ORANG-UTAN BEHAVIOURAL ECOLOGY IN THE SABANGAU PEAT-SWAMP FOREST, BORNEO

by

Helen Celia Morrogh-Bernard

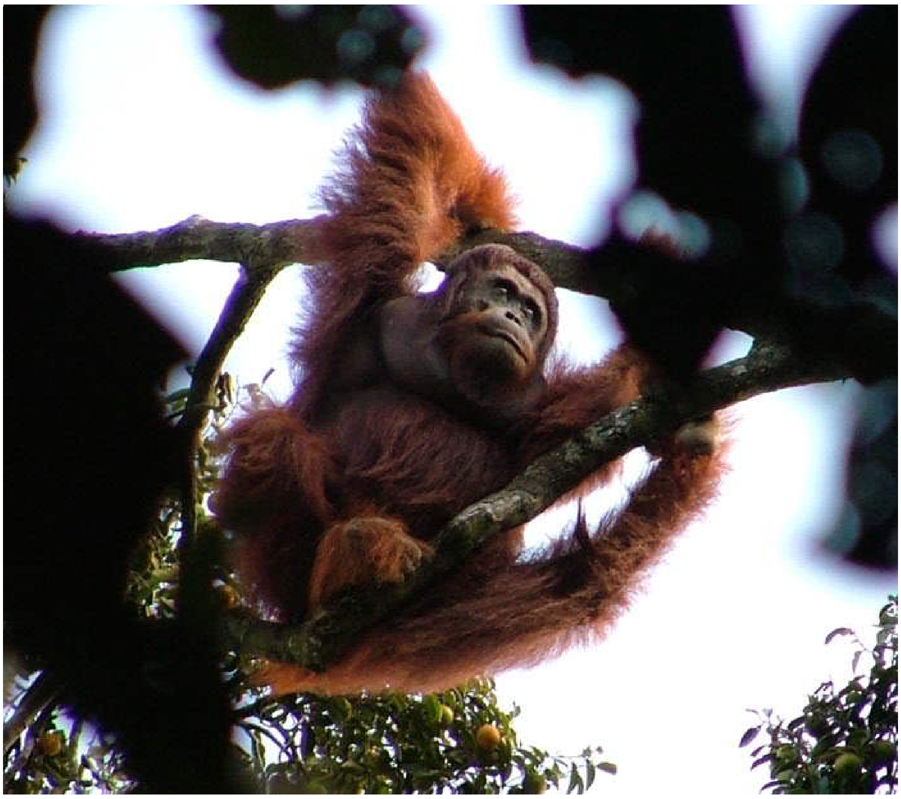
This dissertation is submitted to the University of Cambridge for the degree of Doctor of Philosophy.

Wildlife Research Group, Anatomy School, University of Cambridge.
Wolfson College, Cambridge.

Orangutan Tropical Peatland Project
OuTrop

February 2009

Jupiter kiss squeaking



Mozart looking out for the approach of a flanged male

CHAPTER 5: ORANG-UTAN ACTIVITY PATTERNS 128

CHAPTER 6: FOREST STRUCTURE AND ANTHROPOGENIC DISTURBANCE: ON ORANG-UTAN USE AND BEHAVIOUR 159

TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 8

CHAPTER 9

FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 8

CHAPTER 9

PREFACE

The work described in this thesis was conducted from the Wildlife Research Group, Department of Anatomy, University of Cambridge under the supervision of Dr David. J. Chivers. This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration, except where specifically indicated in the text. No part of this thesis has been submitted to any other University for a degree or diploma.

Helen Celia Morrogh-Bernard.

Cambridge, February 2009.

ACKNOWLEDGEMENTS

First of all I would like to thank my supervisor Dr David Chivers for taking me on as his PhD student, and for all the support he has given me during this long period of research, especially for being so understanding when I told him that I was pregnant and would have to take one year off to look after my daughter Alexandra. Dr Chivers welcomed Alexandra into our Lab for our meetings and considered her an honorary member of the Lab. I would like to especially thank my husband Simon Husson who has supported me throughout my research, both in the field and back in England, I could not have completed this without his help and support. Big cuddles to my daughter Alexandra, who has had to spend many months since the age of 9 months at childcare and nursery school so that I could complete this thesis. I would like to thank the rest of my family: my father Desmond and Julia, Camilla, Martin, Simon and Hannah, the Crawfords: Penelope, Michael, Eddie, Patrick and Anthony and the Hussons: Stephen, Rosalie and Joanna, for not giving up on me and encouraging me to continue when times were hard. I would like to thank all the lab members Marina Kenyon, Shaenandhoa Garcia-Rangel, Natalia Caballos Mago, Gustavo Canale, Rondang Siregar, Thang Long Ha, Gawsia Chowdhury, Mark Harrison, Hannah Trayford, Achmad Yanuar, Kashmira Kakati, Claire Thompson, Monirul Khan, Kim McConkey and Marcela Santamaria, who all gave me fantastic advice and help. They kept my spirits up when all seemed lost, and whose presence created such a friendly atmosphere in the lab, in particular Marina, Shena and Natalia who were always there when I needed help, and made my stay in Cambridge so much fun.

I would like to thank all my sponsors in the field for their support, without which I could not have undertaken this research: Dr Suwido Limin, Director of CIMTROP (Centre of International Co-operation in Management of Tropical Peatlands), Napa J. Awat, former Rektor of the University of Palangkaraya, for supplying me with all the relevant letters and allowing me to do my research in the Natural Laboratory. Thanks you to all the CIMTROP staff, especially Layu, Pak Tampung and Dr Adi Jaya. Thanks to the Indonesian Institute of Sciences, LIPI, for granting me permission to undertake this research project and permission to take orang-utan faecal samples out of the country for genetic analysis, and to Claire McLardy who helped with CITES permits. I would like to thank Dr Cheryl Knott, Professor Carel van Schaik, Dr Birute Galdikas, Dr Serge Wich, Dr Mark Leighton, Dr

Edward Tanner, Professor Jack Rieley, Dr Susan Page and Ashley Leiman for all their help, training and advice on starting and carrying out this project – and particularly to Professor Carel van Schaik, who encouraged me to start behaviour research on this population. I would like to thank Dr Benoit Goossens, Dr Mike Bruford, Dr Michal Krutzen for their collaboration regarding the genetic analysis of my samples, and to Nadja Morf who carried out the analysis. I would like to thank the many funding bodies who gave me financial support which enabled me to carry out this research: Wildlife Conservation Society (WCS), The US Fish and Wildlife Service Great Ape Conservation Fund, Orang-utan Tropical Peatland Project (OuTrop), Primate Conservation Inc, the L.S.B. Leakey Foundation; Wolfson College who funded my travel expenses to Uganda to attend the 2006 IPS (International Primatological Society) Congress and the Cambridge local authority, who funded childcare expenses.

I would like to thank all those people who read and gave very constructive comments on my thesis: Dr David Chivers, Dr Kim McConkey, Dr Serge Wich, Dr Cheryl Knott, Dr Andrew Marshall, Dr Michael Krutzen and Simon Husson; thank to Professor Mascie-Taylor and Dr Brian McCabe for all their help with statistics; and to my examiners Dr Bill McGrew and Dr Susannah Thorpe for their comments; everyone’s help and advice was instrumental in me being able to complete this piece of work. Thank you to Dr Marie Lovatt, my tutor in Wolfson College who was very supportive and understanding during my time at Cambridge. Thanks also to Wolfson College for taking me on as a member of the college, and to the Anatomy School who accepted me as a postgraduate student, and gave permission for me to be away for two years collecting data in Indonesia. Thanks very much to Elaine Murdie for granting me a car permit, which enabled me to commute from Harston. Also thank you to the late Photini who was so helpful in the library, and was always willing to help obtain obscure journals for me.

I would especially like to thank all my field assistants: Ciscoes, Santi, Twenty, Thomas, Zery, Ari, Darsono, Otto, Ahmat, Iwan, Sahdo, Mark Harrison, Carly Waterman, Nick Marchant, Anna Lyons and Tris Allinson for all their hard work and dedication in the field. They all put up with very early morning starts and extremely wet conditions for many months. I would like to thank Erna Shinta from CIMTROP Herbarium for identification of specimens and Zery for his local knowledge of all the trees. Thanks also to Ibu Yanti who cooked wonderful food, which kept us all going, and to Ibu Yana who supplied fresh fruit and vegetables each week. I would also like to thank Serge Wich and Tine Geurts for all their support and friendship while out in the field, our visits to the local restaurants with them were a nice break from the field, in which we could relax, and exchange ideas and information about orang-utans. Thank you very much to Angela Benton-Brown and Apekonity who were instrumental in negotiations with the local community. Thanks to Angela and YCI who worked on community awareness about our research and the role our project would play in the wider community. Also thanks to the CIMTROP patrol team, especially Krisyoyo, Hendri, Idrus, Udin, Bina and Yanto whose efforts stopped the illegal logging in the area, and whose enthusiasm for protecting the forest was amazing and inspiring. Thanks also to all the transect cutters who spent months cutting all the transects so that research could be undertaken especially Ma'mun the team leader. Thanks also to all the 2002 OuTrop volunteers who measured and tagged all transects, and to Sean Bennett who was reported lost during tagging transects. He had collapsed with malaria, he was eventually found at 3 in the morning, and stretchered out by 12 CIMTROP staff. He spent the next two weeks in hospital, but was not put off and was back working once recovered. Thanks also to Laura Darcy and Claire McLardy for all their help and support in setting up and undertaking this project.

Lastly I would like to thank all those individuals whom I may have forgotten and to all the orang-utans for letting me into their secret world.

SUMMARY

Orang-utan numbers are in fast decline throughout their range due to logging and habitat clearance for agriculture. In 2003 I began the first-ever study of orang-utan behaviour and ecology in a peat-swamp forest habitat. My objectives were to understand the behavioural ecology of orang-utans in this habitat and the effects of disturbance on their behaviour, and to compare my findings to orang-utans in other habitats. Research was carried out in the Sabangau Forest, an extremely important tropical peatland, which holds the largest population of orang-utans in the world (Singleton *et al.,* 2004; Marshall *et al*., 2009a), but was subject to intense illegal logging. Substantial differences between peat-swamp forests and the better-known dipterocarp-dominated dry forests have been discovered.

Tree reproductive patterns in peat-swamp forests were found to differ greatly from those in dipterocarp-dominated masting forests. In peat-swamp forests the fruiting cycle was more regular, with a high level of asynchronicity, meaning that fruits and flowers were available for orang-utans all year round. In Sabangau, flowers were very important in the diet, in contrast to dry-forest sites where flower eating is almost absent. During low fruit periods ketones were found, thus orang-utans were in a negative energy balance during these times.

Fruit and flower availability was found to affect the activity budget of orang-utans, leading to different foraging strategies being adopted in different habitat-types. Orang-utans in peat-swamp forests were found to adopt a *'search-and-find'* foraging strategy, whereby they are continuously feeding or travelling in search of food; whereas orang-utans in dipterocarp-dominated forests adopt a *'sit-and-wait'* foraging strategy, where they store fat for lean periods by conserving energy. This emphasises how influential fruiting patterns are on orang-utan behaviour.

Habitat destruction, particularly through commercial logging, is a major issue for orang-utan conservation, although orang-utans are known to cope with light disturbance (see Chapter 6). I identified different classes of habitat quality in the forest, and found that orang-utans showed preference for certain classes over others. They preferred the taller forest classes, regardless of the completeness of canopy, because these have the largest trees with the largest fruit crops, indicating that maintaining unbroken travel routes is not a major requirement. The most heavily-disturbed classes were rarely visited and hardly fed in, hence there appears to be a clear threshold at which logging becomes incompatible with orang-utan survival. This highlights the need for patches of large trees to be left in logging concessions, as orang-utans need large fruiting trees to meet their nutritional needs.

Although the Sabangau has been subject to heavy logging, it has not been fragmented. Thus ranging patterns and dispersal are assumed to be normal, in regards to field observations from primary undisturbed habitats elsewhere. Range size is similar to other sites and the theory that male orang-utans disperse away from their natal range and females remain philopatric was confirmed by genetic data for the first time. Females from the same maternal line had little range overlap with each other, with the locations of ranges of closely-related females resembling that of a flower, in which the female offspring are the petals. I call this my 'Petal Theory' for range overlap. This arrangement is different from other sites, where high overlap between related females occurs. Orang-utans in Sabangau seem to live in more 'open societies', and interact more with individuals from different maternal lines, with whom they had more range overlap.

Dispersal and social interactions influence reproductive strategies. In the Sabangau, orang-utans adopt both the 'roving-male promiscuity' model and the 'female-preference' model, similar to findings from other sites in Borneo, but different to those from Sumatra. The presence of dependent infants of cycling females is of great importance in the 'female preference' model, as cycling females with infants choose to avoid males if they have the chance, unlike cycling females without infants, who would approach the dominant resident male.

Overall, the results of my research highlight differences in orang-utan behaviour between those in peat-swamp forests to those in other habitat types, in particular the effects of habitat homogeneity and regular fruiting patterns on their behavioural ecology. These findings add to our current knowledge of orang-utans, of which there are few data from peat-swamp forests. Data on fruiting patterns, diet and impacts of human disturbances are also extremely important for improving management efforts not only for the Sabangau population, the highest priority population in Borneo, but also for the many populations that remain in logging concessions outside protected areas.

CHAPTER 1

INTRODUCTION

1.1 OVERVIEW

The word orang-utan means “person of the forest” in the Malay language, and they are currently only found in the tropical forests of Borneo and Sumatra in South-east Asia. The high demand for wood and bio-fuels has meant that the lowland rainforests, which are the orang-utans preferred habitat, are being destroyed at an alarming rate. Our knowledge of orang-utans is still very much incomplete compared to African apes. They are found at low densities and are one of the most solitary of all haplorhine primates, which makes them hard to study (Delgado and van Schaik, 2000). Orang-utans are extremely vulnerable to local extinction from both habitat destruction (because of their arboreal lifestyle) and hunting, due of their long life history; they have the longest inter-birth interval of any mammal, ranging from 6-10 years (Galdikas and Wood, 1990; Wich *et al.,* 2004a; van Noordwijk and van Schaik, 2005). The first study of wild orang-utan behaviour was undertaken in the 1960s by George Schaller (Schaller, 1961) in Sarawak. Today, most of our knowledge comes from a few long-term sites in Borneo and Sumatra and, compared to the chimpanzee (*Pan troglodytes*) or gorilla (*Gorilla gorilla*), knowledge about their behavioural ecology is still limited.

The Sabangau orang-utan research project was set up by me in a disturbed, unprotected, ombrogenous (the only external source of nutrients is from rainfall and aerial deposition) peat-swamp forest in Central Kalimantan, Indonesia. At the time (2003) it was the first research site to be set up in an unprotected area, and was the only pure peat-swamp forest habitat in which orang-utans were studied. Although both the Tanjung Puting and Gunung Palung research sites contain areas of peat-swamp, this is not true ombrogenous peat, as it is part of a mosaic containing dryland and freshwater swamp forest. Since setting up the research, one other permanent site at Tuanan in Central Kalimantan was established (in a similar peat-swamp forest, north-west from the Sabangau). At present there are nine different research sites in Borneo and Sumatra, at which research is conducted on wild orang-utans (Figure 1.1), allowing more data to be available for comparisons between sites, habitats and species, which will help us better understand the orang-utans complex behavioural ecology, life history and social system.

The research undertaken for this study will add to our knowledge about orang-utans, as it is the first study of an orang-utan population in an ombrogenous peat-swamp forest, and the first such study in an area heavily disturbed by logging. Data gathered in this study will be given to governmental bodies to help produce management plans for this area. This is one of my primary objectives, as land clearance in Indonesia is accelerating at an alarming rate and with it the disappearance of many orang-utan populations.

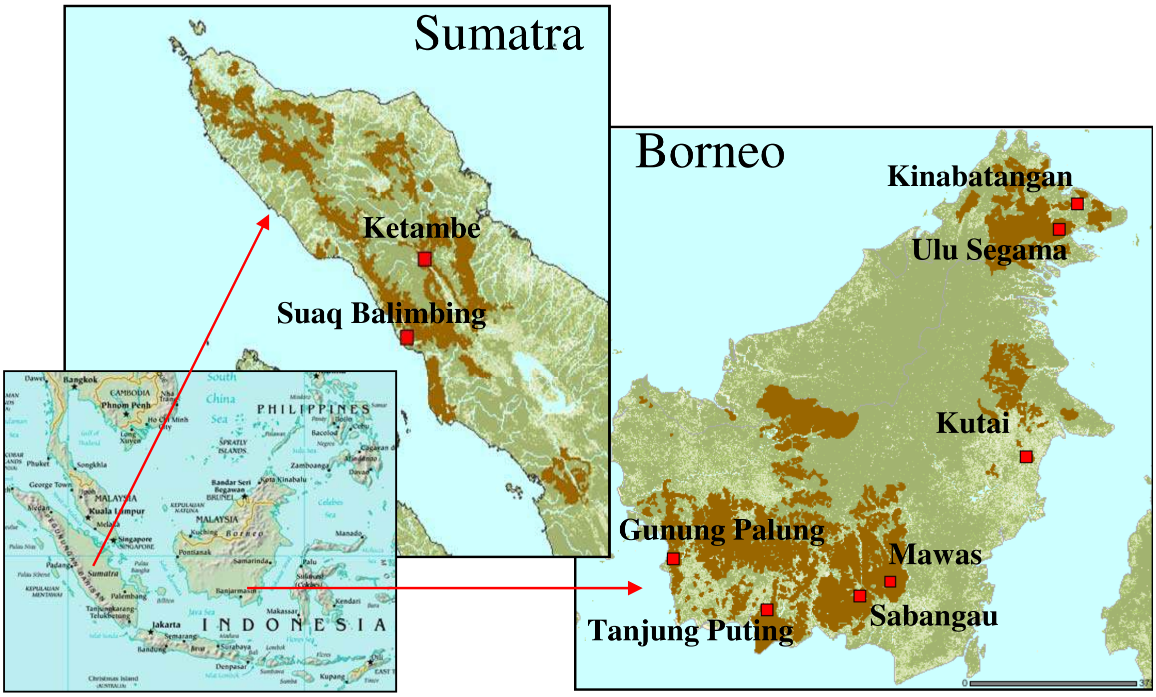


Figure 1.1 Current orang-utan behaviour research sites (adapted from Caldecott and Miles, 2006).

1.2 ORANG-UTANS

Orang-utan taxonomy, distribution, social system and threats to survival will be described in this section. Detailed information on behavioural ecology is covered in the relevant chapters, so that information is not repeated.

1.2.1 Taxonomy

Evidence of the orang-utans (*Pongo spp.*) existence goes back to the Pleistocene epoch (5.2 million years ago) when they inhabited areas of Java and mainland Asia as far north as China (von Koeningswald, 1982). Today however, they are limited to areas of northern Sumatra and scattered areas of Borneo (Singleton *et al.,* 2004) (Figures 1.2 and 1.3).

Figure 1.2 Distribution of the Sumatran orang-utan (from Caldecott and Miles, 2006).

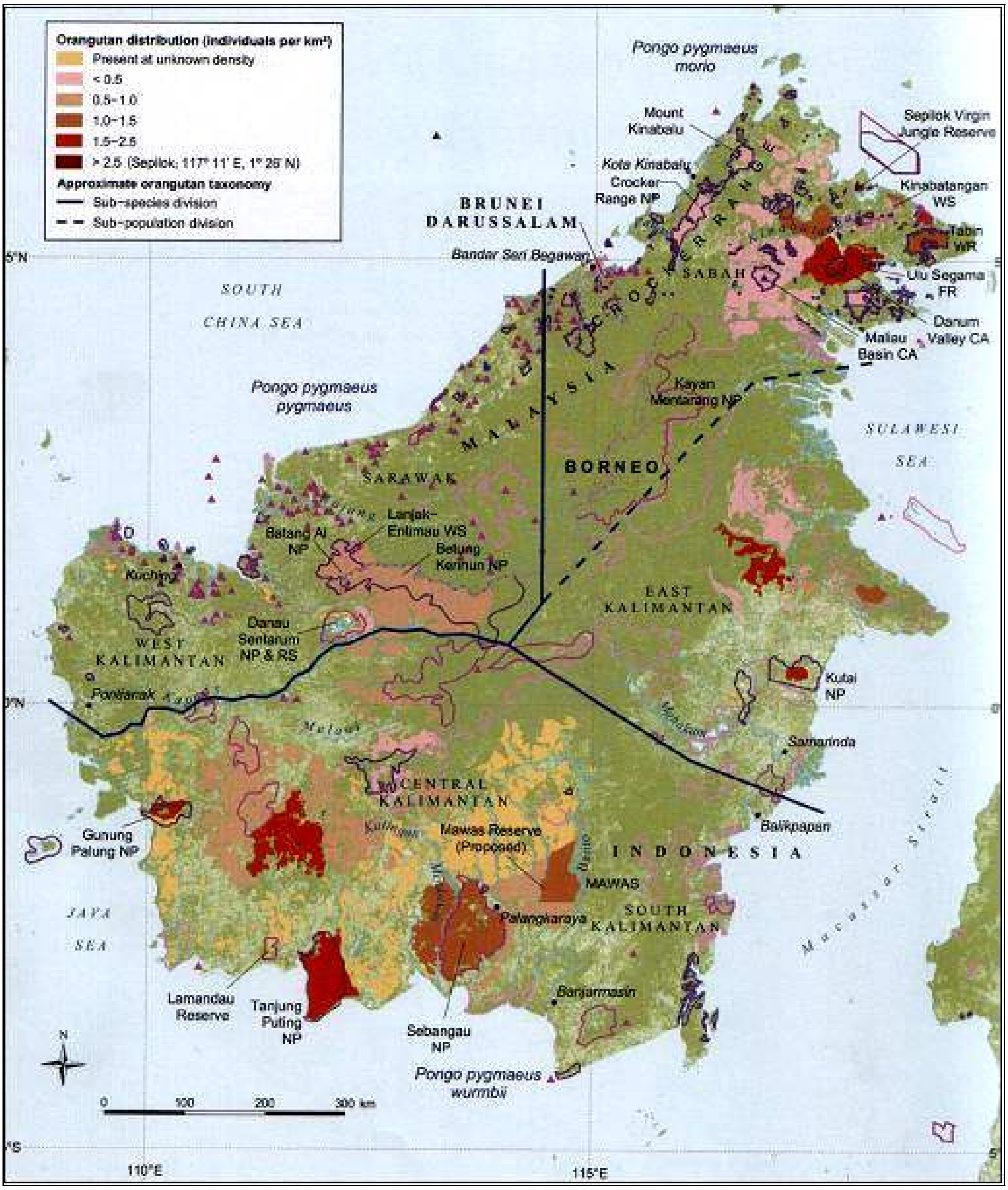


Figure 1.3 Distribution of the Bornean orang-utan (from Caldecott and Miles, 2006).

In the 17th century, when orang-utans were first described by westerners Jacob de Bondt and Nicolaas Tulp (1641), the name *Homo sylvestris* was used to describe them (Figure 1.4). Then in 1758 the name *Simia satyrus* was given by Linnaeus in the Systema Naturae. In 1927 this was changed to *Pongo pygmaeus* (Rijksen and Meijaard, 1999). *Pongo* was originally used to describe orang-utans, gorillas and chimpanzees, but remained to describe only the orang-utan, even though it has been proposed by taxonomists and primatologists, that the name given by Linnaeus, *Simia satyrus,* should be restored (Rijksen and Meijaard, 1999).

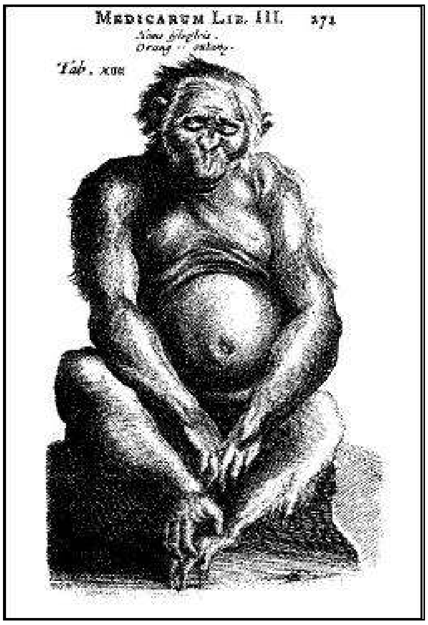


Figure 1.4 Illustration of the first orang-utan described for western science by the Dutch physician Nicolaas Tulp in 1641 and called *Homo sylvestris*. (Taken from Rijksen and Meijaard, 1999).

The Bornean and the Sumatran orang-utan were considered to be two sub-species, *Pongo pygmaeus pygmaeus* and *P.p. abelii* until recently, when Xu and Arnason's (1996) analysis of orang-utan mitochondrial DNA resulted in two separate species being proposed, *Pongo pygmaeus* for the Bornean orang-utan and *Pongo abelii* for the Sumatran (Groves, 1999; Zhang *et al.,* 2001; Warren *et al.,* 2001; Goossens *et al.,* 2009). Although most scientists accept there are now two species, that is not universal and there is still some controversy regarding the re-classification (Muir, 1998), although there are distinct morphological differences between the two species. The Bornean is larger with a darker coat. The shape of the male faces differ with the Bornean's being more square with protruding cheek flanges and short beards, whereas the Sumatran orang-utan has flat cheekpads with long beards and a moustache and white downy hair on their face (Caldecott and McConkey, 2005; Goossens *et al.,* 2009).

Within the Bornean species there are genetic and morphological differences between populations (Groves, 1986; Uchida, 1998; Taylor, 2006; Goossens *et al.,* 2009b), so the Bornean orang-utan (*Pongo pygmaeus*) has been further divided into three sub-species: the western population (*P. p. pygmaeus*) distributed in northwest Kalimantan, north of the Kapuas River and extending into Sarawak, the southern population (*P. p. wurmbii*) found south of the Kapuas River and west of the Barito River, and the northern population (*P. p. morio*) which ranges north-east of the Mahakam River into Sabah (Figure 1.2). Warren *et al.* (2001), however, described four sub-populations for the Bornean species, which may or may not be distinct enough to be classified as separate sub-species. In Sumatra, there is just the one species - *Pongo abelii*.

1.2.2 Distribution, density and effects of disturbance

The Sumatran orang-utan is confined to the northern tip of Sumatra, mostly in the province of Aceh (Figure 1.2), and the Bornean orang-utan is largely absent from the north-west and south-east of Borneo (Figure 1.3). This distribution pattern is the result of extinctions from hunting and land clearance in large areas of their former range and barriers to dispersal such as large rivers and high mountain ridges preventing them reaching some areas. Their preferred habitats are lowland and hill dry forests (<1500 m above sea level (a.s.l.) in Sumatra, and <500 m a.s.l. in Borneo), freshwater swamp and peat-swamp forests (MacKinnon, 1974; Sugardjito and van Schaik, 1991; Leighton, 1993; Knott, 1999a; Morrogh-Bernard *et al*., 2003; Johnson *et al.,* 2005).

Orang-utan densities in these different forest types vary from 5-7 individuals per square kilometre (ind/km^2) in the fertile Leuser region of Sumatra (Rijksen, 1978; van Schaik *et al.,* 1995) to 1-6 ind/km^2 in Borneo (Horr, 1975; Rijksen *et al.,* 1995; Russon *et al.,* 2001; Morrogh-Bernard *et al.,* 2003; Ancrenaz *et al*., 2004a; Johnson *et al.,* 2005). Lower densities of <1 ind/km^2 are found in hill forest, recently-disturbed and heavily-disturbed forests (Rijksen and Meijaard, 1999; Morrogh-Bernard *et al.,* 2003; Ancrenaz *et al.,* 2004a). Various reasons have been suggested to explain their present distribution and densities, which include forest structure and diversity, soil nutrient content, presence/absence of soft-pulp fruits, habitat loss, habitat degradation, fragmentation and hunting (Sugardjito and van Schaik, 1991; Leighton, 1993; Rijksen and Meijaard, 1999; Robertson and van Schaik, 2001; Husson *et al.,* 2002a; Morrogh-Bernard *et al*., 2003, Felton *et al.,* 2003; Ancrenaz *et al.,* 2004a; Johnson *et al.,* 2005; Marshall *et al*., 2006). The most obvious factor today that determines presence and absence of orang-utans is land clearance and degradation from timber extraction and agriculture. Orang-utans are known to move away from active disturbance, but will return when the disturbance ends (MacKinnon, 1971; Morrogh-Bernard *et al.,* 2003), indicating that disturbed habitat retains high conservation value for the orang-utan (Morrogh-Bernard *et al.,* 2003; Ancrenaz *et al.,* 2004a; Marshall *et al.,* 2006). In the past most orang-utan research was concentrated in National Parks and in primary forest. Studies in unprotected and disturbed forest, such as the Sabangau Catchment, and in Kinabatangan in Sabah, have taken place only in the last few years, so the long-term suitability of these areas for orang-utans are not yet fully understood.

The total population size of orang-utans is still uncertain. Previous population estimates for the Bornean orang-utan were 10,282 to 15,546 individuals (Rijksen *et al.,* 1995), but, following extensive orang-utan surveys carried out for the 2004 Population and Habitat Viability Analysis (PHVA) in 2004, the population is now estimated to be between 55,000 and 60,000 individuals (Singleton *et al*., 2004). Figures for Sumatra are better known because of the smaller geographical range occupied by orang-utans there and hence estimates have not changed much over the same time: from 5,000 to 7,000 individuals in 1995 (Rijksen *et al.,* 1995) to 7,500 individuals (Singleton *et al.,* 2004). To simulate changes in population numbers over time a VORTEX model was created (the VORTEX 9.42 computer package was used to conduct a PVA (Population Viability Analysis)) (Singleton *et al*., 2004; Marshall *et al.,* 2009a), which found that populations less than 250 individuals were not viable over the long-term. Because of this, conservation emphasis was shifted to prioritising the largest populations during the 2004 PHVA meeting (Singleton *et al.,* 2004). Of the 13 identified populations in Sumatra, only 7 were estimated to have more than 250 individuals; in Borneo there are many more scattered populations of varying size, with the largest population found in the Sabangau (Singleton *et al*., 2004). Borneo figures have increased from ca. 15,000 to 60,000, because of better surveys over a larger area and not because of any increase in population size. Today, with improved survey coverage and methods, a more accurate figure can be obtained (van Schaik *et al.,* 1995; Buij *et al.,* 2003; Morrogh-Bernard *et al*., 2003; Ancrenaz *et al*., 2004a; Singleton *et al.,* 2004), but it is accepted that orang-utan numbers are still decreasing, due to logging, forest fires and increased land clearance for oil-palm (*Elaeis guineensis*) cultivation, especially in the last

10 years. The loss of central control over forest management and protection systems in 1998, to provincial and regency level, has accelerated forest loss as local councils have promoted logging and conversion for oil palm plantations, even in areas unsuitable for agriculture such as the deep peat-swamps of Central Kalimantan (Singleton *et al.,* 2004). In Sumatra, Rijksen and Meijaard (1999) estimated that orang-utan numbers have decreased by 86% in the last 100 years.

