<0.01
Ride	3.24	0.46	6.98	<0.001
Ride + appendicular	3.38	0.47	7.17	<0.001
Sway	3.49	0.55	6.38	<0.001
Sway + appendicular	3.46	0.59	5.87	<0.001
Size group				
2	2.11	0.48	4.35	<0.001
3	2.77	0.47	5.89	<0.001
4	3.10	0.47	6.66	<0.001
5	3.46	0.46	7.45	<0.001
6	3.50	0.47	7.50	<0.001
Take-off support				
Branch	-1.19	0.07	-18.24	<0.001
Liana	-0.32	0.14	-2.26	<0.05

AGC ~ Size group * type of locomotion + type of locomotion * take-off support + (1 | Individual)

AIC= 3758, n= 10699, Individuals= 17, AGC- actual gap crossed.

Post-hoc analysis was carried out using Tukey's contrasts to determine which of the levels of each of the significant fixed effects differed significantly in their effect on the AGC (Table 4.4). Within size group, size 1 and 2 formed distinct groups, which represent infants and juveniles respectively. Size 3 and 4 form one group and both of these groups contain adolescent subjects. Size 4 and 5 were also grouped together and these represent adult females and males, respectively. The types of locomotor behaviour were separated into three groups; non-compliance utilising and appendicular deformation had significantly different effects on the AGC, and the third group consisted of all of the types of locomotion that involved mass deformation. The supports used in the take-off tree were separated into two groups; branch use had a significantly different effect on the AGC when compared to trunk and liana use, which was grouped together.

Table 4.4 Results of Tukey's contrasts showing the significant groups within each of the model factors that influenced the gap crossed by orangutans when crossing between trees. Data collected at Tuanan Research Station from July 2009- July 2010.

Factor	**Groups**							
Size group (4 groups)	i)	size 1	ii)	size 2	iii)	size 3 size 4	iv)	size 5 size 6
Type of locomotor behaviour (3 groups)	i)	NCU*	ii)	appendicular	iii)	ride ride + appendicular sway sway + appendicular		
Take-off support (2 groups)	i)	branch	ii)	liana, trunk				

Groups significantly different *P*= <0.05. *NCU is non-compliance utilising locomotor behaviour.

The first significant interaction in the model (size group * type of locomotion) is shown in Figure 4.7. This shows that all orangutans cross increasingly larger gaps by employing locomotor behaviours that utilise compliance compared with non-compliance utilising (NCU) behaviours. Appendicular deformation, which involves pulling in supports on the landing tree, increases the size of gap that can be crossed but the behaviours that are used to cross the largest gaps involve mass deformation; ride and sway and combinations of appendicular and mass deformation. Body size also affects the size of gap that can be crossed with larger orangutans crossing larger gaps using each of the different types of gap crossing locomotion.

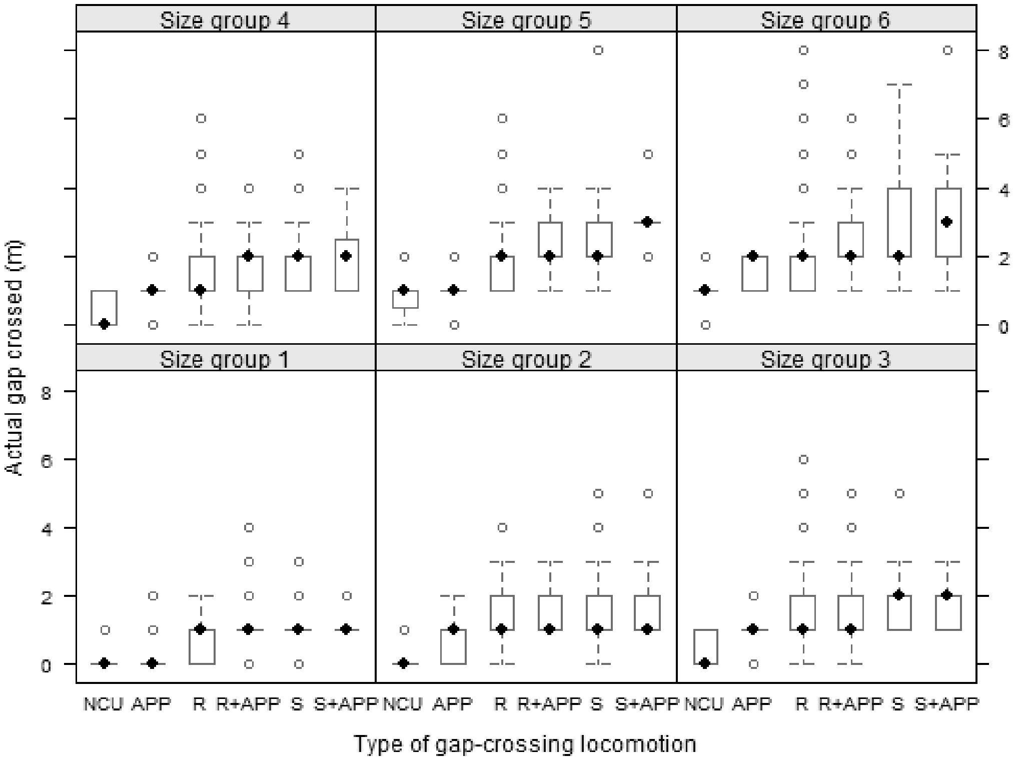


Figure 4.7 The interaction between body size group and type of locomotor behaviour with the effect on the AGC (actual gap crossed) during gap crossing behaviour of Bornean orangutans. Each panel shows the relationship between AGC and locomotor behaviour for each of the six size groups in ascending order of size from bottom left to top right. The boxes represent the inter-quartile range and the solid markers are the median, the whiskers extend to the maximum value excluding outliers and the open circles are the outliers. Types of locomotion as follows: NCU- non-compliance utilising; APP- appendicular deformation; R- ride; R+APP- ride + appendicular deformation; S- sway; and S+APP- sway + appendicular deformation. Data collected at Tuanan Research Station from July 2009- July 2010.

The second significant interaction (type of locomotion * take-off support) is shown in Figure 4.8. Once more, this shows the relationship between type of locomotion and the gap crossed and the panels show how this relationship varies with the type of support used. Orangutans cross larger gaps using trunks and lianas and smaller gaps using branches. When orangutans use the mass deformation types of locomotor behaviour on trunks and lianas they can cross large gaps, and these behaviours are used more often by larger orangutans.

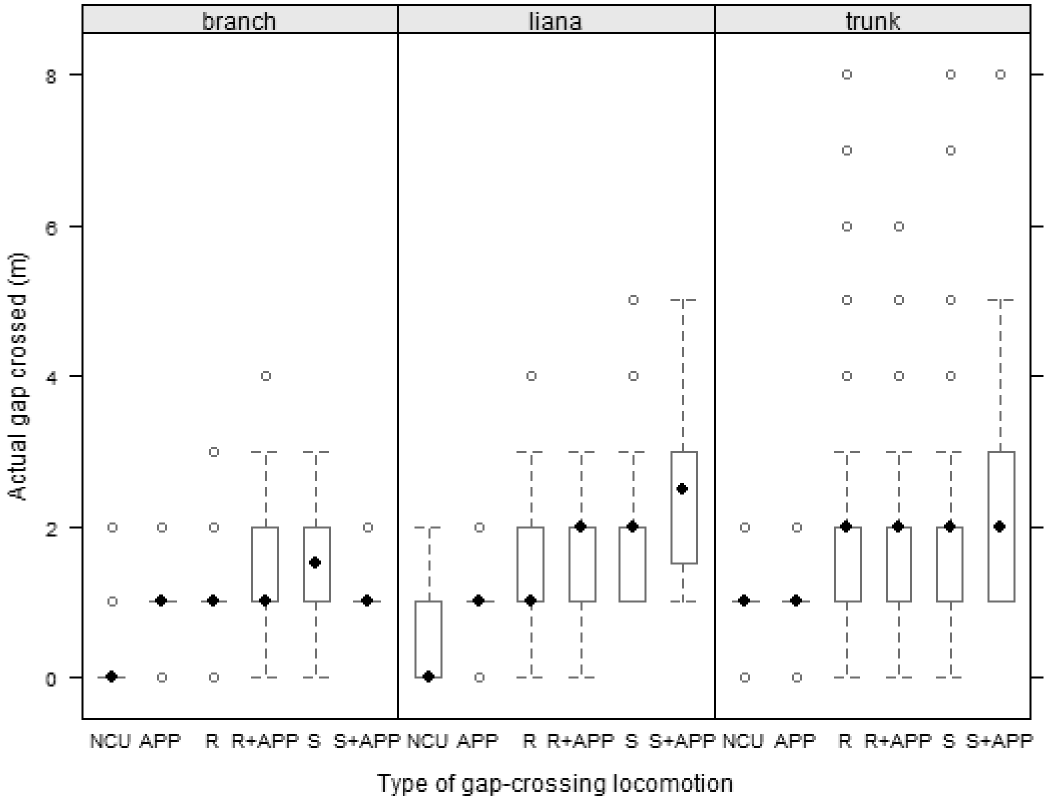


Figure 4.8 The interaction between type of locomotor behaviour and take-off support with the effect on the AGC (actual gap crossed) during gap crossing behaviour of Bornean orangutans. Each panel shows the relationship between AGC and locomotor behaviour for each of the three take-off support types. The boxes represent the inter-quartile range and the solid markers are the median, the whiskers extend to the maximum value excluding outliers and the open circles are the outliers. Types of locomotion as follows: NCU- non-compliance utilising; APP- appendicular deformation; R- ride; R+APP- ride + appendicular deformation; S- sway; and S+APP- sway + appendicular deformation. Data collected at Tuanan Research Station from July 2009- July 2010.

To examine ontogenetic development of gap crossing behaviour further the AGC was plotted against forearm length separately for each type of locomotor behaviour (Figure 4.9). As we wanted to examine the development of skills during immaturity, immature subjects were plotted individually by forearm length and the average of all the adult subjects was used. A linear relationship was found between forearm length and both NCU and appendicular deformation crossings. The mass deformation crossings showed a different trend, with two distinct slopes identified, with an initial steep increase in AGC with forearm length until approximately 24 cm after which the increase in AGC was less. This was confirmed by the 95% confidence intervals for these 2 slopes which did not overlap.

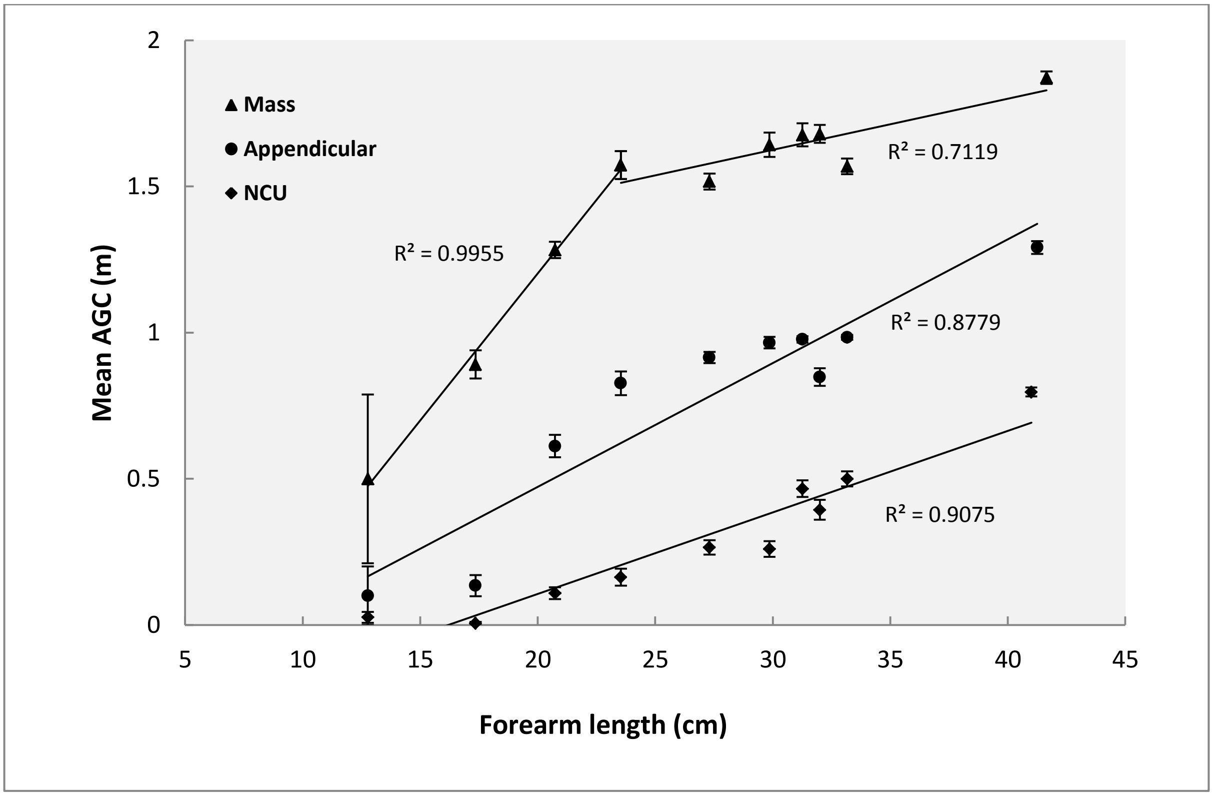


Figure 4.9 The actual gap crossed (AGC) during three types of orangutan gap crossing behaviour: NCU-non-compliance utilising; appendicular; and mass deformation plotted against forearm length. The first nine data points represent immature orangutans and the last point is an average of all the adult data. Error bars represent the standard error of the mean. A linear regression was fitted to NCU and appendicular deformation crossings and two linear regressions were fitted to the mass deformation crossings as these results showed two distinct slopes. This was validated by the 95% confidence intervals for the two slopes of the regression lines for mass deformation, which did not overlap (.08-.12 and .005-.03). Data collected at Tuanan Research Station from July 2009- July 2010.

4.4 Discussion

4.4.1 The relationship between body size and the use of compliance

The aim of this study was to examine the development of gap crossing behaviour during ontogeny. The study found that changes in locomotor behaviour during crossings between trees correlated with body size groups based on forearm length. As predicted, mass deformation locomotion increased in frequency with increasing size group. As larger orangutans cause supports to deform more than smaller orangutans they are both better equipped and have greater need to deform supports to their advantage in order to cross gaps in the canopy.

4.4.2 The relationship between body size and support use

Support use also showed size related trends in line with our initial hypotheses. The use of trunks for gap crossing increased with body size whereas the use of lianas and branches decreased. Trunks tend to have larger diameters than branches and lianas and, therefore, require more force to deform. However, there are advantages of using trunks for gap crossing. When compared to branches trunks tend to have a more vertical orientation that means that when they are deformed they allow the orangutan to cover more horizontal distance than a more horizontal support. Additionally, in the degraded forest around Tuanan tree trunks with a suitable diameter to be readily deformed were far more numerous than lianas with a large enough diameter to support the weight of a large orangutan (pers. obs.). This may explain why smaller orangutans used lianas more frequently than larger orangutans. Furthermore, lianas are often found hanging vertically from trees, which means that they can be oscillated without applying much force making them ideal supports for small orangutans to ride and sway across gaps.

4.4.3 Estimating distance during gap crossing

This was the first study to combine two distance estimates: the distance that was actually crossed and the distance between the trunks during crossings between trees for the largest arboreal primate, the orangutan. Gebo (1992) also estimated distances between the take-off and landing points in his study of platyrrhine monkeys, *Alouatta palliata* and *Cebus capucinus*, but this was only for crossings that used leaping. Cannon and Leighton (1994) used an alternative estimate of distance when comparing the gap crossing behaviour of gibbons *Hylobates agilis* and macaques *Macaca fascicularis*; they measured the distance between the terminal woody supports of gaps rather than the actual distance crossed by the primates. As our study involved a large range of different body sizes we did not measure the distance between the terminal branches because they were deflected according to the mass of the animal, and, therefore, this measure of distance would have varied with body size. Therefore, we chose to measure the distance from take-off to landing point (AGC) but this was particularly complicated for orangutans because they used different methods to cross between trees. Thus, we have provided a new classification system to enable the AGC to be recorded for different types of orangutan gap crossing behaviour, which best reflects the distance that orangutans actually travel without using continuous supports. We were able to use this quantitative variable to model the factors that influence gap crossing ability in this species.

4.4.4 The relationship between body size and the actual gap crossed (AGC)

As predicted, the distance that orangutans crossed when moving between trees (AGC) increased with body size. As larger orangutans have greater mass and longer reach they can deform and grasp supports across larger distances. However, when the average gap size was plotted against forearm length (Figure 4.5), the largest orangutan crossed smaller gaps than expected. This orangutan was observed in a particularly degraded part of the habitat where most of the trees were very young and growing close together. The adult male travelled very near to the ground usually by riding from one tree to the next. He also frequently travelled on the ground, but this was not included in this study of arboreal gap crossing. His arboreal locomotion appeared to require minimal effort as the thin trees bent under his large body weight. This method of travel did not require large amounts of energy-expensive climbing as proposed by Thorpe et al. (2007a) because the food sources in this area were mostly located in small trees and termites were collected from the ground. The behaviour of the largest male in the degraded habitat suggests that he did not cross gaps that were anywhere near the limit of his capability. Therefore, he may not be comparable with the other subjects in this study. Both individual and habitat differences within the study site are likely to affect the locomotor behaviour and gap crossing distances of orangutans.

4.4.5 The relationship between body size and proportion of AGC relative to the distance between the trunks

As the average AGC did not seem to reflect the crossing ability of all of the subjects we also calculated the AGC divided by the distance between the trunks to estimate the proportion of the gap that was crossed. When these values were plotted against forearm length (Figure 4.6) the regression produced a good fit for all of the subjects. This suggests that orangutans in degraded forest use continuous branches for travelling between trees less as their body size increases. However, this relationship may change in different types of forest. In a mature forest where trees are connected by large branches we would expect to see all orangutans taking more continuous routes between trees.

4.4.6 What influences the distance an orangutan crosses?

The results of the GLMM showed that all of the factors tested had a significant effect on the AGC, which suggests that body size is not the only factor that influences the distance an orangutan can cross. The results of the GLMM also support our initial hypothesis (1) that as body size increases orangutans use more complex gap crossing locomotion involving utilisation of compliance. Even though body size was found to correlate with both type of locomotion and take-off support (Figure 4.4), it is clear from the presence of the 2-way interaction between body size group and type of locomotion that both size and gap crossing technique influence the distance that orangutans cross. This is further supported by the interaction between type of locomotion and take-off support, which suggests that orangutans of all body sizes use different combinations of take-off support and locomotion to cross different sized gaps. For the modes of mass deformation locomotion ride and sway there is a further level of detail that may also influence the distance an orangutan crosses. A study of the body posture used during tree sway has been carried out by Myatt et al. (unpublished data) and preliminary results suggest that pronograde suspension is associated with crossing the largest gaps. This posture may allow orangutans greater stability when they oscillate trunks using adjoining branches, a technique that creates a moment arm effect to amplify oscillations.

Although our initial results supported the hypothesis (2) that larger orangutans use larger types of supports, the 2-way interaction size group*take-off support was not present in the model. This may be because smaller orangutans crossed larger gaps using lianas more often whereas larger orangutans usually crossed larger gaps using trunks. This is supported by the Tukey's contrasts (Table 4.4), which group trunks and lianas together in terms of their effect on the AGC but separate them from branches. These results suggest that orangutans of different sizes use different strategies to cross the same distance (AGC). Thus habitat differences such as relative abundance of compliant trunks and lianas may influence the relationship between body size and AGC because smaller orangutans are more able to use lianas to cross large gaps than compliant trunks.

4.4.7 Evidence for cognitive development

The present study found evidence which suggests that cognitive development influences the gap crossing ability of young orangutans. This evidence was only found for gap crossings which involved mass deformation, which are the least intuitive locomotor behaviours and are thought to be the most cognitively challenging locomotor behaviour (Chevalier-Skolnikoff et al. 1982; Bard 1995). The present study found that when AGC was plotted against forearm length (Figure 4.9) for crossings that involved mass deformation there were two different slopes. The AGC of subjects with a forearm length of less than 24cm (aged 1 to 5 years) showed a greater rate of increase than subjects with a forearm length over 24cm (aged 6 to adult). In comparison, the results for non-compliance utilising and appendicular deformation crossings both had a single linear relationship between forearm length and AGC. This evidence suggests that skills required to cross gaps using mass deformation emerge and improve between the ages of 1 and 5 years and during this time the distance an animal can cross is dictated by both body size and skill level. After gap crossing skills are fully mastered, only changes in body size are expected to influence the distance an animal can cross. Therefore, a lower rate of increase from 6 years onwards indicates that orangutans at Tuanan have learnt all the techniques they need to cross gaps in the canopy by 6 years old and are only limited by their smaller body size. This evidence supports our initial hypothesis (5) that skills required to cross gaps using mass deformation develop more slowly than those required for appendicular deformation. Furthermore, these results suggest that infant orangutans are already capable of manipulating compliant vegetation to cross a gap by appendicular deformation by the time they are 1 year old. The apparent difference in age of skill acquisition between appendicular and mass deformation supports the theory that mass deformation is the most cognitively complex gap crossing skill to learn (Chevalier-Skolnikoff et al. 1982; Bard 1995).

4.4.8 Conclusion

This study has found evidence that the gap crossing behaviour of orangutans varies with both physical and cognitive development. As this was the first study to investigate gap crossing behaviour of wild orangutans we cannot be sure how representative of other populations of orangutans in different habitats these data are. As the forests of Borneo and Sumatra become increasingly degraded it becomes more important to understand the influence of habitat degradation on the ability of orangutans to travel between essential resources. This study suggests that orangutans are well adapted to travel in disturbed habitats but more information is required to understand how orangutans deal with gaps in the canopy in a mature forest. This may have implications for orangutan development as habitat differences may affect the age at which orangutans can fully master the skills they need to travel independently of their mother.

4.4.9 Next step

Having investigated how independent gap crossing behaviour changes with growth and maturity and determined the age at which gap crossing skills appear to be fully mastered. The aim of Chapter 5 was to establish the role of the mother in the development of independent gap crossing behaviour. If orangutan mothers provide assistance during gap crossing according to their offspring’s needs then the type of assistance and size of gap where it is provided can be used to establish the competence of the offspring. However, individual differences in maternal style may also influence the development of skills in their offspring. Chapter 5 will additionally address whether maternal parity affects maternal style and how different maternal styles may influence the development of gap crossing skills in their offspring.

5. THE ROLE OF THE MOTHER IN THE DEVELOPMENT OF INDEPENDENT TRAVEL IN WILD BORNEAN ORANGUTANS (*Pongo pygmaeus wurmbii*)

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Abstract

Orangutan life history is characterised by an extended period of immaturity, when orangutans learn the skills needed for an independent life in the forest. Arboreal locomotion presents a particular challenge to orangutans, as the largest arboreal primates, they must learn complex skills in order to utilise compliant arboreal supports to cross gaps in the canopy. Young orangutans receive substantial assistance from their mothers before they are able to cross gaps independently; therefore, maternal assistance is key to understanding the development of independent locomotion in orangutans. This study was carried out from Tuanan field station, Central Kalimantan, Borneo. Data collection focussed on six dependent offspring and their mothers and the ages of the offspring ranged from 1 to 7 years. Independent and maternally assisted gap crossing behaviour was recorded along with gap crossing distance and support use to determine which gaps the offspring were capable of crossing independently. We investigated the mother-infant relationship further by recording the maternal response to her infant crying in the context of arboreal locomotion. Results showed that mothers provided less assistance as offspring age increased. Mothers provided more active types of assistance

that were more costly to younger offspring and more passive assistance to older offspring. Mothers assisted offspring crossing larger gaps than they crossed independently. Overall, these results indicate that mothers reduce the assistance that they provide according to the needs of their offspring. This study found preliminary evidence that maternal style may relate to maternal experience and this may influence the development of arboreal skills in offspring. We also present new evidence of active maternal encouragement of locomotion by a mother orangutan during this study.

5.1 Introduction

Orangutans have one of the longest immature phases of all mammals. Young orangutans spend up to 9 years in exclusive association with their mother before their close bond is broken by the birth of another offspring (Wich et al. 2004; van Noordwijk and van Schaik 2005). In primates an extended period of immaturity has been associated with the need to transfer essential skills and knowledge (Janson and van Schaik 1993; Joffe 1997). For the largest arboreal primates, skills associated with travel in the forest canopy are likely to be amongst the most challenging. Orangutans show considerable variation in their locomotor behaviour (Thorpe and Crompton 2006) particularly in their methods of crossing gaps in the canopy (Povinelli and Cant 1995). Orangutans have been found to utilise the energy in compliant vegetation by bending and oscillating arboreal supports (Thorpe et al. 2007a). These skills allow orangutans to cross gaps between trees without descending to the forest floor, thereby avoiding ground predators and conserving energy (Thorpe et al. 2007a). The manipulation of compliant supports for locomotion is thought to be one of the most complex behaviours that orangutans must learn (Chevalier-Skolnikoff et al. 1982; Bard 1995) and these behaviours require young orangutans to develop both their cognitive and physical skills (see Chapter 4). As orangutans lead semi-solitary lives (Delgado and van Schaik 2000), their offspring receive all of their parental care and the majority of their social learning opportunities from their mothers. Therefore, maternal behaviour is key to understanding the development of independent locomotion in these species.

Studies of rehabilitant orangutans have shown them to be proficient imitators (Russon and Galdikas 1993, 1995; Russon 1999). It is thought that wild infant orangutans acquire technical skills such as nest building and food processing through observation of their mothers (van Noordwijk et al. 2009). This is supported by observations of wild Bornean orangutans, which showed that infants paid closer attention when their mother was processing rare or difficult food items (Jaeggi et al. 2008). Locomotor skills develop slowly during ontogeny and orangutan mothers play an important role in this process (Bard, 1995). These skills are complex to learn and infants require substantial maternal assistance: for the first 2 years of their lives, they are almost always carried by their mothers during travel (van Noordwijk et al. 2009). Once infants start to travel independently they still regularly receive assistance when crossing gaps between trees (van Noordwijk and van Schaik 2005; van Noordwijk et al. 2009). Active types of maternal assistance include carrying, making a bridge by holding two trees together (MacKinnon 1974) and reducing the size of a gap by leaning a tree closer to the infant (van Noordwijk and van Schaik 2005). Offspring may also benefit from passive types of assistance such as riding in the same tree as their mother while she sways it or catching a tree that the mother has already swung and using the back-swing to cross a gap (Bard 1995). Maternal assistance during gap crossing may still occur regularly for offspring up to 6 years old (van Noordwijk et al., 2009) and has occasionally been observed for even older offspring (Bard 1995; van Noordwijk and van Schaik 2005).

According to the theory of parent-offspring conflict (Trivers, 1974), mothers should invest in their offspring when the benefit to their offspring is greater than the cost to them. This includes the cost of reducing the resources they have available to invest in subsequent offspring. In contrast, offspring should demand investment when the cost to their mother is up to twice as much as the benefit they receive because their subsequent siblings will only share half their genetic information. Maternal assistance during locomotion incurs cost to the mother through increased energy expenditure and lost foraging time while waiting for her offspring. Therefore, it is likely to result in parent-offspring conflict. The maternal costs of assisted travel vary according to the type of assistance provided and the mass of the offspring. Carrying is likely to be the most costly form of assistance, especially when the offspring is heavy. Larger offspring may benefit from travelling with their mother without substantially influencing her energy expenditure by riding on the same tree while she oscillates it to cross a gap. The benefits of maternal assistance to the offspring are potentially large because failed crossings can result in falls, which can cause serious injury or death, as observed by Goodall (1986) in chimpanzees. Following Trivers (1974), orangutan mothers are, therefore, expected to provide assistance during gap crossing according to the need of the offspring, but offspring are expected to demand assistance even when they are capable of crossing independently.

5.1.1 Comparison of crying behaviour in orangutans and humans

Crying is used by humans and other mammalian species to promote proximity between mother and infant and has, therefore, been termed an attachment behaviour (Ainsworth 1967). In orangutans, infants solicit the attention of their mothers by making crying vocalisations that sound very similar to the cries of human children (Maestripieri and Call 1996). The theory of Bowlby (1969) states that human infants develop attachment to a caregiver (usually the mother) who attends to their attachment behaviours with an appropriate response. Ainsworth et al. (1971) further defined attachment as either secure or insecure based on whether the caregiver is attentive (i.e. responds promptly to infant's cries) or neglectful (i.e. ignores infant's cries), respectively. Studies of humans suggest that infants with attentive mothers and secure attachments develop alternative forms of communication faster than infants who are ignored (Bell and Ainsworth 1972). Infants with insecure attachments have been found to be less resilient (Cicchetti et al. 1993; Sroufe 1997) and are more prone to anxiety disorders (Warren et al. 1997). However, in the absence of verbal communication, orangutans continue to use crying as a form of communication as they grow older (Maestripieri and Call 1996). Therefore, it may not be appropriate to compare their crying behaviour to that of human infants. Young orangutans often use crying to solicit their mother's assistance when a gap in the canopy separates them from their mother (Bard 1995). However, she observed that when mothers ignored their offspring's cries their offspring usually found a way to cross independently, often by taking a different route. This indicates that offspring solicit assistance even when they are capable of following their mother independently and that mothers may be able to identify this. By ignoring and refusing to provide assistance, mother orangutans can encourage independent behaviour in their offspring (Bard 1995). This can be structured in a manner that is conducive to learning, by withdrawing assistance gradually so that infants are constantly challenged but are not presented with problems that are beyond their capability, a technique known as scaffolding (Wood et al. 1976). By systematically reducing carrying and other assistance during gap crossing, Bard (1995) proposed that orangutan mothers were scaffolding the development of independent locomotor behaviour in their offspring.

5.1.2 Maternal style

Primate mothers are known to vary in terms of mothering style and this has been attributed to both experience and individual differences (Fairbanks 1996). Research has focussed on monkey species with studies of vervet monkeys (*Cercopithecus aethiops*) and rhesus and Japanese macaques (*Macaca mulatta* and *M fuscata*), showing that primiparous mothers are more protective and less rejecting when compared to more experienced mothers (Hooley and Simpson 1981; Berman 1984; Fairbanks 1988; Schino et al. 1995). As with humans, research suggests that maternal style influences infant development in rhesus and Japanese macaques (Simpson and Datta 1991; Bardi and Huffman 2002)

However, in contrast to studies of human development e.g. (Bell and Ainsworth 1972; Cicchetti et al. 1993; Sroufe 1997; Warren et al. 1997), research on macaques suggests that infants with more rejecting mothers are more independent than infants with more restrictive mothers (Simpson and Datta 1991; Bardi and Huffman 2002). By rejecting their infants, primate mothers may encourage infants to develop independent behaviours. In orangutans maternal rejections peak during weaning when mothers are more likely to ignore or act aggressively towards their offspring (Horr 1977). In chimpanzees the increase in maternal rejection associated with weaning has been found to cause a regression back to more infant-like behaviour in the young chimpanzees (Clark 1977). This suggests that there is considerable conflict between mothers and infants regarding the timing of weaning and the withdrawal of maternal assistance.

Maternal encouragement may also facilitate the development of independent locomotor behaviour. Studies of rhesus and pigtail macaques (*Macaca nemestrina*) by Maestripieri (1995, 1996) found evidence that mothers actively encouraged locomotion by leaving their infant then coaxing them to follow by walking backwards making vocalisations and facial expressions (e.g. the pucker face; Maestripieri, 1996). The infants of mothers who regularly encouraged locomotion in this way developed independent locomotion earlier than those that were not encouraged. There is also evidence for maternal encouragement during arboreal locomotion: spider monkey mothers were found to encourage independent locomotion by encouraging their infants to travel in front of them (Milton 1981). This behaviour was also observed by Bard (1995) in Bornean orangutans. These behaviours suggest that some primate mothers may be able to facilitate their infant's locomotor development by actively encouraging infants to move independently.

For developmental studies of animals with slow life histories such as orangutans, long-term studies are required for longitudinal data to be collected. Shorter studies rely on cross-sectional data from multiple individuals to infer approximately when developmental milestones occur. The subjects of the study of Bard (1995) were 14 dependent immature orangutans ranging in age from 2.5 to 8.5 years. This was the first study to quantify broadly the types of maternal assistance that occurred in two age categories: infants (under 5 years) and juveniles (over 5 years). Unfortunately, her sample size did not allow division of her subjects into further age categories to examine the timing of developmental milestones in finer detail. Infant subjects under the age of 2.5 were not sampled by Bard (1995), and although young infants mostly cling to their mother during gap crossing, it is likely that some early independent crossing behaviours begin to develop before the age of 2.5 years. To differentiate further between the gap crossing abilities of different aged orangutans, gap crossing parameters such as crossing distance and support use are required to investigate the gap crossing scenarios that present the greatest challenge to immature orangutans. Therefore, quantitative data from the earliest stages of independent locomotion are required to determine fully when specific gap crossing skills develop.

The aim of this study was to investigate the role of the mother in the development of independent travel in orangutans, by collecting behavioural data and estimates of distance crossed between trees for both maternally assisted and independently crossed gaps. Maternal assistance is expected to decrease with offspring age and in accordance with offspring need. Specifically we hypothesise that: (1) mothers will be more likely to assist their offspring in crossing larger gaps; (2) the type of assistance provided will vary according to the age of the offspring, with younger offspring expected to receive more active forms of assistance and older offspring expected to receive more passive assistance; (3) there will be individual variation in maternal response to crying with more experienced mothers expected to be less attentive; and (4) the offspring of more experienced mothers are expected to be more independent than those of inexperienced mothers.

5.2 Methods

5.2.1 Study site and subjects

This study was carried out at Tuanan research station (2°09'S, 114°26'E) within the Mawas Reserve, Central Kalimantan, Indonesia. The study area consists of approximately 725 ha of lowland peat swamp forest with an orangutan density of 4.25/km^2 (van Schaik et al., 2005). The area is highly degraded and has been subject to selective logging in the early 1990s. Prior to the onset of continuous research at Tuanan in 2003, a grid-based trail system was cut and orangutans in the area were identified and habituated to human observers. Data collection focused on six mother-offspring pairs, and one semi-independent adolescent, the ages of the dependent offspring ranging from 1 to 7 years (Table 5.1).

Table 5.1 Young orangutans in association with their mothers observed at Tuanan Research Station, Central Kalimantan between July 2009 and July 2010. Focal days refers to the number of whole days of observation.

Subject	Age	Sex	Mother	Mother parity	Focal days
Mawas	1	female	Mindy	multiparous	10
Kino	3	male	Kerry	multiparous	10
Jip	4	male	Juni	primiparous	10
Deri	5	male	Desy	primiparous	7
Jerry	6	male	Jinak	multiparous	10
Streisel	~7	female	Sidony	multiparous	9
*Milo	~9	female	Mindy	multiparous	7

*Milo still travelled with her mother and younger sibling at the time of the study but maternal assistance was no longer provided. Only data on travel route were collected.

Ages of the five youngest offspring were known and the ages of the two oldest offspring were estimated on first encounter based on body size and locomotor competence (Jaeggi et al., 2008). Although this is a potential source of bias, Milo was estimated to be 2 years old when research in the area started and Streisel was first encountered in 2007 when she was estimated to be 5 years old. At these ages it was possible to estimate age with reasonable accuracy.

5.2.2 Data collection

The study was carried out from June to November 2009 and from January to July 2010. Continuous observations of focal subjects were carried out from when the subject awoke from their nest in the morning to when they rested in their evening nest, typically from 05:00 to 17:00. As this was a cross-sectional study of locomotor development, data were collected from different aged individuals that were still in constant association with their mother. Subjects were followed for a maximum of 10 days over more than one month to minimise possible bias introduced by temporarily abundant food sources (Thorpe and Crompton, 2005). The interval between observation periods varied, and for immature subjects a maximum sample interval of 6 months was set to ensure they were at the same stage of development. Data collection focussed on travel between trees. Every time a focal infant travelled between two trees, the type of support used, an estimate of the distance crossed and any assistance provided by the mother were recorded (see Table 5.2) using a digital voice recorder (Sony ICD-MX20) to enable the observer to watch and record simultaneously. Additionally, for all independent crossings the direction of travel relative to the mother was recorded. Other mother-infant interactions were also recorded to establish the relationship between the mother and offspring at different stages of development.

5.2.3 Locomotor behaviour

Locomotor behaviour during gap crossing is presented in Chapter 4, but, for the purpose of this chapter it is necessary to define two categories of locomotor behaviour because this determined how support use and distance crossed were recorded. Thus, gap crossing locomotion can be divided into behaviours that cross a gap by using body mass to deform compliant supports (such as ride and tree sway), and those which do not rely on the deformation of compliant supports (such as clamber and transfer) (Cant 1994; Hunt et al. 1996; Thorpe and Crompton 2006).

5.2.4 Support use

Five types of support were distinguished: compliant trunk, rigid trunk, compliant branch, rigid branch and liana. Supports were judged to be compliant if they were observed to deform under the weight of the subject using them and rigid if they did not. Therefore, this was a measure of the effective compliance. This study recorded the support that was used to make the crossing in the tree that the orangutan started in (take-off tree). For modes that involved mass deformation, the support that was deformed to make the crossing was recorded and for all other modes of locomotion, the last support that the subject made contact with in the take-off tree was recorded (see Chapter 4 for further details).

5.2.5 Actual gap crossed (AGC)

This study recorded an estimate of the distance crossed to the nearest metre every time a subject moved between two trees. The actual gap crossed (AGC) was an estimation of the horizontal distance travelled from the take-off point to the landing point. When the gap was crossed using mass deformation locomotion, the take-off point was estimated from the point where the orangutan was prior to support deformation (shown by the dotted outline of the tree in Figure 5.1a and b). For all other types of behaviour the take-off point was the last part of the take-off tree that the orangutan made contact with. If this distance was estimated to be less than 0.5m the AGC was recorded as zero. In cases where a subject crossed a gap to reach a liana and then used the liana to get to the next tree, details of both crossings were recorded (see chapter 4 for further details). Self-training in estimating horizontal distances in the forest was carried out at regular intervals to ensure estimations were accurate.

5.2.6 Maternal assistance

When a mother assisted her offspring in crossing between trees, the support used and distance crossed by the mother were recorded. Information on the gap crossed by the mother was recorded to compare gaps that offspring crossed independently with gaps that they received assistance with to investigate whether mothers provided assistance according to the needs of their offspring.

Five different types of maternal assistance were identified (Table 5.2). These were not mutually exclusive as one crossing could involve more than one type of assistance and in such cases all assistance was recorded. Types of maternal assistance were classed as active or passive. Maternal assistance was considered active when the mother’s behaviour showed obvious intent to aid her offspring’s travel between trees, such as in carry, bridge (Figure 5.1 and 5.2a) and reduce gap (Table 5.2). Offspring also benefitted from passive maternal assistance when they travelled using the same trees that their mother used, such as ride together and backswing (Table 5.2 and Figure 5.1 and 5.2b). Due to low sample sizes it was necessary to combine reduce gap with bridge and back-swing with ride together for the purpose of analysis.

When there was an independent component of a maternally assisted crossing (i.e. the offspring crossed a gap of more than 0.5m independently; see Figure 5.1b), the offspring’s support use and distance crossed were also recorded.

Table 5.2 Maternal assistance provided to young orangutans when travelling between trees. Research carried out at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

Type of assistance	Definition	Active/ Passive
Carry	Mother carries offspring across the gap	Active
Bridge	Mother makes a bridge with her body and pauses. The offspring may travel across the mother's body or at a different level where the mother's bridge has created a continuous path or brought branches close enough for the infant to cross (Figure 5.1a)	Active
Reduce gap	The mother has already crossed, and then she shifts her weight in the landing tree to decrease the size of the gap enough for the offspring to cross. Often in response to crying after failed crossing attempts	Active
Ride together	Mother rides or sways a tree and offspring travels in the same tree taking advantage of, the deformation of the support (Figure 5.1b)	Passive
Back-swing	Mother sways a tree to cross and offspring catches the tree on the backswing and follows mother across	Passive

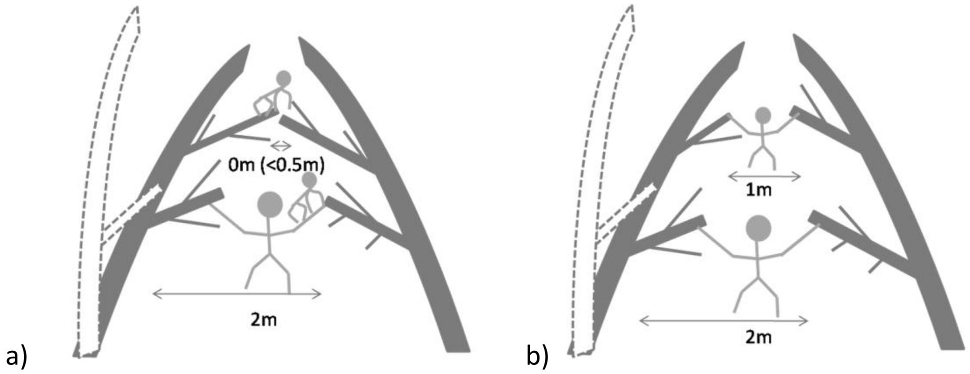

Figure 5.1 Two ways that mother orangutans assist their offspring in gap crossing. a) Bridge: mother makes a bridge and offspring either crosses on her body or at another level where the branches have been brought closer together; b) Ride together: mother deforms a trunk and offspring rides and reaches for the branch of the next tree.

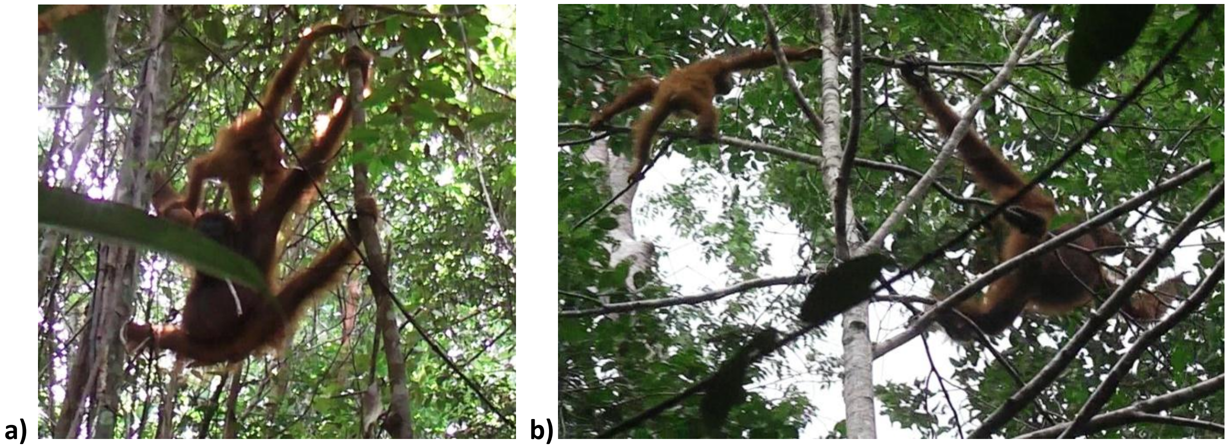

Figure 5.2 Stills from videos of orangutans at Tuanan Research Station in 2010. a) Bridge: Juni makes a bridge for Jip; b) Ride together: Kerry bends a tree and Kino ride with her (Videos: A C Phillips)**.**

5.2.7 Response to crying

When an infant made crying vocalisations whilst travelling or attempting to travel, a crying bout was recorded along with the response of the mother. Crying bouts were variable in duration, and included all crying made within the same locomotor context. Responses were divided into three categories: 1) active- mother comes back/assists/collects infant; 2) passive- mother stops moving/waits until her infant has caught up; and 3) ignore- mother does not change her behaviour on hearing her offspring cry.

5.2.8 Travel route

When offspring travelled between trees independently, their direction of travel with respect to their mother was recorded to establish the extent to which offspring chose their own travel route. Crossings where offspring moved closer to their mother were recorded as ‘towards’, crossings where offspring moved farther from their mother were recorded as ‘away’ and crossings where the offspring had already moved away and then changed direction to move closer again were recorded as ‘come back’. In cases where the mother had moved on before the offspring came back, crossings were recorded as comeback until the offspring reached the area where it had left its mother and towards after that. If it came back but took a different route to meet up with its mother, these crossings were recorded as towards. If the mother and offspring appeared to be travelling parallel to each other no direction was recorded. The percentage of crossings where the offspring took their own route was calculated from these data using the following equations:

$$true\ Away\ (tA) = A - CB \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots. Equation\ 1$$

$$\text{Where A} = \text{ Away and } CB = Come\ back$$

$$\text{Infant takes own route} = \frac{tA}{tA + T} \times I \ldots\ldots\ldots\ldots\ldots\ldots.\ldots\ldots\ldots\ldots\ldots\ldots.. Equation\ 2$$

$$\text{Where T} = \text{Towards}, and\ I = percentage\ of\ independent\ crossings$$

5.2.9 Other mother and offspring behaviour

Additional types of mother and offspring behaviour were recorded to provide further information on the relationship between mothers and their offspring with respect to the level of independence of the offspring and the willingness of the mother to provide assistance to her offspring (Table 5.3). These behaviours were recorded ad libitum for all subjects that associated with their mother.

Table 5.3 Definitions of mother and offspring behaviours recorded in Bornean orangutans at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

Category	Behaviour	Definition
Offspring solicit	Cry	Crying vocalisation in any context
	Food solicit	Any attempt to obtain food from the mother [a]
Offspring locomotion	Practise tree sway	A trunk is swayed back and forth without attempting to cross to another tree
	Alternative route	A gap is obviously avoided- after hesitation or failed crossing another route is found [b]
Mother maintain proximity	Collect	Mother approaches offspring and puts it on her body
	Restrain	The offspring is prevented from leaving by holding part of its body [c]
	Wait	During travel , the mother stops and continues once her offspring has caught up
	Throat scrape	Vocalisation made by mother orangutans to their offspring [d]
Mother encourage	Encourage locomotion	Mother leaves offspring and vocalises for them to come to her [c]
	Play	Mother instigates or actively participates in play with offspring [c]
Mother provide	Food share	Mother offers food or allows food to be taken [a]
	Protect	Mother threatens, chases or attacks another animal to protect her infant [c]
Mother-offspring conflict	Reject	Mother blocks infant from making contact for suckling or travel purposes [c]
	Withhold food	Mother resists infant's solicitation for food [a]
	Scold	Mother exhibits aggression towards offspring
	Chase away	Mother chases offspring and offspring moves away

Behavioural definitions follow previous studies: **a**- Jaeggi et al. (2008); **b**- Bard (1995); **c**- Maestripieri et al. (2002); and **d**- van Schaik et al. (2006)

5.2.10 Statistical analysis

We examined the factors and combinations of factors that influence the ability of a young orangutan to cross a gap independently by fitting a generalized linear mixed model (GLMM) using a binomial response variable ‘success’ with independent crossings coded as successful and assisted crossings as unsuccessful. Subject age, AGC and support type were included in the model as predictors. The GLMM was carried out using R 2.13 (LME4 package, R Development Core Team 2010). As with binomial logistic regression, GLMMs provide parameter estimates that indicate how the predictors influence the probability of obtaining a successful outcome. The advantage of GLMMs is that they can be used for data with repeated measures, which was particularly important for this study as the data consisted of many observations collected from each individual. Individual identity was included as a random effect on the intercept and a binomial distribution family with a logistic link was selected.

5.3 Results

5.3.1 Solicitation of assistance and maternal response

Out of 3566 observations of independent travel there were 160 observations of young orangutans crying while attempting to follow their mother. There was considerable variation in the maternal response to infant crying (Figure 5.3). Overall, mothers responded to crying both actively and passively more when their offspring were younger and ignored older offspring more often (Table 5.4). The 4 year old orangutan, Jip, cried most frequently when travelling, more than twice as often as the 3 year old Kino. Jip’s mother Juni was less likely to ignore Jip’s cries when compared to Kino’s mother Kerry (Table 5.4). At 5 years old Deri cried at a similar rate to 3 year old Kino, but Deri was ignored less than Kino (7.1% and 37.5%, respectively) but Deri’s mother Desy usually responded passively (78.6%). At 6 years old Jerry rarely cried in the context of locomotion and his mother Jinak was not observed to respond actively although she was observed to wait for him. At 7 years old Streisel still cried regularly when travelling. She also cried at a similar rate to Kino and Deri but her mother, Sidony, ignored her on the majority of occasions (84.6%) although she was observed to respond both actively and passively.

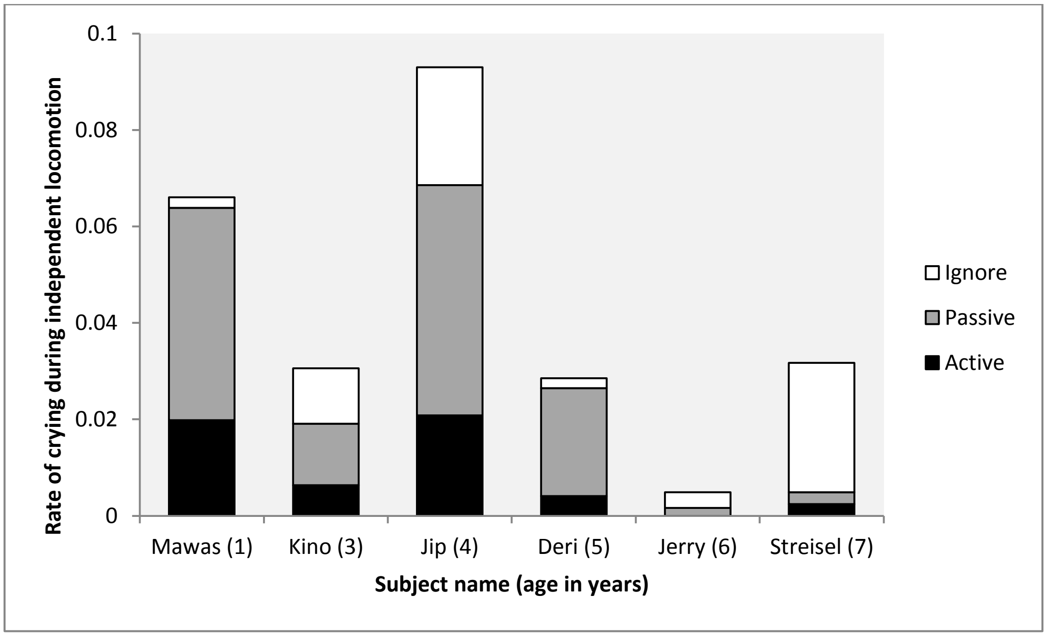

Figure 5.3 Response of orangutan mothers to their infant crying in the context of locomotion. Bar heights represent the number of crying bouts divided by the number of observations of independent travel for each infant. Bars are shaded according to the response of the mother following the cry of her infant. Responses to crying are as follows: Active- mother returns/assists/collects infant; Passive- mother stops moving/ waits until her infant has caught up; and Ignore- mother does not change her behaviour on hearing her offspring cry. Data collected at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

Table 5.4 Response of orangutan mothers to their infant crying as a percentage of total cry observations. Responses to crying are as follows: Active- mother returns/assists/collects infant; Passive- mother stops moving/ waits until her infant has caught up; and Ignore- mother does not change her behaviour on hearing her offspring cry. Data collected at Tuanan Research Station, Central Kalimantan from July 2009- July 2010.

Subject	Age (years)	Number of cries	Active response (%)	Passive response (%)	Ignore (%)
Mawas	1	30	30.0	66.7	3.3
Kino	3	24	20.8	41.7	37.5
Jip	4	76	22.4	51.3	26.3
Deri	5	14	14.3	78.6	7.1
Jerry	6	3	0.0	33.3	66.7
Streisel	7	13	7.7	7.7	84.6

Maternal assistance during crossing between trees was divided into three main types: carry, bridge and ride together. Figure 5.4 shows the percentage of different types of maternal assistance with bar heights representing the percentage of all crossings that were maternally assisted. The results show that older offspring received assistance less frequently than younger offspring. The type of assistance also varied with offspring age with mothers providing active types of assistance to younger offspring such as carry and bridge, whereas older offspring were more likely to receive passive assistance by being allowed to ride together with their mother. Carrying was likely to be the most costly form of assistance for the mother and was only observed regularly in subjects under 4 years old. The 4 year old subject Jip was carried more often than the 3 year old Kino but, otherwise, carrying decreased with age.

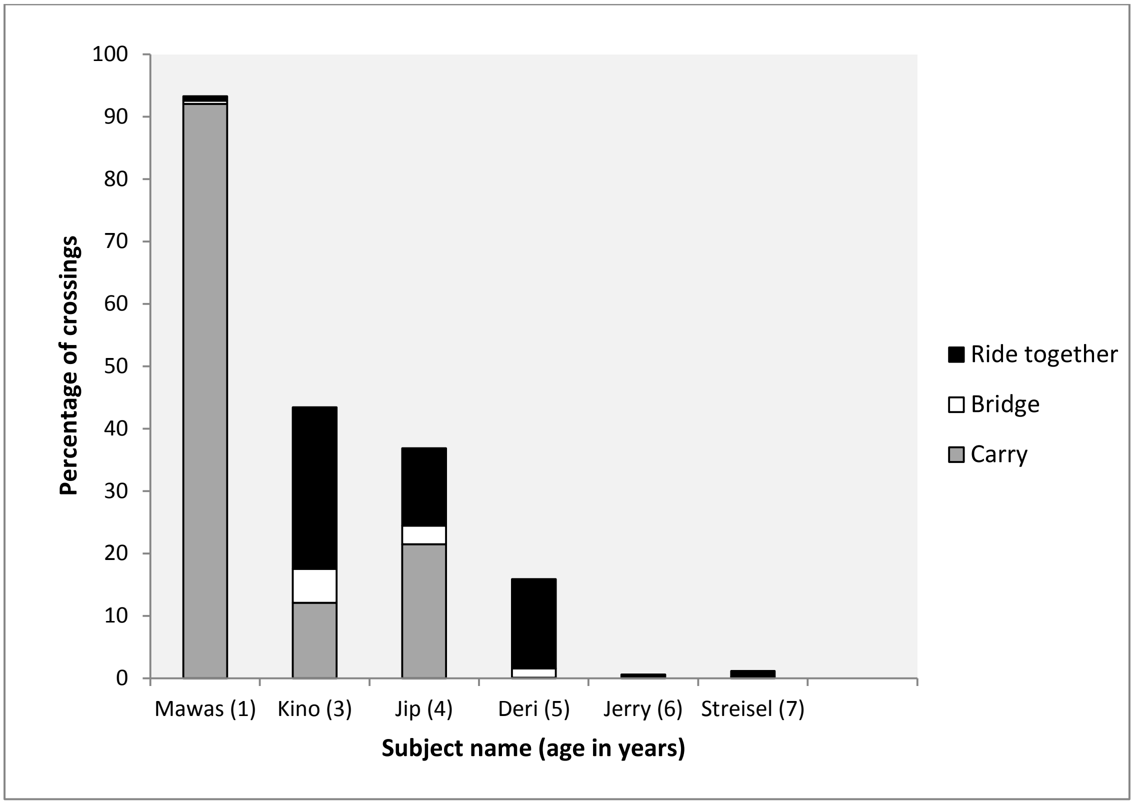

Figure 5.4 Maternally assisted crossings between trees as a percentage of total crossings between trees. Three types of maternal assistance were distinguished: carry- mother carries offspring; bridge- mother makes a bridge between two trees for offspring to cross; and ride together- mother deforms a tree to cross a gap and offspring rides in the same tree. Data from wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Independent crossings yielded a direction of travel relative to the location of the mother which was used to calculate the percentage of crossings where the offspring chose its own travel route (Figure 5.5). Overall, older offspring were found to take an independent travel route more often than younger orangutans, which followed their mothers more often. These data fit the pattern of the other data on maternal dependence shown in Figure 5.3 andFigure 5.4 in that Kino is more independent and Streisel is less independent considering their respective ages.