Although the percentage of pristine forest in Borneo and Sumatra is decreasing due to land clearance, orang-utans are still hanging on in degraded areas. In the Kinabatangan study area in Sabah, an area of degraded and secondary forest, orang-utans are found at densities between 0.7-3.2 ind/km^2 (Ancrenaz *et al*., 2004a), which is similar to those found in the shallow rich primary peatlands of Gunung Palung (Johnson *et al.,* 2005). Densities were higher in the lower parts of the Kinabatangan floodplain where the habitat was less disturbed, indicating that heavy habitat disturbance has a negative impact on orang-utan density (Ancrenaz *et al.,* 2004a). In areas like the Sabangau catchment, which has been subject to intense illegal logging pressures since 1997, densities were found to fluctuate in accordance with the location of disturbance, with orang-utans moving away and returning when the disturbance was over (Husson *et al.,* 2002a). After 2002, however, a sudden decrease of 36 % was recorded (Husson and Morrogh-Bernard, 2003). This decrease was a direct effect of illegal logging, but it took a time lag of 5 years before any true effects could be witnessed (Husson and Morrogh-Bernard, 2003). Orang-utan populations will regulate themselves in accordance to the carrying capacity of the area (density dependent), thus densities will ultimately decrease if resources are removed and not replaced (Marshall *et al.,* 2009a). Disturbed forest, although not ideal, is now the orang-utans' refuge in many locations and are important strongholds which must be protected (Morrogh-Bernard *et al.,* 2003; Ancrenaz *et al.,* 2004a, 2004b; Marshall *et al.,* 2006). Most field research sites in the past were in primary forest, so little is known about orang-utan behavioural ecology in areas of degraded or secondary forest.

The effects of habitat quality and disturbance on the behavioural ecology of orang-utans will be examined (Chapter 6).

1.2.3 Life history and social structure

Life history

Many differences in the behavioural ecology of the Bornean and Sumatran orang-utans have been highlighted in recent comparative studies, so generalisations should not be made (Wich *et al.,* 2009). Most of our knowledge regarding orang-utan social systems, reproductive strategies and ranging comes from the Sumatran species, as they have been studied more intensively and for longer. Orang-utans have the slowest life history of all the extant apes (Wich *et al.,* 2004a; van Noordwijk and van Schaik, 2005), with both species having a slow rate of growth and reproduction and the longest inter-birth interval of any mammal. They have a long period during which offspring are dependent (van Noordwijk and van Schaik, 2005), which may be the reason for the long inter-birth interval.

The Sumatran orang-utan has a mean inter-birth interval of 8 years or more, whereas the Bornean inter-birth interval is 7 to 8 years (Galdikas and Wood, 1990; Knott, 2001; Wich *et al*., 2004a; van Noordwijk and van Schaik, 2005). In comparison, chimpanzees (*Pan troglodytes*) have an inter-birth interval between 4 and 6 years (Nishida *et al*., 1990; Sugiyama, 1991; Boesch and Boesch-Achermann, 2000; Knott, 2001) and gorillas (*Gorilla gorilla*) have an inter-birth interval between 3 and 5 years (Watts, 1991; Yamagiwa and Kahekwa, 2001), much shorter than orang-utans. The life span of wild orang-utans in Sumatra is estimated to be at least 58 years for males and 53 years for females, based on realistic estimates of individual age at death (Wich *et al*., 2004a). This means that a female can give birth to around 4 or 5 offspring within her lifetime, if she starts reproducing at 15 years old (Galdikas and Wood, 1990; Wich *et al*., 2004a). Infants in Sumatra stay with their mother until they are weaned around the age of 7 (van Noordwijk and van Schaik, 2005) compared to chimpanzees, who wean their offspring around 5 years of age (Boesch and Boesch-Achermann, 2000).

Female orang-utans, unlike chimpanzee females, show no sign of sexual swellings to advertise ovulation; instead they develop labial swellings from 2 weeks to over a month after conception (Delgado and van Schaik, 2000). The gestation period is similar to that of humans of 9 months, and she will give birth on her own in her nest. Her older infant will then be pushed out of the nest to sleep alone. It is around this time that the older offspring, now classed as adolescent, starts to become more independent from its mother and starts occupying its own home range. Female orang-utans, again in contrast to female chimpanzees, will set up their home range within or near their maternal range and males will depart to new areas (Singleton and van Schaik, 2002).

Social structure

The nature of the orang-utan social system has been a mystery for a long time, and it is only recently in the last 10 years that it is becoming better understood. The principal factors shaping primate social behaviour and grouping are food resources (their distribution and abundance) and reproductive potential (Cowlishaw and Dunbar, 2000). A non-group-living lifestyle is suitable for areas where resources are limited and patchily distributed, as is the case in Borneo. Orang-utans have therefore been described as 'solitary' or sometimes 'semi-solitary' because the mother-infant relationship is strong (Galdikas, 1979). Van Schaik (1999) describes orang-utans as a semi-solitary fission-fusion species, especially the Sumatran species, which is much more social and sometimes congregates in large groups in large feeding patches (Sugardjito *et al.,* 1987; Utami *et al.,* 1997; Knott, 1999a). Congregations can also be found during times of female receptiveness, when males will accompany females for extended periods (MacKinnon, 1974; Rijksen, 1978; Galdikas, 1985a; Knott, 1999a). Female social groups in the Sumatran orang-utan are called a cluster, defined as a group of females occupying similar home ranges (Singleton and van Schaik, 2002), whereas the social structure of the Bornean orang-utan is far less understood, as they are even more solitary than the Sumatran species (Mackinnon, 1974; Galdikas, 1985a).

Female social structure

Food is the main resource which influences female social behaviour in orang-utans, as the Sumatran species is far more social than the Bornean, owing to higher productivity levels in Sumatran forests (Marshall *et al.,* 2009b). Food competition and resource availability (particularly large fruiting trees) within their home ranges are important. The Sumatran species is far more social than the Bornean, and can be found at densities as high as 7 ind/km^2 (van Schaik *et al.,* 1995; Singleton *et al.,* 2004); it is common to see groups of females with offspring feeding in one tree or groups of adolescents travelling together in bands (Utami *et al.,* 1997). This type of aggregation is rarely seen in the Bornean species and the most probable reason for this difference is resource availability. In Sumatra the soil is more fertile than in Borneo and productivity is higher (Marshall *et al.*, 2009b), so food availability is generally lower in Borneo and it is more advantageous for females to travel alone. Utami *et al.'s* (1997) study in Sumatra found that orang-utan aggregation size at Ketambe was dependent on the availability of ripe fruit. Similar findings affecting ape group size and sociality have been found in Africa (Doran *et al.,* 2002a).

Male Social Structure

Male social organisation is influenced by the distribution of females, especially cycling females which are a limited resource. As a result there is inter-male competition for females (Utami and Mitra Setia, 1995). Male orang-utans of both species exhibit extreme sexual dimorphism and, unlike any other primate, possess two distinct adult morphs: the fully-developed male with flanged cheek pads and a large throat sac for resonating calls (flanged males) and the 'sub-adult' or 'arrested' male state (unflanged males). Unflanged males are smaller than flanged males. They are fertile and are capable of siring offspring. Flanged males of both species are predominantly solitary and will only socialise during courtship, when they will accompany adult females for a number of days or weeks while fertile. There is a distinct difference between the species, with the Sumatran males courting for weeks, and the Bornean only for a few days (Delgado and van Schaik, 2000). This may be explained by home range size and spatial distribution of the Bornean species. Flanged males of both species are dominant over unflanged males, which nevertheless are tolerated within the flanged male's home range (Galdikas, 1985b). Flanged males never associate with other flanged males and, if encountered, will behave antagonistically towards each other (pers obs.). In comparison, the unflanged males of both species are more social and gregarious (Rijksen, 1978; Galdikas, 1985b). The reproductive strategies for both sexes from the Bornean and Sumatran species are summarised here (adapted from van Schaik and van Hooff, 1996 and Delgado and van Schaik, 2000).

- ***Adult female both species:*** prefer male with highest resource holding potential – usually local dominant male. Initiates courtship when high ovarian activity. Resist mating with sub-ordinates and sub-ordinate flanged males. When lactating keep track of familiar flanged male by their long calls for protection against infanticide.
- ***Unflanged male:*** Forced mating with adult female, despite restricted access due to presence of flanged males. More unflanged males in Sumatra than Borneo.

- ***Flanged male:*** Given female preference for high resource-holding potential, they attain local dominant status, and broadcast presence using long calls. Attempt to exclude all other males from receptive females. Courting: Sumatran species courts for weeks; Bornean for a few days. More flanged males in Borneo than unflanged males, so if not locally dominant will force a mating with the female. More forced mating by the Bornean than the Sumatran.
- ***Forced matings****:* *Borneo* (most ± 90 %)*, Sumatra* (lower ± 45%).
- ***Two different mating strategies may exist between the two islands:***

- (1) Roving male promiscuity: males cannot defend access to female ranges and females do not congregate at predictable areas – Bornean strategy

- (2) Spatially dispersed but socially distinct community, organised around one adult male with synchronised births – Sumatran strategy.

Ranging patterns, social interactions and relatedness will be investigated, in order to understand properly orang-utan social organisation (Chapters 7, 8 and 9).

1.2.4 Feeding ecology

Orang-utans have an extremely diverse and adaptable diet compared to many other primates (Ungar, 1995; Russon *et al.,* 2009). They are mainly frugivorous (MacKinnon, 1971, 1974; Rodman, 1977), as their diet consists mainly of fruit, but also includes flowers, leaves, pith, bark, insects, birds eggs and even small vertebrates such as lorises (MacKinnon, 1974; Rodman, 1977; Galdikas, 1988; Utami and van Hooff 1997; Knott, 1999b). Some authors describe orang-utans as an opportunistic forager rather than a true frugivore (McConkey, 2005), as their diet changes in relation to what is available. However, they do spend on average 50-70% of their time eating fruit (MacKinnon, 1974; Rodman, 1977; Rijksen, 1978; Galdikas, 1988; Knott, 1998; Fox *et al*., 2004), of which soft-pulp fruits, figs and berries are their favourite (Rodman, 1988; Djojosudharmo and van Schaik, 1992; Leighton, 1993), usually from trees with large crop sizes (Leighton, 1993). Although fruits are their preferred food, Ungar (1995) found orang-utans at Ketambe in Sumatra to be less selective than many of the other simple-stomached primates there, by eating both unripe fruits and fruits with hard husk. Orang-utans appear to vary their preference for different fruit types at different times. Galdikas (1988) found orang-utans varied their diet quite considerably if a preferred food was unavailable, eating from as many as 78 food types to as little as 4 in one month. Fruiting seasonality, together with presence and absence of certain species, will result in differences in diet between sites.

What plant species are present in the Sabangau peat-swamp forest and which of these are eaten will be identified, along with seasonal availability, orang-utan preference and changes in energy balance (Chapter 4).

1.3 THREATS TO ORANG-UTANS

The major threats affecting the continued survival of the orang-utan are habitat-loss (clearance and fragmentation) and hunting, both for food and for the pet trade (Rijksen and Meijaard, 1999; van Schaik *et al.,* 2001; Robertson and van Schaik, 2001; Singleton *et al.,* 2004; Marshall *et al.,* 2006; Nellemann *et al.,* 2007). The orang-utan is included in Appendix 1 of CITES (the Convention on International Trade in Endangered Species of Flora and Fauna) which prohibits trade in endangered species and is classified as ‘Endangered’ in Borneo and ‘Critically Endangered’ in Sumatra by the IUCN (World Conservation Union). In Indonesia the orang-utan has been protected since 1927 (Rijksen and Meijaard, 1999), but ineffective law enforcement has meant that none of these laws have halted their decline. These threats combined have increased the vulnerability of the orang-utan, the global population of which declined by up to 50% in the last decade alone (Currey *et al.,* 1998). It has been estimated that, if current trends continue, the wild orang-utan faces a high probability of extinction in the wild (Rijksen and Meijaard, 1999; Singleton *et al.,* 2004). In the latest UNEP report, Nellemann *et al.* (2007) report that 98% of Indonesian forest will be lost by 2022 and that many protected areas will be severely damaged and degraded in only 3 to 5 years (by 2012).

1.3.1 Habitat loss

Habitat loss, through clearance for settlements, agricultural conversion, illegal logging, mining and fire, are the major threats to orang-utan survival (Singleton *et al.,* 2004; Buckland, 2005). Between 1900 and 1985 50% of forests in Sumatra and Kalimantan were cleared (Figure 1.5). An estimated 24,000 km^2 of forest has been lost annually since 1986 (Rijksen and Meijaard, 1999).

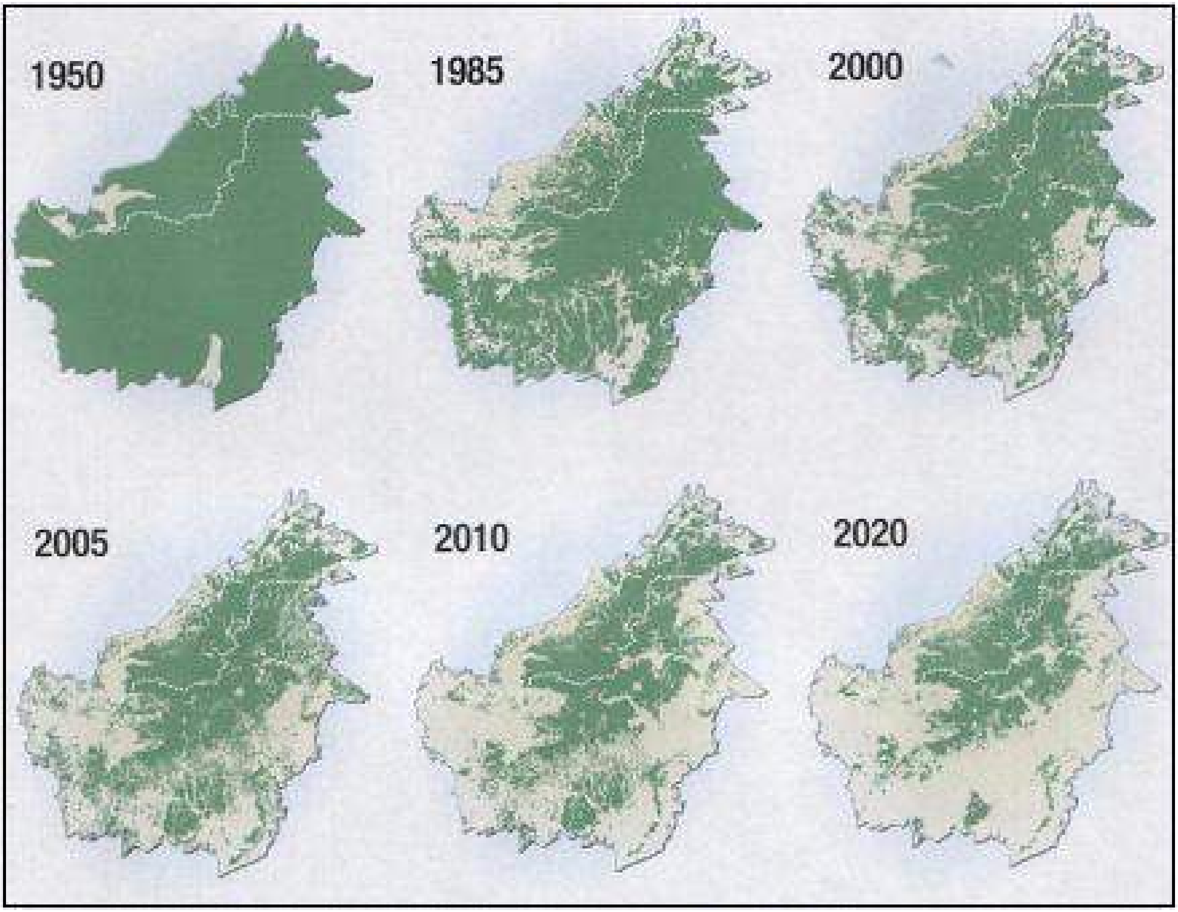


Figure 1.5 Extent of deforestation in Borneo from 1950 - 2005, and predicted forest loss by 2010 and 2020 (Nellemann *et al.,* 2007).

Oil-palm

The major threat facing forests and orang-utans today is conversion to oil-palm plantation (Figure 1.6) (Buckland, 2005). Indonesia and Malaysia are the world's major palm-oil producers, with 83% of the world's production (Commitante *et al.,* 2003; Nellemann *et al.,* 2007) and Indonesia plans to overtake Malaysia as the major palm-oil exporter. Between 1967 and 2000 the area in oil-palm cultivation in Indonesia grew from less than 2,000 km^2 to over 30,000 km^2 (FWI /GWF, 2002 – from Nellemann *et al.,* 2007). The demand for palm oil is expected to increase, so that by 2020 an estimated 30,000 km^2 of forest will be converted annually (Nellemann *et al.,* 2007). It is estimated that 98% of the rain forest in Indonesia and Malaysia will be gone in 15 years due to conversion to oil-palm plantation (MacKinnon, 2007). Indonesia has converted double the amount of land for oil palm compared to Malaysia, but produced only 50% as much oil (WWF Indonesia, pers. comm.). This is due to land suitability and fertility. Soil in Indonesian Borneo is less suitable for oil palm, yet clearance continues, especially in lowland areas below 500 m which are also the orang-utans' preferred habitat.

Most land used for planting is newly-cleared forest, rather than regions with large areas of already cleared land such as abandoned plantations. This is because oil palm concessions can use the money from felling and selling the timber in order to finance the plantation. In some cases a 'hit-and-run' attitude has been adopted, whereby just the timber is taken with no intention to plant crops. It takes 5 years before any crop can be harvested so many companies come in just for the wood. In Kalimantan a mere 250,000 hectares have been planted out of the 6 million allocated for oil-palm (MacKinnon, 2007). Although oil-palm plantations are required to protect 10% of their concession area as natural forest, areas of at least 12,500 ha are needed to support a viable population of 250 individuals (Singleton *et al.,* 2004). As nearly all oil-palm plantations are considerably smaller than the 125,000 ha required, this 10% law is not adequate for orang-utan conservation.

Figure 1.6 Oil-palm plantation.

Most orang-utans in areas where oil palm is grown are wiped out, with a few being rescued by rehabilitation centres. Orang-utans are also killed when they venture into plantations to find food. Many are burned, scalded, shot and even buried alive (MacKinnon, 2007; Droscher-Nielsen, pers. comm.). Many plantation owners pay 150,000 Rupiah (£8.30) for the right hand of an orang-utan to prove that they have been killed (MacKinnon, 2007).

In addition to oil palm, rice and coffee cultivation are also threats. In 1995–1997 then-President Suharto wanted to make Indonesia self sustainable in rice production, so he converted one million hectares within a deep-peat-swamp forest (20% of the remaining orang-utan habitat) for rice production, even after many ecologists told him that the habitat was not suitable for rice cultivation. Rice never grew there and these areas are now wasteland (pers. obs).

Reason for palm oil

By 2020 the European Union aims to cut greenhouse gasses by 20%, partly by raising the number of vehicles fuelled by bio fuels to 10% or higher. This means that the demand for palm oil from western countries could result in the destruction of Indonesian and Malayan forests. Clearing and burning peat-swamp forest for oil-palm plantation to supply the west with biofuel will not cut greenhouse gas emissions, but only exacerbate the problem. A report by UNEP highlights the negative effect of burning peat, as peat-swamp forests store huge amounts of carbon, which are then released when destroyed by drainage, fire or conversion (Page *et al.,* 1999; Rieley *et al.,* 2005). So the conversion of peat-swamp forest for increased production of biofuels will only increase the emission of CO_2 into the atmosphere. Hooijer *et al.* (2006) indicate that the most effective way for the EU to achieve this 20% cut is by conserving remaining peatland forests, alongside rehabilitation of degraded peatlands and improved management of plantations and agricultural areas, rather than increased destruction of forest and peatland for oil-palm plantations.

Logging

Figure 1.7 Illegal logging in the Sabangau research area.

Illegal logging became widespread and indiscriminate throughout Indonesia in 1997 (Figure 1.7); not even the key orang-utan strongholds in Gunung Leuser, Gunung Palung and Tanjung Puting National Parks were spared (van Schaik *et al.,* 2001; Nellemann *et al.,* 2007; Galdikas, pers.com.). Indeed most National Parks in Indonesia are being encroached by plantations or are infested by illegal logging operations (Figure 1.8). Illegal logging is taking place in 37 of the 41 surveyed National Parks in Indonesia; some are also seriously affected by mining and oil-palm plantations. It is estimated that 73-88 % of all wood that comes out of Indonesia has been illegally cut (Nellemann *et al.,* 2007). Less than 20% is smuggled out as logs, the rest is processed in saw, paper and pulp mills and later exported. These mills have a capacity 2 to 5 times greater than the legal supply of timber (Nellemann *et al.,* 2007). From 1993 to 2001 a 43% decrease in orang-utans occurred in the Leuser Ecosystem due to legal and illegal logging in the area (van Schaik *et al.,* 2001), and today over 1000 orang-utans are living in rescue centres in Borneo alone due to land clearance (Nellemann *et al.,* 2007).

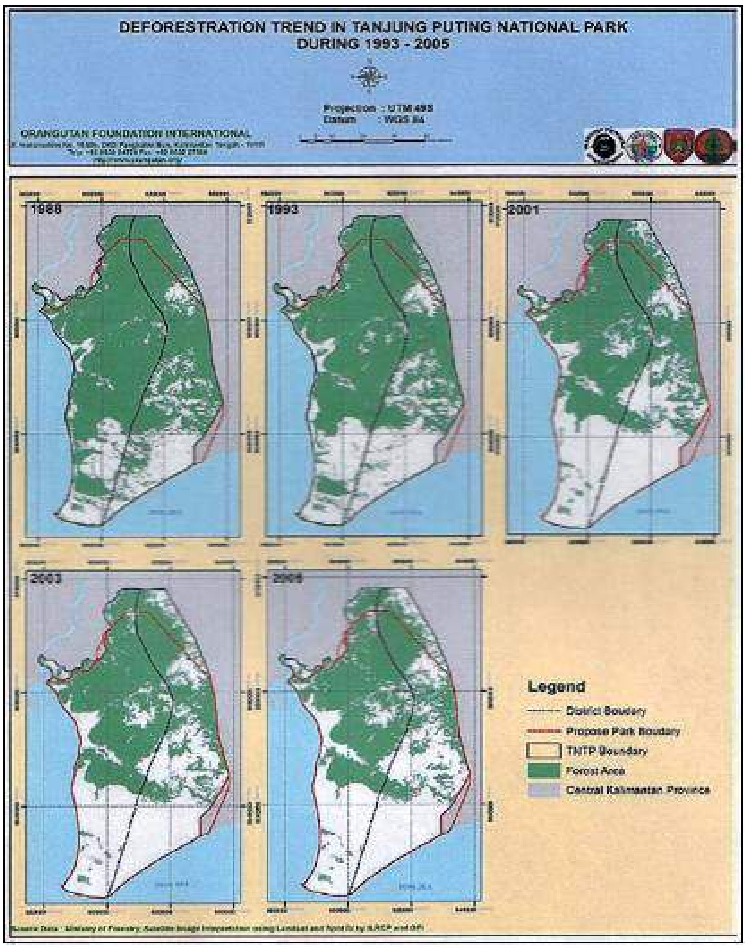


Figure 1.8 Illegal logging and land clearance for oil palm in Tanjung Puting National Park from 1988 – 2005 (from Nellemann *et al*., 2007).

Many forests in Indonesia were selectively logged rather than clear cut, under the Indonesian government's concession system whereby logging concessions are given to companies for a period of 30 years. Upon cessation of logging there is a legal requirement for a 30-40 year recovery period during which no logging is allowed, but instead all were illegally logged at this time (van Schaik *et al.,* 2001; pers. obs.). Illegal loggers are not controlled by regulations that apply to licensed concessions and, as a result, are far more damaging to the forest. Timber is extracted causing much damage to the surrounding trees, with timber from 15 cm dbh upwards removed (pers. obs.). Destruction of the forest in this way is extremely damaging for orang-utans. Densities were found to decrease by 90% within a year after illegal logging started at a site in Sumatra (van Schaik *et al.,* 2001). A similar, but less dramatic, decrease was found in the Sabangau, when selective logging stopped and illegal logging started (Husson *et al.,* 2002a; Husson and Morrogh-Bernard, 2003). Continued logging can effectively eliminate orang-utan populations if the forest is not left to regenerate (van Schaik *et al.,* 2001). The presence of people can be a cause of population decline because resident animals can be eliminated by disease transmitted from humans, or more likely by capture and death (van Schaik *et al.,* 2001). Husson *et al.* (in prep.) describe how a population can decrease rapidly, even when there are enough food resources in the forest as a whole, due to a compression effect. Animals flee from logging areas and, as a result, overcrowd and exceed the carrying capacity of the refuge area, eventually resulting in death, particularly of females and their young.

Forest fires

In 1997/1998 fires raged across the islands of Borneo and Sumatra, destroying in excess of 2 Mha of forested land, including an estimated ½ Mha of prime orang-utan habitat (Trent, 1998; van Schaik *et al.,* 2001; Yeager *et al.,* 2003). Rijksen and Meijaard (1999) estimated a 33% loss to the remaining orang-utan population from these fires. In 2002, 2004 and 2006 fires raged again, covering Central Kalimantan in smog for a period of 2-3 months each year and destroying large areas of forest (pers. obs.). These fires have fragmented remaining orang-utan habitat, which were already irregularly distributed, causing isolation of populations which are now in extreme danger of dying out. Although orang-utan numbers can fall to 50% of their original number in logged forest, in areas affected by fire populations can be completely wiped out. Yeager *et al.* (2003) found that species richness in burned forest decreased substantially, and that peat-swamp forests were more seriously affected by fire than other lowland forests. In Tanjung Puting, species richness was reduced by 59% after the fires, and the area continued to suffer high tree mortality and species loss 8 months after the fire (Yeager *et al.,* 2003).

Figure 1.9 Forest fires in peat-swamp forest burn the surface peat away slowly, exposing roots and causing trees to fall over.

Fire is of great concern as severe El Niño events are becoming more frequent, and these events usually result in extended droughts in South-east Asia. Many fires are associated, not just with El Niño events (Mongabay.com, 2007), but with plantation owners setting fire to forests as a quick and easy way for clearing large areas of land (MacKinnon, 2007; Mongabay.com, 2007). These fires are then exacerbated by El Niño droughts, particularly in the drained swamp areas, where the extremely-flammable degraded peat easily catches fire (Figure 1.9); as a result, smoke from these fires blankets much of South-east Asia each year (Figures 1.10 and 1.11). While the 2006 El Niño was relatively weak, increased land burning by plantation owners resulted in massive forest fires across Borneo and Sumatra, with some of the highest deforestation rates (more than 30,000 km^2) ever recorded in Indonesia (Mongabay.com, 2007). Indonesia is estimated to generate 1,400 tonnes of carbon dioxide each year, making Indonesia the worlds 3rd largest producer of CO_2 (after the United States and China) if both CO_2 from forest fires and CO_2 from degraded peat are included (MacKinnon, 2007), despite being only the world's 22nd largest economy (Mongabay.com, 2007). Not only is CO_2 released from these fires, but large amounts of carbon monoxide are produced, which can cause detrimental health effects to both fauna and flora (Mongabay.com, 2007).

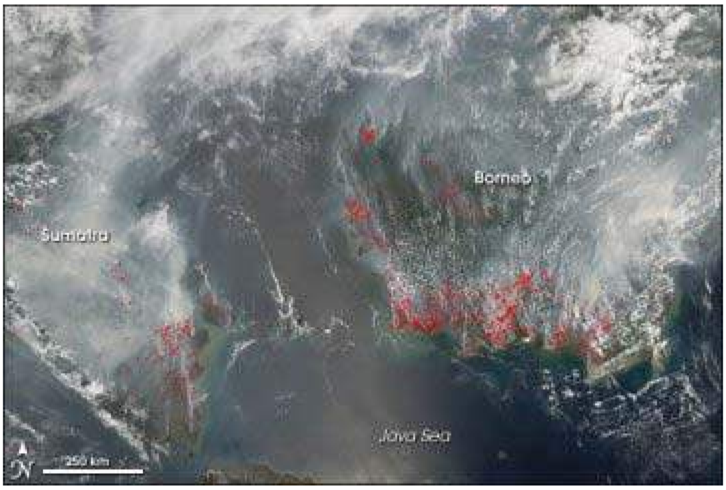


Figure 1.10 Smoke pollution from forest fires in Borneo in 2006 (Mongabay.com, 2007).

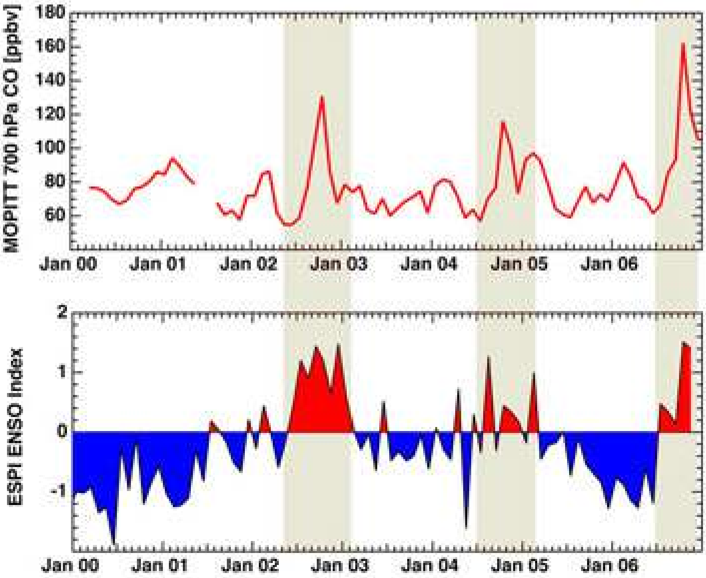


Figure 1.11 Pollution from forest fires in 2007.

Peaks of Indonesian carbon monoxide pollution (top) coincide with the warm phases of El Niño (bottom) over the past 7 years. The inter-annual variability of atmospheric carbon monoxide at an altitude of about 3 km (1.9 miles) was measured by the Measurements of Pollution in the Troposphere (MOPITT) instrument. The El Niño warm phase conditions led to a reduction in rainfall and an increase in fire occurrence over Indonesia (red). (from Mongabay.com 2007)

As well as habitat loss, many orang-utans are killed in the fires (Sastrawan, 2006) and those that try to flee are usually butchered and killed by locals. Orang-utans rescued by local NGOs are commonly treated for burns and smoke inhalation. Those that escape the fires and remain in the forest can be affected by decreased food availability, as much of their home range may have been destroyed, potentially resulting in overcrowding and starvation (Husson *et al.,* 2002a; in prep).

1.3.2 Hunting

Hunting of orang-utan has been prohibited in Indonesia since 1924 (Rijksen and Meijaard, 1999), but is still a major problem. Many people do not know it is illegal, and even if they do, the law is weakly enforced. Poaching occurs for food, as orang-utans are slow moving and therefore easier to catch than other animals, or they are shot for crop raiding, but the majority of hunting is for the local or international pet trade, where a baby orang-utan can fetch up to U$10,000 (Nellemann *et al.*, 2007). A VORTEX model was used to estimate survival rates for populations of different size and rates of hunting (Singleton *et al.,* 2004) with natural orang-utan mortality rates depending on age/sex class and the quality of habitat the orang-utan is in (Table 1.1).

Table 1.1 Mortality rates for different age/sex classes in various habitat types (from Singleton *et al.,* 2004).

Age and sex-class	High quality (lowest mortality) %	Medium %	Low quality (highest mortality) %
Females 0-5	1.0	1.5	2.0
Females 5+	0.5	1.0	1.5
Males 0-5	1.0	1.5	2.0
Male 6-12	0.5	1.0	1.5
Male 12+	1.0	1.5	2.0

The VORTEX model confirmed that, if hunting causes this figure to increase by 1%, it would not cause the collapse of a population in good habitat because natural mortality is low but would lead to a depressed population size. In sub-optimal or logged habitats, natural mortality is higher, and in these circumstances hunting could cause a decline to extinction (Singleton *et al.,* 2004). It is estimated that if the rate of poaching exceeds 1% above natural mortality in many populations, it would only take one or two hunters targeting females to achieve this increase in mortality, and hence cause a population crash, particularly in small isolated populations of less than 250 individuals which are not considered viable over the long-term (Figure 1.12) (Singleton *et al.* 2004). Marshall *et al.* (2006) studied the density of orang-utans in relation to distance from the nearest hunting village and found there to be a positive correlation, concluding that hunting was a far more serious threat to orang-utans than light to moderate logging.

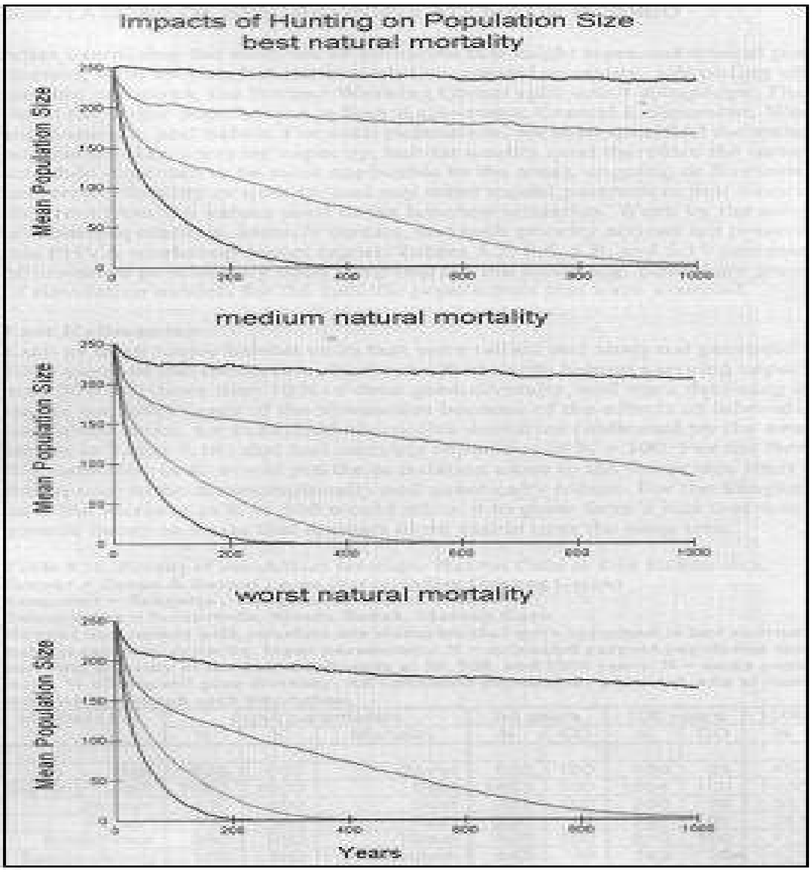


Figure 1.12 Impact of hunting on Bornean populations of 250 individuals with best, medium and worst natural mortality (Singleton *et al.* 2004). Lines in the graphs are population size trends resulting from hunting rates of 0%, 1%, 2% and 3% (from top to bottom).

Within the Sabangau catchment hunting has occurred at a lower level than expected, thought to be due to religious beliefs. Many of the transmigrants living along the surrounding Sabangau and Katingan rivers are Muslim, and it is against their faith to eat animals with canines. Many indigenous people are also scared of orang-utans. For example, most Dayak communities living along the Sabangau are scared of orang-utans, due to legends passed down of male orang-utans abducting females and taking them to their nest, where they are kept and mated by the orang-utan. There are many different stories about orang-utans depending on where you are in Borneo. Not all Dayaks are scared or have religious taboos forbidding hunting (Rijksen and Meijaard, 1999; pers. obs.); some tribes consider orang-utans necessary for certain ceremonies and medicinal purposes, whereas others see them as food. Today, many indigenous people have converted to Islam and abandoned their animist traditions (Rijksen and Meijaard, 1999), so hunting in some areas has decreased. On the western side of the Sabangau Forest, the majority of people are Muslim, compared to the eastern side, where they are mainly Christian, and the density of orang-utans here was much higher (Morrogh-Bernard and

Husson, 2002) possibly due to religious traditions. On the opposite side of the Sabangau, where the old PLG conversion project was based, patches of forest are left and it is in this part that hunting is high (pers. obs). People from the transmigration village nearby use the open forest fragments to hunt orang-utans, and many in this area had machete wounds or missing hands and limbs (Marchant, pers comm.). Hunting is a big problem for these small populations but one that can be tackled if the laws set down to protect orang-utans are implemented.

1.4 TROPICAL PEAT-SWAMP FOREST

Tropical peatlands are a unique dual ecosystem, being both peat-forming and supporting tropical forest cover (Rieley, 2001). Tropical peatlands are found in Asia, the Caribbean and Central and Southern America (Rieley, 2001). Around 70 % of tropical peatlands, or 260,000 km^2, occurs in South-east Asia (Rieley *et al.,* 2005) with 50 % occurring in Malaysia and Indonesia. Indonesia has the largest amount of tropical peatland in the world (Rieley, 2001) Kalimantan contains over 60,000 km^2 of peatland, half of which is in Central Kalimantan (Page *et al.,* 1999) (Figure 1.13).

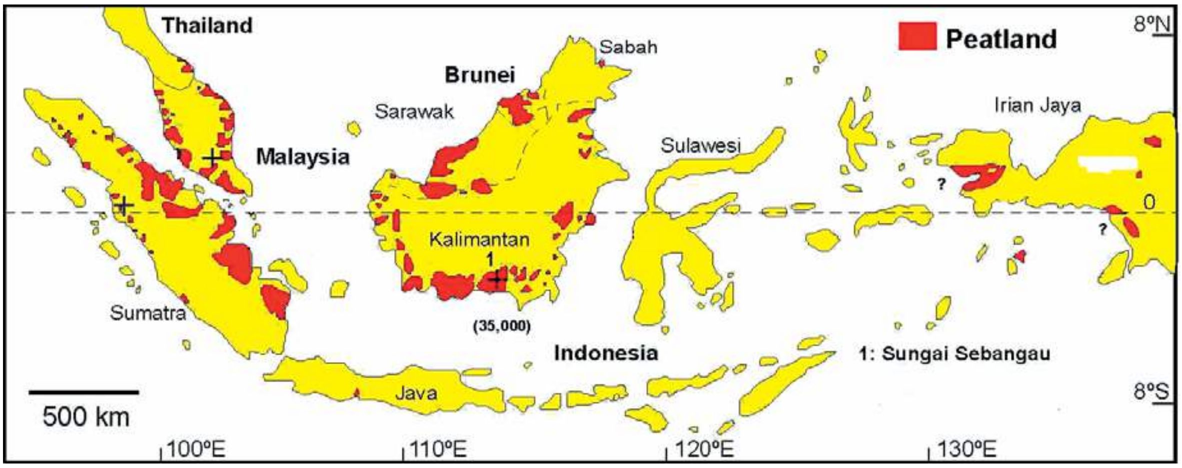


Figure 1.13 Peatlands in South East Asia (Page *et al.*, 2006)**.**
The figure in brackets is the age of the initiation of peat accumulation, and is calculated in years BP (Before Present – Present being AD).

1.4.1 Peatlands

Two types of peatland are found in Kalimantan, the fertile shallow coastal peatlands formed 4,000 - 5,000 years ago (Anderson, 1983), and the deep interior peatlands which were formed more than 10,000 years ago (Rieley *et al.,* 1992; Page *et al.,* 1999). Tropical peat-swamp forests have received little attention in the past, due to beliefs that they were low in biodiversity and unimportant for conservation. Only 3 % are protected in Indonesia, with the majority designated as either production forest for selective logging or conversion forest for agriculture. Recent research has discovered that they are rich in species diversity of, both fauna and flora however (Page *et al.,* 1997; Morrogh-Bernard and Husson, 2002; Dragiewicz and Husson, 2007; Dragiewicz *et al.*, 2007; Husson *et al.,* 2007) and, therefore, important for conservation. Peatlands are extremely important for regulating the hydrology of surrounding areas and as a major carbon store in both the peat and the trees (Rieley *et al.,* 2006). Thus, if peatlands are deforested, drained, burned or developed, huge amounts of carbon are released into the atmosphere which adds to the greenhouse effect and global warming (Page *et al.,* 2002; Rieley *et al.,* 2005).

Deep-peatlands

The deep-peatlands of Central Kalimantan are ombrogenous ecosystems (Rieley *et al.,* 1997), receiving all their water and hence dissolved nutrients from rain water and other precipitations as opposed to water courses or below-ground drainage. These areas are very acidic (PH < 3) and poor in nutrients, due to the thickness of the peat which does not allow the root system to reach the mineral rich soil anywhere other than the margins. Deep-peatlands usually form in domes between rivers; they are an accumulation of organic material and can be up to 20 m thick in the centre (Page *et al.,* 1999). All nutrients in a peatland are contained in the first few surface metres, meaning that all trees have very shallow roots. The area is usually flooded most of the year, with the water table above the surface during the wet season reaching depths of 1 m and more in some areas. Trees have adapted to these conditions by producing either breathing or stilted roots. The difference in the water table over the dome affects the distribution of nutrients, and in turn divides the area into defined habitat sub-types. The stability of peatlands is governed by the water levels. If it is upset by drainage and forest clearance the stability of the peatland can be lost, making the area susceptible to flooding in the wet season and fire in the dry season.

1.4.2 Importance of tropical peat swamp forest

Diversity

Pristine tropical peatlands are important for the conservation of biological diversity (Page *et al.,* 1997; Rieley, 2001; Morrogh-Bernard *et al.,* 2003). Although diversity is lower than that found in other lowland forests, many species are peatland specialists that are not associated with any other wetland or forest habitat; making the area important for regional and global diversity (Rieley, 2001). There are also many types of peat-swamp forest (Anderson, 1964; Shepherd *et al.,* 1997; Page *et al.,* 1999) and this heterogeneity is a key conservation issue (Page *et al.,* 2006). Recent studies have identified a number of endangered or endemic mammal and avian species in this habitat, including the orang-utan (*Pongo pygmaeus*), agile gibbon (*Hylobates albibarbis*), sun bear (*Helarctos malayanus*), clouded leopard (*Neofelis nebulosa*), leopard cat (*Prionailurus bengalensis*), rhinoceros hornbill (*Buceros rhinoceros),* storms stork (*Ciconia stormi*), grey-breasted babbler (*Malacocincla albogulare*) and white-winged duck (*Cairina sculata*), the latter two being found in no other wetland or forest type (Page, *et al.,* 2006).

In the Sabangau peat-swamp forest over 150 species of bird have been identified and over 50 species of mammal (Page *et al.,* 1997; Morrogh-Bernard and Husson, 2002). The Sabangau peat-swamp forest is also important as a breeding ground for fish, with a high diversity (Dragiewicz, 2006). Mansor *et al.* (2001) identified 66 different fish species in Malaysia of which many were endemic to the peat-swamp ecosystem. The Sabangau forest is one of the largest contiguous areas of peat-swamp forest left in Kalimantan, supporting the largest orang-utan population in the world (Singleton *et al.,* 2004) and possibly also the largest population of agile gibbon in Borneo (Buckley *et al.,* 2006). These areas are therefore extremely important for biodiversity conservation and every effort must be made to save these and other peatlands from conversion pressures.

Use of peatland

Most deep-peat-swamp forests in Indonesia are designated as production forest for selective logging. Extraction methods are selective with strict regulations. The main commercial tree species exploited in these areas include ramin (*Gonystylus bancanus*), agathis (*Agathis dammara*) and meranti (*Shorea* spp). These species represent 10% of Indonesia’s forest exports (Laurent, 1986). Peat swamps are not only important for timber but also for many non-timber products, including jelutong (latex from the wild rubber tree *Dyera lowii*), rattan, gemur (bark of *Alseodaphne coriacea* used for making mosquito coils) and many kinds of medicinal plants (Shinta, pers. comm.). They are also very important breeding grounds for fish and thus, extremely important for the local economy. In contrast to these deep-peatlands, shallow coastal peatlands less than 3 m deep are important for agriculture and, as a result, most areas have already been converted.

Carbon storage

Tropical peatlands are one of the largest near-surface reserves of terrestrial organic carbon and thus, its destruction has major implications for climate change (Page *et al.,* 2002). During the 1997 forest fires in Borneo, vast areas of peatland (796,906 ha) in Central Kalimantan were destroyed (Siegert *et al.,* 2001) releasing huge amounts of carbon into the atmosphere. Page *et al.* (2002) estimated that the amount of CO_2 released from Indonesian's peatland fires was equivalent to 13-40% of the mean annual global carbon emissions from fossil fuels. This contributed to the largest annual increase in atmospheric CO_2 since records began in 1957 (Page *et al.,* 2002). Peatlands are an important carbon store and, as such, they must be maintained and managed appropriately.

1.4.3 Threats to tropical peat-swamp forests

Recent threats to tropical peatland are agricultural conversion (for rice and oil-palm plantations), illegal logging, drainage and fire. Tropical peat-swamp forest is a very sensitive ecosystem and any disturbance can take years to recover, and in some cases can be irreversible. The deep-peatlands of Central Kalimantan were protected from conversion to agriculture under presidential decrees due to their unsuitability (Marr, 1996). In 1995-1997, however, nearly 2 Mha of deep-peat in Central Kalimantan was cleared for rice production, and 150 Mha of peatland was drained (Rijksen and Meijaard, 1999). The project known as the Mega Rice Project (PLG) was former-President Suharto's plan to try and make Indonesia self sufficient in rice, but, due to the low nutrient value of the peat, no rice ever grew and the area was turned into a wasteland. The project was a monumental disaster on a global scale, but plans are still being put forward to convert deep-peatland for agriculture. These drained areas now burn annually (pers. obs.). In 1997, in conjunction with the Asian economic crash and the fall of President Suharto, illegal logging in Indonesia became widespread, resulting in the near extinction of ramin (*Gonystylus* *bancanus*), an indigenous swamp species. In 2001 ramin was put on Appendix 2 of CITES in an effort to crack down on illegal trade in the species, but illegal logging is still rife and conducted with no regulations. Although illegal logging is conducted selectively, when one species is finished they will log the next and so on, until there are no trees of commercial value left. Mass corruption within the government, army and police has allowed this rampant theft to continue as many top officials own the illegal logging companies. When President Susilo Bambang Yudhoyono came to power in 2006, however, he ordered the army to stop illegal logging in National Parks, which was a success.

As well as the removal of timber, the methods used to extract wood in deep-peat-swamp forests are very damaging. Illegal loggers dig small canals into the peat in order to transport logs to the river, which in turn drain this sensitive ecosystem, thus destroying the hydrology, drying the peat and exposing it to fire risk. Most of Central Kalimantan's peat-swamp forests have been heavily disturbed as a result. Fires are now common phenomena each year during the dry season, blanketing Kalimantan and neighbouring countries in smog (Mongabay.com, 2007).

The Sabangau Forest was designated the 'Sabangau National Park' in October 2004, but it is still in danger as plans have been put forward to increase the areas of land under plantation (for oil palm) to support the increased numbers of people translocated to Kalimantan under Indonesia's transmigration policy (Rieley *et al.*, 2005). This encroachment and land conversion is devastating for the peat-swamps and its wildlife. Not only have plans been put forward to convert land, but a road through the centre of the Sabangau was planed so that transmigration villages near the coast could be connected to towns within the interior. These attempts failed and the project abandoned in 2007, due to the depth of the peat, and frequent fires, which were a result of drainage. There are still plans, however, for the road to run along the Katingan River instead.

1.5 PROJECT DESIGN

1.5.1 Previous Research

In 1995 the first-ever study on orang-utans within the Sabangau peat-swamp forest was undertaken (Figure 1.3; Chapter 2). At this time the Sabangau was still under logging-concession management. Our findings identified the presence of a large sustainable population of orang-utans (Morrogh-Bernard *et al.,* 2003). Orang-utan monitoring has continued since 1999, to monitor the effects of these disturbances upon the population.

Summary of Major Findings from the Sabangau Study Site.

The summaries below come from the following reports and papers; Hearn, 2002; Nesbitt, 2001; Husson *et al.,* 2002a; Husson *et al.,* 2002b; Morrogh-Bernard and Husson, 2002; Husson and Morrogh-Bernard, 2003; Morrogh-Bernard *et al.,* 2003.

A. Orang-utan movements in response to logging.

Orang-utan nest monitoring has been conducted since 1999 in all three major habitat sub-types (mixed swamp forest, low pole forest and tall interior forest – for descriptions of these habitat sub-types see Chapter 2), to identify orang-utan density, distribution and effects of logging. Standardised orang-utan nest-survey techniques developed in Sumatra were adapted for Borneo and used here (van Schaik *et al.,* 1995; Morrogh-Bernard *et al.,* 2003). The following trends were found:

- Habitat destruction caused by illegal logging and fire led to large shifts in orang-utan distribution from the 'normal' distribution of 1995 and 1996, when the mixed swamp and tall interior forest supported stable high densities of orang-utan.
- 1999 and 2000: Orang-utan distribution shifted greatly, with large rises in density in the interior mixed swamp and low pole forest; and sharp decreases in the tall interior and mixed swamp forest near to the river, due to illegal logging activities in those areas. Despite the shift in distribution, overall numbers appeared to remain stable.
- 2001: There was a sharp decrease in density in both the mixed swamp and low pole forests, but an increase of 30% in the tall interior forest. The latter was due to orang-utans moving back from the low pole into the tall interior forest following cessation

of logging. Overall densities were low and it was not known if this was just a blip or a long-term trend.

- 2002: Overall densities were again low, confirming 2000 results that logging was eventually affecting orang-utan numbers, with an overall density decrease of 36%. Densities within the mixed swamp forest near to the river (1-3km) and the tall interior forest were higher, again following cessation of logging in these areas. Orang-utan distribution appears to be returning to the norm with the tall and mixed forest sub-types supporting the highest densities.

B. Distribution and fruit availability

- Orang-utan distribution was related to fruit abundance. Within the mixed swamp forest 17 tree species were found to be fruiting (July- September 2001). The area with the most abundant fruiting was 2km from the forest edge. A significant negative correlation between both fruit abundance and fruiting species diversity with increasing distance from the river was discovered. One area with the highest fruit abundance had the lowest orang-utan densities, but the highest evidence of logging, indicating that habitat disturbance overrides fruit availability when it comes to orang-utan distribution (Nesbitt, 2001).

C. Habitat Damage

- Illegal loggers use canals and skids to extract the timber. These extraction canals have been found to drain the peat rapidly, with flow rates exceeding natural drainage through the uppermost peat layer (the acrotelm) by a factor of between 100 and 3000, resulting in peat desiccation and aeration. Logging skids were found to cause considerable damage to forest structure, devastating over 40% of the immediate forest area. Forest within 50m of the extraction railway was severely damaged, with the canopy above 10m height reduced in extent. In logged areas within the tall interior forest an entire layer of emergent trees had disappeared. The only positive effect was that tree species richness and diversity may be increased (Husson *et al.,* 2002b).
- According to nest-site choice orang-utans avoided areas of disturbance, but preferred nesting in open areas. Whilst an apparent contradiction, this suggests that orang-utans prefer nesting near open areas on a localised scale, whereas logging disturbance

affects their overall distribution and population size. The location of nests adjacent to open areas may be a behavioural strategy employed to increase detection of predators or conspecifics (Hearn, 2002).

Overall it is apparent that orang-utans are moving away from areas of disturbance, but are moving back when logging operations cease. Intense logging activity has lowered habitat quality by reducing the density of large fruiting trees and, as a result, a fall in orang-utan density has been recorded.

1.5.2 Justification for research

Information on orang-utan behavioural ecology comes mainly from long-term studies in primary dryland forests. There have been no studies in deep-peat-swamp forest habitats, presumably because this habitat has been hard to access and work in. Since the earlier studies, however, many forested areas have been subject to logging activities and land clearance, and peat-swamp forest has assumed much more importance for orang-utans. There is also a realisation that orang-utans do not behave the same way in every habitat, and we cannot completely understand a species unless we study them in every habitat under all conditions. Additionally, the study of orang-utans in logged forest (and indeed forest actively being logged) will also tell us much about their behaviour, their adaptability and their ability to survive habitat degradation. There has been research conducted in old logged and secondary dipterocarp forest in Sumatra (Rao and van Schaik, 1997) and in Sabah (Lackman-Ancrenaz and Ancrenaz, 2006) in the last few years, although the first of these studies was very short, and the second is in very heavily disturbed and fragmented forest. This study is one of two long-term studies of orang-utan behaviour in a peat-swamp forest, both started at the same time (2003). The other is at Tuanan in the old PLG area, north-east of the Sabangau. At Tuanan there is more emphasis on pure behavioural studies, including development and learning, whereas this study is more ecological and thus more focused on the effects of habitat differences on orang-utan behaviour.

I started orang-utan research in the Sabangau in 1995, when the first nest surveys were carried out, and research has continued since. The deep peatland here is physically very different from the shallow peatland of Tanjung Puting nearer the coast, the only long-term study site in Central Kalimantan, and thus the behaviour of orang-utans may be expected to be different. Meanwhile, a large decline in orang-utan density, and hence population size, resulting from illegal logging has been recorded, but the precise means of this decline is not known, and thus it is imperative for orang-utan conservation that an intensive study takes place in order to understand this population's ecology and the effects that habitat disturbance has had. The demographic structure of the population and physical health of the animals is probably far more important information for conservation management than the actual number of surviving animals, although this information is important for identifying priority populations and for monitoring purposes.

This behavioural ecology research project was devised in order to enhance our knowledge of this population, so that appropriate management plans are implemented in the future. This research project was designed for the collection of data on behavioural ecology in order to: (1) identify aspects of orang-utan behaviour unique to peat-swamp forest; (2) evaluate the impact of disturbance on orang-utan behaviour and ecology; (3) assess the general health of the population; and (4) identify ranging patterns and social structure.

1.6 AIMS AND OBJECTIVES

1.6.1 Aims

To describe orang-utan behaviour, ecology and demography, by investigating orang-utan activity patterns, dietary composition, relatedness and ranging patterns, in relation to food availability and habitat quality within the Sabangau peat-swamp forest.

- Initiate a comprehensive study of orang-utan behaviour and ecology in a peat-swamp forest.
- Evaluate the impact of habitat disturbance on orang-utan behavioural ecology
- To collect general behaviour data for comparison with other sites.

1.6.2 Objectives

To elucidate:

- Population composition.
- Fruiting patterns and productivity levels.
- Dietary composition.
- Orang-utan activity patterns.
- Home and day ranges.
- Relatedness between individuals and social interactions in order to understand orang-utans social organisation.
- Effects of fruit availability on orang-utan behaviour (activity patterns and ranging).
- Habitat quality and habitat degradation throughout the study site, and orang-utans use of areas of differing habitat quality.
- Human disturbance levels, and how they affect orang-utans.

Results from Sabangau will also be compared with findings from other sites and habitats in Borneo and Sumatra.

By answering these questions it is hoped that we will get a better understanding of orang-utan behaviour in peat-swamp forest, and the affects of disturbance on their behaviour. By comparing my findings with other sites I should advance our knowledge and highlight similarities or differences between different populations in different habitats. Answers to these questions will also be incorporated into management plans for the Sabangau forest, and other peat-swamp forests nearby, which hold large and sustainable orang-utan populations.

Orang-utans feeding behaviour and fruiting patterns were investigated in Chapters 3 and 4, activity budgets and habitat use in Chapters 5 and 6 and ranging, dispersal and social organisation in Chapters 7, 8 and 9.

CHAPTER 2

STUDY AREA AND METHODS

2.1 STUDY AREA

2.1.1 Location

The study site is located in the NLSPSF (*Natural Laboratory for the Study of Peat Swamp Forest*), an area of 500 km^2 within the Sabangau River catchment (Figure 2.1). The Sabangau River is a minor black-water river in southern Borneo, in the Indonesian province of Central Kalimantan. The catchment covers an area of some 9,200 km^2, a major part of the 22,000 km^2 of tropical peat-swamp forest found in the south of this province. The catchment is boarded by the Kahayan River to the east and the Katingan River to the west. The area bordered by the Sabangau and Katingan rivers includes about 6,000 km^2 of forest and is where the NLSPSF is located; the forested area was given National Park status in 2004.

Most of the area is continuous forest, with villages located on the banks of both rivers, but to the south there is encroachment from the transmigration settlement near the coast. The NLSPSF was designated for the purpose of scientific research in 1997, when the Setia Alam Jaya timber concession ended. It was established by the then Governor of Central Kalimantan, to be managed by CIMTROP (the Centre for International Co-operation in Management of Tropical Peatland) and the University of Palangkaraya. The base camp is located 20 km south-west of Palangkaraya, the provincial capital, at coordinates 2^o 19‘S and 114^o 00‘E.

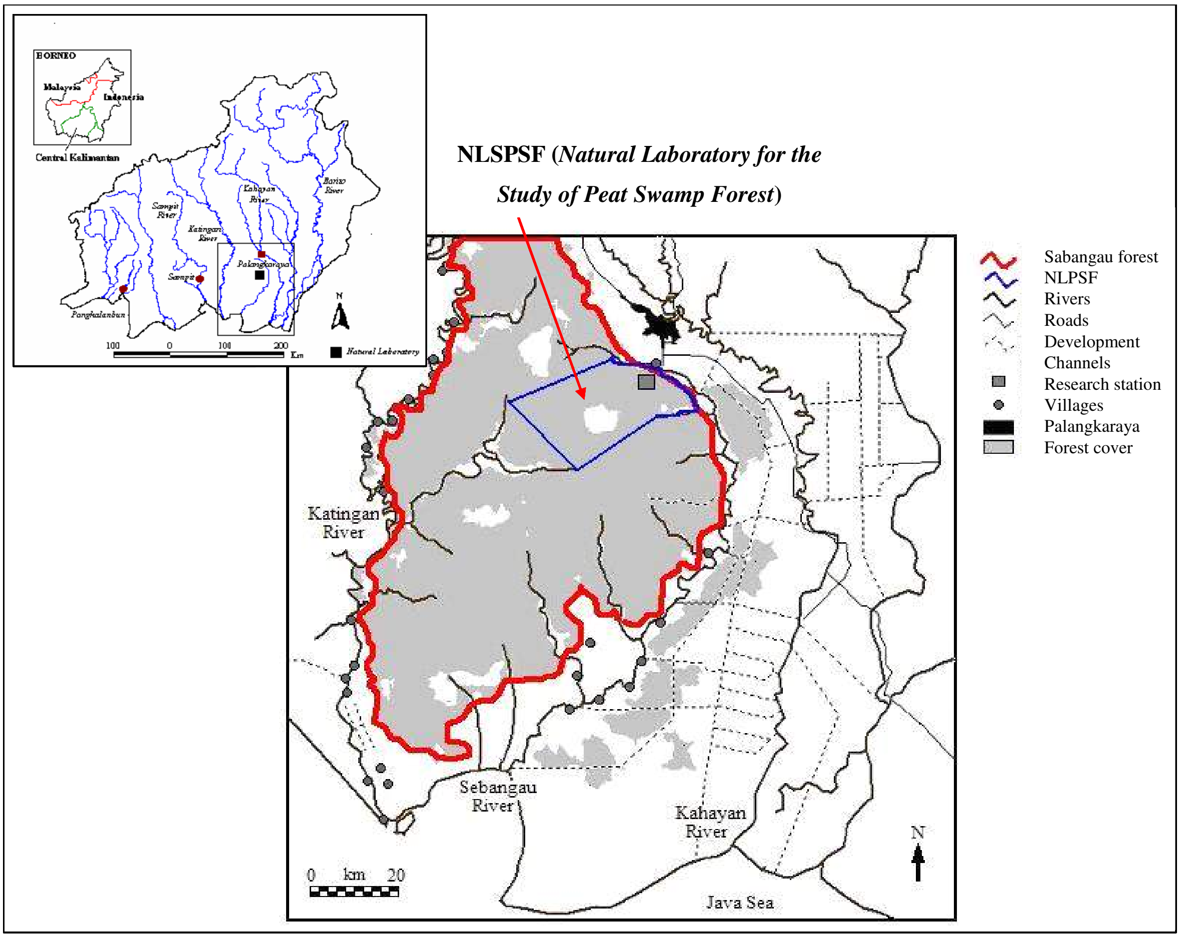


Figure 2.1 Central Kalimantan and the Sabangau peat-swamp forest.