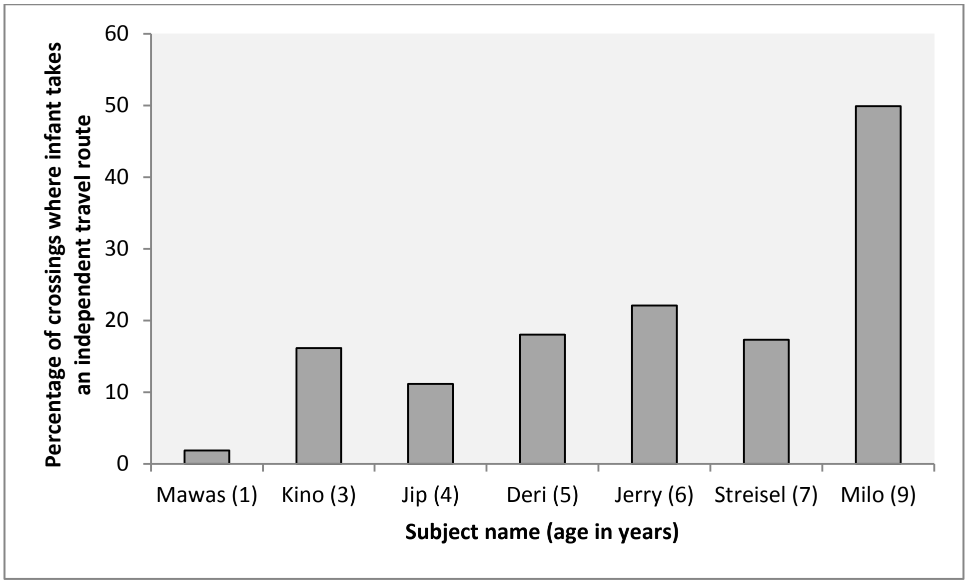

Figure 5.5 Percentage of independent crossings where infant takes their own route. Data from wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

Frequencies of specific mother and infant behaviours are presented in Appendix C. These results can be used to establish broad trends in age-related behavioural variation and to investigate individual differences in maternal style (Fairbanks 1996). Solicitation of maternal care was lower for the youngest infant when compared with the 3 and 4 year old subjects Kino and Jip. After 4 years old offspring solicited their mother's care less frequently. At 4 years old Jip had the highest number of observations of soliciting behaviours. The mother of the youngest offspring had the highest number of behaviours that maintained proximity and the number of these behaviours decreased for mothers with older offspring. Individual differences were most striking between 3 year old Kino and 4 year old Jip; Jip's mother exhibited almost twice as many behaviours that maintained proximity as Kino's mother. Overall, mothers with older offspring provided food and protection to their offspring less than those with younger offspring. Maternal encouragement in the context of play and locomotion was only observed in mothers with young infants. Mothers with older offspring had higher frequencies of behaviours associated with mother-offspring conflict. This was most obvious for Streisel and her mother Sidony, who was particularly aggressive towards her daughter.

The GLMM tested the fixed effects of take-off support (a categorical variable) and two continuous covariates of AGC (the actual gap crossed either by the infant or the mother in the case of mother-assisted crossings) and subject age. The final model of best fit following an iterative model selection and criticism process was:

Success ~ age * AGC + take-off support * AGC + (1 | Individual)

The model was selected based on the value of the AIC and the significance (*P*- value) of the interactions contained within it. The distribution of the residuals was checked, but there were no obvious patterns of over or under-dispersion, non-homogeneity of variance, or other features that might invalidate the model. The model of best fit included two 2-way interactions and three main effects. All levels of the main effects and interactions between them were found to be significant ($P<0.05$) apart from the take-off support compliant trunk (Table 5.5). These results show that the probability that a young orangutan will independently cross between two trees is influenced by three factors: the age of the orangutan, the size of the gap and the type of support that is used in the take-off tree. Both the interactions between age and AGC and the interaction between the take-off support and the AGC influence whether a young orangutan will independently cross a gap.

The parameter estimates, shown in Table 5.5 indicate by their size and sign (+/-) how the levels within the factors influence the probability of a young orangutan successfully crossing a gap independently. As the AGC increases, the level of success decreases, shown by the negative parameter estimate. As age increases, the level of success increases, shown by the positive parameter estimate. The negative effect of AGC, however, is larger than the positive effect of age on the probability of success. The small, positive parameter estimate (0.36) for the interaction between AGC and age does not alter the overall trend that, within this age range, as AGC increases the likelihood of success decreases.

The parameter estimates for take-off support, listed in Table 5.5, are relative to the support of rigid trunk. These indicate that all other support types are associated with higher levels of success, the greatest being liana. The interaction between AGC and the take-off support of compliant trunk has the least negative estimate, which indicates that as AGC increases young orangutans are most likely to cross using a compliant trunk successfully.

Table 5.5 General linear mixed model- fixed effects that influenced whether young orangutans crossed between trees independently or were assisted by their mothers. Data from wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

	Estimate	**Std. Error**	**z value**	***P***
Intercept	-3.07	0.97	-3.15	<0.01
AGC	-2.40	0.43	-5.63	<0.001
age	1.29	0.20	6.56	<0.001
Take-off support	0.11	0.46	0.24	0.81
rigid branch	1.89	0.78	2.44	<0.05
compliant branch	2.58	0.49	5.27	<0.001
liana	5.01	1.29	3.89	<0.001
Interactions				
AGC*age	0.36	0.07	5.21	<0.001
compliant trunk*AGC	-0.70	0.35	-1.98	<0.05
rigid branch*AGC	-2.00	0.82	-2.43	<0.05
compliant branch*AGC	-1.48	0.39	-3.77	<0.001
liana*AGC	-2.80	0.84	-3.31	<0.001

Success ~ age * AGC + take-off support * AGC + (1 | Individual). AIC= 2467, n= 5989, Individuals= 6. Success defined as successfully crossing a gap without assistance from mother.

Post-hoc analysis was carried out using Tukey's contrasts to determine which of the levels of the significant factor take-off support differed significantly in their effect on the probability of a successful independent tree crossing. The test separated the support types into two groups that had a significantly different influence on success (*P*<0.05). The first group consisted of compliant trunks and rigid trunks and the second group included compliant branches, rigid branches and lianas.

The model interaction between the two continuous covariates AGC * age is represented in Figure 5.6. It graphs shows that mother-assisted crossings occur on larger gaps than independent crossings for all ages. Older immature orangutans cross larger gaps independently and they also tend to receive assistance only when crossing larger gaps compared with younger orangutans. This evidence supports the hypothesis that mother orangutans provide assistance when the offspring cannot cross the gap independently.

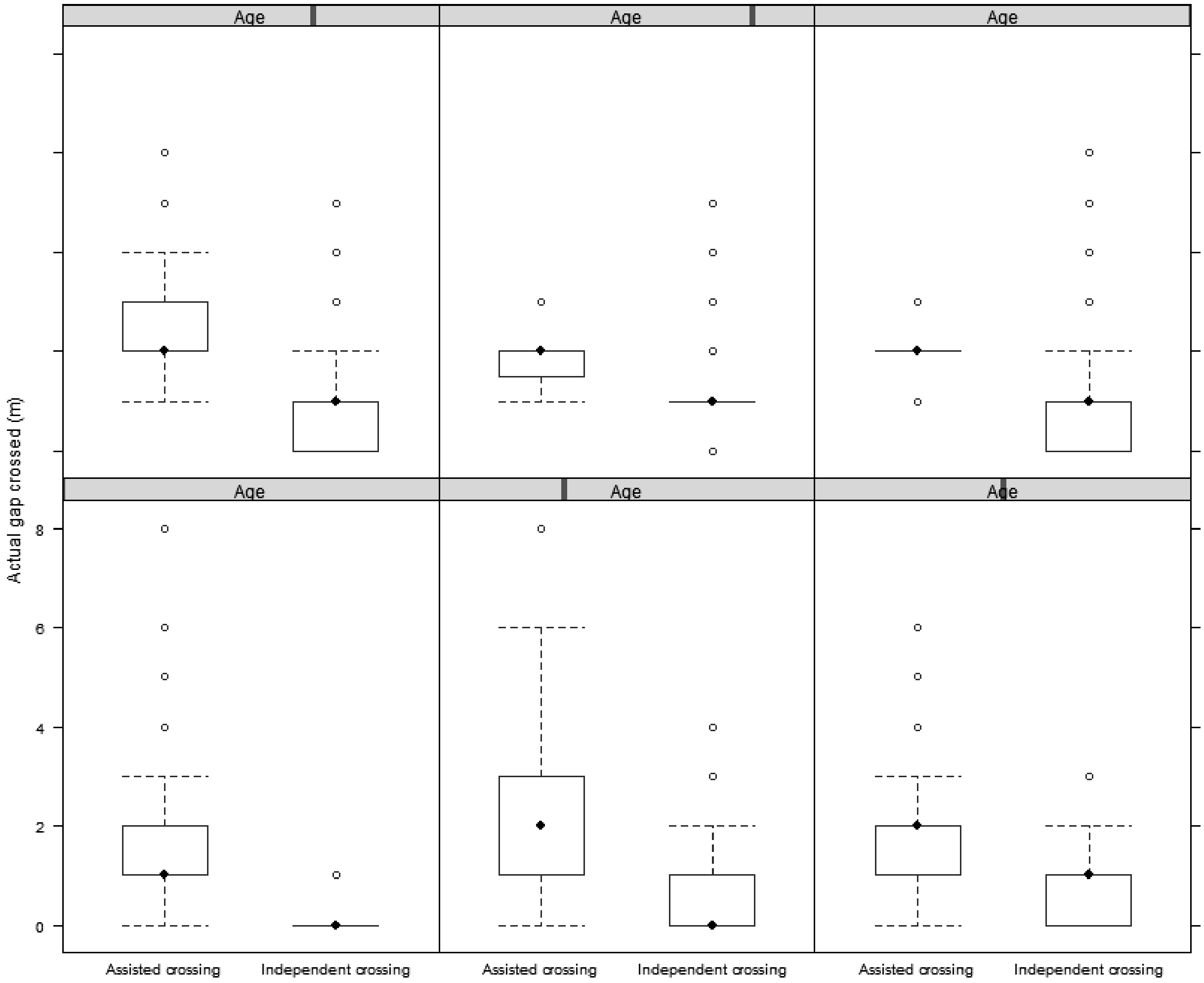

Figure 5.6 The interaction between offspring age and actual gap crossed (AGC) when travelling between trees with the effect on successful independent crossing. Panels represent the different ages, the grey bands show the position of the individual on the age scale, which runs from 1 to 7 years. The boxes represent the inter-quartile range and the solid markers are the median. The whiskers extend to the maximum value excluding outliers and the open circles are the outliers. Data from wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

The second model interaction AGC * take-off support is shown in Figure 5.7. This shows that larger gaps are crossed when mothers provide assistance compared to when infants cross independently. The difference is greatest when comparing crossings where the take-off support is a compliant trunk. Mass deformation of trunks allows heavier orangutans to cross larger gaps but lighter orangutans have more difficulty deforming trunks, while they can deform compliant lianas and branches more easily. Therefore, the difference in AGC is less pronounced for these types of supports. All orangutans cross smaller gaps when using rigid supports which do not allow mass deformation and, therefore, differences between independent and maternally assisted crossings are less for these types of take-off support.

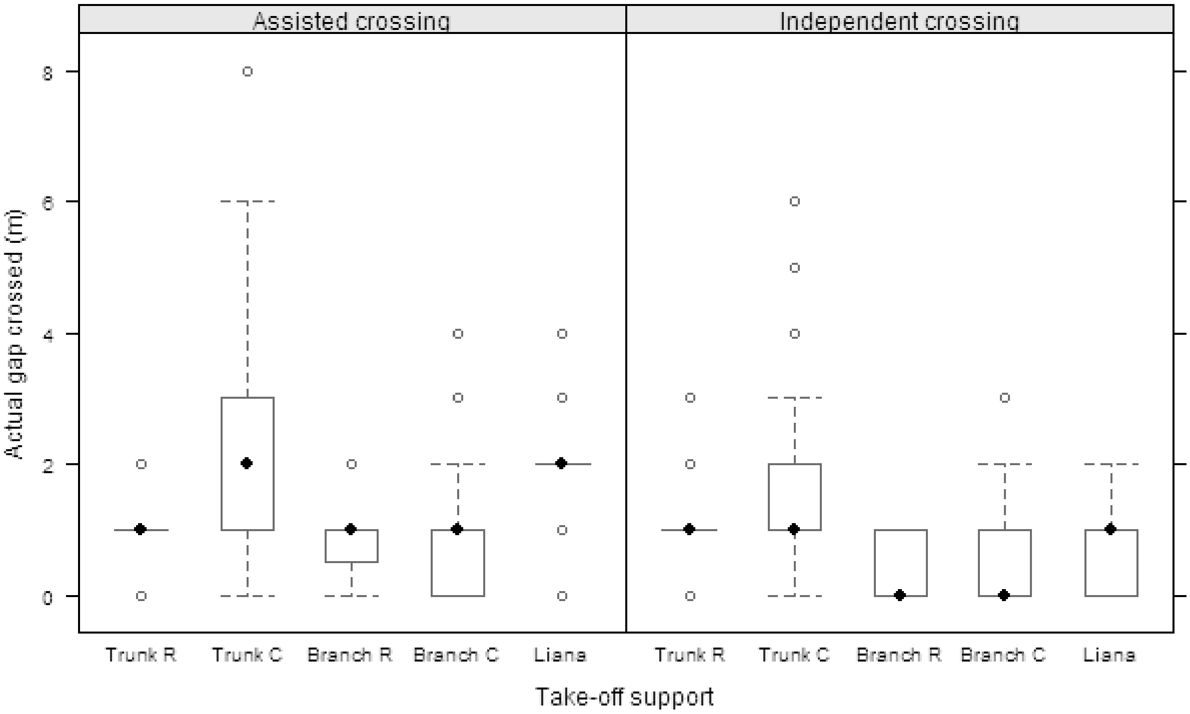

Figure 5.7 The interaction between the take-off support used for gap crossing and the actual gap crossed (AGC) with the effect on successful independent crossing. The boxes represent the inter-quartile range and the solid markers are the median. The whiskers extend to the maximum value excluding outliers and the open circles are the outliers. Types of take-off support as follows: Trunk R- rigid trunk; Trunk C- compliant trunk; Branch R- rigid branch; Branch C- compliant branch; and liana. Data from wild Bornean orangutans collected from July 2009- July 2010 at Tuanan Research Station.

5.4 Discussion

According to the theory of parent-offspring conflict (Trivers 1974), mothers should provide assistance when the benefit to the offspring is greater than the cost to the mother. Therefore, maternal assistance was expected to correlate with offspring need. As expected, this study found that maternal assistance correlated with age, with older orangutans receiving less assistance when crossing between trees. This was also found by Bard (1995) in her study of Bornean orangutans. The type of maternal assistance provided also varied with age. As expected, younger offspring were given more active types of assistance such as carrying and bridging which are more energetically costly for the mother. Older offspring received more passive types of assistance, such as predominantly ride together with is much less costly for the mother. The results broadly support the findings of Bard (1995) although there were some interesting differences. Bard (1995) found that mothers regularly made bridges for offspring up to 8 years old whereas our study found that bridging rarely occurred after 5 years old. Our study found that riding together was very frequent between the ages of 3 and 5 after which all assistance declined dramatically. In contrast, Bard (1995) found the level of ride together was similar between the ages of 2.5 and 6 years and far lower than the frequency observed at Tuanan. Habitat differences may account for the differences in the amount of ride together. The habitat at Tanjung Puting was mainly composed of undisturbed mixed dipterocarp forest (Galdikas 1988) which is characterised by tall, thick tree trunks when compared to the heavily disturbed peat-swamp forest found at Tuanan (van Schaik et al. 2005). Tuanan had an abundance of thin trunks that were closely spaced and may allow orangutans to cross independently of their mother by riding one tree to the next at an earlier age. Habitat differences may also account for the differences in type of assistance: if mothers are also frequently crossing between trees by ride then offspring can take advantage of this by riding together with their mother. Overall, these results support the theory that mothers provide assistance according to offspring need and that they reduce the costs associated with assisting their offspring by using less energetically expensive types of assistance, primarily by riding together at Tuanan.

By recording the AGC and take-off support each time an orangutan crossed between trees, this study was able to examine which gaps young orangutans were capable of crossing independently and those which presented problems for them. Across the range of ages, orangutans were assisted with larger gaps than they crossed independently. This evidence supports the hypothesis that orangutan mothers provide assistance according to the needs of their offspring. The model of gap crossing success also shows that take-off support type influences the gap crossing abilities of young orangutans. The greater disparity in AGC between independent and assisted crossings using compliant trunks as the take-off support suggests that young orangutans may lack the physical ability to deform trunks to cross larger gaps and this is where they are most likely to need assistance from their mothers. Bending and swaying large trunks are likely to be the most physically challenging aspects of gap crossing behaviour that young orangutans must master. Younger orangutans may also be constrained by their cognitive abilities as bending and swaying compliant supports requires an understanding of the affordances of the supports.

Young orangutans solicit their mother’s assistance by crying (Bard 1995). Data from this study did not permit analysis of whether offspring still solicited for assistance once they were capable of crossing independently. However, observations of offspring that were ignored suggest that in the absence of maternal assistance offspring were usually able to take an alternative route to circumvent gaps that they could not cross independently, as observed by Bard (1995) and Noordwijk et al. (2005). This evidence suggests that orangutan mothers may be able to predict which gaps their offspring can circumvent and only provide assistance when absolutely necessary. This is supported by evidence from Bard (1995) who found that a mother with an injured infant provided more assistance than previously observed before the injury. In our study offspring solicitation appears to correlate with maternal response. In general, offspring that solicited more had mothers that responded more often and offspring that solicited less had mothers that were more likely to ignore them. There were, however, two exceptions: Deri and

Streisel. At 5 years old Deri's rate of solicitation was one third of the rate of 4 year old Jip. Deri almost always got a response from his mother, but she usually responded passively by waiting rather than returning to assist him. At 7 years old Streisel still solicited her mother's assistance regularly even though her mother almost always ignored her. Streisel's immature behaviour may have been a reaction to her mother's rejections (Appendix C) as she was pregnant at the time of the study. Therefore, this behaviour may have been a temporary phase that occurred in response to her mother re-establishing the boundaries of their relationship. This has been observed in chimpanzees where an increase in maternal rejections associated with weaning was found to cause offspring to regress temporarily to more infantile behaviours (Clark 1977). Correlations between offspring solicitation and maternal response suggest either that mothers with offspring that rarely solicited assistance became less receptive to this signal or that offspring with mothers that regularly ignored them learnt that vocalising for assistance was futile. This may also indicate that as a result of being ignored, offspring developed independent gap crossing behaviours faster and, therefore, had less need to vocalise for their mother's assistance. This theory is supported by studies of rhesus and Japanese macaques, which showed that infants with more rejecting mothers developed independent behaviour earlier than those with more attentive mothers (Simpson and Datta 1991; Bardi and Huffman 2002). However, this goes against the findings of human studies which suggest that children with rejecting mothers develop insecure attachment, which has been associated with lower resilience (Sroufe 1997), greater anxiety (Warren et al. 1997), less social competence (Troy and Sroufe 1987)and poorer performance at problem solving tasks (Matas et al. 1978). This may reflect differences in learning mechanisms for the skills being recorded in studies of humans and non-human primates.

Among primate mothers, differences between individuals lead to variation in maternal style (Fairbanks 1996). Maternal experience has been found to lead to variation in maternal style, with less experienced mothers being more attentive than more experienced ones (Hooley and Simpson 1981; Berman 1984; Fairbanks 1988; Schino et al. 1995; Fairbanks 1996). In order to assess whether maternal parity affected maternal behaviour and the development of offspring we compared individuals of similar ages with mothers, which differ in their parity. Firstly we considered the differences between 3 year old Kino and 4 year old Jip and their respective mothers, multiparous Kerry and primiparous Juni. As predicted by our initial hypothesis regarding the influence of maternal experience on maternal style, Kerry was found to reject and ignore Kino more frequently than Juni did with Jip even though Jip was 1 year older than Kino. Also in agreement with our maternal experience hypothesis, Juni showed more maternal behaviours aimed at maintaining proximity and was more likely to respond to solicitations from Jip than Kerry did with Kino. We also found evidence that the younger Kino may be more independent than Jip. Kino solicited his mother's assistance less, was carried less and rode together more when crossing between trees and took an independent travel route more often than Jip. Although he was 1 year younger, Kino exhibited less infant-like behaviour than Jip. Deri's mother, Desy, was also primiparous. During the study Deri was 2 years older than Kino. In comparison to Deri, Kino cried more often and his mother, Kerry, exhibited more behaviour which maintained proximity and shared food with Kino more often (Appendix C). She also rejected Kino less often than Desy and Deri. However, Kino and Deri had similar rates of solicitation during travel and similar percentages of crossings where they took independent travel routes. However, results for travel route were broadly similar for 5 year old Deri, 6 year old Jerry, and 7 year old Streisel. Overall, there is some evidence for experience-related maternal variation affecting offspring development but the sample size is too small to draw any firm conclusions.

Active maternal encouragement of locomotion is known to occur in macaque species, with offspring that were encouraged developing independent locomotion earlier (Maestripieri 1995, 1996). During our study, active maternal encouragement was observed on two occasions by the same individual, Kerry with her infant Kino. The behaviour sequence was the same on both occasions and occurred in quick succession; firstly, Kerry carried Kino from one tree to another, then she let him go and crossed back to the first tree. Kino then cried, and Kerry moved off in the opposite direction to Kino and made throat scrape vocalisations, whereupon Kino found a way to follow his mother. Another way primate mothers can encourage independent locomotion is by encouraging their offspring to lead during travel. This involves waiting for the offspring to move and then following, as previously observed in spider monkeys and orangutans (Milton 1981; Bard 1995). This behaviour was also observed when following Kerry and Kino and may explain why Kino's percentage of crossings (see Figure 5.5) where he took an independent route was particularly high. Kerry was the only mother that was observed to perform these types of maternal encouragement. This may further explain the apparent precocity of 3 year old Kino in comparison to the other subjects.

Individual differences were also in observed in the two oldest subjects, 6 year old Jerry and 7 year old Streisel. Jerry's mother, Jinak, was thought to be one of the older orangutans in the area as genetic tests indicate that Jerry has three older siblings in the area- Kerry, Mindy and Juni (van Noordwijk, pers. comm.). When compared to Streisel, Jerry was rejected less, benefitted from food sharing more and was still observed suckling whereas Streisel was not. These differences may be due to maternal age. The terminal investment hypothesis (Williams 1966) suggests that older mothers should be more willing to invest in their offspring as they are closer to reproductive senescence. Streisel's mother, Sidony, was known to be pregnant at the time. Therefore, she would be expected to cease investment in her older offspring to prepare for the birth of her new offspring.

Information on the role of the mother in the development of arboreal skills may be particularly valuable given the number of young orphaned orangutans that currently reside in rehabilitation centres across

Borneo and Sumatra. In order to release these orangutans back into forests, rehabilitation staff must ensure that they have all the skills they need to survive. The results of our study may be used to help facilitate learning of arboreal skills in orphaned orangutans undergoing rehabilitation.

This study has provided detailed information on the role of the mother in the development of independent travel for six wild Bornean orangutans that were still in constant association with their mothers. While the sample size is small, the study indicates that mother orangutans provide assistance during travel according to the needs of their offspring as the assistance provided to younger offspring was more frequent and more energetically expensive. Furthermore, by modelling the factors that influence whether an orangutan will cross a gap independently, we have shown that offspring are more likely to be assisted crossing larger distances of AGC. The type of support used to make the crossing also influenced the success of young orangutans' independent crossings with lianas being used more to cross large gaps. This suggests that habitat variables may influence the development of gap crossing behaviour in this species. This study provides preliminary evidence to support the theory that more experienced mothers are less attentive and that their offspring are more independent within the context of arboreal gap crossing. We also provide the evidence of active encouragement of locomotion by a mother orangutan. This information may be used to help facilitate the learning of arboreal skills in orphaned orangutans at rehabilitation centres and improve their chances of successful reintroduction to the wild.

5.4.1 Next step

After thoroughly investigating the development of positional behaviour and gap crossing in wild orangutans I was interested to know whether captive orangutans would have a similar course of development. As wild orangutan positional behaviour is adapted to their complex arboreal habitat, the highly simplified environment experienced by most captive orangutans may promote different types of positional behaviour and influence the development of these behaviours during ontogeny. Changes in positional behaviour during ontogeny can affect the development of muscle and bone. Therefore positional behaviour during ontogeny is particularly important for the long-term health and suitability for reintroduction of captive orangutans.

6. A COMPARISON OF THE DEVELOPMENT OF POSITIONAL BEHAVIOUR IN CAPTIVE AND WILD BORNEAN ORANGUTANS

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Abstract

Wild orangutans are the largest primates to live a predominantly arboreal lifestyle and their varied positional behaviour reflects the complexity of their forest habitat. In contrast, captive environments offer a far less challenging habitat where terrestrial behaviours are common. These alternate environments encourage different types of positional behaviour. Although some comparison has been made of adult captive and wild orangutan positional behaviour, these studies have not included immature animals, which is a particularly important developmental stage because this is when bones form and establish the maximum stresses that they will be able to bear in adulthood. This study recorded wild orangutans at Tuanan, Central Kalimantan, Indonesia and captive orangutans at Apenheul and Ouwehands zoo in The Netherlands. Bornean orangutans ranging from infant to adult were sampled in both environments. We recorded the positional behaviour and support use of all age groups and analysed the development of these behaviours. Although captive and wild subjects showed similar frequencies of locomotion relative to posture, the types of behaviour were very different. Wild orangutans had much higher frequencies of suspensory behaviours whereas captive orangutans showed more compressive behaviour. Locomotor behaviour showed more variation across environment than posture, which suggests that captive management should focus on promoting more natural locomotion.

When associations between locomotion and support use were examined captive and wild subjects were similar, which suggests that providing supports that mimic those found in their natural habitat could encourage more natural locomotor behaviour. When the development of positional behaviour was examined, young captive orangutans were found to exhibit a positional behaviour repertoire that was most similar to wild counterparts. However, with increased age, captive orangutans showed less similar behaviour to their wild counterparts. As activity during immaturity influences musculoskeletal development, this developmental pattern may suggest that captivity puts the musculoskeletal systems of immature orangutans under lower stresses than in the wild, and this may serve to further limit their positional behaviour repertoire in adulthood.

6.1 Introduction

Wild orangutans lead an almost exclusively arboreal lifestyle. Their diverse repertoire of positional behaviour allows them to travel and feed on thin, compliant supports within the complex forest canopy (Cant 1987a, b; Thorpe and Crompton 2005, 2006; Thorpe et al. 2007a; Thorpe et al. 2009; Myatt and Thorpe 2011), which they achieve most often by spreading their weight over multiple supports and using all four limbs to bear weight in suspension and compression (e.g. orthograde quadrumanous clamber; Thorpe and Crompton 2005, 2006). When large animals travel on small branches, they are theoretically more stable in suspensory positions compared with above branch positions because they have, in effect, already fallen off the branch (Cartmill and Milton 1977). This theory is supported by studies of both Sumatran (Thorpe and Crompton 2005) and Bornean orangutans (Chapter 2), which found that orthograde suspensory locomotion was most associated with the smallest diameter branches. These thin flexible branches typically occur at the periphery of tree crowns (Grand 1972), which orangutans must use to access fruit and travel between trees. In contrast, pronograde compressive types of locomotion (tripedal and quadrupedal walking) are associated with the least challenging substrates, namely large single supports (Thorpe and Crompton 2005) and interwoven small supports (Chapter 2). Captivity on the other hand presents a far less varied and challenging environment for orangutans, which is likely to be reflected in their positional behaviour. By providing a secure ground environment with plenty of food, zoos promote terrestrial behaviour in orangutans. This has the potential to alter drastically the composition of terrestrial and arboreal positional behaviour in captive orangutans. Therefore, encouraging arboreal behaviour is one of the greatest challenges facing orangutan captive management.

As the largest predominantly arboreal animals, wild orangutans have received considerable interest in their positional behaviour. Studies of Sumatran orangutans (Sugardjito 1982; Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2005, 2006; Thorpe et al. 2007a; Thorpe and Crompton 2009; Thorpe et al. 2009; Myatt and Thorpe 2011) and Bornean orangutans (Cant 1987b; Manduell et al. 2011; Chapter 2 and 3) have enhanced our understanding of positional behaviour and habitat use in these species. However, few studies have recorded the positional behaviour of orangutans living in captive environments or examined the differences between wild and captive positional behaviour (Crompton et al. 2003; Isler and Thorpe 2003; Hanson 2008). To date, only Sumatran orangutan positional behaviour has been examined in captivity (Crompton et al. 2003; Isler and Thorpe 2003; Hanson 2008). Isler and Thorpe (2003) focussed on vertical climbing because it places the greatest stresses on the musculoskeletal system as it opposes gravity. They recorded the climbing behaviour of wild, rehabilitant and captive Sumatran orangutans including adults and immature subjects and found that the captive orangutans were faster, with a shorter cycle of limb movements than their wild counterparts. They attributed this to the captive animals using less cautious climbing because they were more familiar with the supports in their enclosure. Crompton et al. (2003) refer to a short study of orangutan locomotion at Chester Zoo which highlights the key differences in the locomotor behaviour of captive and wild

Sumatran orangutans. The captive orangutans exhibited much higher frequencies of quadrupedal and tripedal walking than wild orangutans, which are associated with a more terrestrial lifestyle. Crompton et al. (2003) (Crompton et al. 2003)also found that several modes of locomotion that are common in the wild were absent in the behaviour of the captive orangutans. These included bridging, oscillation and torso pronograde suspensory locomotion (see Appendix A for definitions of positional behaviour), which are complex locomotor behaviours particularly adapted for dealing with compliant arboreal supports. There are several possible explanations for the absence of these behaviours: the enclosure may have lacked the supports necessary to elicit them, their motivation to use arboreal supports may have been very low or the sample of 279 observations of locomotion may have been too small to detect behaviours that only occurred rarely. Such behaviours are generally reliant on small, compliant vegetation (Thorpe et al. 2009), which is particularly difficult to emulate in captive conditions. Since the study of Crompton et al. (2003) was carried out at Chester Zoo, the orangutans have been transferred to a more naturalistic enclosure. A recent study of Chester Zoo orangutans was carried out in their new enclosure (Hanson 2008). Levels of pronograde walking were still much higher than found in the wild by Thorpe and Crompton (2005, 2006). However, this study found that although frequencies of positional behaviours were substantially different from those recorded in wild orangutans, the overall repertoire of behaviour was broadly similar, suggesting that the new enclosure was successful in promoting natural behaviours.

The type and frequency of different positional behaviours that an animal exhibits have implications for the development and maintenance of a healthy musculoskeletal system. Exercise can increase bone mineral density (BMD) and enlarge muscle (Vicente-Rodríguez 2006). However, the modification of bones by the processes of modelling and remodelling is mainly achieved during the immature phase of life (Gunter et al. 2008). If optimum BMD is not achieved by adolescence, this may increase the chance of osteoporosis in later life (Khan et al. 2000) and although new muscle tissue can still be generated in older animals, deterioration also occurs in old age (Lindle et al. 1997). Therefore the immature phase is a particularly important time for captive orangutans, and deviations from natural positional behaviour during immaturity may contribute to adults being less able to exhibit their full repertoire of positional behaviour. For large bodied orangutans modes of positional behaviour that put the most stress on muscle and bones are those that oppose gravity, such as vertical climbing and suspensory locomotion (Isler and Thorpe 2003). When orangutans adopt a predominantly terrestrial lifestyle this puts very different demands on their body (Isler and Thorpe 2003). There is evidence that the skeletons of captive orangutans also adapt to a terrestrial way of life. For example, Sarmiento (1985) found that torsion was higher in the long bones of captive orangutans than wild orangutans and the shape and direction of their pisiform bones was modified so that they were similar to those of the African apes, which exhibit significant adaptations to quadrupedal knuckle walking (Richmond et al. 2001). Such changes are likely to hinder an orangutan's ability to clamber and climb. There are also welfare implications for animals that are physically unable to use suspensory behaviours and access their entire enclosure. A major concern for reintroduction and welfare of captive orangutans is, therefore, whether their environment can encourage sufficient arboreal positional behaviour to allow the musculoskeletal system to develop so that it continues to function in adulthood. In addition, exercise in humans has been shown to benefit mental health (for a review see Penedo and Dahn 2005), and it may therefore help alleviate symptoms of boredom and depression associated with living in confinement.

Thorough studies of wild animals help us to understand how their positional behaviour is adapted to the habitat in which they live. However, positional repertoires assembled from studies of wild individuals may not represent the whole spectrum of positional behaviours that orangutans are capable of, which Prost (1965) has termed totipotentiality. For example, a study found that a captive white-handed gibbon (*Hylobates lar*) was capable of brachiating with only one arm, whilst the other was used to carry objects.

This behaviour had never been observed in wild gibbons (Gibbons and Lockwood 1982). To understand fully the locomotor capabilities of a species, it is best to combine wild studies with zoo or lab-based studies (Prost 1965; Dunbar and Badam 1998; Wells and Turnquist 2001).

In primates, novel forms of positional behaviours also emerge during play behaviour, which contribute to juveniles having a larger repertoire than adults (Dunbar and Badam 1998; Wells and Turnquist 2001). Play behaviour is said to be training for the unexpected (Pellegrini and Smith 2005) and tends to involve faster, more risky types of locomotion (Thorpe and Crompton 2005). In positional behaviour, risky behaviours are those that are most unstable and are, therefore, associated with the greatest risk of falling. In captive environments, where animals are familiar with their surroundings, play behaviours may become even more dramatic in order to create the same level of risk. For example, captive Delacour's and red-shanked douc langurs (*Trachypithecus delacouri* and *Pygathrix nemaeus*) were found to perform locomotion with their eyes closed during bouts of play behaviour (Workman and Covert 2005). Therefore, in this study we predict that young captive orangutans will perform novel types of positional behaviour, and in particular fast, risky types of locomotion. These are likely to improve locomotor skills and aid healthy muscle and bone development.

When designing their exhibits, zoos have many important considerations. Zoos need to balance their animals’ need to have a naturalistic environment with making it attractive to visitors and allowing it to be easily maintained by staff whilst ensuring the safety of all inhabitants (Rosenthal and Xanten 2010). Orangutan enclosures typically contain climbing structures and ropes. One easy way to increase the area for captive orangutans to climb on is to use wiremesh in place of smooth walls and ceiling. This can encourage climbing and suspensory locomotion, particularly if it is used on the ceiling and animals are fed from above. However, zoos may be reluctant to use wiremesh as it does not have a very natural appearance and may spoil visitors’ photographs. Providing orangutans with free-hanging rope facilitates the oscillatory behaviours ride and sway, but this is often viewed as dangerous as it may increase the risk of animals injuring themselves or may be used to try and escape. Zoos prefer to attach ropes at both ends to limit the distance an animal can sway. This can still promote oscillatory behaviour providing the ropes are loosely attached.

Sumatran and Bornean orangutans are classified as critically endangered (Singleton et al. 2007) and endangered (Ancrenaz et al. 2007), respectively and their numbers continue to decline in the wild as a result of loss of habitat from forest destruction and conversion to plantation. As a consequence of human-orangutan conflict, thousands of orangutans currently reside in rehabilitation centres across Borneo and Sumatra, most of which are infants that have been snatched from their mothers. In order to successfully rehabilitate these orphaned orangutans they must be prepared by human care-givers for an independent life in the forest. Understanding how development of positional behaviour differs between captive and wild environments is also useful for improving the design of captive environments to elicit more natural behaviours. Education is one of the primary goals of modern zoos, and exhibiting animals performing natural behaviours is one of the best ways to educate the public about the ecology and conservation of threatened species. Furthermore, by identifying the key differences in the positional behaviour of wild and captive orangutans, it may be possible to evaluate the suitability of orangutans that have grown up in confinement for release into the forest.

The aim of this study was to compare the positional behaviour repertoires of Bornean orangutans living in captive and wild environments to investigate the influence of habitat on the development of positional behaviour and examine the potential suitability of captive orangutans for future release into natural forest habitat. We expect that the less complex and more familiar surroundings in captivity will elicit differences in the positional behaviour repertoires of captive and wild orangutans. Specifically, we hypothesise that: (1) captive orangutans will exhibit higher frequencies of pronograde walking; (2)

captive orangutans will exhibit modes of behaviour not seen in the wild, specifically fast, risky forms of locomotion that are expected to be most common in the behaviour of younger subjects; (3) enclosure design and support availability will influence frequencies of positional behaviours between captive environments, specifically enclosures with larger areas of wiremesh are expected to elicit higher levels of suspensory locomotion and enclosures with a greater number of ropes are expected to elicit higher levels of oscillatory behaviour; and (4) the positional behaviour of wild and captive orangutans is expected to be less similar (e.g. in terms of body orientation, method of weight-bearing and limb use) as age increases because deviations from natural behaviour during immaturity are expected to have negative effects on musculoskeletal development and this is expected to cause further divergence between adults.

6.2 Methods

6.2.1 Subjects and study sites

Tuanan field station (2°09’S, 114°26’E) is located within the Mawas Reserve, in Central Kalimantan, Indonesia. The study area consists of approximately 725 ha of lowland peat-swamp forest with an orangutan density of 4.25/km^2 (van Schaik et al. 2005). This area has been subjected to selective logging and as a result the forest is dominated by young, small trees. Data were collected from June to November 2009 and January to July 2010. The study analysed data from 12 wild Bornean orangutans, which ranged from infant to adult. Ages of younger orangutans were known to be accurate but older orangutans were assigned to age groups based on estimated age at first encounter. Five wild adults were excluded from this analysis to balance the wild and captive datasets in terms of the proportion of data from different age-sex categories. Less data were obtained for captive adults because older individuals were highly inactive, in particular the flanged males, which were not sampled in captivity.

Therefore, wild flanged males were excluded from this analysis along with two of the sub-adult males and one of the adult females, which were chosen randomly.

Captive orangutans were observed at two zoos in the Netherlands- Apenheul Primate Park in Apeldoorn, and Ouwehands Dierenpark, Rhenen (Table 6.1). Both zoos kept Bornean orangutans of unknown subspecies and all of the 12 captive subjects were captive born. Data collection was carried out from January to March 2009 when winter temperatures meant that orangutans were not given access to their outdoor enclosures. Apenheul had four indoor enclosures and each contained climbing structures made of wood logs bolted together and interspersed with knotted rope hammocks (see Figure 6.1). Some of the enclosures also had climbing structures made of metal bars. All enclosures contained ropes that were attached at both ends yet loose enough to allow orangutans to oscillate them. There were some panels of wiremesh between the enclosures and the keeper area but the majority of walls and the ceilings were solid. The enclosures were more spacious in the vertical plane with platforms at different levels to encourage orangutans to make use of the vertical space. Seven subjects were observed at Apenheul including individuals from each age group.

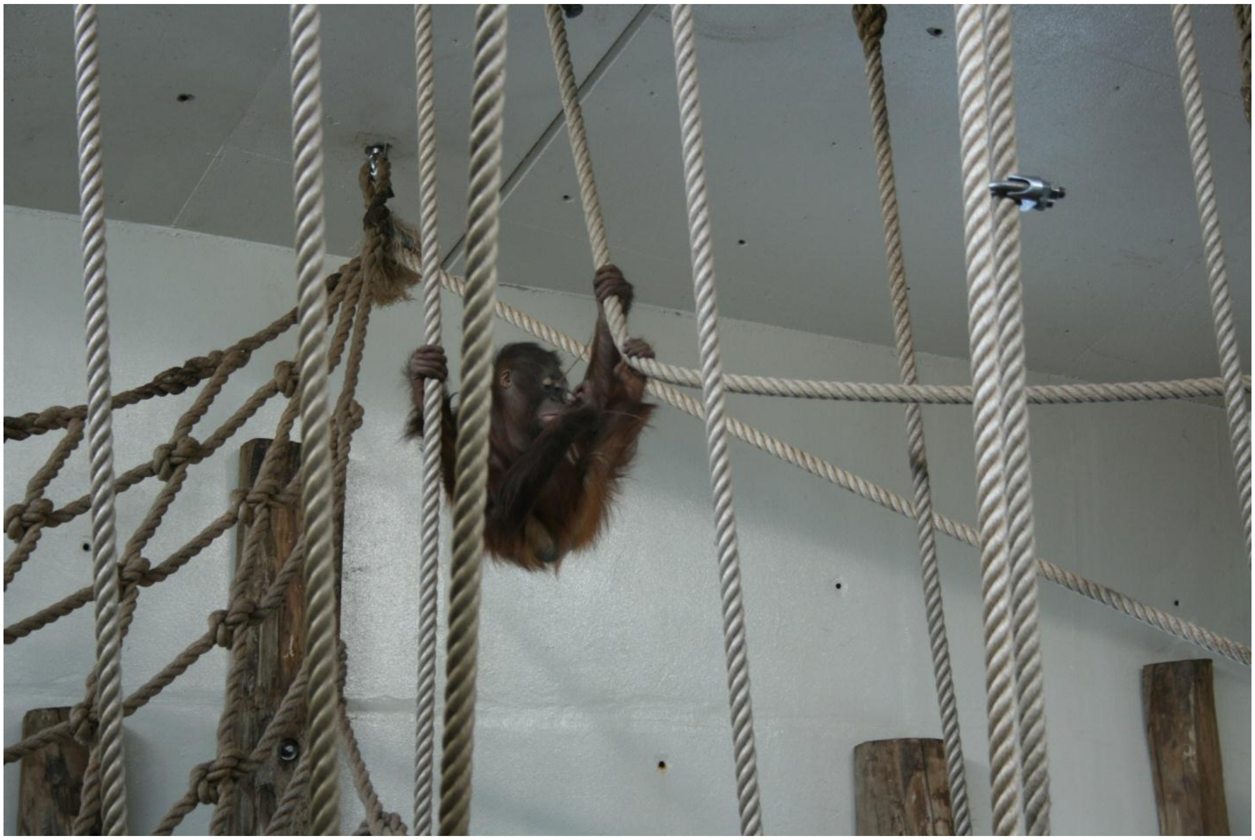

Figure 6.1 Orangutan indoor enclosure at Apenheul Primate Park, Apeldoorn, The Netherlands (Photo: A C Phillips).

A further five captive subjects were observed in Ouwehands Dierenpark. The three indoor enclosures at Ouwehands also contained climbing structures made of wood logs and many shelves and platforms (see Figure 6.2). In comparison with Apenheul the enclosures had less vertical space and more horizontal space. There were fewer ropes at Ouwehands (only 50% of the number found at Apenheul). There were fewer hammocks available to orangutans at Ouwehands but there was a larger area of climbing surface available as the sides of all enclosures and the ceilings of two of the enclosures were made of wiremesh allowing the orangutans to access all parts of their enclosure.

At both zoos the orangutans were given access to different parts of their enclosure by opening and closing sliding doors, so the amount of space available to them varied over the sample period. Therefore, it is not valid to compare overall enclosure sizes between the two zoos.

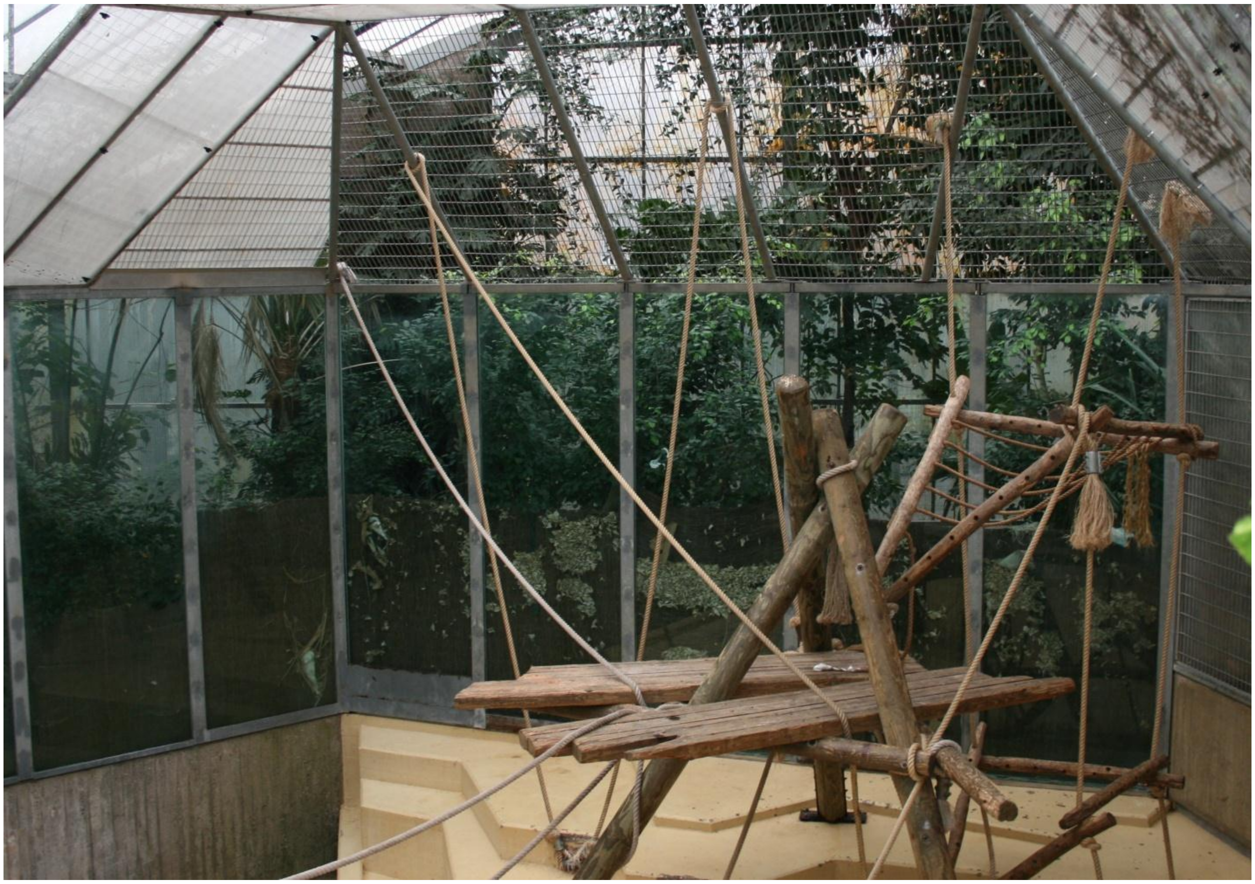

Figure 6.2 Orangutan indoor enclosure at Ouwehands Dierenpark, Rhenen, The Netherlands (Photo: A C Phillips).

Table 6.1 Wild and Captive orangutans sampled at Tuanan Research Station, Central Kalimantan, Ouwehands Dierenpark, The Netherlands and Apenheul primate Park, The Netherlands. Observations refers to the number on 1-minute instantaneous samples of positional behaviour recorded.

Subject	Location	Age (years)	Sex	Age group	Observations
Mawas	Tuanan wild	1	F	Infant	3352
Kino	Tuanan wild	3	M	Infant	3438
Jip	Tuanan wild	4	M	Juvenile	3418
Deri	Tuanan wild	5	M	Juvenile	2310
Jerry	Tuanan wild	6.5	M	Juvenile	3954
Streisel	Tuanan wild	~7	F	Juvenile	2851
Ido	Tuanan wild	~8	M	Adolescent	1950
Milo	Tuanan wild	~9	F	Adolescent	3011
Kondor	Tuanan wild	~11	F	Adolescent	4124
Juni	Tuanan wild	-	F	Adult	1954
Kerry	Tuanan wild	-	F	Adult	2162
Gismo	Tuanan wild	-	M	Sub-adult	1590
Jingga	Ouwehands zoo	1	M	Infant	1441
Yuno	Ouwehands zoo	2.5	M	Infant	1373
Merah	Apenheul zoo	2.5	F	Infant	1411
Dayang	Apenheul zoo	3	F	Infant	1345
Samboja	Apenheul zoo	3.5	F	Juvenile	1417
Damai	Ouwehands zoo	5.5	M	Juvenile	1370
Willie	Apenheul zoo	6.5	M	Juvenile	1440
Amos	Apenheul zoo	8	M	Adolescent	1443
Bako	Ouwehands zoo	13	M	Sub-adult	763
Josje	Apenheul zoo	16.5	F	Adult	719
Tjintah	Ouwehands zoo	25	F	Adult	646
Sandy	Apenheul zoo	27	F	Adult	718

6.2.2 Data collection

Focal animal sampling (Altman 1974) was used to sample the behaviour of wild and captive orangutans. Wild subjects were followed continuously for a maximum of 10 days. Data were recorded from when the focal animal emerged from their nest in the morning until they lay down in their nest in the evening, typically between 05:00 and 17:00. Captive subjects were sampled for 1 hour each and the order of sampling was rotated daily to ensure all subjects were sampled at all times of day. Due to constraints of the zoo opening hours it was only possible to record data for 6 hours each day, between 10:00 and 16:00. Instantaneous sampling at the 1-minute mark was used to sample positional behaviour and support use. A digital watch with an auto-repeat countdown vibration alarm function was used to ensure that instantaneous sampling was accurate without disturbing the orangutans. Locomotor behaviour was described according to the classifications of orangutan positional behaviour by Thorpe and Crompton (2006) which is based on the standardised classification system of Hunt et al. (1996). Where necessary, additional modes of positional behaviour observed in the study subjects, but not represented in the classification of Thorpe and Crompton (2006), were described according to the principles proposed by Hunt et al. (1996). Thus, positional modes were assigned based on the orientation of the body, which limbs were bearing weight and whether they were bearing weight in suspension or compression. Locomotor modes were further differentiated into sub-modes according to the gait pattern (regular or scramble) and whether limbs were flexed or extended (Hunt et al. 1996).

6.2.3 Support use

The number and type of weight-bearing supports were recorded for positional behaviour involving up to four supports (Thorpe and Crompton 2005). If more than four supports were used only the type of the main weight-bearing support was recorded (Cant 1987b). In addition, diameter was recorded for each weight-bearing support in the wild, but this could not be replicated in captivity because many supports had large surface areas, in which case diameter was meaningless. Instead, support flexibility was used as a substitute for diameter because flexible supports are functionally similar to supports with small diameters. To facilitate comparison between wild and captive orangutan support use, wild supports were classed as flexible if they had diameters of less than 4cm and rigid if they had diameters of more than 4 cm because 4cm branches were found to deflect under the mass of all of the size groups that were observed. In captivity supports that were made up of multiple smaller ones were recorded as multiple support use if their components could move independently (e.g. rope hammock), and single support use if they could not (e.g. wiremesh).

All data were collected by a single observer (ACP) and periods of self-training in classifying behaviour and estimating support diameters were undertaken prior to and during data collection to ensure consistency and accuracy.

6.2.4 Statistical analysis

Statistical analysis was carried out using SPSS (version 18, Chicago, IL). Chi-squared tests of independence were used to examine the associations between different aspects of positional behaviour and different environments. P-values were used to assess whether the observed behaviours were significantly different in captive and wild environments. Adjusted standardised residuals (ASRs) were generated to examine relationships among the variables; they indicate by their size and sign the strength and direction of the relationship. Absolute values greater than 2 indicate a significant association between the variables.

6.3 Results

In total 48125 instantaneous observations of positional behaviour were obtained from 12 wild and 12 captive Bornean orangutans. The dataset is comprised of 71% wild and 29% captive observations. Visibility was considerably more obscured in the wild, and, therefore, far fewer observations were recorded per focal hour. However, there was less difference between the numbers of observations collected per day as we were limited by zoo opening hours. We acknowledge that differences in time of day, restricted visibility and overall sample size may have contributed some bias to this dataset. As the captive dataset was smaller, there is a chance that some behaviours that occurred very rarely may have been under-sampled in captivity. Poor visibility is associated with sampling bias because inconspicuous behaviours can be under-sampled and animals may seek privacy when carrying out certain types of behaviour more than others (Martin and Bateson 1993). When recording positional behaviour in the wild, fast types of locomotion were particularly hard to record if foliage was obscuring part of the focal animal's body. Therefore, these types of locomotion may have been slightly under-sampled in wild orangutans, in particular the supports that were used.

6.3.1 Locomotion

Locomotion accounted for on average 16.5% of captive and 15% of wild positional behaviour. There was a difference between the two zoos with locomotion accounting for 15% of positional behaviour at Apenheul and 19% of positional behaviour at Ouwehands. Captive orangutans used ground supports as the main weight bearing support in 41% of locomotor behaviour whereas ground locomotion in wild orangutans was rare, accounting for only 2% of observations. Captive orangutans used single supports for locomotion more often than wild orangutans- 64% and 41%, respectively. Frequencies of different locomotor modes varied with habitat; in general, captive orangutans used more compressive forms of locomotion (62%) than suspensory locomotion (38%) whereas wild orangutans used predominantly suspensory locomotion (77% of observations). The frequencies of locomotor modes were found to be significantly different between the three study sites, (χ^2= 1449.6, DF 20, P<0.0001). Figure 6.3 shows the frequencies of different modes of locomotion as percentages of total observations for each of the three study sites and shows that the primary differences occur between wild and captive animals. The captive orangutans used pronograde and orthograde walking more often and they also used more 'risky' forms of locomotion such as descending by sliding. Wild orangutans used more orthograde suspensory locomotion and more gap crossing locomotor behaviours such as bridging, riding and swaying in arboreal supports.

While the locomotor behaviour of the orangutans at the two zoos was broadly similar when compared with locomotion of wild orangutans, there were some differences (Figure 6.3). Apenheul orangutans used ground locomotion less than orangutans at Ouwehands- 37% and 48% respectively. Orangutans at Apenheul exhibited greater levels of orthograde walking than pronograde walking compared to the Ouwehands orangutans, and they also exhibited greater frequencies of vertical climb and ride. In contrast, Ouwehands orangutans used both orthograde and pronograde suspensory locomotion more often than orangutans at Apenheul.

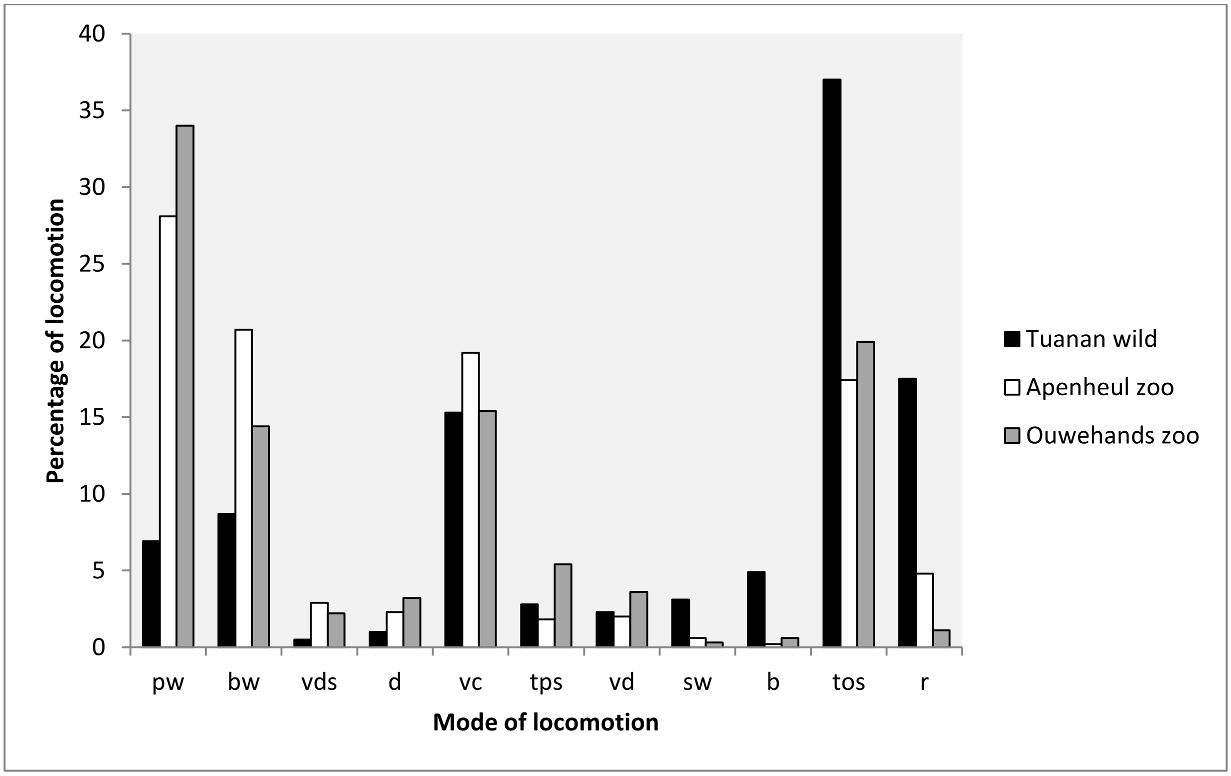

Figure 6.3 Locomotor mode frequencies of orangutans in wild (Tuanan) and in Zoos (Apenheul and Ouwehands- see text for further details) as percentages of total locomotor observations for each study site. Locomotor modes are as follows: pw- pronograde walk; bw- bipedal walk; vds- vertical descent slide; d- drop; vc- vertical climb; tps- torso pronograde suspensory; vd- vertical descent; sw- sway; b- bridge; tos- torso orthograde suspensory; and r- ride.

6.3.2 Posture

Orangutans used ground supports more often for posture than for locomotion. Captive orangutans used ground supports in 60% of postural behaviour compared with only 3% for wild orangutans. The use of single supports was also more common during posture than during locomotion; captive orangutans used single supports in 67% and wild orangutans in 50% of postural behaviour. Overall, there was less variation in the types of postural behaviour exhibited between the study sites when compared to locomotion (Figure 6.4). However, as with locomotion, the posture results showed that pronograde and orthograde compression (standing) were more common in captivity. When the two zoos were compared, Apenheul had higher frequencies of orthograde stand and Ouwehands had higher frequencies of pronograde stand. Suspensory postures, such as orthograde forelimb suspend, forelimb hindlimb suspend and pronograde suspend were used more by wild orangutans than by those in captivity. There was a significant difference between the distributions of postural behaviour at the three study sites, $\chi^2 = 3235.9$, DF= 20, $P<0.0001$.