The base camp, called Setia Alam, is positioned on the edge of the forest bordering the Sabangau river (Figure 2.1), and access into the forest is along the routes of two old rudimentary railways which were constructed by the logging concession. These railways have since rotted away but a basic path remains which extends for 13 km through the three largest habitat sub-types, the mixed-swamp forest, low-pole forest and tall-interior forest. Due to the swampy nature of the peat-swamp forest, a boarded walkway extending 2 km from base camp was constructed to enable fast access into the grid system. The grid covers an area of 9 km^2 within the mixed-swamp habitat sub-type (Figure 2.2) and it was here where this research took place. It was not logistically feasible to set-up the grid system in any other forest sub-type because of the distance from base camp. Trails were cut every 250 m, running north-south and east-west (Figure 2.2), thus allowing easy access into the forest to locate and follow orang-utans.

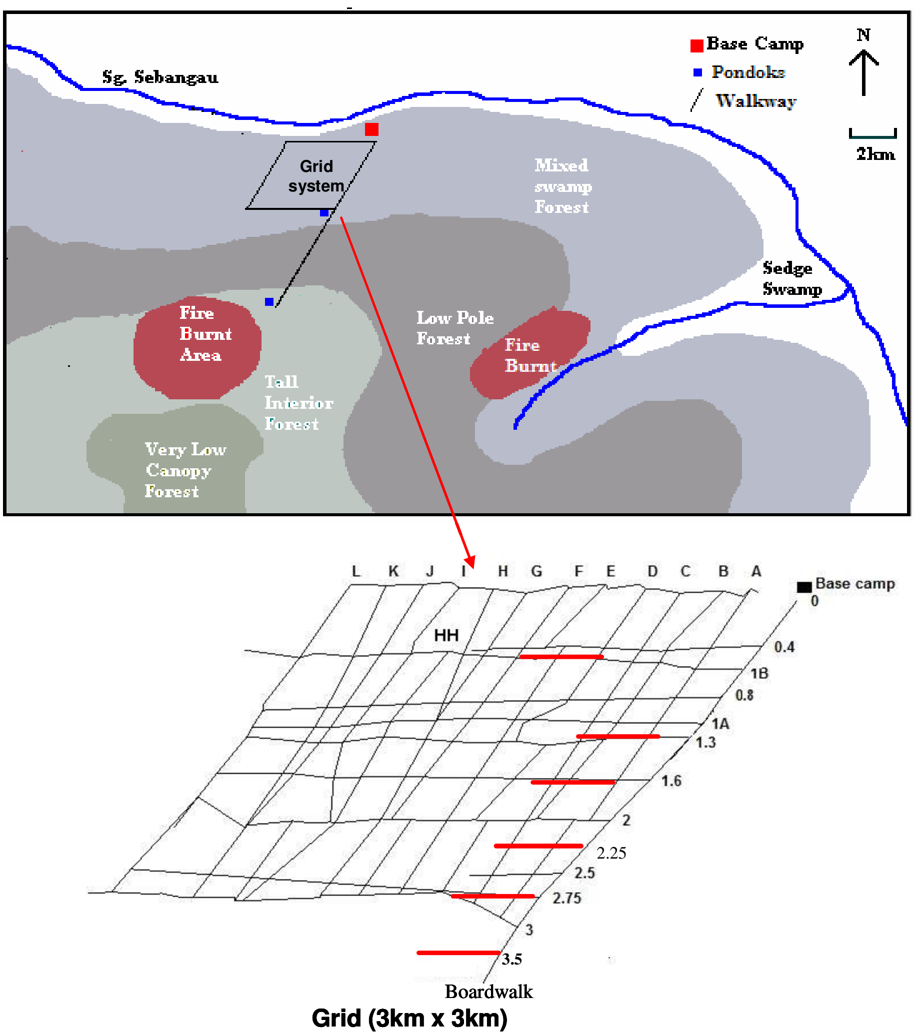


Figure 2.2 The study site with in the Natural Laboratory. Permanent vegetation plots in red.

There are five distinct habitat sub-types identified in the Sabangau Forest (Figure 2.2), all varying in structure and vegetation composition from the impoverished, wet, low-pole forest to the diverse, dry, deep-peat tall interior forest on the watershed (Figure 2.3). The latter forest-type is unique, standing on peat as deep as 13-20 m and over 20,000 years old (Weiss *et al*., 2002), thus the Sabangau peatland is the oldest tropical peatland in the world. The Sabangau forest supports a huge diversity of animal and plant life (Appendix I, II and III), of which many are endemic. It also holds the largest contiguous population of the southern race of Bornean orang-utan existing today (Morrogh-Bernard *et al.,* 2003; Singleton *et al*., 2004).

2.1.2 Habitat types

A catenary sequence of forest sub-types (Figure 2.3) occurs on the peat-covered watershed between the Sabangau and Katingan rivers. Five distinct forest sub-types have been identified based on tree species composition and forest structure (Shepherd *et al.*, 1997; Page *et al.,* 1999). These are:

(i) Riverine forest: Found 0 - 1 km from the river. Located in the flood plain of the Sabangau and subject to much anthropogenic disturbance, such as burning and felling. Under pristine conditions the dominant tree is swamp meranti (*Shorea balangeran*). Successional vegetation is of either primary (impoverished open forest) or secondary (sedge, *Thorachostachyum bancanum*) swamp habitat. Natural areas of this forest sub-type large enough to support orang-utans may only be found in remote areas, as much of this habitat has been cleared. Areas in Figure 2.2 that were previously riverine forest are now covered in sedge swamp.

(ii) Mixed-swamp forest: Found 1 - 6 km from the river with peat up to 6 m deep. Flooded in the wet season. In the dry season the acrotelm (surface peat) slowly drains, but the peat remains saturated with pools of standing water remaining in the hollows in its natural state. Due to drainage, however, this forest type tends to completely dry out by the end of the dry season, leaving no water in the hollows. This is the most extensive of the five habitat sub-types. The forest is tall and stratified, with the upper canopy reaching a height of 35m. Most vegetation growth occurs on ‘peat islands’ or hummocks that rise above the floodplain and subsequent shallow drainage channels. This stratified habitat contains commercially-valuable trees, such as ramin (*Gonystylus bancanus)*, mentibu (*Dactylocladus stenostachys*) and gerrongang (*Cratoxylon glaucum)*, and thus has been intensively logged. Illegal logging was concentrated here and, as a result, most of the remaining commercially-important species have been removed. This is the orang-utans second most preferred habitat sub-type, after the tall-interior forest, and supports the bulk of the orang-utan population in the Sabangau (Morrogh-Bernard *et al.,* 2003).

(iii) Low-pole forest: Found 6 - 11 km from the river on peat between 7 and 10 m deep. Permanently flooded in both the dry and wet season in its natural state, but due to artificial drainage this forest type is now dry during the dry season. In its natural state, this is an extremely wet and low-productive forest type. The canopy reaches a maximum height of 20 m. Growth is still restricted to hummocks, including many trees with pneumatophores (breathing roots). This low-canopy forest contains very few trees of commercial size; reasonably high light penetration and water levels results in a dense growth of *Pandanus* spp. Thus, sapling growth and small tree establishment is restricted. Orang-utan densities are found to be lowest in this habitat sub-type (Morrogh-Bernard *et al.,* 2003).

(iv) Tall-interior forest (Tall pole forest): Found 13 km from the river on peat deeper than 12 m. There are few hummocks and hollows and few trees have pneumatophores. The peat surface remains dry during both the dry and wet seasons. A small yet important habitat type, well stratified with trees reaching a maximum height of about 45 m; as a result, this habitat contains the majority of the commercially-logged genera including *Agathis, Koompassia, Shorea* and *Palaquium*. High, closed canopy, resulting in low forest-floor light and lower water level gives a much lower shrub, herbage and sapling population than the other habitats in this area. This forest-type has been logged extensively, and has also suffered from fire damage, but is still in good condition in parts. This is the preferred habitat type, with the highest density of orang-utan (Morrogh-Bernard *et al.,* 2003).

(v) Very low forest (low interior forest): Found on the highest point of the peat dome, occupying an area of 13 x 6 km^2, surrounded by tall forest. Characterised by very small trees less than 15 m tall, and large pools (200 m across). Pneumatophores are abundant, protruding high above the surface of the pools. There is high light penetration, so high diversity, and the peat surface is covered in bryophytes. No orang-utans found here (Morrogh-Bernard *et al.,* 2003).

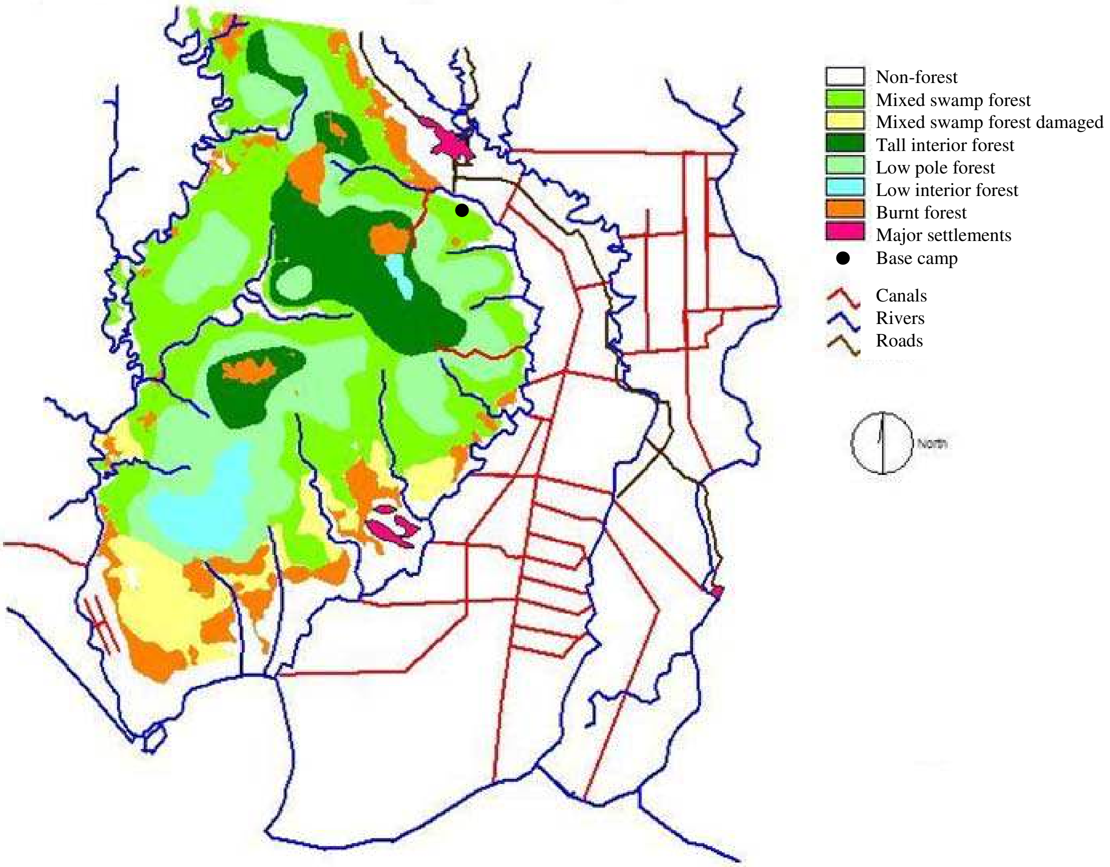


Figure 2.3 Distribution of habitat sub-types and locations of settlements within the Sabangau forest.

2.1.3 Fauna

154 species of bird and 65 species of mammal have been identified in the Sabangau (Appendix I, II, III), of which many are endangered or endemic to this habitat, e.g. storms stork (*Ciconia stormi*) and grey-breasted babbler (*Malacocincla albogulare*). There are 9 species of primates, including the orang-utan (*Pongo pygmaeus*), agile gibbon (*Hylobates albibarbis*) and proboscis monkey (*Nasalis larvatus*), which are all listed as endangered or near threatened. Not only have birds and mammals been recorded, but over 43 species of reptiles have been identified, including 22 snake species, 2 crocodilians, 3 turtles, 11 lizards and 3 frog species. This area is an incredibly diverse ecosystem and those species identified are only a fraction of the species likely to occur in the Sabangau.

2.1.4 Climate

Indonesia straddles the equator, with the peat-swamp forests of Central Kalimantan not very far to the southof the equatorial line. There are two distinct seasons, a dry season between July and September and a wet season between October and June. Borneo is generally hot and humid.

In peat-swamp forests the climate is extremely hot and humid all year round, with frequent tropical downpours in the wet season. In the past 10 years extended droughts have occurred during the dry season, resulting from more frequent El Niño events, a probable result of global warming. These droughts have contributed to the dramatic rise in fire events over the same 10-year period, which now occur almost every dry season in heavily logged and/or drained peatland areas.

Climate within the Sabangau peat-swamp forest

The weather at the study site was monitored from our base-camp weather station; sited at the edge of the forest. The temperature gauge was positioned under the trees in the shade and the rain gauge was in the open. The maximum and minimum temperatures were taken each morning, and rainfall was measured twice daily; once in the morning at ca. 0600 h for night-time rainfall and once in the late afternoon at ca. 1800 h for day-time rainfall. Data were collected for 24 months from September 2003 to August 2005.

Monthly rainfall at the study site ranged from a minimum of 0.5 mm in August 2004 to a maximum of 632 mm in February 2005. The most rain recorded in one day was 127 mm on 15th February 2005. Annual rainfall was almost identical during the two years of my study; in the first year from September 2003 to August 2004, 2960 mm of rain fell compared to September 2004 to August 2005 when 3013 mm fell. In the first year of my study the wet season started in October 2003 and ended in July 2004, and in the second year it started in November 2004 and ended in May 2005 (Figure 2.4). Thus, the dry months varied from year to year. The driest months were recorded during August, September and October 2004. Over the two years seven major storms were recorded, where rainfall exceeded 100 mm in a 24 hour period. These torrential downpours were usually accompanied by strong wind and thunderstorms and would cause large trees to come crashing down, pulling many others with them. The most damaging storm was recorded on the 5th December 2005 (124 mm of rain; see Chapter 6), when high winds caused many trees to fall. The many tree falls during windy conditions in the peat-swamp was due to a combination of reasons: (i) logging, which opened up the canopy so that exposed trees received the full force of the winds, (ii) the shallow root system of most peat-swamp species, (iii) the peat itself is a low density substrate, thus providing little counter-resistance to the wind and (iv) peat drainage from illegal logging canals which aerates the top surface, which oxidises and degrades as a result. As the peat degrades, the surface area becomes unstable, and tree roots are undermined.

The average minimum temperature was 22.2°C and the average maximum was 29.4°C (Figure 2.5). The highest shade temperature was recorded on August 17th 2004, when it reached 38°C, and the lowest, 18°C was recorded during the night of April 18th 2004. The lowest temperatures were usually recorded on days when it rained, due to cloud cover. Smoke from the forest fires often blocked out direct sunlight during the dry season.

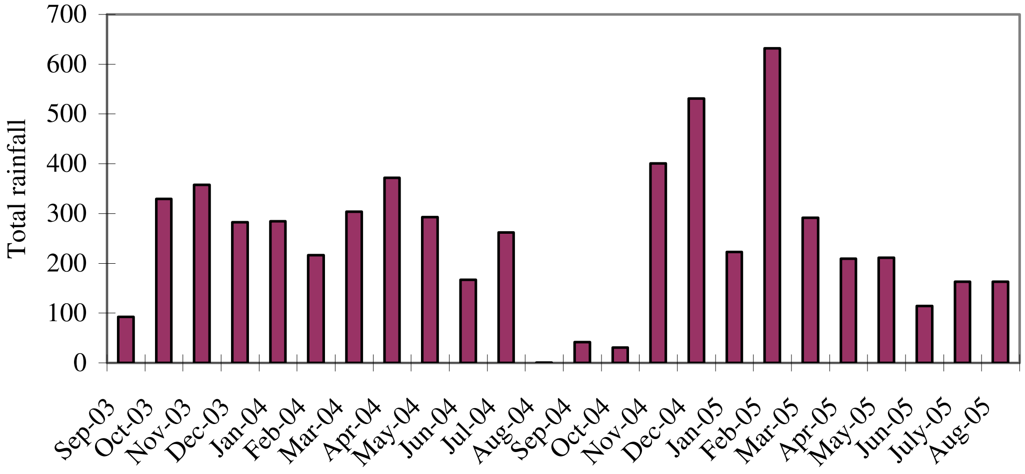


Figure 2.4 Monthly rainfall in mm in the Sabangau Forest from September 2003 to August 2005.

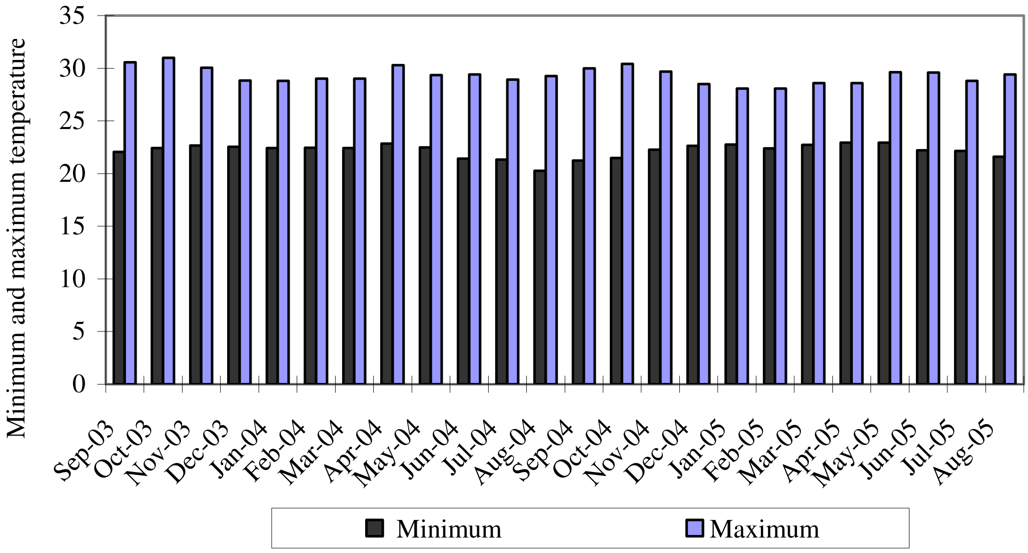


Figure 2.5 Minimum and maximum monthly temperatures in degrees Celsius in the Sabangau Forest from September 2003 to August 2005.

2.1.5 Human disturbance

There are various activities and disturbance within the forest (Table 2.1)

Table 2.1 Types of human disturbance.

Activity within the research site	Dates
Illegal logging for large timber	November 03 – March 04 – ended in March 04
Illegal logging for scaffolding	December 03 – January 05
Bat hunting	February-April, September-November each year
Other forms of hunting (pigs, birds)	All year round
Jelutong collecting	May – November each year
Gemur collecting	All year round

- **Illegal logging of big trees*:*** Trees with a dbh over 20cm were cut for timber; and many trees smaller than this, but over 10cm dbh, were also cut for the construction of rails (skids) used to extract the timber. Most large trees were taken, no matter what species, as many of the preferred large timber species had already been removed.
- **Illegal logging for scaffolding:** Timber that was cut was usually less than 10 dbh and was only taken from the very edge of the forest, usually from the species Galam (*Syzygium* sp.*)*.
- **Bat hunting:** This took place during the night. Bat hunters cleared areas of forest 30 x 30 m next to large fruiting trees, usually from the genera *Palaquium* and

Calophyllum, which are favoured by the large fruit bat (*Pteropus vampyrus*). The hunters set up mist nets at canopy level across these clearings, in order to catch the bats. This activity only took place during the fruiting season of the above genera, when the fruit bats arrived to forage.

- **Other forms of hunting:** Pigs and deer were hunted by small groups of men armed with spears (occasionally shotguns) and with several dogs used to chase and catch the prey. Snares were very rarely used. Certain species of bird were caught for sale, and recreational hunters were seen once or twice, using basic blow pipes to hunt small birds. No large animals other than pigs, deer and fruit bats were known to be hunted during the course of my study, although previously every kind of animal, including orang-utans, have been hunted in this area.
- **Jelutong collecting:** The latex from the jelutong, or wild rubber, tree (*Dyera lowii*) was tapped for its sap. Jelutong collection was practised throughout the forest as this species occurs at high density.
- **Gemur collecting:** Bark from the gemur tree (*Alseodaphne coriacea*) was stripped for use to make mosquito coils. There was not much gemur collection during my study, as most of the trees had already been removed.

2.2 METHODS

Standardised field data collection procedures, that were designed at the Leakey Foundation Orang-utans Compared Workshop held in San Anselmo, California in 2002 (Morrogh-Bernard *et al*., 2002), were used and adapted for this socio-ecological study. All data were collected on a focal animal, using instantaneous sampling methods.

2.2.1 Habituation

Habituation is the relatively-persistent waning of a response as a result of repeated stimulation (Thorpe, 1963). This persistence eventually leads to a reduction in fear and eventually the animals will ignore the human observer. Habituation allows the observer to approach closely to observe subtle behaviours, such as social interactions and feeding techniques, and allows behaviour to be sampled consistently (Williamson and Feistner, 2003).

In order to habituate orang-utans to my presence, and that of my assistants, we all wore the same matching uniforms of green clothing, so that orang-utans could distinguish between researchers and those not associated with research, such as loggers and hunters, who usually wore bright colours.

Orang-utans show fear by kiss-squeaking and displaying at the intruder, including approaching aggressively, throwing branches, breaking branches and pushing over dead trees. Orang-utans, if alarmed, would approach aggressively and, in some circumstances (even when habituated), would give chase. This was usually only by the large flanged males. When this occurred observers would sit still and not run, taking up a submissive posture (sitting down as small as possible with head down and no eye contact, pretending to groom or feed) and wait until the threat was over. If the threat continued, however, the observer would slowly move away, both to reduce the pressure on the orang-utan and to avoid the risk of personal injury resulting from a pushed-over tree. In circumstances where a large flanged male was on the ground, again the observer would remain still. In circumstances when the observer moved off, a flanged male orang-utan sometimes gave chase, but when the observer stayed put and was submissive, the male would stop a few metres from the observer, stay for a while, and then move off. Only once did a male stay watching the observer for over one hour, before the observer was able to leave and abandon the follow.

Finding orang-utans

Although many researchers working with apes use natural forest trails for following their target species, this was not possible in the peat-swamp forest, due to the nature of the habitat, which was extremely dense with visibility less than 5-10 m in some places. Thus, a trail system was cut to facilitate movement within the study area, especially when searching for orang-utans.

One or two teams of two people would search the grid system systematically for signs of orang-utans. Teams would split up, so each person was searching on their own with radio contact, resulting in less disturbance. Orang-utans were located either by (i) movement in the canopy, (ii) falling fruit or noise of feeding, such as sucking termites and breaking open seeds; or (iii) calls, either kiss-squeaks (alarm calls) or long calls from adult flanged males.

Approaching orang-utans

Two approaches were used: (i) the researcher would directly approach the individual as quietly as possible – this did not always work, due to the noise made when going through the undergrowth – and if the researcher was too quiet, this would often surprise the orang-utan who might then run off; and (ii) allowing the orang-utan to see and hear the researcher from a distance. At all times it was important to approach gradually over the course of many days, until the individual becomes accustomed to your presence, allowing you to be close enough to take good data. Once an individual was fully habituated they would completely ignore the researcher in most cases. Noise was limited by not talking loud and, if researchers were trying to communicate with each other from a distance, they whistled.

Only two observers followed the orang-utans, except on training days when three observers were permitted; this was to keep human disturbance to a minimum. The reason for following in pairs was for security in case of an accident, and it also meant more data could be taken than would have been possible with only one observer.

Signs that animals were habituated

- When the frequency of resting behaviour, kiss-squeaks, defaecating and throwing of branches levelled out or stopped.
- When fleeing and hiding behaviour became uncommon.

For the purposes of my study, I defined an orang-utan as habituated when it made fewer than 15 kiss squeaks/hour during the follow. Although this seems a lot, it was a good cut-off to distinguish between truly unhabituated animals and those that were merely briefly disturbed. An unhabituated orang-utan frequently made over 50 kiss squeaks per 5 minute period, and several hundred each hour. Generally, a newly-habituated orang-utan would behave perfectly normally for 95% of the day, but might make a few kiss-squeaks when leaving a feeding tree, or if their chosen travel route passed over the researchers. In those cases I would move slowly out of the way.

Individual recognition

Checklists were used to help identification of individuals. This included a detailed description of the individual, identifying any distinguishing marks, such as cuts, scars, missing digits, warts, size of throat sac and shape of cheek flanges, etc. A detailed drawing, photographs and video film were also taken of all new individuals, who were given names. The first orang-utan identified was given a name starting with A, the next a name starting with B, and so on. Infants were given a name starting with the same letter as their mother in most cases.

2.2.2 Age/sex class classifications

All individuals were classified as one of the age/sex classes listed below (Figure 2.6), with the abbreviations used throughout this thesis.

Infant: dependent on mother (suckling), travelling primarily on their mother's body.
Juvenile: independent but, not yet sexually mature, travelling primarily off their mother's body; normally still nursing from their mother at least once each day (often in nest).
Non-sexually-active female / male (NSAF / NSAM): adolescent and sexually inactive; living independent of their mother.
Sexually-active female (SAF): adult females which have given birth and are accompanied by infant or baby.
Nulliparous female (NLF): sexually-active adult female with no accompanying offspring.
Unflanged male (UFM): undeveloped sexually-mature male stage – no cheek pads.
Flanged male (FM): fully developed sexually-mature male with large cheek pads and throat sac.

Four age/sex classes were used for most analyses, with NLF and NSAM being combined with other age/sex classes due to small sample sizes for these two classes. NLF were combined with NSAF and NSAM combined with UFM. The reason why the NLF was included as a NSAF instead of a SAF was because her activity and ranging patterns more closely resembled adolescent females, probably because she did not have the added responsibility of a dependent infant.

Infant (19 months old) Juvenile (3-4 years old)

Adult flanged male (FM) Unflanged male (UFM)

Adolescent female (NSAF) Adult sexually-active female (SAF)

Figure 2.6 Age/sex classification

2.2.3 Follow protocol

Two-person teams would follow individual orang-utans during their period of daily activity (nest-to-nest) for a maximum of 10 consecutive days per individual, if not lost before. To avoid causing distress to the orang-utans, if one individual was followed for 10 consecutive days they would be abandoned and only followed again after 10 further days had passed. One person would take the main behavioural data and map the location of the orang-utan within the grid system and the second person would take the GPS points and tag all feeding trees.

The first individual found when searching was followed. The follow continued until the orang-utan nested. If another individual was seen while following the focal, the follow was only changed if data were needed on that other age/sex class. Orang-utans are very sensitive to body language, so researchers would keep their distance. Direct eye contact was avoided. A submissive and non-threatening posture was necessary in order to collect normal data. When leaving the orang-utan after it has nested for the night, the researcher would wait to make sure the orang-utan did not move again, as unhabituated orang-utans commonly leave when the researcher has left.

2.2.4 Data collection

The methods used for collecting behaviour data were based on the standardised orang-utan data-collection protocols (Morrogh-Bernard *et al.*, 2002) and from Martin and Bateson (1986). All data were collected on a single focal animal using instantaneous sampling to record general behaviour (once every 5 minutes) and continuous sampling every time the orang-utan was observed to feed. Descriptive information on rare behaviours, such as playing, mating and fighting, was taken when witnessed (Appendix IV- data sheets used).

Instantaneous sampling gives a good approximation of the proportion of time spent performing a behaviour (Martin and Bateson, 1986). If the sample interval is too short, however, then the practical benefits of instantaneous sampling are lost and the sample interval must be lengthened. Chivers (1974), found there to be no significant differences in results when using 5- or 10-min sampling intervals for gibbons. Most previous orang-utan studies used sampling periods of 2-3 minutes, but for this study I used 5 minutes as also recommended in the standardisation, (Morrogh-Bernard *et al.,* 2002). I was concerned that a shorter interval would compromise the quality of the data collected due to the number of different data sheets, and in particular the nature of the logged peat-swamp forest habitat which is very dense. Instantaneous sampling is not suitable for recording discrete events of short duration, such as feeding bouts or rare and interesting behaviours (Martin and Batson, 2007), so continuous sampling and written descriptions were used respectively whenever the orang-utan was observed to engage in these behaviours. Times for these activities were rounded to the nearest minute.

Instantaneous Sampling

I recorded the time I found the orang-utan, or the time the orang-utan started its active period (see Section 2.2.5 for definition), to the nearest minute. I then took my first sample at the next multiple of 5 minutes; for example if I found the orang-utan at 0911 h, I took my first sample at the stroke of 0915 h.

Every 5 minutes I recorded the following information on my main datasheet (Appendix IV, Sheet 1):

- Primary activity. The major activity (e.g. Feeding; Resting; Travelling etc.) in which the orang-utan was engaging at that exact point in time. See Section 2.2.5 for a list of primary activities.
- Secondary activity. For most primary activities there are a number of secondary activates that further describe what the orang-utan was doing, for example different types of food or different modes of travel. See Section 2.2.5 for description of secondary activities.
- Distance travelled in metres during the preceding 5 minutes.
- Direction of travel in degrees
- Height of orang-utan in the following classes: 0 m (on ground); 1-5; 6-10; 11-15; 16-20; 21-25; 26-30; 31-35 m.
- Height of the tree in which the orang-utan was, in the following classes; not in tree (on ground); 1-5; 6-10; 11-15; 16-20; 21-25; 26-30; 31-35 m.
- Forest Quality. See section 2.2.7 and Chapter 6 for description and definitions.
- Human Disturbance. See section 2.2.13 and Chapter 6 for description and definitions.

- Number of kiss-squeaks made by the orang-utan during the preceding 5 minutes.
- Party Size. See section 2.2.10 for definition

Training

All assistants were trained by me. They were first trained on taking GPS data and mapping. They then started tagging the feeding trees to become familiar with the forest, and to start learning to identify trees. Before an assistant was trained in taking behavioural data they were first trained on the definitions used for the different behaviours (Figure 2.6). Once they were familiar with these they would join the behaviour team as the third person shadowing the main data collection person. In order to assess that they were fully trained, their data would be compared with that of the main data person, usually me, with inter-observer reliability assessed using the concordance method (Martin and Bateson, 1986). The assistant was not considered trained until his data was a near match of mine (< 90%).

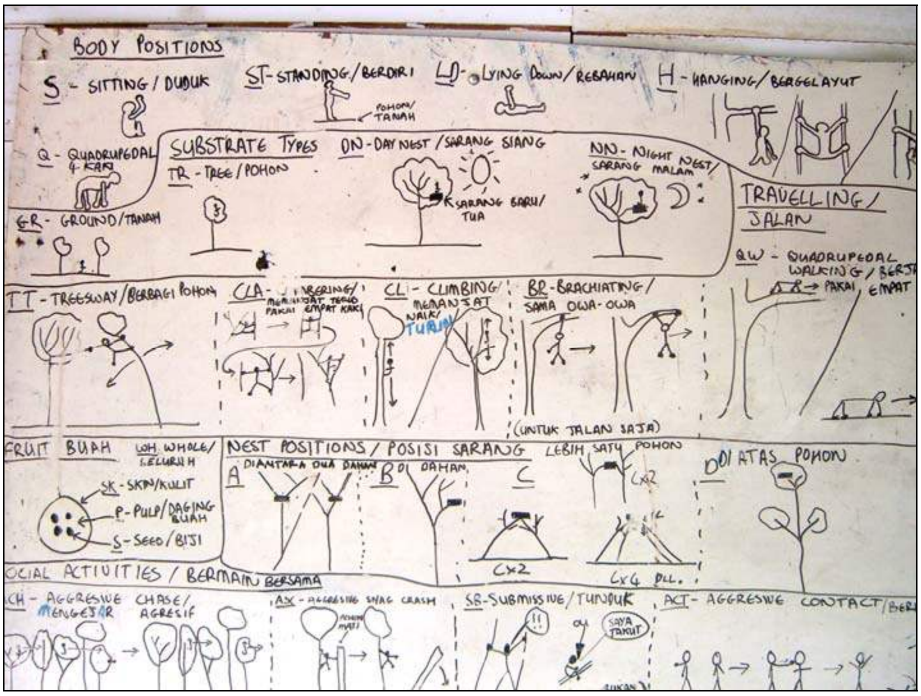


Figure 2.7 Illustrations of the different behaviour activities for training purposes.

2.2.5 Behaviour activities

All definitions for behaviour data collection were based on the standardised field data collection procedures for orang-utans (Morrogh-Bernard *et al.*, 2002).

Active period

The definitions for the active period are:

- **Start of daily active period:** defined as the time of day when the orang-utan first sat up at the edge of its nest (or performs a behaviour other than reclining).
- **End of daily active period:** defined as the time of day when the orang-utan reclines in the nest and performs no further observed behaviours.
- **Active period:** the length of time in minutes between the start and the end of the daily activities.

Primary Activities

Eleven different primary activities were identified. Only one primary activity could be recorded at any one time, so if two activities were being performed at the same time, for example feeding while travelling, the one higher up in the hierarchical list below was adopted. Thus, in this example feeding would be recorded on the datasheet. For most primary activities a secondary activity was also recorded, for example different types of food or different modes of travel (see Appendix IV, sheet 6 for definitions).

Data was recorded for a number of primary activities which are listed here in hierarchical order. This order is described in the standardised field data procedures, so that activity budgets can be analysed in the same way across sites.

1. Foraging: this class can be separated into i. Feed, ii. Co-feed, and iii. Food search.
2. Self-play
3. Nest build
4. Social (including long calls)
5. Aggression to observer (usually during habituation period only)
6. Aggression to other person
7. Travel
8. Rest

(1) Foraging

i. Feed (includes co-feed)

Any type of feeding behaviour in which the animal was actively eating (including reaching for food, food processing, preparing food item or drinking). Moving within a **food patch** was included as feeding.

Food patch: a food patch was defined as either one individual food tree or liana in which the individual was feeding; or more than one separate trees or lianas of the same food species with interlocking crowns.

Food type was recorded as the secondary activity, with the following categories

- **Fruit (ripe or unripe)**-part(s) eaten: pulp, seeds, skin (or combination of these)
- **Leaves:** shoots (new leaves) or mature leaves,
- **Pith of monocots:** such as rattans, pandans and other monocots
- **Flowers:** flower bud or mature flower
- **Other vegetable:** roots, epiphytes
- **Bark**
- **Invertebrates**
- **Honey**
- **Fungi**
- **Meat** (vertebrates)
- **Other** e.g. soil, rotten wood.
- **Water**

ii. Co-Feed

Co-feeding was recorded when another independent individual was in the same feeding patch as the focal animal. Food-type recorded as above.

iii. Food Search

Searching for food, while not actively engaged in feeding, for example breaking open wood to search for termites. This was not recorded when simply travelling through the forest looking for feeding trees.

(2) Self-play

Engaging in behaviour alone, that was judged by the researcher to represent play; included playing with food, playing with leaves/twigs/branches.

(3) Nest Build

When the orang-utan was actively making a new nest or rebuilding an old nest.

(4) Social

When an individual actively interacts with another individual this was recorded as social behaviour. Descriptive information about the interaction was recorded separately, as described in section 2.2.10.

- **Mate:** all activities involved in mating or attempting to mate. This included courtship (record whether focal individual solicits), attempted to mate, struggles relating to mating and copulation (forced/unforced).
- **Calls:** all kinds of social calls including long-calls, kiss-squeaks, and rumbles. Detailed information on long calls made by flanged males recorded separately (Section 2.2.9). Not all calls are social, especially kiss-squeaks, which were mainly directed at people. If directed at observers / other people then the primary activity was ‘Aggression to Observer’ or ‘Aggression to Other Person’ respectively, not ‘Social’.
- **Social play:** behaviour that involved play with another orang-utan.
- **Aggression:** behaviour that included aggressive elements. Included fighting; branch breaking, snag crashing; brief chase i.e. <1 minute, further sub-divided into two categories
  - Aggression with physical contact: contact between individuals.
  - Aggression with no physical contact: aggressive behaviour but no contact.
- **Submit:** behaviour that included submissive elements. Included fleeing in a brief chase i.e. <1 minute; trying to avoid rough play and begging behaviour.
- **Groom:** actively grooming or being groomed by another individual.
- **Touch:** - non aggressive physical contact.

(5) Aggression to observer

Throwing branches; pushing over dead trees; chasing or making kiss-squeaks towards observer.

(6) Aggression to other person

Throwing branches; pushing over dead trees; chasing or making kiss-squeaks towards a person not in the follow team.

(7) Travel

Any movement within the feeding patch was recorded as feeding, but type of locomotion was recorded as the secondary activity, with the following five categories:

- **Tree-sway:** the orang-utan would use its own weight to bend the tree or branch it is on, in order to reach another tree.
- **Clamber:** the orang-utan would use both its hands and feet equally.
- **Climb:** the orang-utan would ascend or descend a tree trunk.
- **Brachiate :** the orang-utan would travel primarily through suspension from both hands (similar to a gibbon).
- **Quadrupedal Walk:** the orang-utan's weight was distributed equally on its hands and feet, while on a horizontal substrate.

(8) Rest

The orang-utan was not engaged in any other primary activity.

Body Position and support were recorded as the secondary activity, with the following categories:

Body position:

- **Sit:** The majority of the orang-utan's weight was supported on its rear end, and the upper body was upright.

- **Stand:** The majority of the orang-utan's weight was distributed on two legs and was standing upright on a horizontal surface.
- **Lie Down**: the majority of the orang-utan's weight was supported on its torso and was in a horizontal or reclining position.
- **Hang:** the majority of the orang-utan's weight was supported by suspending from one or more hands or feet.
- **Quadrupedal:** the orang-utan's weight was distributed equally on its hands and feet while on a horizontal substrate.

Support types**:**

- **Tree:** the majority of the orang-utan's weight was distributed on a tree.
- **Liana:** the majority of the orang-utan's weight was distributed on a liana
- **Ground:** at least one of the orang-utan's feet was on the ground.
- **Day Nest:** this was built during the active period.
- **Night Nest:** this was the nest which the orang-utan built to sleep in over night.

2.2.6 Feeding bouts

Feeding bouts were recorded separately on my second data sheet (Appendix IV, Sheet 2). A feeding bout started when the orang-utan put food in its mouth and ended when the individual stopped eating, changed food type, engaged in another activity for more than 5 minutes or changed food patch.

For each feeding bout the start and end times were recorded to the nearest minute; the species and type of food eaten were recorded, and a specimen collected from all species eaten for later identification by a botanist. Every feeding tree was tagged, the diameter at breast height (dbh) measured and the tree height estimated in 5 m classes. If feeding on fruit or flowers, crop size was estimated using the same classes defined in 2.2.14 (ii) and feeding technique described for each species eaten.

2.2.7 Home range

Garmin 121 GPS units were used to record orang-utan position every half hour in order to identify home range; to map the location of feeding trees and to map the location of nests. This information was recorded on my third datasheet (Appendix IV, Sheet 3). The location of the focal individual was also recorded continuously on the grid map.

2.2.8 Long calls

Long calls are sex-specific calls made by adult males, usually flanged males (Delgado *et al.,* 2009). Whenever a long call was made by the focal animal, the following information was recorded on the fourth datasheet (Appendix IV, Sheet 4):

- Direction of long call.
- Length of long call (the start and stop time).
- Activity of the focal before, during and after making the long call.

Whenever a long call was heard from another individual, the following information was recorded

- Time long call heard
- Direction from where the call came from.
- Distance of individual (estimated).
- Reaction of focal to long call.

2.2.9 Social interactions

Every time the orangutan was in a party of 2 or greater, information on interactions between the orang-utans was recorded on datasheet 5 (Appendix IV, Sheet 5). Party Size was defined as the number of independent orang-utans present within 50 m (or line of sight) of each other. A female with a dependent offspring (baby or young infant) was classed as having a party size of 1. Orang-utans were only considered to be social when they were in a party of 2 or more.

The identity of the orang-utans present; the time the orang-utans came into party; and every time that interactions took place between the two animals was recorded on the social sheet, together with a description of the behaviour of both individuals at that time.

2.2.10 Assessing urinary ketones as a proxy for orang-utan energy balance.

Urine was collected once a day, and tested for the presence of ketones (Appendix IV, Sheet 6). These appear in the urine if body fats have been metabolised, and the presence or absence of ketones indicates whether orang-utans were in negative or positive energy balance at the time. This method for analysing weight loss has been used and tested by Knott (1999b) at Gunung Palung, West Kalimantan.

Urine was collected first thing in the morning, as the orang-utan would usually urinate when it left its nest. Two methods were used: (i) a plastic bag was positioned under the nest to collect the urine and (ii) urine was collected off vegetation and stored in a vial or syringe. At first, samples were brought back to camp for analysis and tested in the evening after the follow had ended, but often samples would change colour from an opaque white to a dark brown, which meant that no test could be carried out, so tests were performed on the urine as soon as it was collected. This change in colour was thought to be due to tannins in the urine.

Urine sticks (Multistix 10 SG) made for human clinical analysis were used and stored in a dehumidifying cupboard, with only one or two sticks being taken into the field at any one time. The presence of ketones was indicated by changes in colour as either: negative, trace, positive, or positive +. Samples were collected each month for 18 months from October 2003 to July 2005. For analysis, samples were scored using a binary scale (1 = negative, 2 = trace, 3 = positive and 4 = positive +.

2.2.11 Genetic analysis

Faecal samples were collected every time the orang-utan defaecated. Between 1 and 3 samples for each individual were collected for later DNA analysis. Samples were stored in 100% alcohol, and then refrigerated to help preserve sample integrity. An export permit and CITES import permit were obtained in order to transfer these samples from Indonesia to the University of Zurich, Switzerland, where DNA was extracted and analysed by Dr Michael Krutzen and Nadja Morf. Full details can be found in Chapter 8.

2.2.12 Disturbance

Human Disturbance

The presence or absence of humans, other than the observers, was recorded together with the normal behavioural data every 5 minutes, in order to assess the orang-utans reaction. Only data from habituated orang-utans were used, as these should display normal behaviour when the researcher was around.

If other humans were present, the kind of disturbance they were causing was recorded, including, for example, talking, logging, tapping trees and dogs barking.

The distance from the focal was also recorded.

Forest Quality

Habitat quality was assessed visually by the observer and recorded every 5 minutes, along with the main behaviour data. Seven habitat classes were defined in advance on a scale of most disturbed to least disturbed, based on the height of canopy and the percentage completeness of the canopy at 20 m and above. Using these same classes I identified the overall condition of the forest, by assessing habitat quality at fixed distances along transects within the grid. Finally, to confirm that these classes were distinct from each other, I measured a number of habitat variables including large-tree density, sapling density and canopy cover, among others, at a number of locations within the forest. See Chapter 6 for a full description of these methods.

2.2.13 Vegetation plots

Six permanent vegetation plots were set up along six transects to assess species diversity and identify fruit and flower production. The first plot was 400 m from the forest edge and each subsequent plot was further into the interior, at 1.1 1.6, 2.25, 2.75 and 3.5 km (Figure 2.2). Each plot contained two sub-plots (belt transects) set up in the following way: a belt transect measuring 5 x 300 m (0.15 ha) on the south side of the transect with all trees >6 cm dbh tagged, measured and identified; and a belt transect 5 x 500 m (0.25 ha) on the north side of the transect with all trees >20 cm dbh tagged, measured and identified. In all, 2.4 ha of forest were monitored for trees >20 cm dbh; whereas only 0.9 ha was monitored for trees >6 cm dbh. As well as trees, in all sub-plots lianas and figs >3 cm in diameter were also tagged and identified. Fruiting and flowering patterns were assessed using all sub-plots (2.4 ha), in which values for trees 10-19.9 cm dbh were corrected to take into account the smaller plot area for this size class.

.

Fruiting patterns were assessed in the middle of each month on the same day by the same team. The presence or absence of fruits (ripe or unripe), flowers (mature flowers or buds) and new leaves was recorded for all trees, figs and lianas using binoculars. Crop sizes for fruits, flowers and leaves were estimated using percentage cover.

Percentage cover:

> The proportion of the canopy containing the crop under investigation was given an abundance score (Chapman *et al.,* 1994; van Schaik, 1986).

1 = 1 – 25; 2 = 26 – 50; 3 = 51 – 75; 4 = 76 – 100 %

Samples of all leaves, flowers and fruits were collected from all trees within the permanent plots for identification, and stored at the CIMTROP herbarium. All samples were identified to family, genus or species. Samples from trees on which orang-utans fed were also collected for identification. Pictures of all orang-utan foods were taken in order to compile a food identification book.

2.3 RESEARCH PERIOD AND ACCOMPLISHMENTS

2.3.1 Grid system

In 2002 four months were spent designing and cutting a 9 km^2 grid system within the mixed-swamp forest. It was necessary to have a grid system due to the extremely dense nature of the habitat with much thorny pandan (*Pandanus* spp) making moving around the forest very difficult. The grid system extended 3 km west from the main walkway and 3 km south from the river (Figure 2.2). Transects were then cut every 250 m north to south, and east to west. This allowed easy access to the forest for searching. Transects were measured using a 50 m tape measure and marked every 12.5 m with red-and-white material in order to make it easy to locate the transect and locate one's position in the grid. All east-west transects were given a number and all north-south transects were given a letter (Figure 2.2).

2.3.2 Field research

Field research was carried out for 24 months, from August 2003 to September 2005 during which period 5519 hours of behaviour data were collected (Table 2.2). The first 3 months involved the finding and habituation of orang-utans, the setting up of the phenology plots in order to examine fruiting patterns, the classification of the different habitat classes and the clearing and marking of the grid system as many of the transects were overgrown.

Table 2.2 Total hours followed.

Follow type	**Number of follows**	**Hours**
All follows	669	5519
Nest-to-nest (full day) follows	329	3669
All habituated data (<15 Kiss Squeaks / hour)	594	5062
Habituated - nest-to–nest follows	313	3497
Habituated - all follows >3 hours	534	4954

Number of hours of habituated data (follows with <15ks/hour) including follows longer than 3 hours for all orang-utans are shown in Table 2.3. The first 15 individuals are those orang-utans with more than 50 hours.

2.3.3 Study animals

In all, 32 orang-utans were identified, of which 5 were still dependent on their mother (2 infants and 3 juveniles). Out of the 27 dependent individuals, 6 were flanged males, 10 were unflanged males, 5 were sexually-active females, 1 was a nulliparous female, and 5 were adolescent (NSAF and NSAM) (Table 2.3); of the independent individuals I managed to habituate 18.

Table 2.3 Orang-utans identified and followed during my study.

Orang-utan	Age/sex class	Date found	Habituated	Number of hours followed	Offspring
Beethoven	FM	September 03	Yes	432	
Franky	FM	November 03	No	207	
Hengky	FM	November 03	Yes	726	
Jupiter	FM	November 03	Yes	153	
Wallace	FM	August 04	Yes	276	
Drake	FM	July 04	Yes	24	
Kay / Darwin	UFM	November 03	Yes	112	
Leonardo	UFM	August 04	No	9	
Mozart	UFM	November 03	Yes	68	
Newton	UFM	March 04	No	5	
Oscar	UFM	March 04	No	2	
Qu	UFM	March 04	No	34	
Romeo	UFM	April 04	Yes	81	
Zeus	UFM	October 04	No	26	
Archimedes	UFM	February 05	Yes	12	
Shogun	UFM	March 05	Yes	33	
Cleo	SAF	September 03	Yes	509	Infant – Chivers (male)
Indah	SAF	November 03	Yes	1128	Juvenile – Indy (female)
Teresia	SAF	July 04	No	46	Infant – sex not known
Willow / Gracia	SAF	September 03	No	2	Juvenile – sex not known
Potret	SAF	April 04	Yes	31	Juvenile - Picasso
Viola	NLF	November 04	Yes	192	
Chopin	NSAF	September 03	Yes	40	
Feb	NSAF	September 03	Yes	940	
Shima	NSAF	May 04	Yes	191	
Einstein	NSAM	August 04	Yes	146	
Bengy	NSAM	February 05	No	0	

FM: Flanged male; **UFM**: Unflanged male; **SAF**: Sexually-active female; **NSAF**: Non-sexually-active female; **NSAM:** Non-sexually-active male; **NLF** = nulliparous female. Unidentified orang-utans are not included. An individual with two names is the same individual but originally thought to be different.

The age/sex ratio (Table 2.4) at Sabangau was found to be male biased with 1.9 males to each female overall, and 2.7 males to females for adults only.

Table 2.4 Sex Ratio.

Age/Sex Class	Sex Ratio Male / Female
Total male / Total female	1.9
Adult male / Adult female	2.7
Adolescent male / Adolescent female	0.8
Flanged males / unflanged males	0.6

2.4 DATA SET AND ANALYSES

2.4.1 Data set

I have behaviour data on 27 individuals, distributed unequally amongst all individuals as some were followed more than others, and some were not habituated. Thus, I only used data from habituated individuals. Both full-day and partial-day follows were used, except for follows <3 hours in length. See individual chapters for data sets which were used.

For all analyses I used all those individuals for which I had more than 50 hours of behaviour data after the exclusions listed in the above paragraph (Table 2.5), to make sure that I had a sufficiently large sample to represent that individual. The exception to this was the analysis of activity budgets between '*food*' availability classes, which were based on full day follows. To be included, an individual had to have a full day follow in two out of the three '*food*' availability categories.

Table 2.5 Number of habituated follows on each individual (excluding follows < 3 hours long).

Orang-utan name	Number of follows	Nest-to-nest follows	Hours followed
Indah	102	81	1044
Feb	96	55	916
Hengky	73	41	647
Cleopatra	48	28	444
Beethoven	46	26	418
Wallace	32	11	270
Shima	20	15	191
Viola	19	14	187
Jupiter	13	10	127
Einstein	11	8	120
Kay-Darwin	15	2	110
Franky	9	3	84
Romeo	9	4	77
Mozart	8	3	61
Hengky - Injured	*6*	*4*	*52*
Fenser	5	2	44
Chopin	4	1	39
Potret	5		28
Shogun	2	2	23
Unknown flanged	2		15
Zeus	1		11
Unknown individual	2		10
Gracia	1		7
Qu	1		7
Archimedes	1		7
Unflanged male	1		6
Teresia	1		6
Leonardo	1		4
Grand Total	534	310	4954

The follows on Hengky injured, were excluded for most analysis.

For a period of the study Hengky (FM) had a badly injured leg, and did not exhibit normal behaviour. The six follows in which he spent the majority of time in his nest were excluded from any activity analyses. Six follows on Indah were also excluded from some analyses, as she was being followed and harassed by an UFM, causing her not to exhibit normal behaviour but instead spending upwards of 8 hours a day sitting still.

2.4.2 Analyses

As there are no standardised methods for working out or presenting orang-utan activity data (Fox *et al.,* 2004), I presented a mean for each age/sex class (obtained by taking a mean for each individual for primary activities), and took a mean from this to get an overall mean for the population.

In order to standardise activity data between individuals and age/sex classes, I calculated the length of time spent performing each activity as minutes of a 12-hour day for individual means. Minutes were used, rather than percentages, for comparing primary data (feeding, travelling, resting, and social) between individuals and age/sex classes, as percentages can be misleading due to differences in active period length for individuals and age/sex classes.

Sample size

Due to the solitary nature of orang-utans it is difficult to get a large sample size for analysis. Thus other researchers have presented percentages only, or have analysed their data using individual means, monthly means of individuals or individual follow days as independent data points, due to having a low number of individuals. Having such a small number of individuals has caused considerable problems for orang-utan researchers in the past in regards to how one analyses and presents their data (Fox *et al.,* 2004), which is why so many different methods have been used. This small sample size, with uneven number of follows for each individual, or uneven number of individuals in each age/sex class, can increases the likelihood of type II errors (Fox *et al.,* 2004), i.e. 'false negatives', thinking there is no relationship when there is. Here I have used 'Individual means'. Due to the likelihood of type II errors, trends were discussed when no significant result was found. See specific chapter methods sections for detailed analysis used. Only habituated data and data >3 hours were used for most data sets. The exception was ranging, as all data were used for identifying range size.

Statistical analysis

For associations between two variables Pearson's correlation was used. For normally-distributed data, t-tests or ANOVA's, with Tukey *post-hoc* comparisons to determine significant pairwise differences, were used to test for differences. Chi-squared tests were also used for differences. Where data did not conform to the normal distribution, or where Levene's Test for Homogeneity of Variance produced a significant result, I used a Mann-Whitney test or a Kruskal-Wallis test followed by a Dunn's *post-hoc* test (Siegel and Castallan, 1988), in lieu of t-tests/ANOVA. Multivariate statistics used included Ordinary Least-squares Regression with dummy variables, Multinomial Logistic Regression (MLR) and General Linear Models (GLM) with repeated measures. These multivariate statistics were considered more robust than testing each variable separately in an ANOVA, and allow both ordinal and categorical data to be used. Both SPSS 11 and Gen-stat were used for analysis.

All tests were two-tailed unless otherwise stated, and a p-value of 0.05 was used for significance, as most tests were planned. For those that were not the Bonferroni correction was used.

Behaviour Data

Activities: activity data were described in two different ways. Primary activities were described by taking an average for each individual, using full-day follows only, which were then averaged to give a figure for each age/sex class. All analysis on primary activities was done on full nest-to-nest follows. Secondary activities were analysed by taking an absolute average for each age/sex classes, using all follows with >3 hours (see analysis section in all subsequent chapters).

Ranging: home range sizes were calculated using ArcView 3.2. Individual home ranges were estimated using two methods: (i) Minimum area polygon method (Hayne, 1949), (ii) Circle method (Hayne, 1949; Trevor-Deutsch and Hackett, 1980), whereas core area was estimated using the fixed kernel method (Worton, 1989).

Day ranges were calculated using distance estimates for each individual, which were then averaged to get a mean for each age/sex class (See Chapter 7 for detailed analysis).

Feeding and diet: The percentage of feeding time an orang-utan feeds on different food types was analysed overall, and by month (Chapter 4). To assess changes in diet between seasons, individual days were used as independent data points and for this all follows with less than 2 hours feeding were excluded. All species which were fed on for only 1 bout or less than 6 minutes in total were called ‘try foods’ based on the same criteria as Harrison (2009); and thus were not included when working out productivity levels, but were included in the food list.

CHAPTER 3

FOREST COMPOSITION, SEASONALITY AND PRODUCTIVITY

3.1 INTRODUCTION

Assessing forest diversity and productivity are important components of most ecological studies. The knowledge of what plant species are present in the habitat and their reproductive cycle with regards to seasonal flowering and fruiting patterns is extremely important for understanding the behavioural ecology of a primate. The diversity of tropical peat-swamp forest has been studied mainly in Sarawak and peninsular Malaysia (Anderson, 1963; Janzen, 1974; Ibrahim, 1997; Hanum and Lepun, 1999; Asyraf and Mansor, 2002), and has also been the focus of some studies in the Sabangau forest (Shepherd *et al.,* 1997; Page *et al.,* 1999; D'Arcy and Page, 2002); but no studies into reproductive cycles or fruiting phenology have yet been done here.

Asian forests are more temporally and spatially variable in fruit production than other tropical forests (Fleming *et al.,* 1987), and exhibit community-wide supra-annual masting events (SAM), which are well documented in Asian forests (Janzen, 1974; Ashton *et al.,* 1988; Cannon *et al.,* 2007a; Curran and Leighton, 2000; Wich and van Schaik, 2000; Brearley *et al.,* 2007). These masting events occur in most dipterocarp-dominated forests, during which a number of taxa fruit at the same time and are linked to the El Niño-Southern Oscillation (ENSO) phenomenon in most areas, but with varying strength (Wich and van Schaik, 2000). These masting events have been found to be asynchronous between nearby areas in Sumatra (Wich and van Schaik, 2000), thus allowing frugivorous vertebrates to migrate between forest types. In Borneo, the ENSO effect is stronger, and masting events are more synchronised (Curran *et al*., 1999; Wich and van Schaik, 2000). Peat-swamp forest, on the other hand, does not participate in these masting events and some forests do not have one large peak in fruit, which can be classed as a single fruiting season, but instead exhibit many fruiting peaks (Cannon *et al.,* 2007a, 2007b). Thus, unlike dipterocarp-dominated forest-types, peat-swamps have a more regular and even fruiting pattern (Cannon *et al.,* 2007a, 2007b, Marshall *et al*., 2009b).

Because most research has been conducted on examining SAM events in dipterocarp-dominated forests, little in-depth research has been done into the reproductive patterns of peat-swamp forest species, although Marshall *et al.* (2009b) suggests, in a recent comparative study, that Sumatran peat-swamp forests are more productive than ones in Borneo, owing to more fertile soils; and that dipterocarp-dominated forests are more likely to experience extreme temporal fluctuations in fruit availability due to masting events.

Most tree species have a reproductive cycle which is influenced by climatic parameters (Bendix *et al.,* 2006) and individuals of those species fruit in synchrony with each other. Some of the explanations why species fruit in synchrony include greater seed output and thus fitness, as flowering in synchrony increases the number of plants an individual can exchange genes with; also pollinators behave in a density-dependent manner, being more attracted to higher abundances of flowers. Plants that are asynchronous have a lower reproductive output resulting from low pollination levels, and high seed predation, as predators are more attracted than pollinators to lower abundance of flowers and fruits (Augspurger, 1981). Temporally-segregated fruiting (asynchronous species) may minimise competition and maintain resident populations of dispersal agents, whereas temporally-aggregated fruiting (synchronous species) may enhance dispersal, and be influenced by dispersal agents which vary seasonally (Poulin *et al.,* 1999). Production in peat-swamp forests is spatially separated and does not exhibit a synchronised SAM as discussed above, hence, fruit availability is regular and evenly distributed over time. There are two potential systems in which this can occur, either: (i) this forest has a high proportion of species that have a synchronised fruiting cycle, i.e. all individuals of that species fruit at once, but the fruiting cycles for the various species are temporally separated from each other; or (ii) this forest has a large number of species that have asynchronous fruiting cycles, i.e. not all individuals of that species fruit at once, so there are nearly always individuals of that species in fruit. Either system provides a near-continuous supply of fruit which is available to animals, and a combination of strategy (i) synchronous species which are temporally separated and (ii) asynchronous species, will allow a wide variety of fruits to be available all year round.

3.2 OBJECTIVES

In this chapter I will try to identify the reproductive cycles for species within the Sabangau, to explain the observed productivity patterns. I will calculate overall monthly fruit and flower availability, and provide estimates of the amount of '*food*' (fruits and flowers) available for orang-utans on a monthly basis. Although food clearly includes all items eaten by orang-utans, including leaves, bark and termites, in this analysis and subsequent discussion when food appears in italics and between apostrophe marks ('*food*'), it stands for 'seasonally-limited food, i.e. fruits and flowers, and will always appear this way unless otherwise stated. Using these data I will classify each month as high, medium or low production. These productivity levels will be used to assess the effect of *'food'* availability on orang-utan behaviour, as well as setting guidelines for future comparisons of this type in the Sabangau peat-swamp forest. Species dominance and composition will also be examined.

Questions addressed in this chapter:

- What tree species and families were dominant in the forest?
- What were the fruiting and flowering patterns and what was influencing them?
- What were the productivity levels and how were they defined?

What reproductive strategies (synchronous or asynchronous) were used, on both a species and community level?

3.3 METHODS

In 6 phenology plots all trees > 6 cm dbh (2574 stems), lianas > 2 cm dbh (37) and figs > 2 cm dbh (10) were checked once a month, for 24 months from September 2003 to August 2005, for the presence of fruits, flowers and new leaves (see Chapter 2 for a detailed description of plot set-up and field methods).