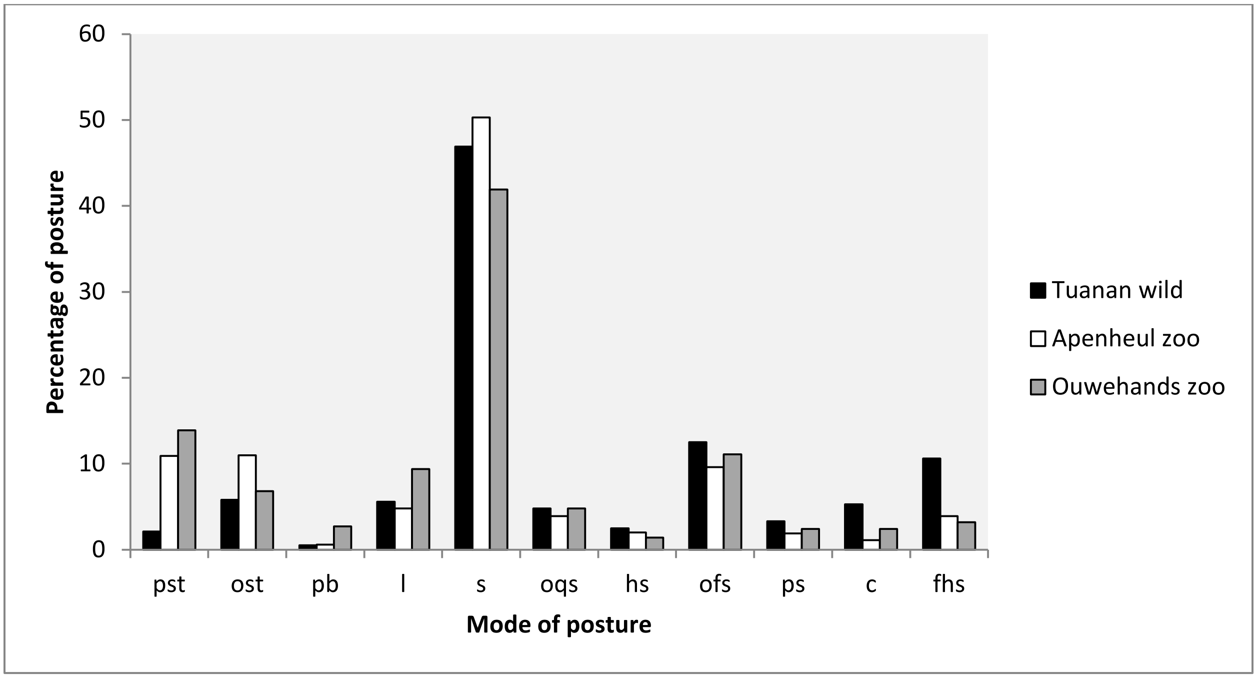

Figure 6.4 Postural mode frequencies of orangutans in wild (Tuanan) and in Zoos (Apenheul and Ouwehands- see text for further details) as percentages of total posture observations for each study site. Posture modes are as follows: pst- pronograde stand; ost- orthograde stand; pb- pronograde bridge; l- lie; s- sit; oqs- orthograde quadrumanous suspend; hs- hindlimb suspend; ofs- orthograde forelimb suspend; ps- pronograde suspend; c- cling; and fhs- forelimb hindlimb suspend.

Positional behaviour was also examined at the submode level and full lists of positional submodes are presented in Appendix D (posture) and E (locomotion). This study found some novel types of positional behaviour that were only observed in captive orangutans. Novel types of locomotion included rolling and sliding across the ground. These behaviours were usually associated with play in younger orangutans. Previously undescribed forms of posture were also seen in the captive environments, including suspension by holding a support in the mouth and compression on the head or hands in an orthograde position.

6.3.3 Support associations

Both wild and captive orangutans used different types of locomotor behaviour when using different support combinations. Different locomotor behaviours were associated with different numbers of supports- in the wild: $\chi^2 = 519.3$, DF =4, P<0.0001; and in captivity- $\chi^2 = 357.3$, DF =4, P<0.0001 (Table 6.2). Different locomotor behaviours were also associated with different types of supports - in the wild: $\chi^2 = 320.0$, DF= 4, p<0.0001; and in Captivity- $\chi^2 = 655.8$, DF= 4, p<0.0001 (Table 6.3). The associations between type of locomotion and the number of supports and type of support were broadly similar in wild and captive environments, with the exception of vertical climbing (see Table 6.2 and Table 6.3). Orthograde locomotion was most associated with multiple supports and pronograde locomotion was most associated with single supports in both captive and wild orangutans, as shown by the positive residuals in Table 6.2. However, vertical climbing and descending were most associated with multiple supports in captivity and single supports in wild orangutans.

Table 6.2 Contingency table for the association: locomotion * number of supports for captive and wild orangutans. Wild data collected at Tuanan Research Station, Central Kalimantan and captive data collected at Ouwehands and Apenheul, The Netherlands.

		orthograde suspension	**orthograde compression**	**pronograde suspension**	**pronograde compression**	**vertical climb/descent**	**Total**
Captive	**1 support**	18.1 (47.8) *-8.3*	13.4 (45.9) *-7.9*	5.2 (81.1) *3.6*	44.5 (90.0) *17.8*	18.8 (52.3) *-5.7*	100 (63.0)
	>1 support	33.6 (52.2) *8.3*	26.8 (54.1) *7.9*	2.1 (18.9) *-3.6*	8.4 (10.0) *-17.8*	29.2 (47.7) *5.7*	100 (37.0)
	Total	23.8 (100)	18.3 (100)	4.1 (100)	31.2 (100)	22.6 (100)	100
Wild	**1 support**	46.8 (37.6) *-7.4*	1.9 (7.3) *-16.9*	14.0 (69.9) *11.3*	10.8 (57.3) *5.9*	26.6 (58.8) *10.7*	100 (42.7)
	>1 support	57.9 (62.4) *7.4*	17.7 (92.7) *16.9*	4.5 (30.1) *-11.3*	6.0 (42.7) *-5.9*	13.9 (41.2) *-10.7*	100 (57.3)
	Total	53.1 (100)	11.0 (100)	8.5 (100)	8.0 (100)	19.3 (100)	100

Each cell contains the row %, (column %) and the adjusted standardised residual (ASR), shown in italics. For example, 18.1% of captive locomotion on 1 support was orthograde suspension and 47.8% of orthograde suspension observed in captivity was on 1 support.
Captive: χ^2 =357.3, DF =4, P<0.0001, n=2221; Wild: χ^2 =519.3, DF =4, P<0.0001, n=4511.

In wild orangutans all orthograde locomotion was associated with flexible supports (those with smaller diameter) whereas in captivity orthograde suspension was associated with flexible supports but orthograde compression was associated with rigid supports (shown by the ASRs in Table 6.3). Pronograde suspensory locomotion did not show an association with either flexible or rigid supports and pronograde compression was associated with rigid supports in both captive and wild environments. Vertical climbing and descending was strongly associated with flexible supports in captivity but in the wild it was strongly associated with rigid supports.

Table 6.3 Contingency table for the association: locomotion * compliance of main support for captive and wild orangutans. Wild data collected at Tuanan Research Station, Central Kalimantan and captive data collected at Ouwehands and Apenheul, The Netherlands.

		orthograde suspension	**orthograde compression**	**pronograde suspension**	**pronograde compression**	**vertical climb/descent**	**Total**
Captive	**Rigid support**	15.6 (40.7) *-11.6*	23.0 (78.0) *7.3*	3.5 (53.3) *-1.7*	46.9 (93.4) *20.5*	11.0 (30.0) *-16.8*	100 (62.0)
	Flexible support	37.2 (59.3) *11.6*	10.6 (22.0) *-7.3*	5.0 (46.7) *1.7*	5.5 (6.6) *-20.5*	41.8 (70.0) *16.8*	100 (38.0)
	Total	23.8 (100)	18.3 (100)	4.1 (100)	31.2 (100)	22.6 (100)	100
Wild	**Rigid support**	43.2 (37.4) *-12.6*	8.8 (37.8) *-3.9*	8.0 (43.0) *-1.3*	11.7 (68.4) *8.6*	28.4 (68.0) *14.2*	100 (46.3)
	Flexible support	62.3 (62.6) *12.6*	12.5 (62.2) *3.9*	9.1 (57.0) *1.3*	4.6 (31.6) *-8.6*	11.5 (32.0) *-14.2*	100 (53.7)
	Total	53.4 (100)	10.8 (100)	8.6 (100)	7.9 (100)	19.3 (100)	100

Captive χ^2 655.8, DF 4, p<0.0001, n=2218, Wild χ^2 320.0, DF 4, p<0.0001, n=4408

6.3.4 Locomotor development

Overall, suspensory locomotion was much lower in captivity when compared to wild orangutan locomotion. In captivity, suspensory locomotion was found to decrease with age as shown by the increasingly negative ASRs in Figure 6.5. In contrast, wild infant orangutans had the lowest frequency of suspensory locomotion (ASR= -4.2), significantly lower than juveniles (3.7) and older orangutans (-0.2).

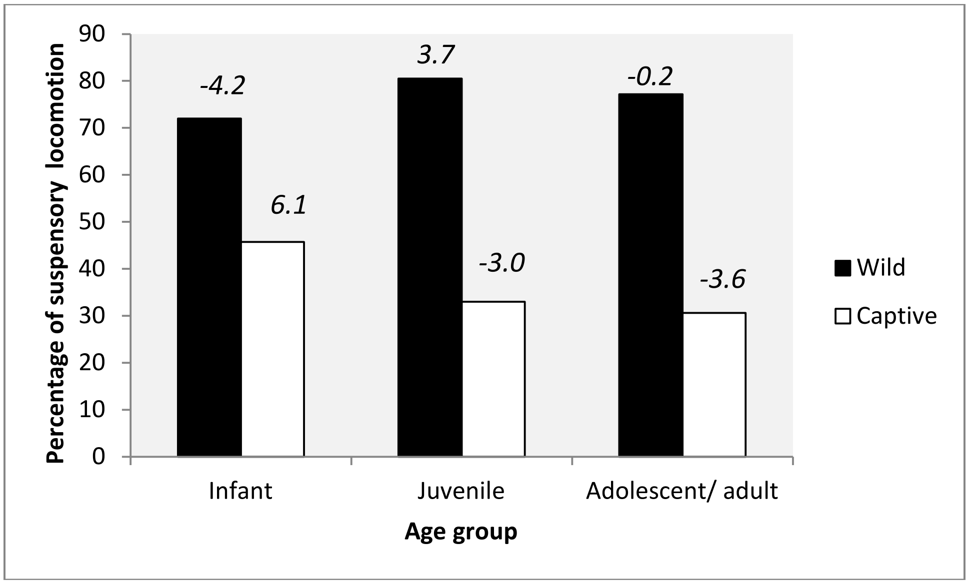

Figure 6.5 The percentage of suspensory locomotion for three age groups of wild and captive orangutans. Infants were aged between 1 and 3 years, juveniles between 3 and 7 and the final age group was made up of orangutans over 7 years old. The remainder of locomotion that is not shown is locomotion where weight is borne in compression. Adjusted standardised residuals (ASRs) are shown in italics above each bar. Wild χ^2= 22.2, DF= 2, p<0.0001, n=3898, Captive χ^2= 37.3, DF= 2, p<0.0001, n=1897.

In captive orangutans orthograde locomotion followed the same developmental pattern as suspension, with older orangutans using increasingly less torso orthograde locomotion and more pronograde locomotion (Figure 6.6). There was no significant difference in the orientation of the torso for the locomotion of wild orangutans at different ages as shown by the high P-value of 0.96 and similar ASRS (Figure 6.6).

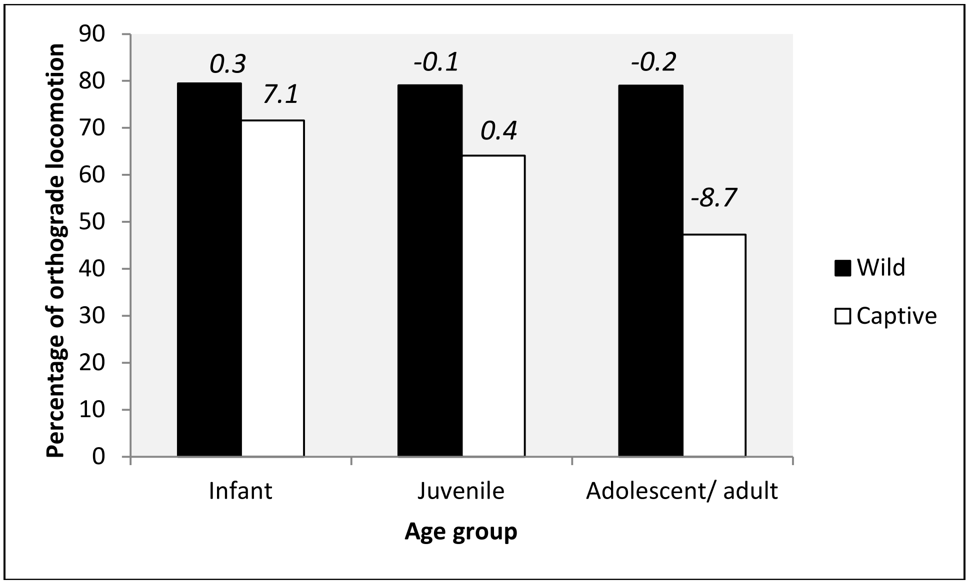

Figure 6.6 The percentage of orthograde locomotion for three age groups of wild and captive orangutans. Although not represented on the chart, the remainder of locomotion was pronograde in orientation. Wild: χ^2= 0.1, DF= 2, P=0.96, n=4937, Captive: χ^2= 86.0, DF= 2, P<0.0001, n=2219.

The main weight-bearing limb used in locomotion was examined for the different age groups of wild and captive orangutans (Figure 6.7). Captive orangutans used their forelimbs to bear the majority of their weight much less than wild orangutans. Contrasting developmental patterns in forelimb use were found in wild and captive orangutans. Forelimb use increased with age in the wild and decreased in captivity. Levels of hindlimb use were found to be similar across age groups and environments. Captive orangutans showed equal use of the fore and hindlimbs more often than wild orangutans and this type of limb use was negatively correlated with age in wild orangutans and positively correlated with age in captivity. Collectively these results indicate that disparity between locomotor behaviour of captive and wild orangutans increases with age with infant locomotion being the most similar across environments.

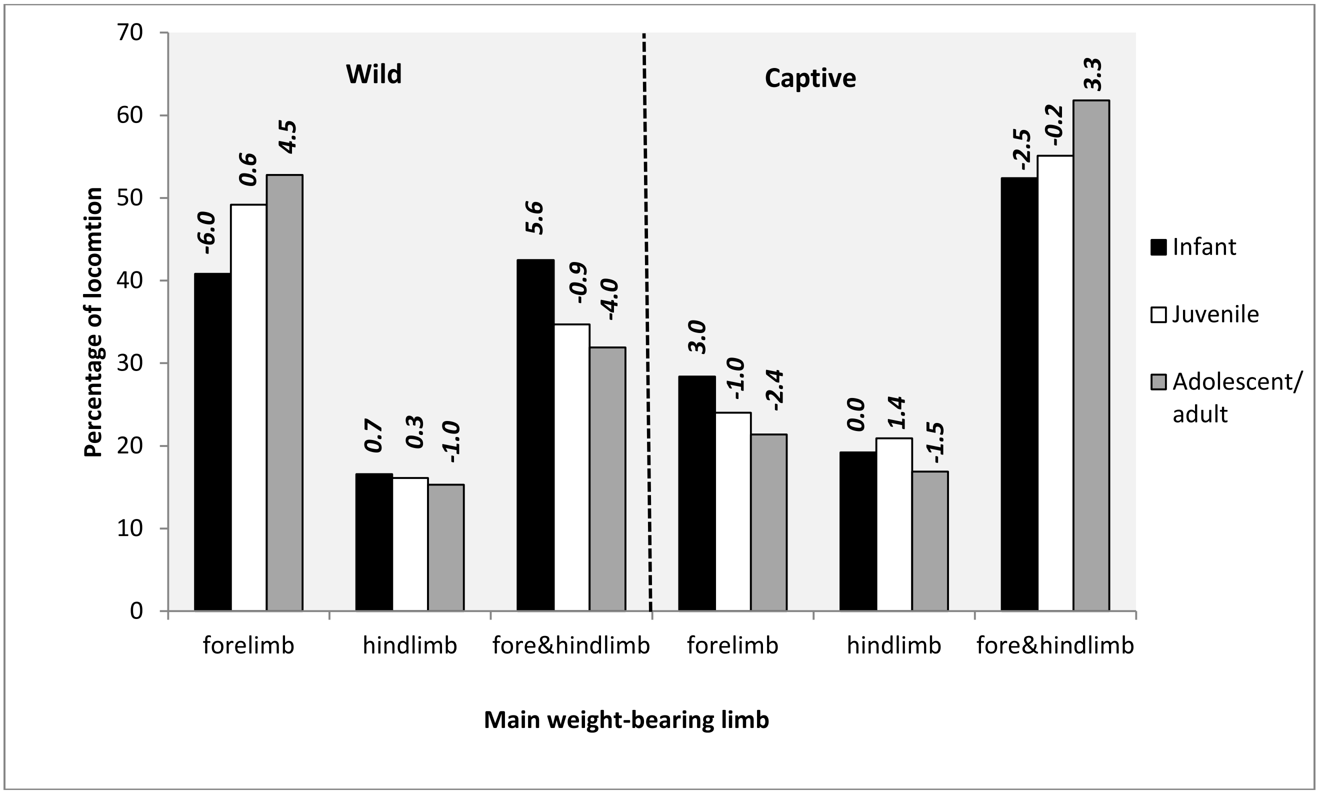

Figure 6.7 The main weight bearing limb used during locomotion by orangutans of different age groups in wild and captive environments. Wild: χ^2= 44.4, DF= 4, P<0.0001, n=4969, Captive: χ^2= 15.2, DF= 4, P<0.01, n=2232.

6.3.5 Postural development

In both wild and captive environments older orangutans were found to use suspensory postures less frequently (Figure 6.8). While all age groups of wild orangutans had higher frequencies of suspensory posture than captive orangutans, the developmental pattern was the same in wild and captive environments.

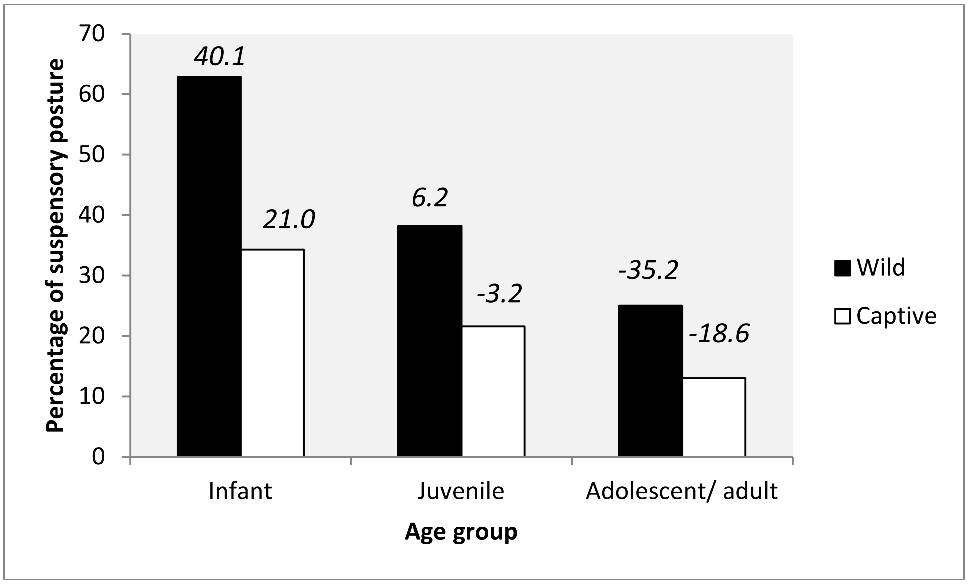

Figure 6.8 The percentage of suspensory posture for three age groups of wild and captive orangutans. Infants were aged between 1 and 3 years, juveniles between 3 and 7 and the final age group was made up of orangutans over 7 years old. Although not represented on the chart, the remainder of locomotion was compressive. Adjusted standardised residuals (ASRs) are shown in italics above each bar. Wild: χ^2= 2038.5, DF= 2, P<0.0001, n=27308, Captive: χ^2= 516.3, DF= 2, P<0.0001, n=11474.

In contrast to the results for locomotor behaviour, the orientation of the trunk during posture showed very little environment or age-related variation (Figure 6.9).

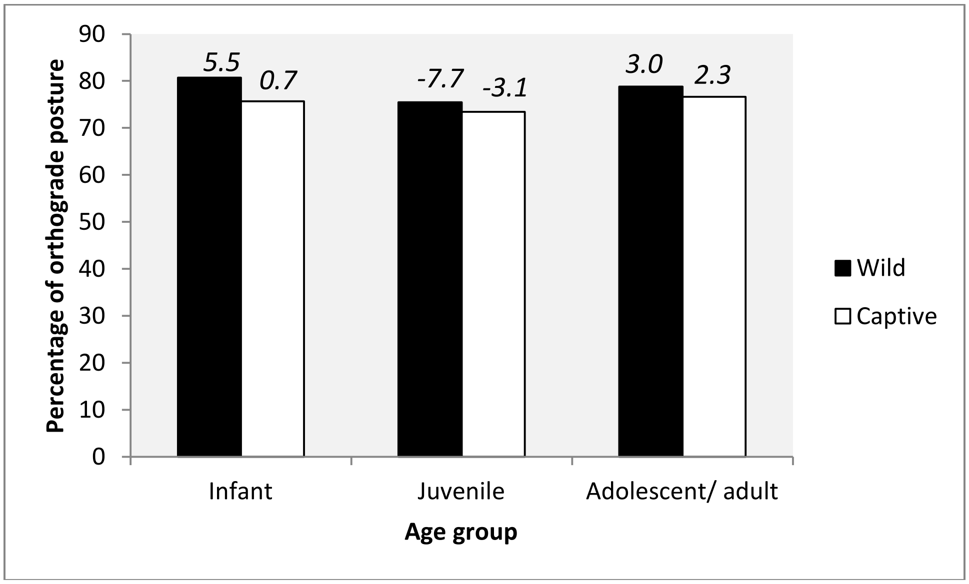

Figure 6.9 The percentage of orthograde posture for three age groups of wild and captive orangutans. Although not represented on the chart, the remainder of locomotion was pronograde in orientation. Wild: χ^2= 66.9, DF= 2, P<0.0001, n=29000, Captive: χ^2= 10.7, DF= 2, P<0.01, n=11703.

Orangutan postural behaviour was dominated by the positions sit and lie where weight was borne in compression by the ischia and/or torso. The frequency of ischia and torso compression was positively correlated with age in both captive and wild orangutans (Figure 6.10). Postures where the majority of weight was borne by the forelimbs decreased in frequency as age group increased. Equal use of the fore- and hindlimbs decreased with age in the wild but did not show age-related variation in captivity. As with locomotion, hindlimb suspend did not show environment or age related variation. In general, postural behaviour was more homogeneous across different environments and age groups when compared with locomotor behaviour.

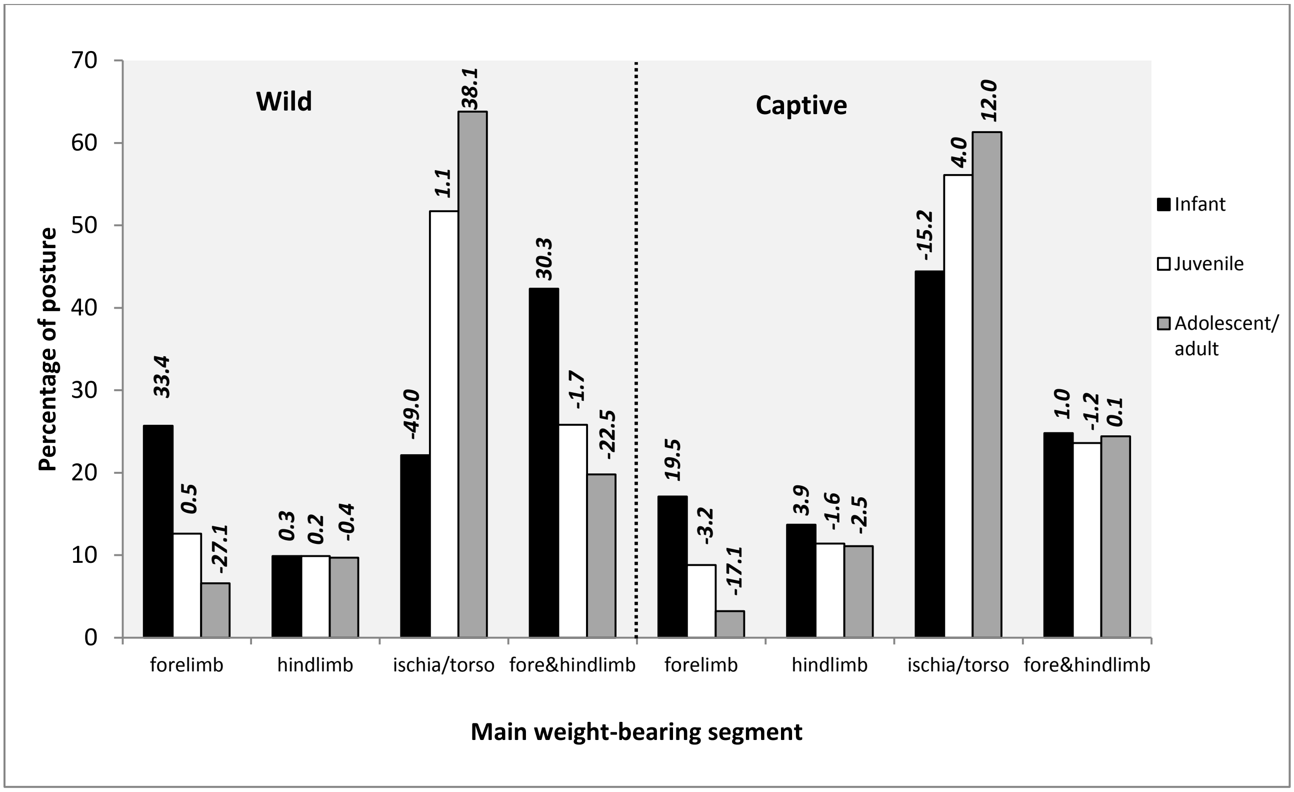

Figure 6.10 The main weight-bearing segment used in posture by orangutans of different age groups in wild and captive environments. Wild: χ^2= 3235.3, DF= 6, P<0.0001, n=29001, Captive: χ^2=527.9, DF= 6, P<0.0001, n=11691.

6.4 Discussion

The aim of this study was to compare the positional behaviour of wild and captive Bornean orangutans and examine how habitat influences development in this species. Overall, the frequencies of different positional behaviours were found to differ in captive and wild environments. However, there was no difference in the percentage of locomotion relative to the amount of posture observed in wild and captive orangutans. This indicates that the captive orangutans did not move less than their wild counterparts despite living in a confined space. However, the modes of locomotion used in captivity may not have applied the same forces to the body, which can make them less strenuous. Also, the method of sampling did not give any indication of the distance travelled, and this is likely to be considerably less in captivity. If older adult subjects had been included in the study (the oldest was 27 years old) the proportion of locomotion relative to posture may have been smaller than found in the wild as the older captive subjects were very inactive (pers. obs.). Although we do not know how old the wild adult subjects were, all were reasonably active.

As expected, the amount of ground use was far greater in captivity. However, there may be some bias here as some wild orangutans may have been more reluctant to descend to the ground in the presence of observers. Additionally, ground use by wild orangutans differs by species and age-sex (Thorpe and Crompton 2009). Sumatran orangutans rarely come down to the ground (Sugardjito and van Hooff 1986; Cant 1987a; Thorpe and Crompton 2006) and, therefore, we would expect differences between wild and captive Sumatran orangutans to be greater. In Borneo flanged adult males use the ground far more than animals in other age-sex categories (Cant 1987b; Galdikas 1988; Manduell et al. 2011). Therefore, the positional behaviour of wild and captive Bornean flanged males may show more similarity than that of Sumatran flanged males. As predicted, captive orangutans had higher frequencies of terrestrial types of positional behaviour. In particular, the frequency of pronograde walking was much greater in captive orangutans. Increased ground use in captive orangutans is likely to account for this, although captive and wild orangutans both used this type of locomotion on certain combinations of arboreal supports. In wild orangutans pronograde walking was most associated with single large supports (Thorpe and Crompton 2005 ; Chapter 2) and was also been found to be associated with multiple small supports in the disturbed peat-swamp forest habitat, (Chapter 2). In captivity orangutans may use pronograde walking on platforms, large logs and hammocks.