3.3.1 Forest composition

Dominance

The total number of tree families present in the plots was counted, and each assessed for dominance using Ganzhorn's (2003) categories for dominance ratings: (i) "Eudominant" (E) – if family accounts for >10% of individuals; (ii) "Dominant" (D) - 5-10% individuals; (iii) "Subordinate" (S) - 2-5% individuals.

Species density

The number of trees/hectare (ha) was counted for three different size classes: >6, >10 and >20 cm dbh, in order to identify the dominant size class of trees in the study area. Species density/ha was also calculated for trees >10 cm dbh in order to work out dominant species. A cumulative frequency curve of new species encountered in the plots against number of stems identified was used to see if most species represented in the forest had been in the plots. For this analysis trees >10 cm dbh were used.

3.3.2 Fruiting, flowering and new-leaf phenology.

Forest Structure

First I examined the fruiting data to estimate the size at which trees became reproductive. Although this inevitably varies between species, I examined this at a community-level, because the small sample sizes in many cases for many species (only 1 or 2 stems) precluded this kind of analysis. I also examined the orang-utan feeding-bout data to see in what size of tree they most commonly fed. These data combined (see section 3.4.2) showed that trees below 10 cm dbh rarely fruited, and were rarely fed in by orang-utans, so I discarded all data from trees smaller than 10 cm dbh for the purposes of working out monthly fruit and flower availability for orang-utans.

Reproductive phenology

For each month, I calculated the percentage of stems with fruits, flowers and new leaves, and calculated this separately for trees >10 cm dbh, lianas and figs. The percentage of fruit available was also calculated with the most dominant species, *Palaquium leiocarpum*, excluded, to see how much influence this species had on overall tree fruiting patterns. The phenology plots were set up in such a way that trees >20 cm dbh, lianas and figs were in a total plot area of 2.4 ha, whereas trees 10-19.9 cm dbh were in a plot area of 0.9 ha. In order to (i) include all sampled trees in these analyses and (ii) represent each size class in proportion to their availability, I used the following equation to estimate monthly fruit availability:

$$\text{Fruit availability} = [\ F_{10} / N_{10} * P_{10}\ ] + [\ F_{20} / N_{20} * P_{20}\ ]$$

where: F = the number of trees in fruit for each size class (10 = 10-19.9 cm dbh; 20 = >20 cm dbh), N = the total number of trees sampled for each size class and P = the proportion of trees that are in each size class (calculated from the 0.9 ha subset of the plots; $P_{10} + P_{20} = 1$).

This was then repeated for flowers and for new leaves.

Orang-utan food availability

For this analysis I included only those species for which either the fruits or flowers were eaten by orang-utans (see dietary list in Chapter 4). The fruits or flowers of a species had to have been eaten in at least 2 feeding bouts or eaten for more than 6 minutes to be considered food (Harrison, 2009). Because these data will be compared against activity budgets, I felt it necessary to get the most accurate figure for '*food'* availability, which will ultimately affect activity budgets and energy gain due to fluctuations in their availability. Because flowers are an important part of the orang-utan's diet in Sabangau, with some species preferred over fruits (Chapter 4), it was necessary to include flowers with fruits as *'food'* availability, rather than just using fruit availability. This is in contrast to most great ape research, including orang-utans, where just the availability of fruit has been used to investigate foraging behaviour and energetics (Galdikas, 1988; Knott, 1998, 1999b, 2005; Wich *et al.,* 2006a). In past studies flowers were not considered important in orang-utans diet (Knott, 2005), as they appear less in the diet than leaves at most sites except Sabangau (Chapter 4 Table 4.7). Thus, flowers are ignored in some studies, or lumped together with leaves or other items and referred to as *'fallback'* foods; these are foods which are permanently or frequently available but are usually ignored (Tutin *et al.,* 1991).

All species of tree, fig and liana that were eaten by orang-utans were grouped and referred to as 'stems'. Stems from which orang-utans eat fruit are referred to as 'Orang-utan Fruit

Stems', and stems from which orang-utans eat flowers are referred to as 'Orang-utan Flower Stems'. When fruits and flowers were combined together, they were referred to as '*food'* stems.

I used the following equation to measure monthly '*food*' availability:

'*Food*' availability = $[\ (Fr_{10} + Fl_{10}) / N_{F\ 10}\ * P_{10}\ ] +\ [\ (Fr_{20} + Fl_{20}) / N_{F\ 20}\ ] * P_{20}\ ]$

where: Fr = the number of Orang-utan Fruit Stems in fruit for each size class, Fl = the number of Orang-utan Flower Stems in flower for each size class, N_F = the total number of Orang-utan Fruit and Flower Stems sampled for each size class. P = the size classes are as before. If a stem had both fruit and flowers available, it was only counted once, i.e. it is only one available '*Food'* stem.

The percentage of trees flowering (buds and flowers were grouped together), and fruiting (ripe and unripe fruits grouped together) were investigated in three ways: (i) all trees within the phenology plots, (ii) only orang-utan feeding trees (species that were fed on by orang-utans), and (iii) orang-utan feeding trees excluding hangkang (*Palaquium leiocarpum*) (Figure 3.7), as hangkang was a very dominant tree in the forest, but was not a major orang-utan food (Chapter 4).

3.3.3 Fruit and flower productivity levels

Productivity levels refer to the different levels of fruit and flowering phenology. For all productivity analyses, I used orang-utan (OU) *'food'* stems (only species that orang-utans fed from) rather than using all species, as this was a more accurate figure when comparing activity budgets with '*food'* availability.

Productivity measurements were split into 3 levels, in order to compare activity budgets and diet with various levels of '*food'* availability. The maximum monthly productivity was just below 12%, and the productivity levels were then worked out by dividing this into 3 equal classes. Each month was assigned a productivity level of high, medium or low:

Level 1 – Low (< 4 %); Level 2 – Medium (4-8 %); Level 3 – High (> 8 %)

These productivity levels will be the standard for any future comparative studies in the Sabangau.

3.3.4 Degree of synchrony

Although data are limited for assessing reproductive cycles because of the short study, an attempt was made to classify tree species (lianas and figs were not included due to small sample size) as either synchronous or asynchronous by examining their flowering patterns. Because these data were worked out using monthly data, the standardised formula of Bolmgren (1998) could not be used. Most datasets used for assessing reproductive patterns are long-term datasets (more than 10 years), or individual trees which have been assessed over days and months for classifying whether they have a synchronous or asynchronous reproductive cycle. Asynchronous species are more likely to have individuals reproducing all year round, and thereby be important for orang-utans. For this assessment, as data were limited to 24 months and were only taken once a month, I was not able to classify species as annuals or not. Instead, I have used a very simple classification system to classify whether a species is synchronous or asynchronous. This system, which may or may not be fool-proof as arbitrary cut-off points have been used, enabled me to classify whether a species had a precise flowering peak, or if it was available all year round, and thus help explain why some foods were appearing in the orang-utans diet more than others. The rationale used is as follows:

If a species had at least 1 month with 50% or more of reproductive individuals flowering together and if, in 50% or more of the remaining months, only 10% or less of the reproductive individuals flowered together, the species was classified as synchronous. If a species had no months where 50% or more individuals flowered, then it was classified as asynchronous.

The number of months that fewer than 10 % of stems were flowering was divided by the total number of ‘low-flower’ months, i.e. the number of months that flower production was < 50 %, to give a ‘synchronicity’ score. The species with the highest values for this score were considered to be the most synchronous.

In order to calculate this score, all trees >6 cm dbh were included in the analysis, with the following exceptions: All individual trees which did not flower at least once during the 24-month study were not considered reproductive individuals and were thus excluded, and all species which had less than 5 individuals in the sample were excluded.

Thus, although this rationale may not be accurate with regards to individual synchrony, it allows me to get an idea of species which may exhibit a synchronous or asynchronous reproductive cycle. It recognises those species that had flowering peaks, in which many individuals flowered at the same time, and flowering troughs, during which very few individuals flowered.

3.4 RESULTS

3.4.1 Forest composition

Species Dominance

In 0.9 ha of forest 2108 trees >6 cm dbh were tagged and measured. In all 138 species in 38 families were identified (Table 3.1; see Appendix V for species list and species density).

Table 3.1 Number of species, genera and families identified in the phenology plots.

Trees Only	Species	Genus	Family
Number > 6 dbh	138	74	38
Number > 10 dbh	110	62	33
Number > 20 dbh	79	48	29

The cumulative frequency of new species is shown in Figure 3.1. The curve starts to level off after 800 stems, which indicates that most species are represented in the plots, except for some very rare species, which were present in orang-utans diet, but were not present in the phenology plots.

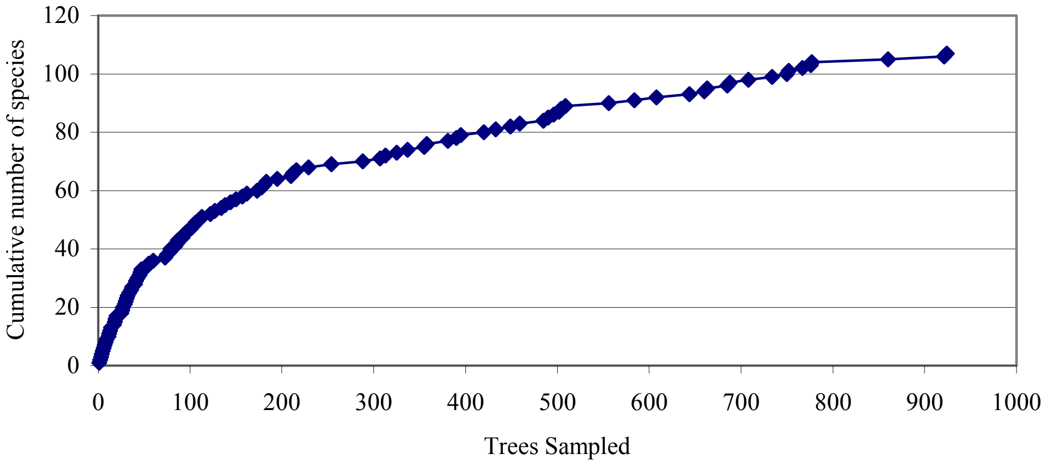


Figure 3.1 Species-collection curve (trees >10 cm dbh)

All 38 families found in the phenology plots were assigned a dominance rating of Eudominant, Dominant or Subordinant (Ganzhorn, 2003) (Table 3.2).

Table 3.2 Family dominance within the phenology plots.

Family	% Stems > 6 cm dbh	**Rating**
Myrtaceae	12.21	E
Clusiaceae	8.4	D
Annonaceae	6.11	D
Euphorbiaceae	6.11	D
Fagaceae	6.11	D
Sapotaceae	5.34	D
Burseraceae	4.58	S
Ebenaceae	4.58	S
Lauraceae	4.58	S
Dipterocarpaceae	3.82	S
Sapindaceae	3.82	S
Myristicaceae	3.05	S
Anacardiaceae	2.29	S
Elaeocarpaceae	2.29	S
Icacinaceae	2.29	S
Melastomataceae	2.29	S
Fabaceae	1.53	R
Hypericaceae	1.53	R
Meliaceae	1.53	R
Moraceae	1.53	R
Rubiaceae	1.53	R
Sterculiaceae	1.53	R
Theaceae	1.53	R
Anisophyllaceae	0.76	R
Apocynaceae	0.76	R
Aquifoliaceae	0.76	R
Celesteraceae	0.76	R
Crypteroniaceae	0.76	R
Linaceae	0.76	R
Magnoliaceae	0.76	R
Myrsinaceae	0.76	R
Pittosporaceae	0.76	R
Rhizophoraceae	0.76	R
Rutaceae	0.76	R
Simaroubaceae	0.76	R
Tetrameristaceae	0.76	R
Thymelaeaeceae	0.76	R
Tiliaceae	0.76	R

E: Eudominant; D: Dominant; S; Subordinate; R: Rare

Only 1 family, Myrtaceae, was classed as ‘Eudominant’, and 5 were classed as ‘Dominant’ - Annonaceae, Clusiaceae, Fagaceae, Euphorbiaceae and Sapotaceae. Ten families were classed as ‘Subordinate’, and the 23 families with a value less than 2% were considered rare.

Species density

The top 20 commonest tree species are shown in Table 3.3. The commonest is *Palaquium leiocarpum* (268 individuals/ha), followed by *Shorea teysmanniana*, *Calophyllum hosei, Horsfieldia crassifolia* and *Blumeodendron elateriospermum* (see Appendix V for density of all species).

Table 3.3 Density of the 20 commonest species in the Sabangau.

Family	Genus	Species	Density / ha	N
Sapotaceae	*Palaquium*	*leiocarpum*	267.9	241
Dipterocarpaceae	*Shorea*	*teysmanniana*	141.1	127
Clusiaceae	*Calophyllum*	*hosei*	116.7	105
Myristicaceae	*Horsfieldia*	*crassifolia*	113.3	102
Euphorbiaceae	*Blumeodendron*	*elateriospermum / kurzii*	77.8	70
Euphorbiaceae	*Neoscortechinia*	*kingii*	62.2	56
Annonaceae	*Mezzetia*	*leptopoda / parviflora*	57.8	52
Myrtaceae	*Syzygium*	*havilandii*	56.7	51
Anacardiaceae	*Campnosperma*	*coriaceum*	53.3	48
Clusiaceae	*Mesua*	sp. 1	52.2	47
Meliaceae	*Sandoricum*	*beccanarium*	52.2	47
Ebenaceae	*Diospyros*	*bantamensis*	51.1	46
Myrtaceae	*Syzygium*	sp. 3 *cf. nigricans*	51.1	46
Icacinaceae	*Stemonurus*	*cf. scorpiodes*	48.9	44
Rutaceae	*Tetractomia*	*tetrandra*	46.7	42
Annonaceae	*Xylopia*	*fusca*	44.4	40
Myrtaceae	*Syzygium*	sp. 2	38.9	35
Lauraceae	*Litsea*	sp. 1 *cf. resinosa*	36.7	33
Fagaceae	*Lithocarpus*	sp. 1 *cf. dasystachys*	35.6	32
Hypericaceae	*Cratoxylon*	*glaucum*	35.6	32

N=Number of stems > 6 cm dbh in 0.9 ha

Forest structure

Over 50 % of all trees measured were in the size class 6-10 cm dbh (Table 3.4), with trees >30 cm dbh representing only 1.8 % of all trees measured; 90 % of all trees have a dbh of less than 20 cm. (See Chapter 6 for detailed forest structure analysis and description).

Table 3.4 The number of trees in six tree size classes.

Dbh	N	%
6-9.9	1122	53.0
10-14.9	580	27.5
15-19.9	207	9.8
20-24.9	110	5.2
25-29.9	51	2.4
>30	38	1.8
Total	2108	100

3.4.2 Reproductive phenology

Size of reproductive and feeding trees

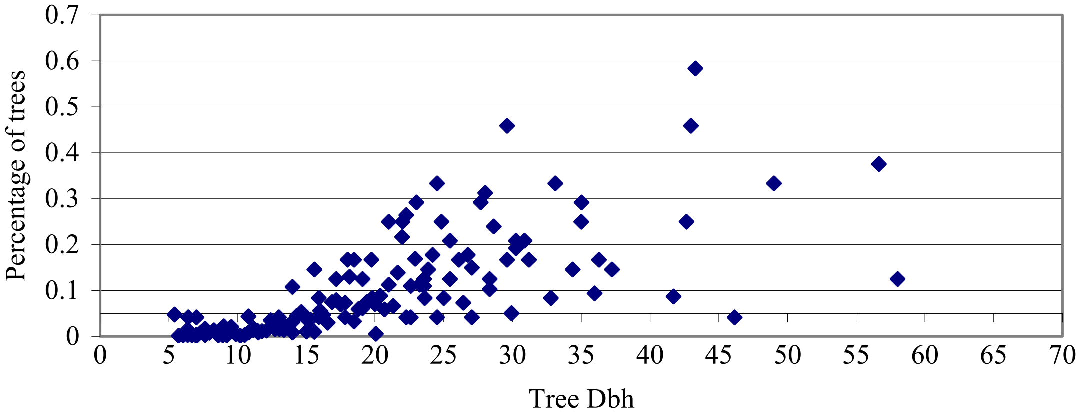


Figure 3.2 Percentage of trees with fruits or flowers from different size trees (cm dbh)

It seems that many species do not become reproductive until larger than 10 cm dbh (Figure 3.2). There is a marked difference in the percentage of trees with fruits, flowers and new leaves when using different cut-off points (>6 cm, >10 cm and >20 cm). The class with trees >20 cm dbh had the highest percentage of trees with fruits, flowers and new leaves (Figure 3.3).

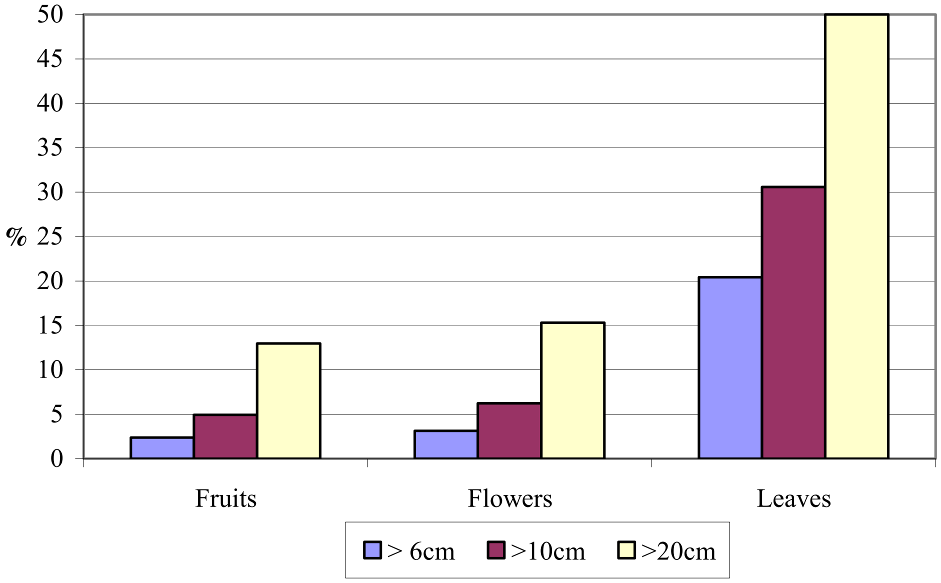


Figure 3.3 Mean monthly percentage of trees with fruits, flowers and new leaves using different dbh cut-off points.

For analysing *'food'* availability for orang-utans, it was important to know from which size class of trees orang-utans were feeding in order to choose which size class to use (>6, >10 or >20 cm dbh). The mean size of trees from which orang-utans fed was 27.7 cm dbh (*sd 14.0*), and the 95 % cut-off for bouts ($p<0.05$) was 12 cm dbh (Figure 3.4). Thus, trees <10 cm dbh were rarely fed on. I used trees >10 cm dbh for all analyses, as this fell into one of the size class ranges already used for assessing fruiting and flowering patterns. This cut-off is also more comparable with other sites, rather than 12 cm dbh when assessing *'food'* availability.

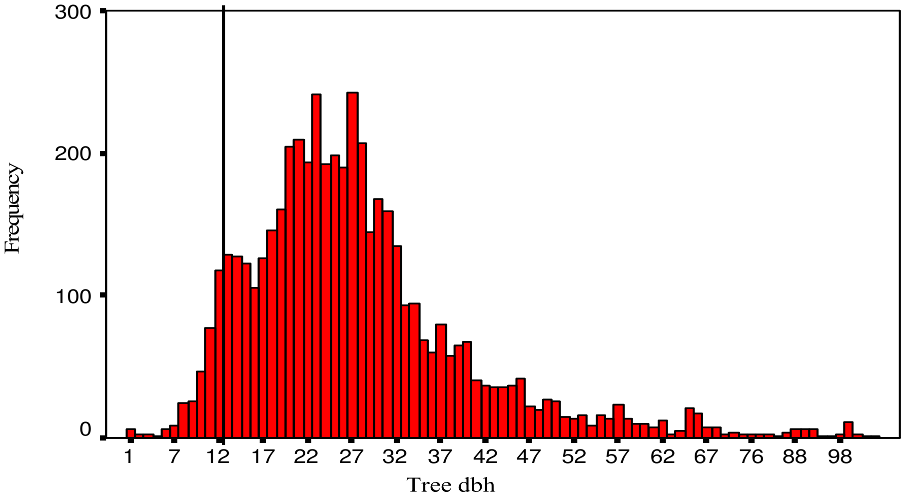


Figure 3.4 Size of trees from which orang-utans fed (fruit and flower feeding bouts). (The black vertical line indicates the 95% bouts cut off).

Reproductive patterns

The percentage of trees with fruits, flowers and leaves fluctuated from month to month (Figure 3.5). Flowering stems did not exceed 12 %, whereas fruiting stems did not exceed 10 % over the 2-year period, In 13 of the 24 months the number of trees fruiting was less than 5 %, and in 3 months (May, June and July 2004), the number of trees in fruit was less than 3 % (Figure 3.6). Flowering only dropped below 5 % in 5 months, but exceeded 10 % in September and October 2004. New leaf production, on the other hand, did exceed 50 %, and only once was lower than 10%, indicating that although new leaf production did fluctuate, it remained above 20% for most of the study period, and thus was not considered a limited resource in the same way that fruits and flowers were (Figure 3.5).

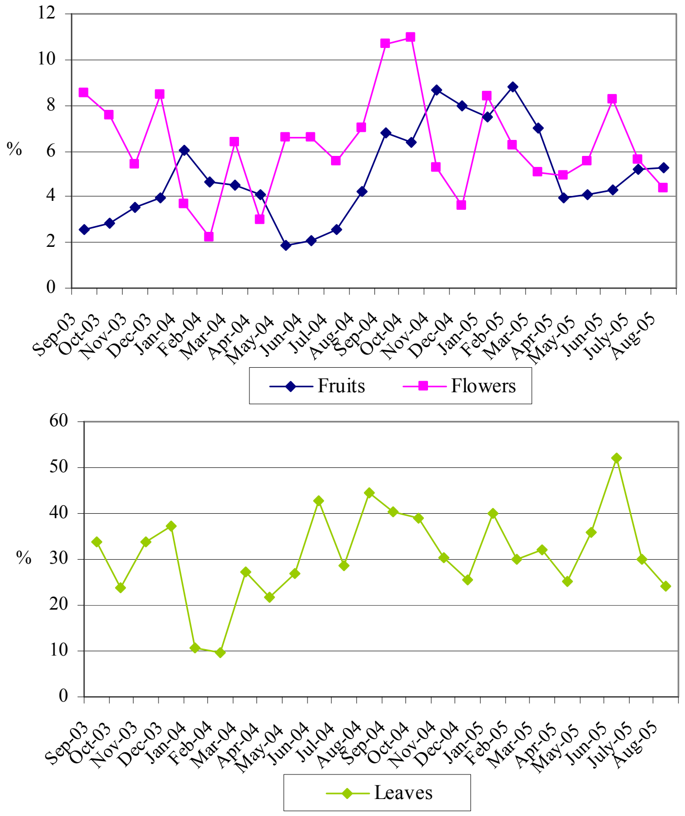


Figure 3.5 Monthly percentage of trees with fruits, flowers and new leaves >10 cm dbh.

Flowering and fruiting events were usually synchronised, with one occurring after the other, but, on a community level there was no correlation between the two (Pearson correlation; r^2=-0.09, n=24, p=0.889 (ns). If fruit production was displaced, however, it took 4 months until the correlation was found to be significant (r^2=0.24, n=20, p=0.014), whereas Figure 3.5 appears to suggest only a 1 or 2 month displacement.

Influences of rainfall and temperature on production

When comparing fruiting, flowering and new-leaf production with rainfall (Figure 3.6) and temperature (Figure 3.7), only rainfall was correlated. A significant negative correlation was found between flower and new-leaf production and rainfall (Pearson correlation; flowers: r^2=-0.24; n=24, $p<0.014$ (large effect); new leaves: r^2 =-0.18, n=24, p=0.038 (large effect), but no significant correlation was found for fruits (r^2=0.138, n=24, p=0.082 (ns)), although the direction was positive indicating that fruit production increased with rainfall, whereas flowers and new-leaf production increased with decreased rainfall. Thus, rainfall plays an important role in both fruit and flower production, with peak flowering occurring during the dry season, and peak fruiting occurring during the wet season (Figure 3.6). No correlation was found for fruits, flowers or new leaves against temperature (fruits: r^2=-0.065, n=24, p=0.229, (ns); flowers: r^2= 0.092, n=24, p=0.656, (ns); new leaves: r^2=0.0051, n=24, p=0.738, (ns)).

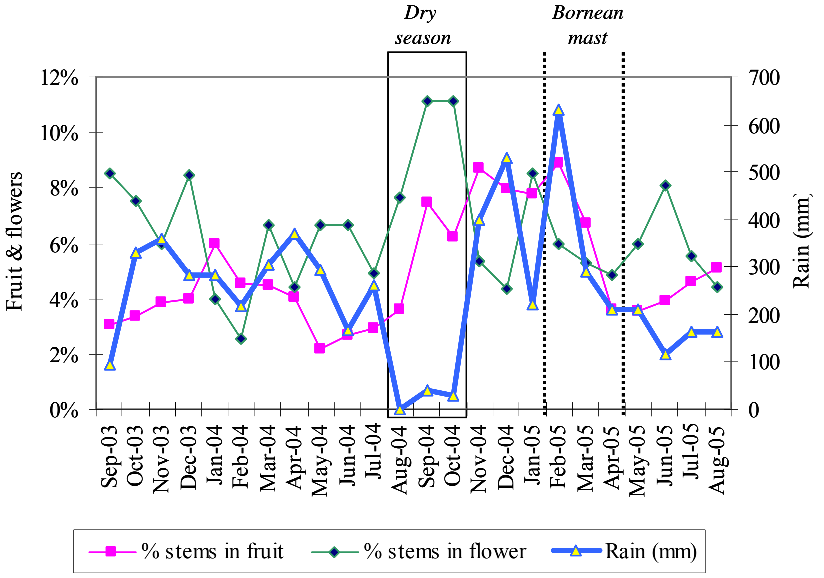


Figure 3.6 Fruiting and flowering patterns in relation to rainfall. February to April 2005 there was a mast fruiting event in Borneo

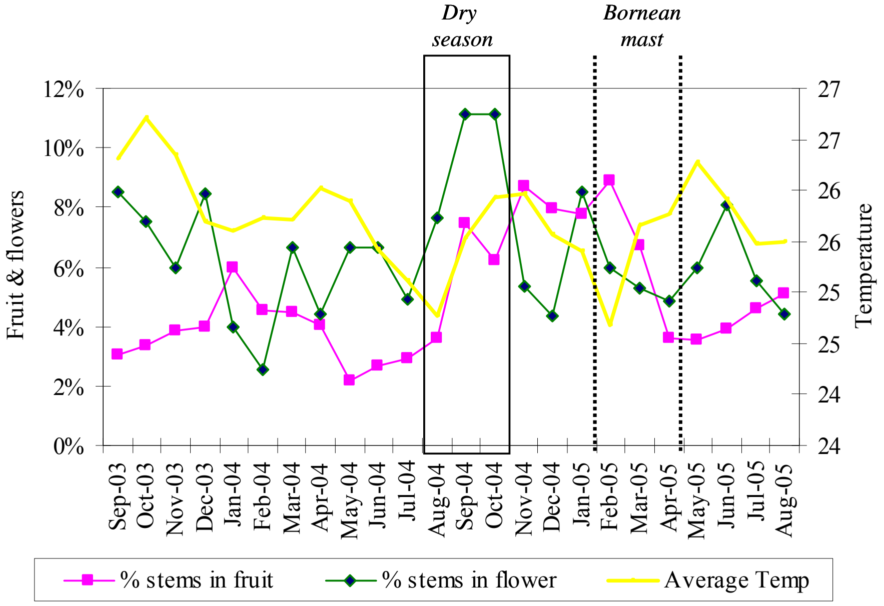


Figure 3.7 Fruiting and flowering patterns in relation to temperature. February to April 2005 there was a mast fruiting event in Borneo.

Fruiting trees

Fruiting patterns for all trees, orang-utan food trees only and for orang-utan food trees excluding hangkang (*Palaquium leiocarpum*), were calculated to see if there were any differences in the fruiting pattern when these different criteria were applied (Figure 3.8).

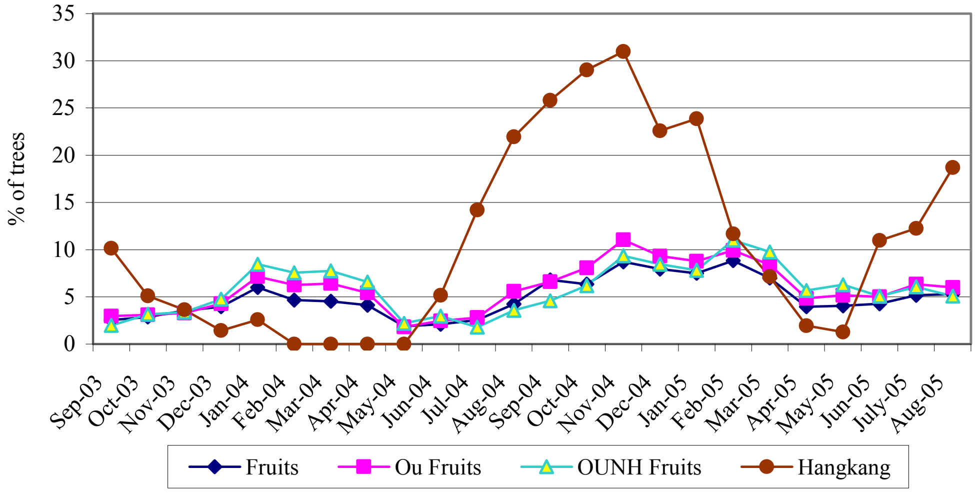


Figure 3.8 Percentage of trees fruiting for (i) all species (ii), for only those species eaten by orang-utans, (iii) for those species eaten by orang-utans excluding hangkang, and (iv) hangkang only. (Trees = all trees in the phenology plots; Ou Fruits=orang-utan feeding species only; OUNH Fruits = orang-utan food species excluding *Palaquium leiocarpum (*Hangkang)).