Captive orangutans used suspensory positional behaviours much less than their wild counterparts. In wild orangutans the predominant mode of locomotion was torso orthograde suspension whereas in captivity it was pronograde walk. When compared to pronograde walking, orthograde suspensory locomotion such as clambering with all four limbs requires muscles to generate greater stresses to cope with the uneven distribution of body mass, the majority supported by the forelimbs, and to be able to apply force at a greater range of joint angles (Isler and Thorpe 2003). When muscle use is less strenuous, muscle shrinkage (atrophy) takes place and results in reduced strength (Booth and Criswell 1997). Orangutan skeletons are well adapted for orthograde suspension, yet there is evidence to suggest that when orangutans adopt a predominantly terrestrial lifestyle, the shape of their bones may become modified in ways that facilitate pronograde walking and preclude orthograde suspension (Sarmiento 1985; Richmond et al. 2001). Sarmiento (1985) also found that torsion was higher in the long bones of captive orangutans when compared to wild orangutans and attributed these skeletal differences to differences in positional behaviour during growth. In humans, new bone formation predominantly occurs during immaturity, after which it can only be maintained (Vicente-Rodríguez 2006; Gunter et al. 2008), and this is likely to apply to all mammals as their bone is similarly structured (Katz et al. 1984). Therefore, the immature period is crucial for ensuring lifelong bone health and mobility. These positional behaviour differences may impact the health and welfare of older orangutans in captivity as low bone mineral density can cause osteoporosis (Khan et al. 2000; Vicente-Rodríguez 2006), and this is likely to reduce further the locomotor repertoire in later life.

In the wild orangutans manipulate compliant arboreal supports to cross gaps between trees (Cant 1994; Thorpe et al. 2007a; Chapter 4). Orangutans can save energy by crossing trees in the canopy thereby avoiding the costs associated with descending to the forest floor and ascending the adjacent tree (Thorpe et al. 2007a). Wild orangutans have two ways of utilising the compliance of supports to cross gaps: (1) appendicular deformation where a support is pulled towards the animal so that a more stable support can be reached to cross a gap, as in bridge; and (2) mass deformation where body mass is used to bend or oscillate a support to move across a gap, as in ride and sway (Cant 1994). These are expected to be among the most physically and also cognitively challenging skills an orangutan must learn (Chevalier-Skolnikoff et al. 1982 Chapter 4). In the wild we found that the modes of locomotion of bridge, ride and sway made up approximately 25% of locomotor behaviour, while in captivity they constituted less than 5%. This reflects the nature of the habitat: in general captive orangutans are provided with few flexible types of support, and those that are provided have very different material properties from the compliant branches and lianas found in their natural environment. Furthermore, they have less motivation to travel within their enclosure without using the ground. If orangutans that have had limited exposure to compliant supports are released into the forest they will not be familiar with the properties (affordances) of vegetation in their habitat which is likely inhibit their ability to move around their habitat. A lack of familiarity with natural support characteristics could put reintroduced orangutans at greater risk of falling when attempting to use compliant supports. If they are not able to cross gaps in the canopy, reintroduced orangutans may be forced to make energy-expensive detours (Thorpe et al. 2007a) or risk travelling on the ground where they may be exposed to ground-dwelling predators such as clouded leopards and tigers in the case of Sumatran orangutans.

As expected, this study found that captive orangutans exhibited types of positional behaviour that were rare or absent in the positional repertoires of wild orangutans. This has not been reported in previous studies of captive orangutans and provides information about the totipotentiality (Prost 1965) of orangutan positional behaviour. Furthermore, fast uncontrolled locomotor behaviour was observed more often in captivity than in the wild and, specifically, the method of descending by sliding. This agrees with our prediction that over-familiarity with the habitat would cause captive orangutans to exhibit more risky types of locomotor behaviour. However, support availability may have also influenced this result as the abundant vertical ropes in captivity were ideal supports for orangutans to slide on. In the wild, sliding was confined to smooth, vertical supports without intersecting branches. When orangutans descended using multiple branches they were more likely to use a controlled gait pattern. Additionally, other types of positional behaviour associated with increased ground use were observed in captivity that have not been observed during wild studies. These include rolling and sliding along the ground and the postures hand stand and head stand. Suspension from the mouth was also only observed in captivity and is likely to reflect that the captive orangutans could be confident that the supports in their enclosure would not break if they bit down on them. It may also reflect a natural tendency to use the mouth in tension as this is how wild orangutans strip the bark from trees (Taylor 2006). Overall, these differences can be attributed to the less complex nature of the captive habitat compared to that of wild orangutans. However, over-familiarity with the environment may convey certain advantages to young orangutans. By encouraging vigorous play behaviours like leaping, dropping, sliding and fast climbing and suspensory locomotion, captive habitats may help maintain healthy musculoskeletal development in young orangutans and offset some of the detrimental effects of excess ground use.

Wild orangutans have been found to use different types of positional behaviour for different combinations of support number and diameter (Cant 1987b; Thorpe and Crompton 2005; Thorpe et al. 2009; Myatt and Thorpe 2011; Chapter 2 and 3). Their complex repertoire of positional behaviour reflects the complexity of their arboreal habitat. Our study found that the associations between locomotor modes and the number and flexibility of supports used were broadly similar for wild and captive orangutans. The main difference was the supports used for vertical climbing. Our study found that single rigid supports were most associated with climbing in the wild whereas in captivity, multiple flexible supports were most associated with climbing. Habitat differences may account for this: at Tuanan orangutans often climbed up rigid tree trunks whereas in captivity the main vertical supports are flexible ropes and, as these supports are quite thin, orangutans are more likely to use more than one support when climbing on ropes. The similarity between the support associations found in wild and captive environments has important implications for captive management because altering the supports provided to orangutans may strongly influence their positional behaviour. Differences between the positional behaviour of orangutans housed in the two zoos support this conclusion. Apenheul had twice as many ropes as Ouwehands and the majority were attached at both ends with excess slack, which allowed them to be swung. As hypothesised, in comparison to Ouwehands, the orangutans at Apenheul had higher frequencies of oscillatory behaviour frequently moving around their enclosure by riding and swaying ropes. Also in line with our predictions, the orangutans at Ouwehands were found to exhibit higher frequencies of suspensory positional behaviour than those at Apenheul in particular pronograde suspension. This difference can be explained by the larger area of wiremesh at Ouwehands compared to Apenheul. Enclosures at Ouwehands had wiremesh walls and ceilings, which allowed the orangutans to use all available surfaces. When orangutans used the horizontal wiremesh found on the ceiling they either used pronograde or orthograde suspensory positional behaviours. In wild orangutans these behaviours are important for feeding because they allow access to the thin terminal branches where the majority of fruit is located (Cant 1987a; Thorpe and Crompton 2005; Thorpe et al. 2009; Myatt and Thorpe 2011). By using wiremesh instead of smooth walls zoos can encourage captive orangutans to exhibit more natural levels of suspensory locomotion and posture.

The use of suspensory locomotion showed opposing developmental trends in wild and captive orangutans. Suspensory locomotion was found to increase with age in wild orangutans and decrease with age in captive orangutans. In wild orangutans suspensory behaviour has been predicted to increase with increasing body size as animals are more stable on thin branches when weight is borne in suspension rather than compression (Cartmill and Milton 1977; Cant 1987a; Chapter 2). However, the material properties of supports used in zoos are very different from those found in the wild and thin man-made supports may still be rigid and,, therefore, captive orangutans cannot use diameter to predict support compliance. However, orangutans in captivity have less need to use external factors to predict the properties of supports in their enclosure because they are already very familiar with all the supports that are available to them. In the absence of compliant supports, captive orangutans may experience less motivation or opportunity to use suspensory behaviours as they grow. Other aspects of captive locomotor behaviour were also correlated with age; both orthograde and forelimb-dominated locomotion decreased with increasing age. Orthogrady and forelimb-dominated locomotion were all more frequent in the wild compared with in captivity. Therefore, as predicted, the locomotor behaviour of captive infants was most similar to their wild counterparts with a trend of increasing disparity with age. This may reflect increasing muscle and bone deterioration associated with insufficient levels of stress applied to the skeleton during development. Overall, postural development showed less age-related variation than locomotion in both environments, which indicates that encouraging arboreal *locomotion* is more important for development than simply keeping orangutans off the ground.

The results of this study have important implications for the development of positional behaviour in captive orangutans. As positional behaviour has strong associations with support use, the type of supports provided in captive environments influence the type of positional behaviour exhibited. To promote natural behaviour zoos should include ample climbing structures and flexible supports that can be oscillated. Wiremesh is particularly useful because it elicits climbing, orthograde and pronograde suspensory locomotion (Figure 6.11). If orangutans are fed from above a wiremesh ceiling they are able to exhibit suspensory postures and locomotion that are similar to those found in wild orangutans feeding on fruit in terminal branches (Myatt and Thorpe 2011). Ropes are also important for eliciting the oscillatory behaviours ride and sway as they can be oscillated in a similar way to lianas that are used by wild orangutans. The attachment points may be different for ropes and lianas and zoos can promote oscillatory behaviour in captive orangutans by attaching ropes vertically with plenty of excess. Wild orangutans also sway and bend compliant trunks and branches to cross gaps in the canopy. These behaviours are not easily replicated in captivity, as few man-made supports have the same properties as compliant vegetation. One solution is to allow natural vegetation to grow in the enclosure. However, orangutans must be rotated in different enclosures to allow vegetation to recover; therefore, this is only suitable when space is not limited. Alternatively, vertical fibreglass poles can act as artificial tree trunks which allow orangutans to practice oscillatory behaviour (as used in the outdoor enclosure at Apenheul). Finally, by providing enclosures that are elongated in the vertical plane, ground use is discouraged. However, this must be coupled with the provision of plenty of climbing structures and thin flexible supports with few large platforms to maximise the frequency of natural arboreal behaviour.

Figure 6.11 Orangutans at the zoo in Ouwehands Dierenpark, The Netherlands, using suspensory postures on the wiremesh ceiling (Photo: A C Phillips).

6.5 Conclusions

Overall, this study has found clear differences in the positional behaviour of wild and captive orangutans. Locomotor behaviour showed greater differences across habitat than posture, which is likely to reflect the greater musculoskeletal stresses involved. Captive and wild orangutans showed similar associations between positional behaviour and support use and this indicates that modifying the support composition of captive enclosures can have a substantial and, most importantly, predictable influence on the positional behaviour exhibited. By investigating the developmental changes for different aspects of positional behaviour, we have demonstrated that the positional behaviour of captive orangutans becomes increasingly less like their wild counterparts with age. This trend has worrying implications for healthy musculoskeletal development in captivity and indicates that captive management must focus on promoting active arboreal behaviour in immature orangutans to improve health and welfare in later life.

7. GENERAL DISCUSSION

The aim of this thesis was to explore how orangutans solved problems related to life in a complex fragile environment and how this changed with growth and development. I addressed this firstly by examining how positional behaviour and support use changed as body size increased. Secondly, I examined how orangutans solve one of the most complicated problems in their habitat: travelling between trees using compliant supports to establish whether skills related to locomotion during gap crossing may contribute to the extended period of maternal dependence in this species. Finally, I compared locomotor behaviour in wild and captive orangutans to examine whether captivity can provide an environment that encourages natural development of positional behaviour. This is particularly important because as the forests of Borneo and Sumatra are cleared, more and more young orangutans are held in rehabilitation centres and successful rehabilitation may help save these endangered animals.

7.1 Summary of findings

By examining the positional behaviour of wild orangutans from infant to adult I found that body size influenced both locomotion and postural behaviour (Chapters 2 and 3). In contrast to previous studies of orangutan locomotion (Sugardjito and van Hooff 1986; Thorpe and Crompton 2005; Thorpe et al. 2009), I found that larger orangutans did use more suspensory locomotor behaviours than smaller orangutans, which supports the hypothesis of Cartmill and Milton (1977) that larger animals gain stability on thin branches by bearing their weight in suspension rather than compression. However, when the influence of body size on postural behaviour was examined, I found the opposite trend. Larger orangutans used more compressive postures than smaller ones. The conflicting results suggest that during posture larger orangutans seek more stable supports that can bear their weight in compression. They may still be able to feed from thin terminal branches because they have a greater reach than smaller orangutans.

Analysis of both posture and locomotion revealed that larger orangutans used larger supports. This was in contrast to the findings of Thorpe and Crompton (2005) for the locomotor behaviour of Sumatran orangutans. They found that adult female Sumatran orangutans used larger supports than the males despite being considerably smaller; this was attributed to their more cautious nature and linked to having given birth. The work on Bornean orangutans reported in this thesis did not find evidence to suggest that adult females were more cautious than males. A possible explanation is that the lower height at which orangutans travel in disturbed forest reduces the need for caution.

Body size was also found to influence the gap crossing behaviour of wild orangutans (Chapter 4). Larger orangutans were found to cross greater distances, favour compliant trunks for gap crossing and use the oscillatory behaviours ride and sway more often when compared to smaller orangutans. However, body size was not the only factor that influenced the distance an orangutan crossed: gap crossing technique was also important. Orangutans of all sizes used more complex behaviours involving the manipulation of compliant supports to cross larger gaps. Complex skills that involved bending and swaying compliant supports were not fully mastered until orangutans reached 6 years old. This corresponds with the age at which the locomotor behaviour of immature orangutans was found to be broadly comparable to that of adults (Chapter 2). When examining the role of the mother in gap crossing (Chapter 5), I found that maternal assistance was rarely provided after 6 years old, although it was observed on a few occasions during follows of a 6 and 7 year olds. Carrying during gap crossing was observed regularly between the ages of 1 to 4 years, but only once in a 5 year old orangutan. When compared with an earlier study of the development of gap crossing behaviour by Bard (1995) at Tanjung Puting, the orangutans at Tuanan appeared to acquire gap crossing skills earlier. In Tuanan, independent gap crossing behaviour began to develop as early as 1 year of age and infants were able to practice gap crossing skills by using thin trees that were abundant in the disturbed forest. In contrast, Bard (1995) did not include orangutans that were younger than 2.5 years old in her study because she observed that they were always carried by their mothers when crossing between trees. Bard (1995) also found that 6 year old orangutans still regularly received assistance from their mothers in the form of bridging and riding together and she even observed these behaviours on a few occasions when following mothers with 8 year old offspring. As the habitat where Bard (1995) carried out her study was considerably less disturbed, I propose that habitat disturbance may advance the development of gap crossing behaviour in orangutans.

In Chapter 5 I also examined the influence of maternal style on gap crossing development and related this to maternal experience. Although the sample size was very small I found some evidence that more experienced mothers were less attentive than primiparous mothers and their offspring learnt independent gap crossing behaviour faster. This has also been found by studies of rhesus and Japanese macaques (Simpson and Datta 1991; Bardi and Huffman 2002). Overall, the results of my study supported the theory of Bard (1995) that by ignoring their offspring's cries for assistance and gradually reducing the assistance that they provide, orangutan mothers are 'scaffolding' the development of independent gap crossing behaviour.

Finally, Chapter 6 compared the positional behaviour of wild and captive orangutans. In agreement with previous studies (Crompton et al. 2003; Hanson 2008) captive orangutans were found to use terrestrial positional behaviours where body weight was borne in compression much more frequently than wild orangutans. These positional behaviours put lower stresses on the musculoskeletal system of developing orangutans than suspensory positional behaviours; therefore, captive orangutans may not develop maximum muscle strength and bone density during immaturity as has been found in humans with restricted exercise (Lindle et al. 1997; Gunter et al. 2008). My results showed that the positional behaviour of captive orangutans increasingly diverged with that of wild orangutans as age increased. Worryingly, these results supported my hypothesis that the positional repertoire of captive orangutans does not facilitate species-typical bone and muscle development, which appears to cause further positional behaviour disparity as the orangutans age. However, it may be possible to reverse this trend; my study also found that positional behaviour had similar support associations in wild and captive environments, which suggests that providing captive orangutans with supports, which mimic the mechanical behaviour of those found in the wild, could encourage more natural positional behaviour. Therefore, providing types of supports that are functionally similar to the supports that wild orangutans use for locomotion should be a major focus for captive management of orangutans.

7.2 Does the development of positional behaviour and gap crossing help to explain the length of inter-birth intervals in orangutans?

Orangutans have the longest inter-birth interval of any mammal and this is associated with a long period of exclusive maternal dependence (Galdikas and Wood 1990; Wich et al. 2004; van Noordwijk and van Schaik 2005). Variation in the length of inter-birth intervals across Borneo and Sumatra has been found to correlate with forest productivity and availability of fruit (Wich et al. 2009). These results led to the hypotheses that higher mortality occurs in less productive forests (Knott 1998) and that this has led to intrinsic differences in the life history of genetically isolated populations of orangutans (Wich et al. 2009). However, the analysis of life history data from captive orangutans by Anderson et al. (2008) contradicted the concept of intrinsic differences (see General Introduction, Section 1.10) and, instead, proposed that there is a high degree of phenotypic plasticity in the length of orangutan inter-birth intervals. This suggests that orangutans may be able to increase their rate of reproduction in response to living in a simplified environment where food is guaranteed and infants can be expected to survive without their mother at an earlier age. Therefore, I suggest that environmental changes, which affect the availability of resources and the development of skills in wild orangutans, may result in changes in inter-birth intervals. I propose that forest disturbance is one such factor.

Previous studies of orangutan development did not find evidence to support the development of skills hypothesis, which states that orangutans have longer inter-birth intervals because they need to learn essential skills before they can range independently from their mother (van Noordwijk and van Schaik 2005; van Adrichem et al. 2006). I suggest that this may in part be because they failed to consider key locomotor skills, in particular the ability to travel across discontinuous forest canopy using compliant supports, which is essential for independent ranging. This thesis examined the development of positional behaviour and gap crossing in a highly degraded forest and found that orangutans learned gap crossing skills faster than had previously been found for the same sub-species inhabiting a more pristine swamp-forest at Tanjung Puting (Bard 1995). Infant orangutans at Tuanan practised the complex gap crossing behaviours ride and sway using thin, compliant saplings that were abundant in the disturbed forest within the field site. If the vegetation structure at Tuanan allowed orangutans to develop gap crossing skills faster, they may have been capable of ranging independently from their mother at a younger age. However, this would only help to reduce their period of maternal dependence if other skills were already mastered. Van Noordwijk and van Schaik (2005) noted that by 3 years old orangutans could make their own nests (although they slept in their mother's nest until they were approximately 7 years old). In Borneo orangutans were capable of processing all of the foods eaten by their mothers when they were between 3 and 5 years old (van Noordwijk et al. 2009). In Sumatra there was one feeding technique that involved using stick tools to remove seeds from between poisonous hairs of a *Neesia* fruit, which was not mastered until approximately 7 years old (van Noordwijk and van Schaik 2005). But this is unlikely to be essential for survival. In Chapter 5 I found that young orangutans hardly ever received maternal assistance when travelling between trees after 6 years of age, yet at 5 years old, assistance was still regular but mostly consisted of riding together on the same tree, which was largely passive on the part of the mother. This thesis found that at 6 years of age the locomotor repertoire of young orangutans was broadly similar to adults and the complex gap crossing skills ride and sway were fully acquired. Although comprehensive data on inter-birth intervals are not yet available for Tuanan as the site was only established in 2003, the first known inter-birth interval was recorded in 2010 at just over 6 years (although, previous data from Tuanan based on estimated ages found inter-birth intervals between 7 and 8 years; van Noordwijk pers. comm.). In conclusion, essential skills required for foraging and nest building are already acquired before orangutans cease to receive assistance during gap crossing. Therefore, changes in forest structure that lead to orangutans mastering gap crossing skills at an earlier age could lead to earlier independence in orangutans. Overall, these preliminary data from Tuanan provide support for the theory that inter-birth intervals are related to the development of locomotor skills in orangutans and mothers may delay conception until their previous offspring no longer requires assistance with travel.

7.3 Can my results be applied to other populations of Bornean and Sumatran orangutans?

A comparison of the development of independence in Bornean and Sumatran orangutans carried out by van Noordwijk et al. (2009) using data from two Sumatran sites (Ketambe and Suaq Balimbing) and one Bornean site (Tuanan) concluded that the development of independent travel was broadly similar in both species. Their study defined travel competence by measuring the percentage of time that offspring were carried during travel. The results showed that Bornean orangutans were carried slightly more between the ages of 2 to 4 years than Sumatran infants. Van Noordwijk et al. (2009) attributed this difference to the more uneven canopy in the disturbed forest at Tuanan. In the more pristine forest of Sumatra trees are larger and, therefore, orangutans would be expected to spend more time travelling within trees than between trees when compared with disturbed forest. If infant orangutans only needed to be carried when moving between trees, they would be expected to spend less time being carried in Sumatra. Chapters 4 and 5 of this thesis recorded gap crossing behaviour every time orangutans moved between trees as this was considered to be more challenging than moving within trees. Therefore, my results are not directly comparable to those of van Noordwijk et al. (2009). However, van Noordwijk et al. (2009) also found that Sumatran orangutans still received assistance in the form of maternal bridging after 6 years of age whereas Bornean orangutans did not, suggesting a slightly later age for complete competence in Sumatra. This is supported by the findings of Chapter 5 and agrees with my theory that forest disturbance may allow young Bornean orangutans at Tuanan to develop gap crossing skills earlier than they would in a pristine habitat. Overall, the results of this thesis may not translate to other species and populations of orangutans living in different habitats and further research is required to examine how habitat structure influences the development of locomotor behaviour in orangutans.

Differences in forest structure may explain the differences in age that complete competence was reached in Bornean and Sumatran orangutans because Bornean orangutans may be able to cross larger gaps by oscillating thin compliant trunks at a younger age than Sumatran orangutans because the trunks in Sumatra are larger and therefore more difficult to oscillate. This hypothesis is supported by comparing the gap crossing behaviour of Bornean orangutans recorded during this study with the study by Bard (1995) at Tanjung Puting, which indicates that gap crossing skills are learnt at an earlier age in the disturbed forest and orangutans require maternal assistance crossing gaps at a later age in the less disturbed forest. Overall, these studies suggest that habitat differences are likely to influence the development of gap crossing behaviour of orangutans and, therefore, my results may not be representative of orangutans living in more pristine habits. Unfortunately, it is not possible to draw any conclusions about species differences that may influence the development of positional behaviour and gap crossing skills because no study has been carried out in similar habitats in Borneo and Sumatra.

7.4 Recommendations for future research

Although this study was only carried out at one site the results have generated predictions for the development of gap crossing behaviour in other habitat types. In order to test these predictions I recommend that future studies record gap crossing behaviour and maternal assistance every time subjects cross between trees in order to standardise the results. This method was chosen because it is difficult to quantify the size of a ‘gap’ for different sized subjects because the branches deform in proportion to body mass and the distance an orangutan can reach is determined by body dimensions. I further recommend that future work adheres to the methods set out in this thesis for recording the actual distance crossed (AGC) during crossing between trees for different types of locomotor behaviour. It is important to record the AGC to compare the gap crossing abilities of orangutans living in different habitats.

I acknowledge that this study of gap crossing behaviour was somewhat limited in the data that could be collected as in Tuanan gap crossing events often occurred in quick succession and the gap crossing data were recorded concurrently with 1 minute instantaneous sampling of posture and locomotion by a single observer. If a study were just focussing on gap crossing behaviour I would recommend recording further information that could more accurately determine which gaps orangutans of different ages and body sizes will be able to cross (e.g. could a 4 year old orangutan cross a distance of 3m by oscillating a trunk of 10cm diameter?). The diameter of the supports used is particularly important for establishing competence in the oscillatory behaviours ride and sway, and this information would help distinguish between different habitats where the composition of different sized supports varies. In order to enhance the detail and accuracy of the data collected it would be useful to video crossing events to examine behaviours in further detail later. If this were combined with tagging and recording GPS locations of all the trees that the orangutans crossed between then more detailed measurements of support diameter and distance between the trunks could be recorded at a later date. This would require a field assistant to tag the trees and record the GPS locations. However, I recommend that AGC be estimated whilst observing the animal because this would be very difficult to determine from video because the angle of filming alters the appearance of distances on video. A further measure that may also be useful to determine which gaps present the greatest challenges for different sized orangutans is the distance between the terminal branches of the two trees. This could be measured if the location was marked with brightly coloured tagging for measurement at a later date. Studies of wild orangutans are always limited by sample size and it may take many years to find enough different aged orangutans to make a full comparison of the development of gap crossing behaviour in different habitats.

7.5 Recommendations for captive care and reintroduction

One of the greatest challenges associated with keeping orangutans in captivity is promoting natural arboreal behaviour. By providing suitable climbing structures and implementing simple routine changes such as feeding animals from above, zoos and sanctuaries can encourage more arboreal behaviour in orangutans. For caged orangutans, providing suitable types of supports is very important for locomotor development. For logistical reasons, it is not always possible to provide captive orangutans with living vegetation to use for locomotion. However, it is important that zoos provide supports that mimic the properties of different types of vegetation. Ropes and polyester webbing have been shown to elicit oscillatory behaviours in zoo subjects (Hanson 2008; Chapter 6). Although the material properties of these man-made fibres are not the same as the lianas used by wild orangutans (as they have different strengths and surface texture), they may still elicit the same types of behaviour in orangutans if they are attached vertically with plenty of excess material to permit oscillation. This is a relatively easy addition to zoo enclosures and most already include some loosely attached ropes in their orangutan enclosures. However, it is much more difficult to mimic the properties of compliant tree trunks. In the wild orangutans can cross gaps of up to 8m by oscillating compliant trees back and forth (Chapter 4). Specially designed poles have been used to mimic the properties of compliant woody supports in the outdoor enclosure of Apenheul Primate Park using fibreglass and by Coward et al. (unpubl. data) at Chester Zoo using carbon fibre. However, it is difficult to find a pole that is flexible enough to permit oscillation yet strong enough to withstand daily use by orangutans without breaking (S. Coward, pers. comm.). Longer poles are easier to oscillate but there is also a greater risk of injury if a tall pole breaks or the orangutan falls while oscillating it. Therefore, safety concerns can stop zoos from providing these types of supports. Unfortunately, safety concerns forced Apenheul to tie the tops of their fibreglass poles together, which prevented orangutans from oscillating them (pers. obs.). At the Great Ape Trust in Iowa, USA, they designed poles from steel (R. Schumaker, pers. Com to S Coward.), which could be oscillated by orangutans without risk of breakage, as steel bends when overloaded rather than fracturing like composite tubes. The ability to cross gaps by swaying compliant trunks is an essential gap crossing skill for wild orangutans. Therefore, in order to maintain locomotor skills for possible release back to the wild, captive institutions will have to find ways to incorporate flexible poles safely in their exhibits.

7.6 Assessing the viability of captive orangutans for release into forest habitat

Rehabilitant orangutans undergo forest training in small fragments of forest around rehabilitation centres in Borneo and Sumatra. The methodology that I used to assess the gap crossing skills of wild orangutans in degraded forest habitat could be used to assess the suitability of rehabilitant orangutans undergoing forest training, for successful release into forest habitat. At Tuanan I found that 6 year old orangutans had the gap crossing skills they needed to travel independently from their mothers. Therefore, my data on the gap crossing behaviour of 6 and 7 year old orangutans could be used as a threshold by which to judge whether a rehabilitant orangutan has the locomotor skills needed to survive in a forest habitat. However, it may be necessary to adjust these recommendations for different types of forest habitat.

7.7 Personal reflections

When I started my PhD research in October 2007 I knew little of the challenge that lay ahead. I was familiar with the conditions in the Bornean peat swamp forest where my study species lives yet I knew very little about the great apes which I would spend the next 4 years studying. I spent the first year of my PhD reviewing the extensive literature on orangutan ecology, primate development, positional behaviour and forest structure. Initially I found it hard to devise appropriate methods to test the questions that I wanted to answer as I had never designed my own research before. I was able to practise the methods of recording positional behaviour on captive orangutans in zoos but I struggled to visualise how this could be translated to a study of wild orangutans. However, I was able to benefit from substantial experience of my supervisor Susannah and other students and collaborators who had carried out research on wild orangutans and with their advice I was able to design my research methods.