When hangkang was included the percentage of trees in fruit was about 2 % higher when hangkang was fruiting, and the opposite was true when hangkang was not fruiting. As it was an orang-utan food, and did not appear to change the actual fruiting pattern too much, I decided not to exclude hangkang in all subsequent analyses.

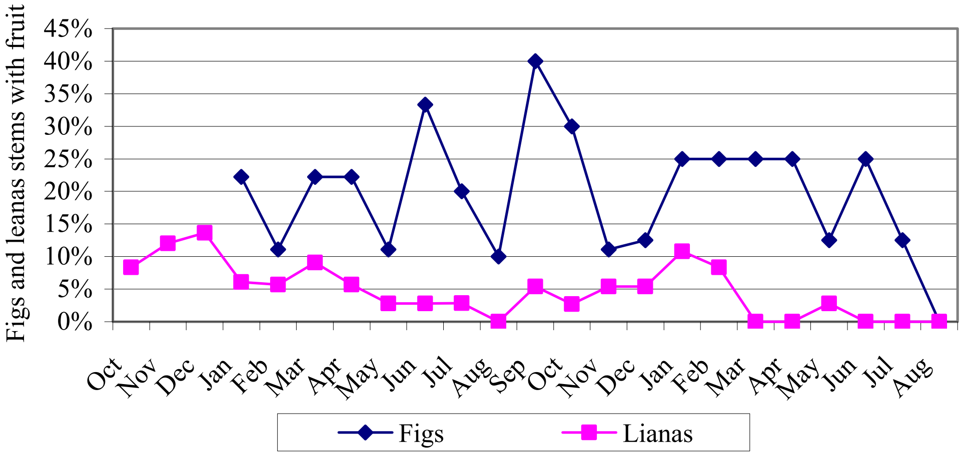


Figure 3.9 The percentage of figs and lianas (>2 cm dbh) with fruit each month.

Figs were found in fruit every month with one exception, and the percentage of figs fruiting rarely fell below 10 %. For lianas, they were found not to fruit for 7 of the 24 months, and rarely exceeded 10 % (Figure 3.9). Due to the low number of figs and lianas (Appendix VI), they were included with trees as *stems*.

3.4.3 Fruiting and flowering stems.

Different flowering and fruiting patterns are shown for a number of different criteria: Figure 3.10: for flowers (all flowering stems and only flowering stems that orang-utans fed from); and Figure 3.11 for fruits and '*foods*' (all stems with fruit (% stems in fruit), all fruit stems eaten by orang-utans (% OU fruit stems) and all fruits and flower stems orang-utans feed from (% OU *'food'* stems)).

The percentage of orang-utan flower stems in flower was not as high as that of all flower stems (Figure 3.10), and the percentage of all stems in fruit were lower than that of orang-utan *'food'* stems (fruits and flowers only eaten by orang-utans) (Figure 3.11). Thus, I decided to use orang-utan *'food'* stems for all analyses, even though the percentage of stems in fruit and percentage of orang-utan *'food'* stems were highly correlated (Pearson correlation: r^2=0.94, n=24; p<0.001), as I considered this a more appropriate figure when comparing food availability against orang-utan activity budgets (Chapter 5).

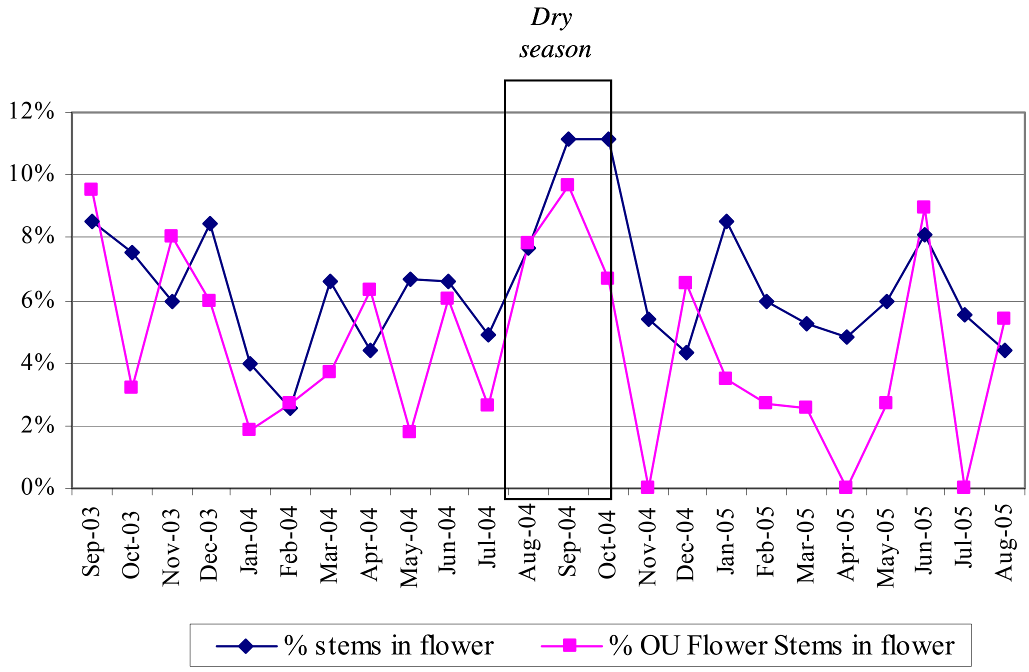


Figure 3.10 Percentage of stems in flower and percentage of orang-utan flower stems in flower. (% stems in flower = all stems in flower; % OU flower stems = only species eaten by orang-utans.

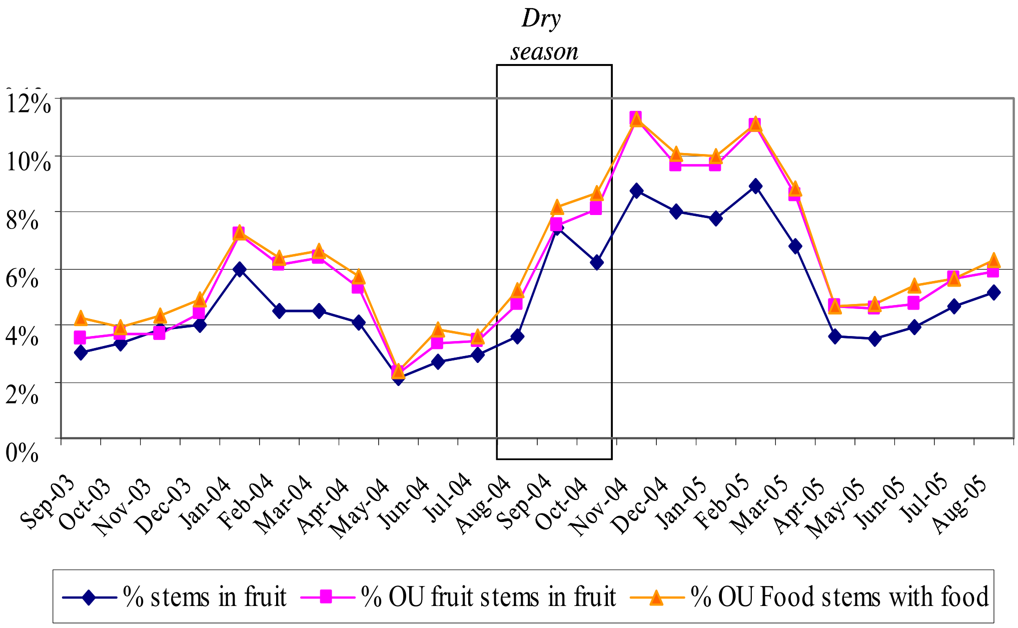


Figure 3.11 Reproductive patterns for three different criteria.

3.4.4 Productivity levels

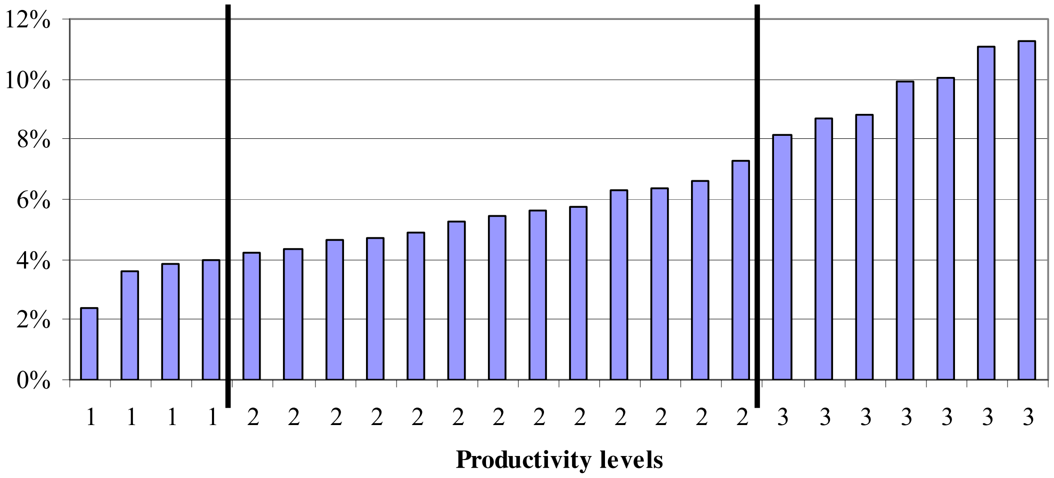


Figure 3.12 '*Food'* availability (the percentage of OU *Food* stems with *Food*) for each month in ascending order and divided into different productivity levels. Black vertical lines separate the three levels.

The productivity level that was commonest during the study period was Level 2, medium productivity, followed by Level 3, high productivity and least common was Level 1, low productivity, with only 4 months (Figure 3.12). This indicates that productivity was medium to high for 20 out of the 24 study months.

Activity budgets and diet were compared to these different levels of '*food'* availability to see if there was any difference in orang-utan behaviour between high *'food'* and low' *food'* periods (Chapters 5 and 6).

3.4.5 Degree of synchrony

Species can have a reproductive cycle which is **synchronous** (all or most of the individuals within that species which are of reproductive age (size) reproduce at the same time), or **asynchronous** (not all individuals reproduce at the same time). For this analysis only stems that flowered at least once were included in order to identify species which had a synchronous or asynchronous reproductive pattern (Table 3.5). In all, 75 % of all tree species were found to have at least one stem reproduce at least once during the 24-month study period. Out of all species identified, only 34 did not reproduce.

Of 42 species that could be classified as having a synchronous or asynchronous reproductive cycle, 62 % were classed as synchronous, and 24 % as asynchronous (Table 3.5). The remaining 14 % were classed as possibly being asynchronous, because, although they had a peak in one month where over 50 % of individuals flowered, and they had high level of background flowering, with between 10 and 50 % of individuals flowering in most of the remaining months, e.g. *Campnosperma coriaceum* had more than 50 % of individuals flowering for 11 of the 24 month study, indicating that this species is flowering for extended periods of time. Figures 3.13 and 3.14 show examples of synchronous and asynchronous flowering cycles. The synchronous species all have a defined peak with over 50 % of individuals flowering at once, e.g. *Calophyllum hosei* flowered in November 2003 and again in December 2004, whereas the asynchronous species have a low level of individuals flowering at any one time, but were found flowering for most months of the year, e.g. *Blumeodendron elateriospermum*.

Of the 13 species from the top 20 list of orang-utan foods (Chapter 4) which could be classified in this way, 53% were synchronous and 23% asynchronous. The reproductive cycle of the synchronous species appear to have defined peaks and troughs, with each species spatially separated or segregated from each other (Figure 3.13), whereas the asynchronous species had low levels of individuals reproducing throughout the year (Figure 3.14).

Table 3.5 Synchronous and asynchronous species of trees.

Family	**Genus**	**Species**	Total number of *rep. ind. for trees	MAX % of ind. trees Fl	No of months > 50 % of ind. trees Fl	No of months < 10 % of ind. trees Fl	Sync. Score
SYNCHRONOUS							
Dipterocarpaceae	*Shorea*	*teysmanniana*	39	70	1	22	**96**
Thymelaeaceae	*Gonystylus*	*bancanus*	6	67	1	22	**96**
Clusiaceae	*Calophyllum*	*hosei*	57	71	2	20	**91**
Euphorbiaceae	*Neoscortechinia*	*kingii*	31	77	1	20	**87**
Hypericaceae	*Cratoxylon*	*arborescens*	10	100	1	20	**87**
Clusiaceae	*Calophyllum*	*soulattri*	7	57	1	19	**83**
Myrtaceae	*Syzygium*	*havilandii*	14	64	1	19	**83**
Clusiaceae	*Garcinia*	*bancana*	6	50	2	18	**82**
Dipterocarpaceae	*Dipterocarpus*	*borneensis*	5	75	1	18	**78**
Hypericaceae	*Cratoxylon*	*glaucum*	18	83	1	18	**78**
Lauraceae	*Litsea*	*cf. elliptica*	11	64	1	18	**78**
Myristicaceae	*Horsfieldia*	*crassifolia*	75	83	2	17	**77**
Myrtaceae	*Syzygium*	*sp. 2*	6	67	2	16	**73**
Anisophyllaceae	*Combretocarpus*	*rotundatus*	11	73	4	14	**70**
Lauraceae	*Litsea*	*sp. 1 cf. resinosa*	5	80	1	16	**70**
Annonaceae	*Xylopia*	*fusca*	33	64	3	14	**67**
Meliaceae	*Aglaia*	*rubiginosa*	10	80	3	14	**67**
Myrtaceae	*Syzygium*	*garcinifolia*	18	78	1	15	**65**
Annonaceae	*Xylopia*	*coriifolia*	6	50	2	14	**64**
Crypteroniaceae	*Dactylocladus*	*stenostachys*	13	54	1	14	**61**
Euphorbiaceae	*Baccaurea*	*bracteata*	13	77	2	13	**59**
Apocynaceae	*Dyera*	*lowii*	21	71	1	12	**52**
Sapotaceae	*Palaquium*	*leiocarpum*	72	63	1	12	**52**
Annonaceae	*Mezzetia*	*umbellata*	5	80	2	11	**50**
Fagaceae	*Lithocarpus*	*dasystachys*	8	50	2	11	**50**
Icacinaceae	*Stemonurus*	*cf. scorpiodes*	11	73	2	11	**50**
ASYNCHRONOUS							
Euphorbiaceae	*Blumeodendron*	*elateriospermum*	14	36	0	17	**71**
Magnoliaceae	*Magnolia*	*bintuluensis*	8	43	0	15	**63**
Myrtaceae	*Syzygium*	*sp. 7*	5	40	0	15	**63**
Sapotaceae	*Palaquium*	*pseudorostratum*	10	33	0	15	**63**
Ebenaceae	*Diospyros*	*bantamensis*	20	44	0	14	**58**
Rutaceae	*Tetractomia*	*tetrandra*	15	33	0	14	**58**
Clusiaceae	*Mesua*	*sp. 1*	6	33	0	13	**54**
Aquifoliaceae	*Ilex*	*hypoglauca*	7	43	0	10	**42**
Myristicaceae	*Knema*	*intermedia*	9	44	0	9	**38**
Tetrameristaceae	*Tetramerista*	*glabra*	6	33	0	6	**25**
ASYNCHRONOUS	?						
Fagaceae	*Lithocarpus*	*sp. 3*	7	60	1	11	**48**
Myrtaceae	*Syzygium*	*sp. 5*	7	57	1	10	**43**
Myrtaceae	*Syzygium*	*sp. 3 cf. nigricans*	9	57	1	9	**39**
Annonaceae	*Mezzetia*	*leptopoda/parviflora*	22	73	1	7	**30**
Sapotaceae	*Palaquium*	*ridleyii*	8	50	1	7	**30**
Anacardiaceae	*Campnosperma*	*coriaceum*	44	74	11	0	**0**

*Reproductive individual; Fl = flowering; species highlighted are in the top 20 most eaten orang-utan foods (Chapter 4).

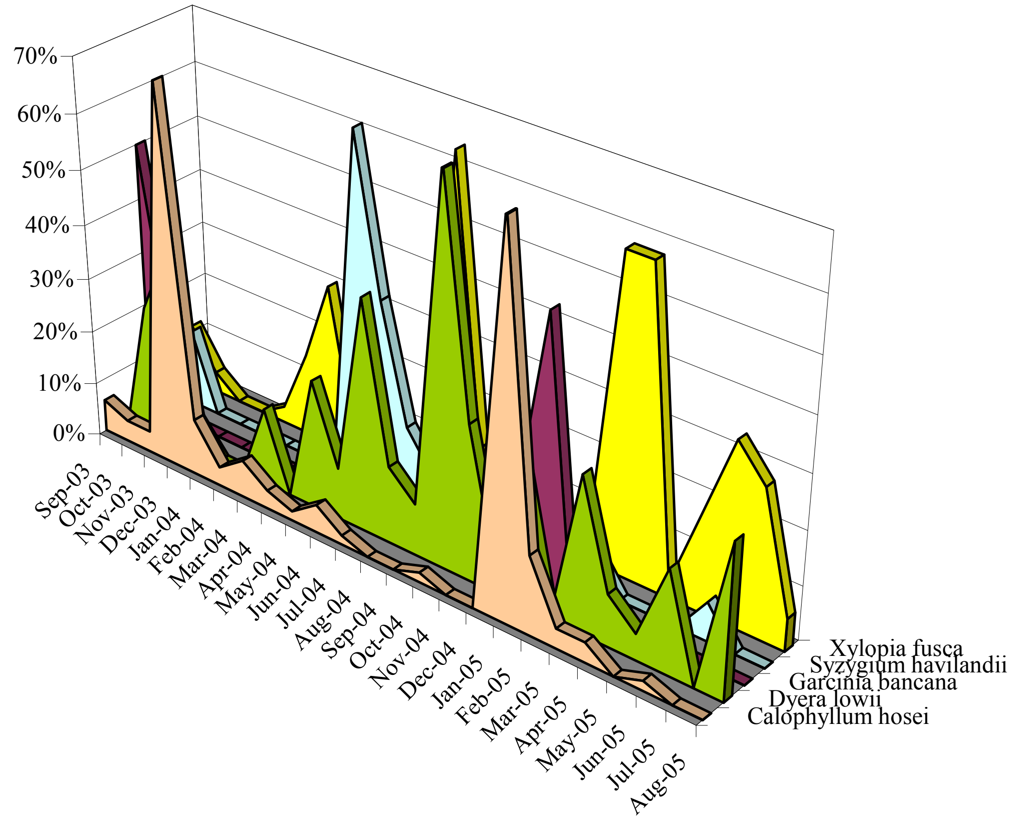


Figure 3.13 Synchronous species flowering patterns.

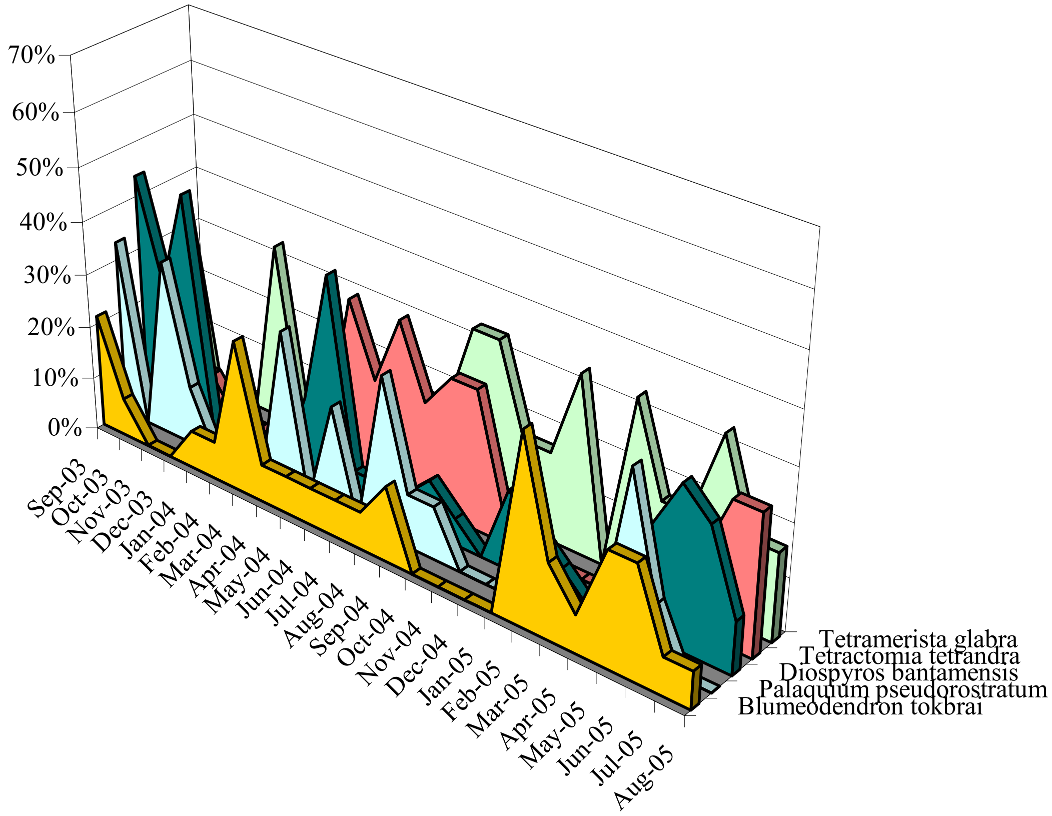


Figure 3.14 Asynchronous species flowering patterns.

3.5 DISCUSSION

3.5.1 Species composition and forest structure

One hundred and thirty eight species were identified in 38 families, which is a similar number to that found in the peat-swamp forests of Tanjung Puting (139 species) (Galdikas, 1988). When the mixed-dipterocarp forest at Tanjung Puting is included, however, the number increases to 177 (Galdikas, 1988), indicating that forest with a mosaic of different habitat-types is more diverse. In Sabangau Myrtaceae was the only 'Eudominant' family, but the dominant species in the forest was *Palaquium leiocarpum* from the family Sapotaceae, followed by *Shorea teysmanniana* from the family Dipterocarpaceae, which was classed as a 'Subordinant' family, representing less than 5% of all species. This demonstrates that the dominant families do not necessarily have the most dominant species, and that, although this forest is not classed as a dipterocarp-dominated forest, *Shorea teysmanniana* was the second commonest species found.

Structure

Forest structure is very important with regards to fruiting patterns, as the larger the tree the more likely it is to fruit or flower and, therefore, to be chosen as an orang-utan feeding tree. Most feeding bouts were on trees >20 cm dbh; 98% of trees in the Sabangau forest are smaller than 30 cm dbh, whereas primary peat-swamp forests in Tanjung Puting have over 20 % of trees larger than 30 cm dbh (Galdikas, 1988). This low number of large trees in Sabangau may be due to past logging. Cannon *et al.* (2007a), however, found that although production in large trees is higher, most large individuals only fruited 2 times during their study period (5.5 years), whereas smaller individuals fruited 3 or more times. Thus, even if the composition of the Sabangau forest has changed with regard to the overall size of trees, '*food*' production may not have decreased much due to smaller individuals reproducing more frequently.

3.5.2 Fruit and flower production and seasonality

Production levels

In the Sabangau, fruit and flower production fluctuated throughout the study period, with '*food*' availability dropping to low levels for 4 months. For most of the study, however, '*food*' availability was medium (13 months) to high (7 months) and therefore, flowers and fruit were only limited for 4 months out of 24. I describe in Chapter 4 how, ketones, a by-product of fat metabolism, were not present in the urine for 3 months from January 2004 to March 2005, when *'food'* availability was high. Whereas from August 2004 to December 2004 there were high to medium levels of ketones appearing in urine samples, which seem to be a result of previously low levels of *'food'* availability from May to July 2004. This indicates that when '*food'* availability is low, orang-utans start losing weight, in turn suggesting that '*food*' availability of 4 % or below may be insufficient to support an orang-utan population, although the quality of available '*food'* is another variable affecting this. Figs, although low in density, appeared to fruit most months of the year compared to lianas which were more seasonal.

Seasonal changes

Seasonal effects were visible in the Sabangau, with leaf and flower production being negatively correlated with rainfall. This indicates that the start of the dry season (typically July) seems to trigger the onset of new-leaf production and flowering, with fruit production increasing as the rains increased. A negative correlation between flowering and rainfall had been found by other researchers (Putz, 1979; Ashton *et al.*, 1988; Brearley *et al.,* 2007). Brearley *et al.* (2007) and Sakai *et al.* (2006) say that drought could be a more important cue for flowering than has been considered previously, and van Schaik and Pfannes (2005) state that it is seasonal droughts that are primarily responsible for seasonality in fruiting and flowering. Peat-swamp forests in their natural state do not dry out during the dry season, but they will experience a drop in the water table, thus triggering flowering. In contrast to tropical peat-swamp forests, van Schaik *et al.* (1993) found that flowering generally occurs at the start of the wet season in seasonally-dry forests.

It seems feasible that the length of the dry and wet seasons can ultimately affect fruiting and flowering patterns and, thus *'food'* availability in the Sabangau. Effects of ENSO (the El Niño-Southern Oscillation) can have drastic effects, by extending the dry season and altering fruiting patterns, as Harrison (2009) found. From Sept 2005 to June 2007 the Sabangau experienced decreased *'food'* availability which never exceeded medium levels. This is probably due to the low amount of rain which only exceeded 300 mm for 7 months of the study period (19 months) (Harrison, 2009). Although temperature was not found to be an influencing factor in this study, some authors support the theory that a drop in night-time temperature triggers the onset of mast-flowering events (SAM) in Asia (Ashton *et al.,* 1988; Yasuda *et al.,* 1999), which are linked to ENSO (Ashton *et al.,* 1988; Wich and van Schaik, 2000). Fredriksson *et al.* (2006) found that the effects of ENSO in Sungai Wain, East Kalimantan caused the local extinction of the fig wasp, the main pollinator of figs, which resulted in some species not fruiting for 2 years.

3.5.3 Fruiting events

In Gunung Palung National Park in West Kalimantan, two mast-fruiting events were documented by Cannon *et al.* (2007a). Both events lasted less than 3 months and plant reproduction increased four fold during this time compared to background levels. Both events were separated by almost 4 years and were driven mainly by species from the Dipterocarpaceae. Outside the mast few apparent seasonal or annual patterns existed, and a large proportion of stems never reproduced, whereas in the mast 8-10 % of stems fruited compared to the normal background level of < 3 % of total stems (Cannon *et al*., 2007a, 2007b). In Sungai Wain , 10-16 % of trees produced fruit in the mast (Fredriksson *et al.,* 2006). In the Sabangau, the number of stems fruiting did not exceed 10 %, but it was at its highest from November 2004 to February 2005 (≥ 8 %). The number of stems flowering exceeded 10 % for 2 months from September 2004 to October 2004. This level of fruiting and flowering in Sabangau has not been recorded before or since (Harrison, 2009; Morrogh-Bernard, unpublished data). During the months of February to April 2005 a mast-fruiting event was documented in Borneo (Fredriksson, G., Padi, G., Curran, L. *in litt.* to E. Meijaard, pers. comm.). Thus, it seems feasible that some trees in the Sabangau peat-swamp forest were participating in the mast, as the observed production in many species was elevated during this period. Bearded pigs are known to time their reproduction with SAM events, and heightened pig activity is a common indicator of a mast having occurred (Dove, 1993). Anecdotal evidence of increased activity of this species in the forest during January-March 2005 (pers. obs.), also indicated that the Sabangau peat-swamp forest could have experienced a ‘mini-mast’ (period of fattening) – namely a period of elevated fruiting that was not centred on dipterocarp species. Cannon *et al.* (2007b) found that many non-dipterocarp species were mast specialists, including Euphorbiaceae*,* Ebenaceae and Myrtaceae and one woody climber *Willughbeia*, which was the only woody climber observed to participate in the Gunung Palung mast.

Thus, as many of those genera which participated in the mast in Gunung Palung are present in the Sabangau, it is possible from the observed elevated fruiting event that the Sabangau peat-swamp forest did participate in the mast. Whether one could call this a ‘mini-mast’, however, or just an ‘elevated fruiting period’ is debatable, as true masting habitats have a high percentage of species which restrict their reproductive activity to these times e.g. 27 genera in 24 families in Gunung Palung (Cannon *et al.,* 2007b). In Sabangau there was no peak in reproduction from the Dipterocarpaceae during this time, the main masting family (Cannon *et al.*, 2007a; Brearley *et al.*, 2007), and all species that did reproduce during the study period, also reproduced at other times and not just during the months of the Bornean mast. In Gunung Palung an elevated reproductive peak in the peat-swamp forest was only witnessed once, during the 1991 mast (Cannon *et al.,* 2007b), but not during any other mast. This implies that the peak in *‘food’* production in Sabangau in early 2005 may be a result of increased rainfall from November 2004-Febuary 2005 and, therefore, a one-off, rather than being a true masting event which is triggered by ENSO (Ashton *et al.,* 1988; Sakai *et al.,* 2006; Curran *et al.*, 1999; Wich and van Schaik,2000 and Brearley *et al.,* 2007). The question, however, of whether the Sabangau forest does exhibit a ‘mini-mast’ – ‘time of fattening’ - which proceeds the true mast cannot be ruled out, until more data are available.

3.5.4 Fruiting cycles

The reason why true SAM events do not occur in peat-swamp forests may not only be due to the absence or low density of dipterocarp species, but also due to different habitat conditions (swamp vs. dry) and evolutionary reproductive cycles. Peat-swamp forests in their natural state should be permanently waterlogged all year round, so their root systems should not be subject to the same stresses as dry forests when extreme droughts occur e.g. El Niño, which is thought to be the trigger for masting events.

In the Sabangau, 75 % of all tree species reproduced in stages over a 2 year period, compared to a masting forest, where at least 80 % of the floral diversity restricts their reproduction to SAM events (Cannon *et al.,* 2007a). The majority of species which could be classified were classed as having a synchronous reproductive cycle, although they reproduced at different times of the year. This indicates that the Sabangau peat-swamp has an asynchronous reproductive cycle at a community level. This pattern of reproducing, together, with a high proportion of asynchronous species, allows *'food'* to be available all year round. Because data are limited to only 24 months, these results must be viewed as preliminary, as it is not usual for assessments of this kind to be made with such a limited data set. Community level asynchrony, however, is probably why peat-swamp forests are considered to have the most consistent reproductive productivity of all forest types in Borneo (Cannon *et al*., 2007a; Marshall, *et al.* 2009b), and why they are so important for orang-utans. Out of the top 20 most important orang-utan food species (Table 4.5, Chapter 4) nearly half (47 %) were asynchronous and thus very important in the diet, e.g. *Mezzetia leptopoda* which was the most eaten food (Chapter 4). The role of these species is similar to figs, which are 'keystone' species for many birds and mammals (Leighton and Leighton, 1983), and are an important 'fallback' food for orang-utans in masting forests in Sumatra (Wich *et al.,* 2006a).