I finally got permission to conduct research in Indonesia half way through the second year of my PhD. The first week I spent at Tuanan we searched every day and did not find any orangutans and I began to worry if I would ever get the data I needed. Then Dr Maria van Noordwijk, who coordinates the research at Tuanan, arrived in camp and she knew just where to find the mother and infant orangutans that we were both so keen to observe. I was very fortunate to be able to learn from Maria on my first days of observing wild orangutans as she has spent many years researching orangutans in both Sumatra and Borneo. It was only through observation of mother and infant orangutans that I was able to refine my methods of recording gap crossing behaviour to enable me to distinguish between the abilities of the different aged infants through observation of their independent and maternally assisted gap crossings.

With hindsight, it would have been extremely useful to carry out a reconnaissance trip to Tuanan whilst I was still at the planning stage of my PhD but unfortunately this would not have been possible due to length of time required for foreigners to get research permits in Indonesia. Still, I was able to devote the first month of my time at Tuanan to practising and refining my methods and learning to estimate diameters and distances in the forest. This period of self-training ensured that my subsequent data collection was consistent and accurate.

The year I spent following orangutans at Tuanan presented many challenges. The seasonal climate meant that I had to deal with both extremes of wet and dry. For the first 6 months of my research there was an exceptionally low rainfall and all of the water in the forest dried up. This led to widespread forest fires across Kalimantan and eventually the fires reached our camp. A team of local fire fighters came to camp and helped put out the fires some 5m from our camp entrance. We were very lucky that the main damage was to previously burnt scrub land and the vast majority of our forest was left undamaged. The fires also generated a lot of smoke and ash which caused poor visibility in the forest but this was offset by the negative impact of the drought on the foliage of the trees, which improved our visibility of the orangutans.

The second half of my fieldwork was carried out during the rainy season and the forest became flooded in places over 1m deep. The water was particularly deep in the transects, which we used to move quickly through the forest. This made walking very tiresome, especially when travelling to the orangutans nest before dawn. It was also hard to walk without making a lot of noise, which hampered our efforts to find orangutans as they would hear us coming and remain silent in their tree. Heavy rainfall also caused us to lose orangutans that we were following because the noise of an orangutan moving could not be detected over the noise of the downpour. Heavy rain during the night sometimes caused orangutans to rebuild their nests in a different location, meaning that we could not find them when we returned the next morning.

Searching for orangutans consumed a large amount of my research time. For my project it was important to find as many different aged individuals as possible, therefore I had to actively search for female orangutans with offspring of known age. I also wanted to keep the sample interval between observation periods short to ensure that subjects were at the same stage of development during all observations. Therefore, I was often searching for specific orangutans. I became familiar with the territories of the females that lived near to our camp and had reasonable success at finding them when I needed them. After a few months of working in the forest I had learned to recognise the subtle clues that indicated orangutans were nearby including sounds, signs and smells, these skills helped me to locate the animals that I was looking for. As a result I was able to obtain data for orangutans aged between 1 and 9 years old with one subject for every age with the exception of a 2 year old. There were two female orangutans known to have 2 year old offspring at the time of my study but their home ranges were far from our camp and they were both unhabituated to human observers therefore they were very difficult to find and follow and I was not able to collect any data on them.

Overall my time in Indonesia was full of immense highs and lows. While working with the orangutans I experienced many wonderful, fascinating and frightening moments and I felt extremely privileged that the orangutans allowed me to share these with them. Through working in the forest alongside Indonesian and foreign researchers I developed the skills required to record accurate behavioural observations of orangutans in dense foliage high up in the rainforest canopy. I also learned how to navigate in the forest and mark orangutan nest sites to return the next day. I adapted to a very basic lifestyle with very limited communication with the outside world. I learned to speak Indonesian and helped to coordinate the local staff to ensure that the field site's other research objectives were carried out.

Over the four years I have spent doing my PhD I have improved my academic skills through completing literature reviews, draft papers and finally my thesis. Before I started my PhD I had only used basic statistics to analyse data. After inputting the data from over 100 full days of observation I had a large dataset consisting of categorical and continuous data with many observations collected from each subject. The analysis called for advanced statistical techniques to establish the complex relationships between the different types of variables whilst, controlling for the repeated measures. The techniques I used required me to learn how to use the statistical packages SPSS and R. I found using R particularly difficult having never done any computer programming, it felt like learning a completely new language. I was fortunate to have help from my supervisor Jackie and also statistics advisors Dr Alan White and Dr Peter Winn and with a lot of hard work I managed to produce valid statistical models.

One of the aspects of doing a PhD that I found very difficult was presenting my research to an audience. As this was an integral part of my PhD I strived to improve my oral communication skills by signing up for extra courses on presentation skills and volunteering to speak at lab meetings whenever I had something new to present. Over the course of my PhD my confidence grew and I was able to present the findings of my PhD at national and international conferences, something I never thought I would be capable of.

7.8 Strengths and weaknesses of the thesis

In my thesis I have presented new information on the development of locomotor behaviour in Bornean orangutans. Although my sample size is very small, I have collected data on a wide range of different aged individuals allowing me to draw some preliminary conclusions about the onset of developmental milestones in orangutan locomotor behaviour. Considering that wild orangutans only give birth once every 7-9 years it is usually very difficult to find enough different aged individuals to get a cross-sectional sample sufficient to investigate development. It was for this reason that I selected Tuanan as my study site as there were a large number of well-known female orangutans with infants of known age.

My study was the first to gauge physical development of wild orangutans by using a non-invasive laser photographic technique. By examining the relationship between physical size and gap crossing distance I was able to infer the age range during which gap crossing skills of young orangutans at Tuanan were limited by their cognitive development. Unfortunately it was beyond the scope of this study to fully address how cognition develops during ontogeny. The cognitive capabilities of young primates are usually assessed through observations of object manipulation. In captivity orangutans were often observed to manipulate objects using complex sequences of goal directed actions including the manufacture and use of tools. However, at Tuanan, orangutans were very rarely observed using detached objects to achieve a goal. Therefore, regrettably my efforts to devise a standardised method of recording manipulative behaviour to infer cognitive ability were abandoned to focus on the more observable locomotor behaviours.

7.9 Broader implications

Overall, my thesis has shown that changes in body size and skill acquisition during ontogeny shape the positional behaviour of young Bornean orangutans. My study has highlighted the importance of the mother in the acquisition of complex gap crossing skills in wild orangutans. In particular maternal scaffolding of gap crossing behaviour is likely to facilitate the learning of these skills. Without their mothers orphaned rehabilitant orangutans will need to be provided with appropriate encouragement from human caregivers to learn the skills they will need to be successfully released back into the forest.

The results of my study also suggest that forest structure may influence the rate of acquisition of gap crossing skills in young orangutans. As the forests of Borneo and Sumatra become increasingly degraded it is important to understand how these changes will impact on all aspects of orangutan ecology.

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APPENDICES

APPENDIX A. Standardised descriptions of primate locomotor and postural modes (Hunt et al. 1996). Additional behaviours specific to orangutans taken from Thorpe and Crompton (2006). Modes shown in bold and sub-modes shown in italic.

Positional Behaviour	**Definition**
MODES OF POSTURE	
Sit	A posture in which the ischia bear substantial portion (usually more than half) of the body weight; the torso is relatively orthograde.
Sit/forelimb-suspend	More than half of the weight depends on the ischia (and the feet, in contact with the support), but one or both abducted forelimbs grasp an overhead branch to stabilise the body and support some body weight.
Sit/hindlimb-suspend	More than half of body weight depends on one or both ischia, but one or both hindlimbs grasp overhead substrate and support more than their own weight.
Sit/forelimb-hindlimb-suspend	As for "Sit/hindlimb-suspend" but a forelimb and a hindlimb support more their own weight in either contralateral or ipsilateral suspensory combination.
Sit/forelimb-compression	As for "*Sit/forelimb-suspend*," but one or both forelimbs are below level of shoulders and support body weight in compression.
Sit/hindlimb-compression	Sit, with one or both hindlimbs supporting body weight in compression.
Sit/forelimb-hindlimb-compression	More than half of body weight is supported by ischia, but a forelimb and a hindlimb support more than their own weight in contralateral or ipsilateral compression combination.
Sit/forelimb-suspend/hindlimb-compression	More than half of body weight is supported by ischia, but weight is also supported by a forelimb in suspension and a hindlimb in compression.
Squat	The body weight is bourne solely by the feet/foot, both hip and knee are strongly flexed. Neither forearms nor ischia bear substantial body weight. The trunk is orthograde or sub-orthograde and the back is typically flexed. The animal often facing at right angle to the length of the support. Sit-in is different to squat in that the ischia bear body weight in sitting.
Squat/forelimb-suspend	Bipedal or monopedal squat in which one or both forelimbs also support weight in suspension.

Squat/forelimb-cling	As for "squat/forelimb-suspend," but one or both forelimbs cling to a vertical substrate, supporting more than their own weight.
Stomach-squat	Body weight is bourne primarily by feet in a squat, but protruding stomach rests on additional support and appears to support significant body mass.
Stomach-squat/forelimb-suspend	As above, but with some body weight borne by one or both forelimbs in suspension.
Cling	Flexed limb posture most common on vertical-subvertical supports.
Bimanual cling	Both hands grasp a support with the elbows flexed; the forelimbs are adducted and the torso is orthograde or sub-orthograde. Hindlimbs are flexed at hip and knee. The foot/feet may or may not grasp the support with a power grip, but support at least a proportional amount of the body weight (usually > half). The ischia bear none of the body weight. The forelimb support may be more horizontal, but in all cases the elbow, knee, and hip are flexed and the hindlimbs bear at least half the body weight.
Cling/forelimb-suspend	As above, except one forelimb is extended in an arm-hanging fashion. More than half of the weight is bourne by the hindlimbs and flexed forelimb in a clinging gestalt.
Cling/sit/forelimb-suspend	One hindlimb is in cling position and supports majority of body mass. This is aided by a forelimb in suspension and one ischium.
Pronograde stand	
Quadrupedal stand	Four-limbed standing on horizontal or subhorizontal supports, the elbow and knee are (relatively) extended and the trunk is near horizontal.
Tripedal stand	As above except with 2 hindlimbs and one forelimb bearing weight.
Tripedal stand/forelimb-suspend	Tripedal posture in which free forelimb is extended in arm-hanging fashion.
Tripedal stand/hindlimb-suspend	Tripedal posture in which free hindlimb supports body weight in suspension.
Crouch	Quadrupedal flexed elbow and/or flexed knee posture.
Quadrupedal full-crouch	*Where both elbows and hindlimbs are flexed.*
Quadrupedal forelimb-crouch	*Wherein the elbows are flexed, but the knees are not.*
Quadrupedal hindlimb-crouch	*Wherein the hindlimbs but not the elbows are flexed.*
Tripedal hindlimb-crouch	Tripedal posture in which elbow is extended, but both hindlimbs are flexed.
Tripedal hindlimb-crouch/forelimb-suspend	As above, but with free forelimb supporting more than its own weight in suspension.

Contralateral compression	Standing with torso pronograde and face downward and weight supported by a forelimb and a hindlimb on opposite sides of the body.
Contralateral compression/hindlimb-suspend	As for “contralateral stand,” but with remaining hindlimb in suspension.
Ipsilateral compression/forelimb-suspend	Torso is pronograde and on its side. Majority of body weight is supported in compression by a forelimb and hindlimb on same side of body. Significant body weight is also supported by a forelimb under suspension.
Ipsilateral compression/hindlimb-suspend	As for “ipsilateral stand-forelimb suspension,” except that mass is partially supported by a hindlimb in suspension rather than a forelimb.
Pronograde stand/forelimb-suspend	Torso is in pronograde position, with one or both hindlimbs in quadrupedal stand position, but one or both forelimbs are abducted and support body mass through suspension above head.
Orthograde stand:	
Extended bipedal stand	Hip and knee are completely extended, but there is no significant support from the forelimb(s). The trunk is near orthograde. This mode best describes human-like bipedal standing. If one foot does not contact a support this term is still recommended.
Flexed bipedal stand	Standing on the hindlimbs with no significant support from any other body part. The torso is typically held at approximately 45° angle. The hip and knees are flexed.
Flexed bipedal stand/forelimb-suspend	More than half of the body weight supported by the hindlimbs, but there is significant support from a forelimb oriented in a fore-limb suspend pattern, hindlimbs flexed; or *Extended bipedal stand/forelimb-suspend* with hindlimbs extended.
Extended bipedal stand/forelimb compression	As for “*extended bipedal stand*,” but one or both forelimbs are below level of shoulders and support body weight in compression.
Bipedal compression	Bipedal posture where legs may be angled in any position below horizontal and may be positioned on variously angled substrates, at different levels and with different degrees of abduction/ adduction and flexion/extension to each other.
Bipedal compression/forelimb-suspend	As above, but with significant support from one forelimb in suspension.
Monopedal stand	Body mass supported by standing on one leg, with insignificant contributions from other body parts.
Monopedal stand/forelimb-suspend	As for “bipedal stand/forelimb-suspend,” but with only one hindlimb.
Monopedal stand/forelimb-compression	As for “bipedal stand/forelimb-compression,” but with only one hindlimb.
Monopedal stand/forelimb-hindlimb-suspend	Majority of body weight is supported by one hindlimb, which in most cases is rather abducted. Torso is often angled, and a fore-and hindlimb support weight on suspension, either in ipsilateral or contralateral combination.
Monopedal compression/	As for “monopedal stand/forelimb-suspend,” but with hindlimb

forelimb-suspend	excessively abducted or adducted. Includes flexed and extended postures.
Monopedal compression/ tripedal-suspend	Majority of body weight is supported by one abducted or adducted hindlimb. But torso is horizontal or near horizontal, and remaining three limbs support body weight in suspension.
Monopedal compression/ forelimb-hindlimb-suspend	Majority of body weight is supported by one hindlimb, which is abducted or adducted. Torso is often angled, and fore-and hindlimb support weight in suspension, either in ipsilateral or contralateral combination.
Monopedal compression/hindlimb-suspend	Posture in which majority of body mass is supported by one hindlimb under compression, but other hindlimb supports substantial body weight under suspension. Torso can be in any position from horizontal to near vertical.
Monopedal stand/sit	More than half body weight is supported by a hindlimb in compression. However, body is leaning in part-sitting posture against angled or horizontal support, and ischia contribute to supporting body mass.
Monopedal stand/hindlimb-cling	Orthograde posture in which majority of body weight is supported by one hind limb, but significant body weight is supported by other hindlimb in "cling" position.
Cantilever	The feet anchor the lower body to a stable near-vertical support. The trunk is held rigid and near horizontal as the individual reaches out to snatch insects with the forelimbs. This behaviour is quite different from bridging and should not be conflated with it.
Extended cantilever	Knees and body are extended, often fully.
Orthograde forelimb-suspend	Posture wherein more than half of the body weight is borne by the forelimb(s) grasping a support above the animal's centre of mass.
Unimanual forelimb-suspend	Suspension by one hand with insignificant support from other parts of the body. The humerus is abducted and the elbow is usually completely extended. The trunk in orthograde. Other body parts may touch a support, but bear no more or little more than their own weight.
Bimanual forelimb-suspend	Suspension from both abducted forelimbs.
Forelimb-suspend/sit	Suspension with approximately half the body weight estimated to be suspended from one or both forelimbs, and the remainder supported by the ischia and/or feet (with hindlimbs flexed). One forelimb may be completely abducted and supporting the body weight in tension, while the other forelimb is orientated in a manner similar to that seen in clinging (humerus adducted and elbow flexed). An individual may be scored as arm-hanging or clinging depending on which forelimb appears to be bearing the most weight. Similar to sit/forelimb-suspend, except that more than half of the weight id borne by the forelimb(s).
Forelimb-suspend/sit/hindlimb compression	Body mass is supported by one or both forelimbs, ischia, and one or both hindlimbs in compression.
Forelimb-suspend/squat	Suspension as above but with the lower body supported by a squatting gestalt.

Forelimb-suspend/hindlimb compression	More than half of body weight suspended from one or both forelimbs. Rest is supported by bipedal or monopedal compression. Trunk is held at least 45° above horizontal. Distinct from Forelimb-suspend/hindlimb cling, because knees and hips may be extended or only slightly flexed, and feet may be placed on supports of any size and orientation, and do exhibit power grip of cling postures.
Forelimb-suspend/tripedal compression	Majority of body weight is suspended from one forelimb, and trunk is held at least 45° above horizontal. Rest is supported by one forelimb and both hindlimbs in compression. Knees may be flexed or extended.
Forelimb-suspend/cling	Hindlimbs flexed, grasping a support and bearing approximately half the body weight; one or both forelimbs under tension similar to forelimb-suspend.
Forelimb-suspend/lie	Suspension as above with the lower body supported by a lying (side or back) posture. The spine cannot be vertical. Some body weight may be borne by an elbow (i.e. the olecranon process of the ulna).
Forelimb-suspend/hindlimb compression/hindlimb cling	One forelimb supports body weight in suspension, but is aided by one hindlimb in compression and other hindlimb is flexed, grasping a support in cling posture, and supporting more than its own weight.
Orthograde quadrumanous-suspend	Orthograde suspend where body mass may be supported by one or both hindlimbs in equal or greater proportion than one or both forelimbs.
Trunk-vertical-suspend	Suspension involving one or both forelimbs and one or both hindlimbs bearing weight in tension, foot/feet above the level of the hip, the trunk orthograde (|). Differs from other suspensory modes in that all the four limbs are in tension and the torso is orthograde.
Orthograde ipsilateral suspend/hindlimb compression	Orthograde suspension by ipsilateral fore- and hindlimb, with other hindlimb supporting more than its own weight in compression, and foot is below level of hip.
Orthograde hindlimb suspend	Orthograde suspension by both hindlimbs, in which hindlimbs are abducted to approximately 45° above horizontal and support all body mass. Forelimbs may be used for balance, but not weight bearing.
Forelimb-hindlimb suspend	Suspension by a forelimb and a foot with the trunk in a subhorizontal orientation. Limbs are typically extended. Differs from forelimb-suspend in the more pronograde orientation of the torso, and in that the forelimb need not be completely abducted.
Ipsilateral forelimb-hindlimb-suspend	Suspension with the torso pronograde by a forelimb and hindlimb on the same side of the body.
Ipsilateral suspend/hindlimb-compression	Suspension by ipsilateral fore- and hindlimb, and compression with remaining hindlimb. Body is relatively horizontal and on its side. All three support limbs bear approximately equal body mass.
Ipsilateral suspend/ipsilateral-compression	As above, but with ipsilateral fore- and hindlimb supporting body weight in compression. Limbs in suspension appear to support most body weight.
Ipsilateral suspend/sit	Majority of body weight is suspended by ipsilateral limbs, but ischia

	support some body mass.
Contralateral forelimb-hindlimb-suspend	Suspension with the torso pronograde by a forelimb on one side of the body, a hindlimb on the other. *Contralateral suspend/hindlimb-compression*: suspension by contralateral for- and hindlimb, with body relatively horizontal and facing downwards, and with other hindlimb supporting more than its own weight in "stand" posture.
Pronograde suspend	
Quadrumanous-suspend	Suspension with the torso pronograde, with all four limbs providing approximately equal support. Orientation of the trunk distinguishes this behaviour from trunk-vertical-suspend. Thorpe: inverted pronograde suspension involving both hindlimbs and one or both forelimbs. Used as feeding posture, generally with one forelimb free to harvest food.
Quadrumanous-suspend-sit	As above, but with additional support from one or both ischia.
Quadrumanous-suspend-lie	As for "quadrumanous-suspend" but with additional support from back in horizontal position.
Forelimb-suspend/pronograde-compression	As for "pronograde stand/forelimb-suspend," but majority of body mass is borne by one or both forelimbs in tension while abducted above head. Distinct from "forelimb-suspend/hindlimb compression" because torso is pronograde. Head faces downward.
Hindlimb suspend	
Extended bipedal hindlimb-suspend	Suspension from both hindlimbs, with both hips and knees extended.
Extended monopedal hindlimb-suspend	Suspension from one hindlimb, with extended hip and knee.
Hindlimb-suspend/forelimb-hindlimb compression	Suspension from one extended hindlimb, with less than half of body weight supported by a fore- and hindlimb in compression. In this study all fore- and hindlimb combinations were ipsilateral.
Hindlimb-suspend/hindlimb compression	Suspension from one extended hindlimb, with other hindlimb under compression. Suspended limb supports majority of body weight, and torso is normally near vertical, with head downward.
Lie	Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso. When an individual grasps a support, the extremity bears little more than its own weight. When lying on a side an individual may support the upper body with an elbow.
Lie/forelimb-suspend	Lie, with one forelimb supporting significant body weight.
Lie/forelimb-hindlimb-suspend	Lie, with one forelimb and one hindlimb supporting significant body weight.
Sit/lie	Sitting with the upper body supported partly by an elbow resting on the same support (or one at a similar elevation) as the ischia and feet.
Sit/lie/forelimb-suspend	As for "sit/lie," but with additional support from one forelimb in suspension.
Postural bridge:	
Pronograde bridge	The feet grasp a support on one side of a gap, the hands grasp

	support on the other side, with the body spanning the gap, in tension. Mothers may use their body as a “bridge” for infants.
Orthograde bridge	Generally one forelimb and one hindlimb hold supports on each side of gap, with body spanning gap in orthograde posture, in tension. Mothers used this posture to reduce size of gap to allow, infant to cross independently at another level.
MODES OF LOCOMOTION	
Quadrupedal walk	Locomotion on top of supports angled at <45°; typically all the four limbs contact the support in a particular sequence. The torso is pronograde or roughly parallel to the support. Walking in distinguished from running periodically by its slow or medium speed.
Symmetrical gait walk	
Crouch walk	As for “Symmetrical gait walk” except that the elbows and knees are flexed, so that the body is held closer to the support for greater stability.
Irregular gait walking	Torso-pronograde, non-suspensory quadrupedal progression lacking a regular gait. Typically supports are small, irregularly placed and variously angled. A locomoting individual may appear quite unstable. Pronograde clamber is most often seen among the terminal branches of trees. Progression is within 45° of horizontal. Speed may be slow to medium fast. This mode is sometimes labeled “climbing”, a practice we discourage
Tripedal walk	Same as quadrupedal walking in its various expressions, except one limb is not used in locomotion, the other often being used to grasp a carried object.
Forelimb tripedal walk	Both forelimbs used in walking, hindlimb may be reserved for carrying.
Hindlimb tripedal walk	Both hindlimbs used for locomotion, a forelimb may be used for carrying. In Thorpe and Crompton (2006) non-locomoting limb is not specified, but was most often a forelimb. Occasionally a forelimb was used in suspension to help support body weight.
Bipedal walk	
Extended bipedal walk	The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. The hip and knee are relatively extended, in a manner similar to human walking. This mode is extremely rare in chimpanzees and probably even more so in other nonhuman primates.
Flexed bipedal walk	As above, except the hip and knee are relatively more flexed
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.
Hand-assisted flexed bipedal walk	As for ‘‘hand-assisted extended bipedal walk,’’ but with hindlimbs relatively more bent.
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.
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.
Vertical climb	
Flexed-elbow vertical climb	Ascent on supports angled at ≥45°. Typically a hindlimb and its contralateral forelimb provide propulsion. The forelimbs help to elevate the body by the retraction (= extension) of the humerus and flexion of the elbow. Limb kinematics follow a diagonal sequence (hand-over–hand, foot-over-foot). The humerus is typically protracted in the process of reaching upward, not abducted. The torso is held orthograde and nearly parallel to the support being climbed. Grasping hands are palmigrade in their contact with the support, and feet are semiplantigrade
Inverted flexed-elbow vertical climb	Ascent only on angled (20–45°) supports, whereby orangutan is effectively hanging underneath support while ascending.
Ladder climb	Similar to flexed elbow-climbing except supports are often relatively horizontal, and are never a single vertical support. Limb kinematics follow a diagonal sequence.
Vertical scramble	Upward (≥45°) progression on multiple often oddly angled supports, typically without a discernible gait pattern.
Extended-elbow vertical climbing	Ascent on larger supports (e.g. > 20 cm in chimpanzees and baboons) angled ≥45° in which the elbow is extended. The gait is a diagonal couplet, i.e. hand-over-hand, foot-over-foot climbing similar to vertical or ladder climb, except the elbow is extended. The support is gripped by the entire volar surface of the hand, including palm and fingers. Foot contact is principally semiplantigrade. Retraction of the humerus and extension of the hip provide most of the propulsive power; elbow flexion provides little propulsive force
Bimanual pull up	A typically horizontal support is grasped by both hands and the body is lifted by retracting the humerus and flexing the elbow; the spine may be flexed to aid bringing the hindlimb on top of the support.
Vertical climb forelimbs only	Vertical climbing in which body mass is borne only by forelimbs in typical forelimb climbing pattern, but hindlimbs are not used for weight-bearing.
Vertical descent	
Rump-first symmetrical descent	Vertical quadrupedal descent of a support angled at ≥45°; rather the kinematic reverse of ascent, but often with more abduction of the forelimb
Rump-first scramble descent	As with rump-first descent, exception multiple supports with odd orientations and diameters.
Rump-first forelimbs only descent	Rump-first descent in which only forelimbs are used. Hindlimbs may be used for balance, but do not bear more than their own weight.
Rump-first cascade descent	Equivalent to ‘‘head-first cascade descent,’’ but rump-first.

Rump-first extended elbow descent	Kinematically reverse of ‘‘vertical climb-extended elbow,’’ with limbs moving in sequence, normally hand over hand, foot over foot.
Fire pole slide	Rump-first, largely passive quadrupedal orthograde sliding on vertical or subvertical support, usually very large (> 20 cm). The support is circumducted by the forelimbs and hindlimbs, after which the animal allows its body to descend by sliding with little other movement. Not infrequently the forelimbs regulate the velocity of the descent with a hand over hand movement.
Head-first descent (scramble)	As with symmetrical head-first descent, except on multiple supports with odd orientation and sizes, and a less symmetrical gait.
Head-first descent (cascade)	As with head-first scramble descent, except supports are still smaller, and radically angled. Limbs grasp briefly and in rapid succession to brake descent.
Pronograde slide	Head-first, quadrupedal, relatively passive descent of smooth oblique branches and boughs wherein the hindlimbs and forelimbs are held steady and the body moves by sliding the hands, feet, and other body contacts against the support. Torso is typically pronograde, and/or held parallel to the support.
Sideways vertical descent	The body is held at right angles to the long axis of the support. The downside fore- and hindlimbs provide most of the braking support.
Cartwheel descent	Descent in which limbs grasp supports in motion which resembles limb sequence of human cartwheels.
Torso-orthograde suspensory locomotion	
Brachiate	Classic hand over hand orthograde suspensory locomotion in which the forelimbs bear more than half of the body weight, but in which some support from the hindlimbs may occur. There is extensive trunk rotation, approaching 180°. The humerus is completely abducted and the elbow is extended, not infrequently completely extended
Forelimb swing	Similar to brachiate but with little trunk rotation.
Flexed-elbow forelimb swing	As in forelimb swing but with elbows bent.
Transfer	This mode often begins with bimanual forelimb-suspension, and may contain a brachiation-like gap-closing motion (a “lunge”), wherein a hand grasps a small support in an adjacent tree, after which a branch is pulled towards the animal with a hand over hand or hand over foot motion. Weight is gradually transferred to the adjacent tree. The torso remains more or less orthograde throughout; more weight is born by the forelimbs than hindlimbs.
Orthograde clamber	Horizontal progression in a forelimb-suspensory torso-orthograde mode, but with the hindlimbs assisting. All the four limbs act as propulsors, with most body weight borne by the abducted forelimbs. Kinematically this mode most resembles brachiation, but it differs in that the hindlimbs provide support for virtually any orientation, including completely abducted. Cant (1987a, 1992) defined the mode as follows: “the body is orthograde with the head superior, and various combinations of all the four appendages attach to substrates in different ways, including suspension by the

	forelimbs from above.”
Arrested drop	Swinging from on top to underneath a support. A bout begins either from sitting or with the body behind a single horizontal substrate supported by adducted forelimbs, elbows extended; the hands are near the hips and bearing most of the weight. From this pose the torso descends while remaining orthograde, so that the individual swings under the branch that had been near or touching the belly or hips.
Torso-pronograde suspensory locomotion	
Inverted quadrupedal walk	All the four hands/feet are used in some combination; the torso is pronograde, and limbs are in tension. Regular gaits are common.
Inverted tripedal walk	As above, but with only three limbs.
Inverted quadrupedal run	As above, but more rapidly
Inverted scramble	As above, except on irregularly angled and sized supports.
Hindlimb swing	Body is held upside-down, and animal swings on one or both hindlimbs. Often used as intermediary form of locomotion to reorient body between two longer bouts of different locomotor modes.
Forelimb-hindlimb swing	Suspensory locomotion which may or may not follow regular limb sequence, utilizing both forelimbs and hindlimbs in both orthograde and pronograde positions.
Cartwheel swing	Sequence of suspensory locomotion on horizontal or negatively inclined support which resembles sequence of limb usage seen in human cartwheels.
Ipsilateral swing	Swinging from ipsilateral fore- and hindlimb. Exhibited as single swing to join two other modes of locomotion.
Bridge	
Cautious pronograde 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.
Inverted pronograde bridge	As above, except with body in inverted pronograde suspension.
Lunging bridge	Feet grasp a support and a lunge (“incomplete leap”) closes the gap, allowing the hands to grasp a distant support. The forelimbs pull the distant support closer with all four limbs in tension. May be followed by a postural bridge.
Supinograde bridge	As with lunging bridge, except suspensory.
Descending bridge	“An incomplete leap yielding hindlimb suspension” that spans a discontinuous gap, followed by grasping a support with the forelimbs, followed by quadrupedal locomotion. Progression is downward at ≥45°.
Leap	Leaping is a gap-crossing movement in which the hindlimbs principally are used as propulsors. The flexed hindlimbs and flexed back are forcefully extended, often aided by the forelimbs. There is an extended period of free flight, distinguishing this mode from bounding.

Pronograde leap	The torso is primarily pronograde at take-off, and the leap may be initiated from either a postural or locomotor position. This type of leap is characteristic of most anthropoids. Longer leaps tend to have a downward component, which increases the horizontal distance covered. Anthropoid leaps effecting ascent are typically over short spaces, with a series of such leaps used to ascend the tree. This mode grades into bounding
Drop	This mode differs from leaping in that takeoffs are initiated not by substantial muscle propulsion, but by falling after releasing a support. It is categorised by the semi-posture ("semi" because there is little pause before dropping) assumed before the drop.
Unimanual suspensory drop	Forelimb suspension assumed before drop. But orangutans often tend to use one limb to maintain contact with support throughout drop, although support does not bear any weight during fall.
Bimanual suspensory drop	Suspension from both forelimbs; not usually preceded by bimanual armswing. Often both hands grasp another support nearly simultaneously on landing. This mode has been referred to as "dropping" or "lowering".
Tree sway	A gap crossing movement used between trees; "swaying a tree to and fro in oscillations of increasing amplitude, or bending a tree by using the body weight until the animal can reach the next tree". Tree sway differs from transfer in that body weight or oscillation are used to deform branches rather than lunging, and often the pre-gap-closing posture resembles clinging more than suspension (exemplar: orangutan). Sway is based on tree sway but expanded to include any locomotion which relies on oscillation of supports to progress forward. Also includes locomotion where orangutan swings on vertical branch/liana.
Ride	Similar to tree sway, but used from tree to ground. A vertical, small diameter support is grasped in a clinging posture and a (sometimes violent) movement or oscillation overbalances the support (typically a small tree). The weight of an individual's body pulls the tree from a vertical orientation toward horizontal. As the tree approaches horizontal a suspensory posture may result, after or during which the grip with the hindlimb is released and the feet contact the ground. Orangutans exhibit ''ride'' to move between different levels in canopy rather than from tree to ground.

APPENDIX B. Generalized linear mixed model: interactions between the fixed effects that influenced the gap crossed by orangutans when moving between trees

Interactions	Estimate	Std. Error	z value	*P*
Size group *type of locomotion				
2*Appendicular	-0.52	0.54	-0.98	0.33
2*Ride	-1.63	0.48	-3.37	<0.001
2*Ride+ appendicular	-1.86	0.49	-3.77	<0.001
2*Sway	-1.80	0.56	-3.19	<0.01
2*Sway+ appendicular	-1.70	0.62	-2.75	<0.01
3*Appendicular	-0.92	0.52	-1.76	0.08
3*Ride	-2.20	0.47	-4.69	<0.001
3*Ride+ appendicular	-2.38	0.48	-4.99	<0.001
3*Sway	-2.35	0.56	-4.18	<0.001
3*Sway+ appendicular	-2.30	0.61	-3.75	<0.001
4*Appendicular	-1.25	0.52	-2.41	<0.05
4*Ride	-2.51	0.46	-5.40	<0.001
4*Ride+ appendicular	-2.62	0.47	-5.53	<0.001
4*Sway	-2.59	0.55	-4.70	<0.001
4*Sway+ appendicular	-2.50	0.61	-4.13	<0.001
5*Appendicular	-1.38	0.52	-2.65	<0.01
5*Ride	-2.77	0.47	-5.95	<0.001
5*Ride+ appendicular	-2.66	0.48	-5.59	<0.001
5*Sway	-2.66	0.57	-4.68	<0.001
5*Sway+ appendicular	-2.46	0.63	-3.92	<0.001
6*Appendicular	-1.19	0.52	-2.27	<0.05
6*Ride	-2.73	0.47	-5.85	<0.001
6*Ride+ appendicular	-2.63	0.48	-5.50	<0.001
6*Sway	-2.67	0.56	-4.78	<0.001
6*Sway+ appendicular	-2.56	0.61	-4.22	<0.001
Type of locomotion * take-off support				
Appendicular *Branch	1.13	0.08	13.80	<0.001
Ride*Branch	0.75	0.08	8.85	<0.001
Ride+ appendicular *Branch	1.06	0.10	10.43	<0.001
Sway*Branch	1.04	0.24	4.39	<0.001
Sway+ appendicular *Branch	0.62	0.32	1.92	0.06
Appendicular *Liana	0.45	0.19	2.40	<0.05
Ride*Liana	0.26	0.15	1.77	0.08
Ride+ appendicular *Liana	0.34	0.17	2.00	<0.05
Sway*Liana	0.39	0.19	2.04	<0.05
Sway+ appendicular *Liana	0.48	0.25	1.92	0.05

AGC ~ Size group * type of locomotion + type of locomotion * take-off support + (1 | Individual)

APPENDIX C. Frequencies of mother and offspring behaviours

Behaviour	**Category**	**Mawas**	**Kino**	**Jip**	**Deri**	**Jerry**	**Streisel**	**Milo**
Cry	Offspring solicit	36	35	89	22	13	19	6
Food solicit		12	22	13	3	5	2	1
		48	**57**	**102**	**25**	**18**	**21**	**7**
Practise tree sway	Offspring locomotion	13	17	38	8	0	0	0
Alternative route		1	4	2	2	2	2	0
		14	**21**	**40**	**10**	**2**	**2**	**0**
Collect	Mother maintain proximity	121	12	48	1	0	0	0
Restrain		66	5	21	1	0	0	0
Wait		25	67	93	13	2	2	0
Throat scrape		14	5	5	4	2	0	0
		226	**89**	**167**	**19**	**4**	**2**	**0**
Encourage locomotion	Mother encourage	0	2	0	0	0	0	0
Play		11	0	1	0	0	0	0
		11	**2**	**1**	**0**	**0**	**0**	**0**
Food share	Mother provide	11	17	12	1	5	0	1
Protect		7	1	0	0	0	0	0
		18	**18**	**12**	**1**	**5**	**0**	**1**
Reject	Mother-offspring conflict	0	1	0	3	2	6	0
Withhold food		1	1	1	1	0	2	0
Scold		0	1	0	1	0	6	0
Chase away		0	0	0	0	0	4	3
		1	**3**	**1**	**5**	**2**	**18**	**3**

APPENDIX D. Frequencies of postural behaviour in Captive and wild Bornean orangutans

Postural mode, *submode*	**Captive freq**	**Wild freq**	**Captive %**	**Wild %**
sit	**4215**	**13469**	**36.02**	**46.44**
sit	3202	8607	27.36	29.68
sit forelimb suspend	348	3091	2.97	10.66
sit hindlimb suspend	34	255	0.29	0.88
sit forelimb hindlimb suspend	185	183	1.58	0.63
sit forelimb compression	137	242	1.17	0.83
sit hindlimb compression	29	390	0.25	1.34
sit forelimb hindlimb compression	0	18	0.00	0.06
sit forelimb suspend hindlimb compression	14	72	0.12	0.25
sit forelimb suspend forelimb compression	0	3	0.00	0.01
sit cling	7	0	0.06	0.00
sit lie	257	518	2.20	1.79
sit lie forelimb suspend	2	87	0.02	0.30
sit lie hindlimb suspend	0	3	0.00	0.01
squat	**1288**	**131**	**11.01**	**0.45**
squat	668	44	5.71	0.15
squat forelimb suspend	512	77	4.37	0.27
squat cling	11	0	0.09	0.00
stomach squat	0	5	0.00	0.02
squat forelimb suspend forelimb cling	1	0	0.01	0.00
squat forelimb compression	95	5	0.81	0.02
squat forelimb compression suspend	1	0	0.01	0.00
cling	**187**	**1551**	**1.60**	**5.35**
cling	159	1532	1.36	5.28
cling forelimb suspend	13	10	0.11	0.03
cling hindlimb suspend	1	2	0.01	0.01
cling sit	7	4	0.06	0.01
cling sit forelimb suspend	5	0	0.04	0.00
cling forelimb compression	1	0	0.01	0.00
cling hindlimb compression	0	2	0.00	0.01
hindlimb cling forelimb compression	1	1	0.01	0.00
Pronograde stand	**1409**	**617**	**12.04**	**2.13**
pronograde stand	18	0	0.15	0.00
quadrupedal stand	344	157	2.94	0.54
tripedal stand	201	163	1.72	0.56
tripedal stand forelimb suspend	36	37	0.31	0.13
tripedal stand hindlimb suspend	5	13	0.04	0.04
quadrupedal full crouch	659	31	5.63	0.11

quadrupedal forelimb crouch	37	3	0.32	0.01
quadrupedal hindlimb crouch	23	16	0.20	0.06
quadrupedal forelimb crouch head compression	1	0	0.01	0.00
tripedal crouch	13	15	0.11	0.05
tripedal forelimb crouch	0	1	0.00	0.00
tripedal crouch forelimb suspend	31	13	0.26	0.04
tripedal crouch hindlimb suspend	0	1	0.00	0.00
contralateral compression hindlimb suspend	0	4	0.00	0.01
tripedal hindlimb crouch sit forelimb suspend	1	0	0.01	0.00
contralateral compression	3	7	0.03	0.02
contralateral compression forelimb suspend	1	1	0.01	0.00
ipsilateral compression	1	0	0.01	0.00
ipsilateral compression forelimb suspend	5	24	0.04	0.08
ipsilateral compression hindlimb suspend	3	15	0.03	0.05
ipsilateral compression ipsilateral suspend	0	14	0.00	0.05
pronograde stand forelimb suspend	27	96	0.23	0.33
pronograde stand hindlimb suspend	0	1	0.00	0.00
pronograde stand hcfs	0	5	0.00	0.02
orthograde stand	**1096**	**1677**	**9.37**	**5.78**
extended bipedal stand	16	26	0.14	0.09
flexed bipedal stand	140	50	1.20	0.17
extended bipedal stand forelimb suspend	41	72	0.35	0.25
extended bipedal stand forelimb compression	7	5	0.06	0.02
flexed bipedal stand forelimb suspend	209	325	1.79	1.12
flexed bipedal stand forelimb compression	96	31	0.82	0.11
flexed bipedal stand head compression	2	0	0.02	0.00
bipedal compression	61	147	0.52	0.51
bipedal compression forelimb suspend	106	361	0.91	1.24
bipedal stand forelimb suspend	2	0	0.02	0.00
monopedal stand	11	20	0.09	0.07
monopedal stand forelimb suspend	114	288	0.97	0.99
monopedal stand forelimb compression	46	8	0.39	0.03
monopedal stand forelimb hindlimb suspend	56	197	0.48	0.68
monopedal stand forelimb compression hindlimb suspend	1	2	0.01	0.01
monopedal stand forelimb suspend forelimb compression	1	0	0.01	0.00
monopedal stand hindlimb suspend	7	52	0.06	0.18
monopedal stand sit forelimb compression	1	1	0.01	0.00
monopedal stand tripedal suspend	15	5	0.13	0.02
monopedal stand forelimb suspend hindlimb cling	0	1	0.00	0.00

monopedal stand sit forelimb compression	0	19	0.00	0.07
monopedal stand sit forelimb suspend	0	5	0.00	0.02
monopedal stand cling	1	1	0.01	0.00
monopedal compression	5	0	0.04	0.00
monopedal compression forelimb suspend	37	26	0.32	0.09
monopedal compression hindlimb suspend	43	10	0.37	0.03
monopedal compression forelimb hindlimb suspend	62	22	0.53	0.08
monopedal compression tripedal suspend	16	1	0.14	0.00
bipedal compression forelimb cling	0	1	0.00	0.00
flexed bipedal stand sit forelimb suspend	0	1	0.00	0.00
cantilever	**6**	**8**	**0.05**	**0.03**
orthograde forelimb suspend	**1191**	**3629**	**10.18**	**12.51**
forelimb suspend	3	0	0.03	0.00
bimanual forelimb suspend	143	135	1.22	0.47
unimanual forelimb suspend	195	1239	1.67	4.27
bimanual forelimb suspend upside down	7	0	0.06	0.00
forelimb suspend sit	11	257	0.09	0.89
forelimb suspend sit hindlimb compression	0	1	0.00	0.00
forelimb suspend sit cling	0	5	0.00	0.02
forelimb suspend squat	10	8	0.09	0.03
forelimb suspend hindlimb compression	333	1565	2.85	5.40
forelimb suspend tripedal compression	3	6	0.03	0.02
forelimb suspend cling	397	292	3.39	1.01
forelimb suspend lie	0	3	0.00	0.01
forelimb suspend hindlimb compression hindlimb cling	89	102	0.76	0.35
forelimb suspend forelimb compression	0	2	0.00	0.01
forelimb suspend ipsilateral compression	0	12	0.00	0.04
orthograde forelimb forelimb suspend hindlimb suspend	0	2	0.00	0.01
orthograde quadrumanous suspend	**623**	**1403**	**5.32**	**4.84**
trunk vertical suspend	425	971	3.63	3.35
orthograde ipsilateral suspend	4	64	0.03	0.22
orthograde ipsilateral suspend hindlimb compression	42	131	0.36	0.45
orthograde ipsilateral suspend sit	0	9	0.00	0.03
orthograde ipsilateral suspend hindlimb cling	0	1	0.00	0.00
orthograde contralateral suspend	1	5	0.01	0.02
orthograde contralateral suspend hindlimb compression	25	60	0.21	0.21
orthograde contralateral suspend sit	0	8	0.00	0.03
orthograde quadramanous hindlimb suspend	81	98	0.69	0.34

orthograde quadrumanous tripedal suspend hindlimb compression	44	42	0.38	0.14
orthograde quadrumanous tripedal suspend forelimb compression	1	1	0.01	0.00
orthograde quadrumanous supend sit	0	12	0.00	0.04
orthograde quadramanous hindlimb suspend hindlimb cling	0	1	0.00	0.00
forelimb hindlimb suspend	**417**	**3085**	**3.56**	**10.64**
forelimb hindlimb suspend	15	1	0.13	0.00
forelimb hindlimb suspend ipsilateral	212	1949	1.81	6.72
forelimb hindlimb suspend ipsilateral suspend hindlimb compression	92	715	0.79	2.47
forelimb hindlimb suspend ipsilateral ipsilateral compression	36	82	0.31	0.28
forelimb hindlimb suspend ipsilateral suspend sit	5	7	0.04	0.02
forelimb-hindlimb suspend ipsilateral suspend forelimb compression	0	3	0.00	0.01
forelimb-hindlimb suspend ipsilateral suspend lie	0	9	0.00	0.03
forelimb hindlimb suspend contralateral	48	297	0.41	1.02
forelimb hindlimb suspend contralateral suspend hindlimb compression	9	22	0.08	0.08
pronograde suspend	249	956	2.13	3.30
quadrumanous suspend	244	910	2.08	3.14
quadrumanous suspend sit	1	0	0.01	0.00
quadrumanous suspend lie	2	38	0.02	0.13
pronograde suspend hindlimb compression	0	8	0.00	0.03
pronograde suspend hindlimb suspend and mouth	2	0	0.02	0.00
hindlimb suspend	**203**	**722**	**1.73**	**2.49**
hindlimb suspend	5	0	0.04	0.00
hindlimb suspend bipedal	106	174	0.91	0.60
hindlimb suspend monopedal	66	433	0.56	1.49
hindlimb suspend forelimb hindlimb compression	3	8	0.03	0.03
hindlimb suspend forelimb compression	0	30	0.00	0.10
hindlimb suspend hindlimb compression	9	62	0.08	0.21
hindlimb suspend hindlimb cling	0	2	0.00	0.01
hindlimb suspend sit	0	1	0.00	0.00
hindlimb suspend lie	0	2	0.00	0.01
hindlimb forelimb suspend	14	10	0.12	0.03
lie	**770**	**1619**	**6.58**	**5.58**
lie	719	1191	6.14	4.11
lie forelimb suspend	27	292	0.23	1.01
lie forelimb hindlimb suspend	11	52	0.09	0.18
lie hindlimb suspend	12	41	0.10	0.14

lie forelimb suspend hindlimb compression	0	1	0.00	0.00
lie forelimb suspend forelimb compression	0	2	0.00	0.01
lie hindlimb compression	0	11	0.00	0.04
lie quadrumanous suspend	1	17	0.01	0.06
lie sit	0	12	0.00	0.04
postural bridge	**36**	**134**	**0.31**	**0.46**
postural bridge	0	1	0.00	0.00
pronograde bridge	28	99	0.24	0.34
orthograde bridge	8	26	0.07	0.09
postural bridge lie	0	8	0.00	0.03
other				
mouth suspend	1	0	0.01	0.00
mouth suspend bimanual forelimb suspend	2	0	0.02	0.00
handstand	1	0	0.01	0.00
shoulder head compression	9	0	0.08	0.00
Total	**11703**	**29001**	**100**	**100**

APPENDIX E. Frequencies of locomotor behaviour in Captive and wild Bornean orangutans

Locomotor mode, *submode*	Captive freq	Wild freq	Captive %	Wild %
quadrupedal walk	**640**	**333**	**27.60**	**6.52**
quadrupedal symmetrical walk	479	181	20.66	3.54
quadrupedal scramble	65	148	2.80	2.90
quadrupedal run	2	3	0.09	0.06
quadrupedal crouch walk	0	1	0.00	0.02
quadrupedal crutch walk	33	0	1.42	0.00
quadrupedal walk backwards	1	0	0.04	0.00
quadrupedal walk slide	1	0	0.04	0.00
quadrupedal scramble crawl	58	0	2.50	0.00
sprawled crawl	1	0	0.04	0.00
tripedal walk	**45**	**19**	**1.94**	**0.37**
tripedal walk	44	19	1.90	0.37
tripedal walk forelimb suspend	1	0	0.04	0.00
bipedal walk	**397**	**440**	**17.12**	**8.62**
bipedal walk	1	0	0.04	0.00
extended bipedal walk	7	1	0.30	0.02
flexed bipedal walk	134	24	5.78	0.47
hand assisted bipedal walk	7	6	0.30	0.12
hand assisted extended bipedal walk	11	15	0.47	0.29
hand assisted flexed bipedal walk	190	235	8.19	4.60
bipedal scramble	2	9	0.09	0.18
hand assisted bipedal scramble	45	150	1.94	2.94
vertical climb	**388**	**774**	**16.73**	**15.16**
vertical climb	7	0	0.30	0.00
flexed vertical climb	277	491	11.94	9.62
inverted flexed vertical climb	18	23	0.78	0.45
vertical climb ladder climb	1	17	0.04	0.33
vertical climb scramble	59	216	2.54	4.23
extended vertical climb	1	1	0.04	0.02
bimanual pull up	17	12	0.73	0.24
unimanual pull up	3	1	0.13	0.02
vertical climb forelimbs only	5	11	0.22	0.22
vertical climb hindlimbs only	0	1	0.00	0.02
vertical climb sideways	0	1	0.00	0.02
vertical descent	**61**	**116**	**2.63**	**2.27**
vertical descent	0	1	0.00	0.02
rump first descent	2	0	0.09	0.00
rump first symmetrical descent	21	39	0.91	0.76
rump first scramble descent	28	27	1.21	0.53

rump first forelimbs only descent	1	3	0.04	0.06
rump first cascade descent	0	10	0.00	0.20
headfirst descent	1	0	0.04	0.00
headfirst scramble descent	0	4	0.00	0.08
head first cascade descent	0	3	0.00	0.06
sideways descent	1	8	0.04	0.16
sideways cascade descent	0	2	0.00	0.04
head first symmetrical descent	1	3	0.04	0.06
headfirst hindlimbs only descent	0	1	0.00	0.02
cartwheel descent	5	11	0.22	0.22
inverted rump first symmetrical descent	1	4	0.04	0.08
torso orthograde suspensory	**411**	**1844**	**17.72**	**36.11**
brachiation	83	248	3.58	4.86
forelimb swing	28	169	1.21	3.31
forelimb swing sliding	2	0	0.09	0.00
flexed elbow forelimb swing	0	2	0.00	0.04
transfer	19	318	0.82	6.23
clamber	279	1107	12.03	21.68
torso pronograde suspensory	**76**	**140**	**3.28**	**2.74**
inverted quadrupedal walk	69	92	2.98	1.80
inverted tripedal walk	2	5	0.09	0.10
inverted quadrupedal run	4	1	0.17	0.02
inverted quadrupedal scramble	1	41	0.04	0.80
inverted tripedal scramble	0	1	0.00	0.02
hindlimb swing	**0**	**4**	**0.00**	**0.08**
forelimb hindlimb swing	**13**	**21**	**0.56**	**0.41**
cartwheel swing	2	4	0.09	0.08
ipsilateral swing	11	17	0.47	0.33
bridge	**9**	**249**	**0.39**	**4.88**
cautious pronograde bridge	4	180	0.17	3.53
inverted pronograde bridge	4	31	0.17	0.61
lunging bridge	1	29	0.04	0.57
supinograde bridge	0	2	0.00	0.04
descending bridge	0	7	0.00	0.14
leap	**7**	**1**	**0.31**	**0.02**
leap	2	1	0.09	0.02
pronograde leap	2	0	0.09	0.00
orthograde leap	3	0	0.13	0.00
drop	**60**	**95**	**2.59**	**1.86**
drop	0	4	0.00	0.08
drop unimanual forelimb	28	35	1.21	0.69
bimanual drop	14	4	0.60	0.08
drop hindlimb bipedal	1	0	0.04	0.00

drop monopedal hindlimb	2	5	0.09	0.10
drop ipsilateral suspend drop	1	2	0.04	0.04
drop pronograde suspend	0	1	0.00	0.02
drop from bipedal stand	3	0	0.13	0.00
drop rolled off edge	1	0	0.04	0.00
drop fall backwards from standing	1	0	0.04	0.00
arrested drop	9	32	0.39	0.63
arrested drop hindlimb	0	10	0.00	0.20
arrested drop ipsilateral suspend	0	2	0.00	0.04
sway	**10**	**156**	**0.43**	**3.06**
sway	0	18	0.00	0.35
sit forelimb suspend	0	4	0.00	0.08
squat	0	1	0.00	0.02
squat forelimb suspend	0	1	0.00	0.02
cling	0	2	0.00	0.04
pronograde stand forelimb suspend	0	1	0.00	0.02
flexed bipedal stand forelimb suspend	0	4	0.00	0.08
bipedal compression	0	1	0.00	0.02
bipedal compression forelimb suspend	0	4	0.00	0.08
monopedal stand forelimb suspend	0	2	0.00	0.04
monopedal stand forelimb hindlimb suspend	0	2	0.00	0.04
cantilever	0	2	0.00	0.04
bimanual forelimb suspend	1	1	0.04	0.02
forelimb suspend hindlimb compression	2	32	0.09	0.63
forelimb suspend cling	1	1	0.04	0.02
forelimb suspend hindlimb compression hindlimb cling	1	3	0.04	0.06
unimanual forelimb suspend	0	13	0.00	0.25
trunk vertical suspend	0	3	0.00	0.06
orthograde ipsilateral suspend	1	11	0.04	0.22
orthograde ipsilateral suspend hindlimb compression	0	1	0.00	0.02
forelimb hindlimb suspend ipsilateral	0	30	0.00	0.59
forelimb hindlimb suspend contralateral	1	0	0.04	0.00
forelimb hindlimb suspend ipsilateral suspend hindlimb compression	0	11	0.00	0.22
pronograde suspend	3	3	0.13	0.06
hindlimb suspend monopedal	0	2	0.00	0.04
hindlimb suspend hindlimb compression	0	1	0.00	0.02
lie	0	1	0.00	0.02
ipsilateral compression hindlimb suspend	0	1	0.00	0.02
ride	**70**	**886**	**3.02**	**17.35**
ride	0	96	0.00	1.88
bimanual forelimb suspend	20	17	0.86	0.33

bipedal compression	0	5	0.00	0.10
bipedal compression forelimb suspend	0	2	0.00	0.04
brachiation	0	3	0.00	0.06
cantilever	0	10	0.00	0.20
clamber	0	1	0.00	0.02
cling	0	4	0.00	0.08
extended bipedal stand forelimb suspend	0	2	0.00	0.04
flexed bipedal stand	0	1	0.00	0.02
flexed bipedal stand forelimb compression	0	1	0.00	0.02
flexed bipedal stand forelimb suspend	1	15	0.04	0.29
flexed vertical climb	0	4	0.00	0.08
forelimb hindlimb suspend contralateral	1	3	0.04	0.06
forelimb hindlimb suspend ipsilateral	5	148	0.22	2.90
forelimb hindlimb suspend ipsilateral ipsilateral compression	0	1	0.00	0.02
forelimb hindlimb suspend ipsilateral suspend hindlimb compression	0	19	0.00	0.37
forelimb suspend cling	2	4	0.09	0.08
forelimb suspend hindlimb compression	6	185	0.26	3.62
forelimb suspend hindlimb compression hindlimb cling	3	4	0.13	0.08
forelimb suspend sit	0	2	0.00	0.04
forelimb suspend squat	1	0	0.04	0.00
forelimb swing	0	1	0.00	0.02
hand assisted flexed bipedal walk	0	2	0.00	0.04
hindlimb suspend bipedal	0	4	0.00	0.08
hindlimb suspend hindlimb compression	0	2	0.00	0.04
lie forelimb suspend	1	0	0.04	0.00
monopedal stand forelimb hindlimb suspend	0	2	0.00	0.04
monopedal stand forelimb suspend	0	8	0.00	0.16
orthograde ipsilateral suspend	8	79	0.34	1.55
orthograde ipsilateral suspend hindlimb compression	0	12	0.00	0.24
orthograde quadrumanous iss	0	1	0.00	0.02
pronograde bridge	0	1	0.00	0.02
pronograde stand forelimb suspend	0	1	0.00	0.02
pronograde suspend	3	11	0.13	0.22
quadrupedal scramble	0	1	0.00	0.02
quadrupedal stand	0	11	0.00	0.22
quadrupedal walk	0	1	0.00	0.02
sit forelimb suspend	0	12	0.00	0.24
sit hindlimb compression	0	1	0.00	0.02
squat forelimb compression	1	0	0.04	0.00
tripedal stand forelimb suspend	0	1	0.00	0.02
trunk vertical suspend	2	3	0.09	0.06

unimanual forelimb suspend	16	205	0.69	4.01
sliding descent	**57**	**27**	**2.46**	**0.53**
sliding descent	2	0	0.09	0.00
bimanual forelimb suspend	13	0	0.56	0.00
cantilever	1	0	0.04	0.00
Cling	6	13	0.26	0.25
forelimb hindlimb suspend	1	0	0.04	0.00
forelimb hindlimb suspend contralateral	0	1	0.00	0.02
forelimb hindlimb suspend ipsilateral	3	2	0.13	0.04
forelimb suspend cling	6	1	0.26	0.02
forelimb suspend hindlimb compression	4	3	0.17	0.06
hindlimb suspend bipedal	1	2	0.04	0.04
hindlimb suspend forelimb compression	2	0	0.09	0.00
hindlimb suspend monopedal	0	2	0.00	0.04
Lie	1	0	0.04	0.00
orthograde ipsilateral suspend	2	0	0.09	0.00
orthograde ipsilateral suspend hindlimb compression	2	0	0.09	0.00
pronograde suspend	4	0	0.17	0.00
quadrupedal stand	2	1	0.09	0.02
trunk vertical suspend	4	0	0.17	0.00
unimanual forelimb suspend	3	2	0.13	0.04
ground sliding	**5**	**0**	**0.22**	**0.00**
Lie	2	0	0.09	0.00
quadrupedal full crouch	2	0	0.09	0.00
sit hand assisted slide	1	0	0.04	0.00
Roll	**69**	**0**	**2.98**	**0.00**
Total	**2319**	**5105**	**100**	**100**