Why the different species have adopted an asynchronous or synchronous strategy is beyond the scope of this chapter, but the fact that most species are asynchronous at a community level indicates that it may be an evolutionary response, in which pollinators and seed-dispersal agents are the driving force, rather than environmental cues, as is the case for synchronised masting species, although certain environmental cues do seem to increase reproductive productivity e.g. high rainfall. Asynchrony, on the other hand, has been found to minimise competition between species and to maintain a resident population of dispersal agents (Poulin *et al*., 1999). As orang-utans have both sedentary (female) and wide-ranging (male) individuals, this combined strategy of having a large number of asynchronous species and overall community asynchrony of synchronised species, may be the reason why Cannon *et al.* (2007b) found peat-swamp to be the most productive forest-type over extended periods of time and, therefore, why peat-swamp forests are so good for orang-utans (Johnson *et al*., 2005; Husson *et al.,* 2009; Marshall *et al.,* 2009b). The length, frequency and intensity of periods of fruit shortage are the key element for determining orang-utan population density (Marshall *et al.,* 2009b), thus explaining why sites with a mosaic of different habitats (e.g. peat-swamp and dry forest) have higher densities of orang-utans (Husson *et al.,* 2009) because the different habitats can have different fruiting patterns.

3.6 CONCLUSION

Masting forests have a fruiting peak that is limited to 3 months or less (Cannon *et al.,* 2007b), whereas the peat-swamp forest of Sabangau exhibited high '*food*' production for 6 months. This indicates that, unlike a masting forest which peaks quickly, the Sabangau peat-swamp forest peak was prolonged. The reason why the peak lasted for so long compared to masting forests is due to temporal segregation of synchronised species, together with the presence of many asynchronous species. The reason why the Sabangau experienced an elevated peak in food production in 2004-2005 may be due to increased rainfall during that time, as rainfall between November 2004 and March 2005, when '*food'* production was high, was 31% higher than in the same period in 2003-2004, when '*food'* production was medium. Thus, high rainfall seems to be the cue for a productive and extended fruiting season. I refer to the elevated period in *'food'* production as a 'mini-mast' (period of fattening), not as a true SAM, as it was not dominated by dipterocarp species, but it was followed by a true SAM in dipterocarp-dominated forests in Borneo.

Flowering was triggered by the onset of the dry season; thus an extended dry season (as sometimes caused by ENSO) is likely to effect the next fruiting season. During this study, *'food'* productivity was high for 6 months, and during these months ketones were not detected in the urine, indicating that high *'food'* production was sufficient for orang-utans to put on weight, as opposed to periods when *'food'* production was low (Chapter 4). Thus, although the forest is mainly made up of small trees <30 cm dbh, production was able to increase to high levels for a number of months, compared to levels recorded since. Overall, both synchronous and asynchronous species occur here, so there is a segregated reproductive pattern, which has allowed sufficient *'food'* to be available for orang-utans in most months of the year.

3.7 SUMMARY

- 138 species were identified in 38 families, of which the Dipterocarpaceae family is not dominant.
- Forest structure is small, as the majority of trees (98%) have a dbh < 30cm, due to past logging.
- Orang-utans spend most of their time feeding from trees >20 cm dbh with the mean feeding size of 28 cm dbh.
- Fruiting and flowering productivity was regular, with most months being characterised as medium or high *'food'* availability. Only 4 months were classed as low *'food'* months.
- Overall production seems to be influenced by changes in the seasons, as fruit production increases with increased rainfall, and flower production was found to be negatively correlated with rainfall.
- As production was elevated during the 2004 to 2005 wet season (a SAM year), this may indicate that the Sabangau peat-swamp forests may participate in the Borneo mast. I prefer to refer to this as a 'mini-mast', or a period of fattening, however, as it was not dominated by dipterocarp species.
- 63% of species were classified as having a synchronous fruiting cycle, with the remainder being asynchronous. The synchronised species appear to be temporally segregated in flowering, which means that the fruit of different species are available at different times of the year.
- Out of all the major orang-utan foods, about half were classed as having a synchronous fruiting cycle and half an asynchronous cycle. Thus, asynchronous species are very important in the orang-utans diet when more preferred foods are not available.

CHAPTER 4

ORANG-UTAN DIETARY DIVERSITY AND EFFECTS OF FOOD AVAILABILITY

4.1 INTRODUCTION

4.1.1 Diet and food availability

Primate population density and behaviour are influenced by the quality, quantity and seasonal availability of food (Chapman and Chapman, 1999; Gupta and Chivers, 1999; Furuichi *et al.*, 2001; Brugiere *et al.*, 2002). In the tropics, plant reproduction is highly seasonal because of changes in climate between wet and dry seasons (Cowlishaw and Dunbar, 2000; van Schaik and Pfannes, 2005), and this has an effect on the food-types and species eaten at different times of the year (Peres, 1994; Knott, 1998; Brugiere *et al.*, 2002; McConkey *et al.*, 2003).

Orang-utans are predominantly frugivorous, as fruits provide animals with more readily available nutrients and energy than leaves (Cowlishaw and Dunbar, 2000), but they supplement their diet with leaves, invertebrates, bark and other plant matter when fruit is scarce. Their diet is thus influenced by seasonal changes, with less fruit in the diet when fruit is less abundant (MacKinnon, 1971; Galdikas, 1988; Knott, 1998; 1999b; Fox *et al.,* 2004; Wich *et al.,* 2006a). The proportion of different food-types in the diet also differs between populations. MacKinnon (1977) found that the Bornean orang-utan fed on a greater amount of fruit species compared to the Sumatran orang-utan, suggesting that the Bornean orang-utan is less selective. In an investigation comparing 11 populations in 15 different sites, Russon *et al.* (2009) also found that Bornean orang-utans feed from more plant families, genera and species than Sumatran orang-utans, thus habitat productivity had an inverse effect on dietary breadth and food used. Habitat differences in diet were weak, however, so habitat differences found in their diet were partly due to differences in orang-utans foraging strategy and dietary flexibility (Rodman, 1988). The eastern Bornean orang-utan, *P.p.morio,* copes better with drier conditions, fire and more frequent El Niño events than the other species and sub-species, and thus has a more folivorous diet (Taylor, 2006) due to more extreme fruiting patterns in eastern Borneo.

The Sumatran species is the most frugivorous of the two species, and this is mainly due to productivity, as Sumatran forests are more productive than Bornean forests (Wich *et al.,* 2006b; Marshall *et al.,* 2009b) and there are also fewer masting species in Sumatra than in Borneo (Marshall *et al.,* 2009b). In habitat types that are not dominated by dipterocarps e.g. peat-swamp forests, fruiting patterns are more regular (Marshall *et al.,* 2009b). In areas which have more heterogeneous habitat like Gunung Palung and Tanjung Puting in Borneo and Ketambe and Suaq Balimbing in Sumatra, orang-utans have been found to utilise different habitat types when fruit availability in their primary habitat is low (Galdikas, 1988; Singleton, 2000; Wich and van Schaik, 2000; Buij *et al*., 2002; Johnson *et al*., 2005), and this has been found in other primates as well (e.g. Kano and Mulavwa, 1984).

Fallback foods

When fruit is not abundant, orang-utans have to feed on other food-types. The term '*fallback food*' is used to describe foods of normally low preference that are eaten when preferred foods are not available (Furuichi *et al*., 2001; Marshall and Wrangham, 2007). The Bornean orang-utan is better suited to resisting large and/or frequent jaw loads compared to the Sumatran (Taylor, 2006). This difference in morphology is presumably an evolutionary adaptation as Bornean orang-utans rely more heavily on bark and tough vegetation during periods of low fruit availability (MacKinnon, 1974; Galdikas, 1988; Rodman, 1988; Knott 1998; Lackman-Ancrenaz and Ancrenaz, 2006). Sumatran orang-utans, by contrast, rely more heavily on figs and termites during periods of food scarcity (Rijksen, 1978; Sugardjito *et al.,* 1987; Fox *et al*., 2004; Wich *et al*., 2006a). Marshall and Wrangham (2007) suggest that the evolutionary importance of fallback foods applies more to adaptations for processing than for harvesting foods. For example, the types of fallback foods eaten affects the thickness of tooth enamel; both chimpanzees and gorillas eat pith as a major fallback food, thus they have thinner enamel than orang-utans who eat more bark as a fullback food (Wrangham *et al.,* 1991; Furuichi *et al.,* 2001). Marshall and Wrangham (2007) have produced two definitions for fallback foods: (1) Staples: those that can represent 100% of the diet at certain times of the year, and (2) Fillers: those that never represent 100% of the diet and are more seasonal. Pith is a staple for gorillas (Doran *et al.,* 2002a), whereas bark is a filler food for orang-utans; bark never constitutes the entire diet of a given day and would probably not maintain the dietary requirements of the individual eating them in the absence of other food resources. It is useful to know which food-types are fallback foods, and which species are important foods in a species' diet when assessing dietary diversity.

4.1.2 Food availability and energy balance

Orang-utans diet varies in response to habitat differences and seasonal changes, eating less energy-rich food in times of low fruit availability and *vice versa*. To cope with these fluctuations in food availability, orang-utans are extremely efficient at storing fat quickly when fruits are available (Wheatley, 1982), but also use up their reserves fast when fruit availability is low (Knott, 1998). Knott (1998) found that both sexes were spending the same amount of time feeding during both fruit-abundant and fruit-scarce periods; but due to reduced food quality in the fruit-scarce period they were not maintaining their body weight. This was especially marked in females which have higher-than-average energy expenditure, due to energetic costs of motherhood and inability to successfully open *Neessia* fruits (large fruits with irritating hairs surrounding the seeds that are common in Knott's study site), to access the oil-rich seeds, unlike males that could access this food during these times (Knott, 1998). During fruit-abundant periods (essentially during the mast) males were consuming an estimated 8422 kcal/day, and females 7404 kcal/day; gaining as much as 0.66 kg/day; compared to only 3824 kcal/day for males and 1794 kcal/day for females during periods of low-fruit availability (Knott, 1998). This is a decrease in caloric intake of 76% for females and 55% for males, a good example of how different levels of food availability can influence energy intake.

The examination of an orang-utan's diet and health in relation to fluctuations in '*food*' (fruits and flowers) availability is important. Classifying each food species in terms of importance will increase our knowledge of orang-utan diet in peat-swamp forest, and aid future management and conservation efforts for the Sabangau. It will also allow for more detailed comparative studies in the future, as most food lists do not categorise species in terms of importance.

4.2 OBJECTIVES

Orang-utan dietary composition will be investigated in this chapter, with regards to food-types, species diversity and their importance in the diet, and the effects of changes in *'food'* availability on diet and health. In addition, dietary composition will be compared to other sites and habitat types using published data.

The questions to be addressed in this chapter are:

Section 1 - Dietary composition

- What is the percentage of each food-type in the diet?
- Does the diet vary between individuals?
- Does the diet vary between age/sex classes?
- Does the diet vary between different levels of *'food'* availability?
- Does *'food'* availability affect energy intake and thus health?
- Does the diet vary between sites?

Section 2 - Important and preferred species

- What species were eaten? (Compile a species list).
- What were the dominant food species in the diet?
- Were there seasonal changes in species eaten?
- Was there an order of preference for species when seasonal changes and species density was taken into account?

4.3 METHODS

To answer the questions on '*food'* availability, I first controlled for *'food'* availability when investigating differences in age/sex classes, and then controlled for age/sex class when investigating '*food'* availability. The normal age/sex classes as described in Chapter 2 were used.

Only dietary compositions were compared between other sites as these data were easily accessible from the literature.

4.3.1 Diet composition

Only follows that had 2 hours or more feeding data were used for analysing diet, as some follows which were longer than 3 hours had very little feeding data e.g. 8 minutes in some follows. All individuals with fewer than 2 follows or if the individual was unidentified were also excluded, which left 17 individuals for the analysis (6 flanged males, 3 sexually active females, 3 non-sexually active females and 5 unflanged males). Means were calculated by taking individual means for each age/sex class, and overall means calculated by taking an average of all age/sex classes. Thus these figures differ from the mean presented in Table 4.7, which were calculated using monthly means, as different computational methods give different results (Harrison *et al.,* 2008).

For this analysis I looked at both food-types and species importance. When I refer to **'food-types',** this includes fruits, flowers, leaves, bark, pith and invertebrates. When I refer to '**species importance'**, I refer to the name of the species regardless of which food-type was eaten, unless otherwise stated e.g. *Dyera lowii* fruits or *Dyera lowii* bark.

4.3.2 '*Food*' availability and effects on diet

As explained in Chapter 3, *'food'* availability (with food written in *italics*) is used for comparing different levels of important seasonally-available foods, rather than just using fruits, as flowers are important in the Sabangau orang-utans' diet. *'Food'* availability is the percentage of tree stems known to be orang-utan food with either fruits or flowers present, and was calculated separately for each month (see Chapter 3). Correlations were carried out between '*food'* availability and the percentage of each major food-type in the diet (fruits, flowers, leaves, bark, pith and invertebrates). To assess whether different food-types were eaten more during periods of high, medium or low '*food*' availability, I divided the months into 3 classes (Table 4.1) (see Chapter 3, Section 3.4.4).

Table 4.1 Productivity classes for orang-utan foods only.

Class	**% stems with '*food*'**	**Number of months in each class**
Low	< 4%	4
Medium	4-8%	13
High	> 8%	7

I assessed differences in food-types eaten between individuals within the same age/sex class, by conducting a series of ordinary least squares (OLS) regressions for each food-type, incorporating *'food'* availability levels. I assessed differences in diet between age/sex classes and periods of different '*food*' availability by conducting a General Linear Model (GLM) with repeated measures, incorporating both *'food'* availability and age/sex class as independent variables. Age/sex class was incorporated as differences between these classes are suggested by examination of the raw data. The proportions of each major food-type in the diet were tested against the three '*food*' availability classes. The GLM was considered the most robust test for my dataset which has a small sample size and a mixture of continuous and categorical variables.

Ketones

In order to asses if orang-utans were in positive or negative energy balance, I used the presence of ketones in the urine as an indicator of energy intake, as ketones are present in the urine when fats have been metabolised, and thus are a good indication of orang-utan health.

One urine sample was collected from each individual orang-utan on each follow when possible, and tested for ketones using Multistix 10 SG urinalysis sticks (Knott, 1998). Four levels of ketones were measured: high ketones (stick readings: large, 0.8-1.6), medium ketones (moderate and small), trace ketones and no ketones (negative). In order to assess the level of ketones present, these levels were converted into a 4 level scale (0 = negative, 1= trace ketones, 2 = medium ketones and 4 = high ketones). Then a score was calculated for each month. This score was used to plot a graph for ketones against *'food'* availability.

A Pearson's correlation between *'food'* availability and the percentage of samples with ketones was tested to see if there was a relationship between the two.

4.3.3 Comparison with other sites

To compare between sites, data for Sabangau were converted into the same format as that available for other sites. Diet was re-calculated as overall monthly means rather than individual means, thus figures for Sabangau will differ from Figure 4.1 (means of age/sex class).

Fruit availability was also used rather than '*food'* availability, thus excluding flower availability from this measure as other sites have done. For fruit availability, this was compressed into two classes: low: < 6 % stems in fruit, and high: ≥ 6 % stems in fruit for Sabangau; for Ketambe, data was used from Wich *et al*. (2006a) where 4 levels were used, which were combined into low fruit availability (levels 1 and 2) and high fruit availability (levels 3 and 4); for Ulu Segama, values were estimated from graphs in MacKinnon (1974).

4.3.4 Species eaten, importance and preference in the diet

A species list was compiled of all species that had been eaten on at least one occasion by orang-utans. A special category of 'try foods' was included. 'Try foods' were food-types which were eaten for less than 6 minutes or for a maximum of 2 feeding bouts (regardless of time). This distinction was made to differentiate between those species that form part of a normal diet, and those that are not but were tried by orang-utans, presumably to see if they liked them. For analysis of food importance and preference, and the affect of changes in '*food'* availability, try-foods were excluded.

Species Importance

1. 'Important Species'

These are species which make up the majority of the diet, thus eaten the most.

The species which formed the largest part of the diet (>1.5 %) were classified as the most important species, and were ordered by the percentage of time spent feeding overall. The time spent feeding on each species was weighted by follow effort in each month (as this varied considerably between months), in order to correct for seasonal changes. This was worked out by calculating a percentage for each month and then averaging across all 24 months of the study. These species were then ranked in order with 1 being the most important species in the diet.

2. 'Seasonally-important species'

These are species that are only eaten at certain periods when in season.

Seasonally-important species were worked out by ordering the species by the number of months they were in the top 3 for time spent feeding (this figure was arbitary). Those that were in the top 3 for the most months were considered common in the diet, thus 'staples', and those that appeared less often were considered rare in the diet, and thus seasonally important.

3. 'Preferred species'

These are species and food-types which are highly selected for when in season. Preferred food-types are *high-quality foods* that comprise a substantial part of the diet during some seasons, and are foods that tend to require relatively little manual or masticatory processing. They are often rare in the environment.

To calculate a Preference Score (Ps) for each species I used the following variables:

- Total percentage of feeding time on each species, calculated separately for fruits and flowers.
- Species density (for trees >6 cm dbh).
- Percentage of stems of each species fruiting (or flowering) in each month.

Preference Score (Ps) =

$$\frac{\text{\% of time feeding on each food-type}}{\text{(stem density for that species x proportion of stems fruiting or flowering)}}$$

This Preference Index (Pi) takes into account fruiting and flowering patterns and density, so that species with the lowest score were those that were least preferred, and those with the highest score were those that were highly selected for (preferred).

Lianas and figs were not included in these analyses, as it was not easy to identify whether they had fruits or flowers each month due to the dense canopy.

4.4 RESULTS

4.4.1 Dietary composition

Food-types orang-utans eat overall are examined in this section, investigating differences between individuals, age/sex classes and sites. All follows with more than 2 hours feeding were included, unless otherwise stated.

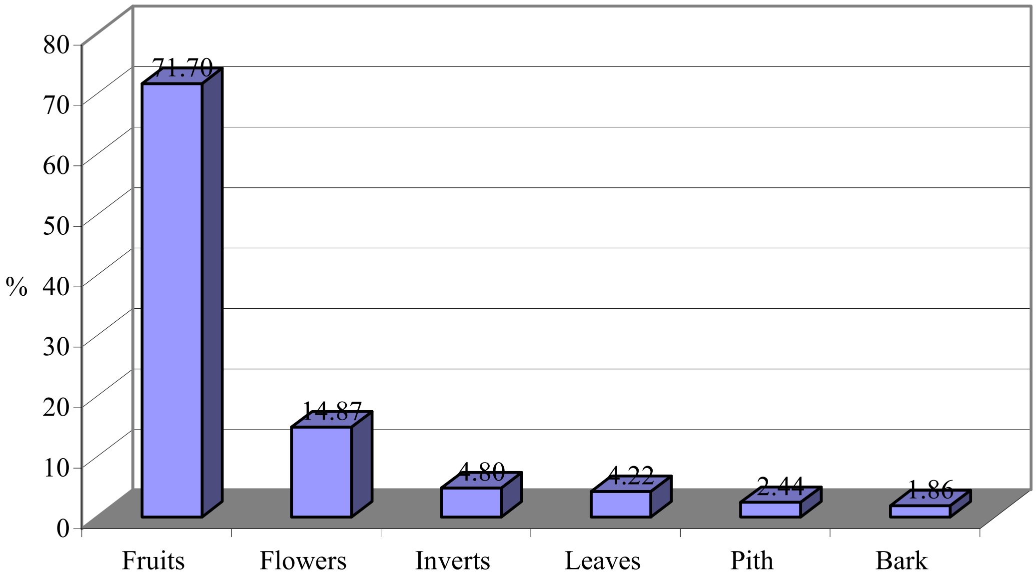


Figure 4.1 Overall percentage of each food-type in the diet (mean of age/sex classes). Inverts are an abbreviation for Invertebrates.

Orang-utans diet in the Sabangau is predominantly fruit (72% - both ripe and unripe), followed by flowers (14% mature and buds), invertebrates (including larvae, ants, termites and caterpillars), leaves (mature leaves and leaf shoots), pith (including stems of pandan) and finally bark (the cambium layer), which represents less than 2% of all feeding time (Figure 4.1). Although pith was fed on more than bark, only half as many species were chosen, with the bulk of pith eating being on lianas and *Pandanus* spp. (Appendix VII).

Individual differences in diet

There is some variation in the make-up of the diet between individuals within each age/sex class (Figures 4.2), probably because not all individuals were followed during the same season, so that the availability of different foods and overall levels of '*food*' availability would have been different. Thus in order to control for these variations, *'food'* availability (high, medium and low) was included in 24 different OLS regression models (one each for all combinations of age/sex class (3 NSAF, 2 SAF, 6 FM and 4 UFM) and food-type) to test for individual differences in diet with in each age/sex class. Overall, 168 pairwise tests were performed, in which 21 (13%) were found to be significant after the Bonferroni correction was applied (4 for NSAF, 1 for SAF, 12 for FM and 4 for UFM – the Bonferoni correction was applied in this circumstance due to the number of pair-wise comparisons compared). The majority of these differences were found for invertebrates (6 pairwise differences) and pith (5 pairwise differences), only 2 pairwise differences were found for fruit and none were found for flowers. With this low number of significant pairwise differences (21 out of 168), I was confident to group individuals into age/sex classes for testing differences in diets between age/sex classes and levels of '*food*' availability.

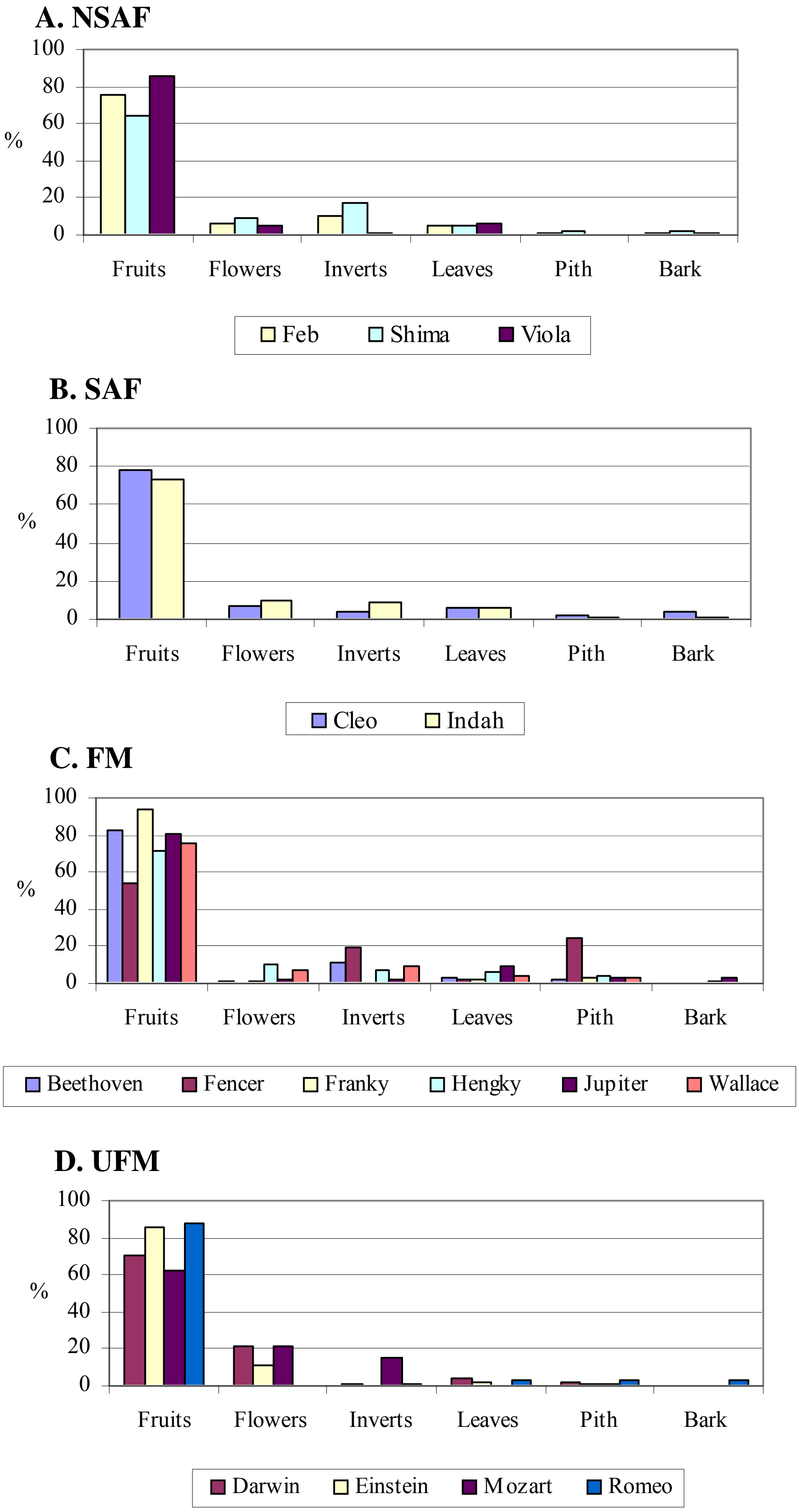


Figure 4.2 Percentage of each food-type in the diet for (A) NSAF– non-sexually active females, (B) SAF – sexually active females, (C) FM– flanged males and (D) UFM– unflanged males. Inverts are an abbreviation for Invertebrates.

Age/sex differences in diet

Diet differences between age/sex classes seem apparent from Figure 4.3. UFM ate the largest amount of fruit, and SAF ate the least. For flowers SAF ate the most, and FM ate the least. For leaves NSAF ate the most and UFM ate the least. For pith, FM ate more pith than any other age/sex class.

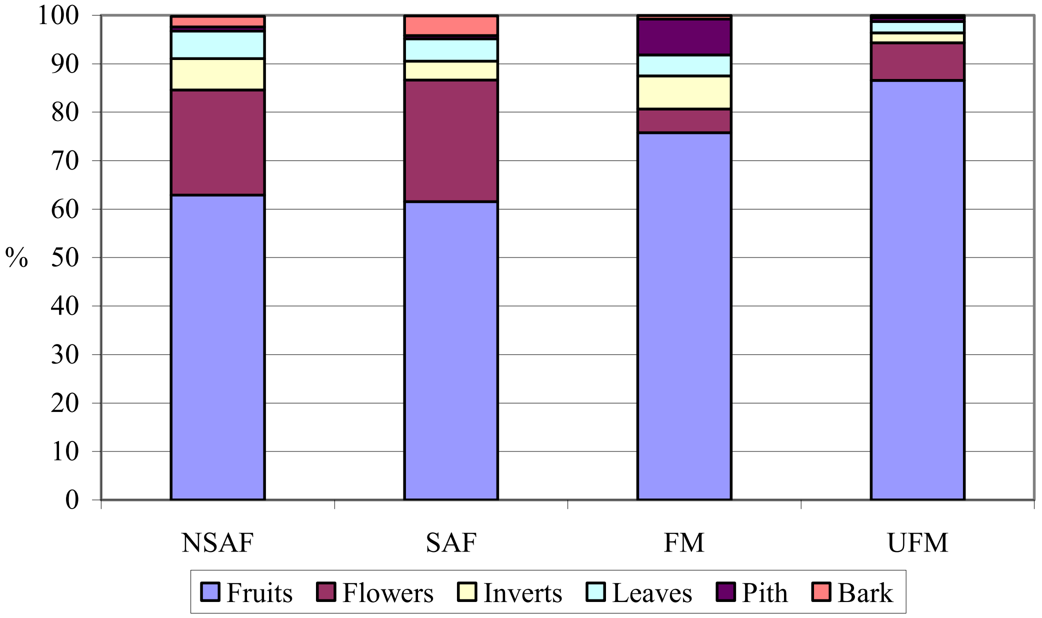


Figure 4.3 Dietary composition for each age/sex class. Inverts are an abbreviation for Invertebrates.

To ensure that these differences are true and not due to age/sex classes being followed at different times of the year, '*food*' availability was incorporated into the GLM model, in which a repeated measures ANOVA with regression model was run, but results were not found to be significant ($F_{15, 137} = 0.90$, $p = 0.561$), although the trends highlighted above still hold true. See table 4.2 for predicted means

Table 4.2 Predicted means from regression model.

		Bark		**Flowers**	
N	*Age/sex*	*Means*	*s.e.*	*Means*	*s.e.*
5	FM	1.05	2.899	9.44	2.899
3	NSAF	1.84	3.931	17.72	3.931
2	SAF	4.63	3.931	7.89	3.931
5	UFM	0.56	3.260	13.53	3.260
		Fruit		**Inverts**	
		Means	*s.e.*	*Means*	*s.e.*
5	FM	75.39	2.899	5.38	2.899
3	NSAF	67.99	3.931	5.54	3.931
2	SAF	76.95	3.931	4.60	3.931
5	UFM	79.26	3.260	3.08	3.260
		Leaves		**Pith**	
		Means	*s.e.*	*Means*	*s.e.*
5	FM	4.49	2.899	4.21	2.899
3	NSAF	6.02	3.931	0.77	3.931
2	SAF	4.64	3.931	1.11	3.931
5	UFM	2.12	3.260	1.37	3.260

N=Number of individuals. Predictions are estimated mean values formed only for those combinations of factor levels for which means can be estimated. The predictions have been standardised by averaging over the levels of some factors: '*Food*' availability is constant over levels of other factors. Standard errors are appropriate for interpretation of the predictions, as summaries of the data, rather than as forecasts of new observations.

Although there are differences in the predictions (Table 4.2), food-types eaten were not found to differ between age/sex classes. This may be due to the high standard errors.

Food parts in the diet

When fruits in the diet were broken down into different parts (seeds, pulp, skin, whole fruit), seeds were the part of the fruit eaten most often; for flowers, mature flowers were eaten the most, and for leaves, leaf shoots were eaten the most (Figure 4.4).

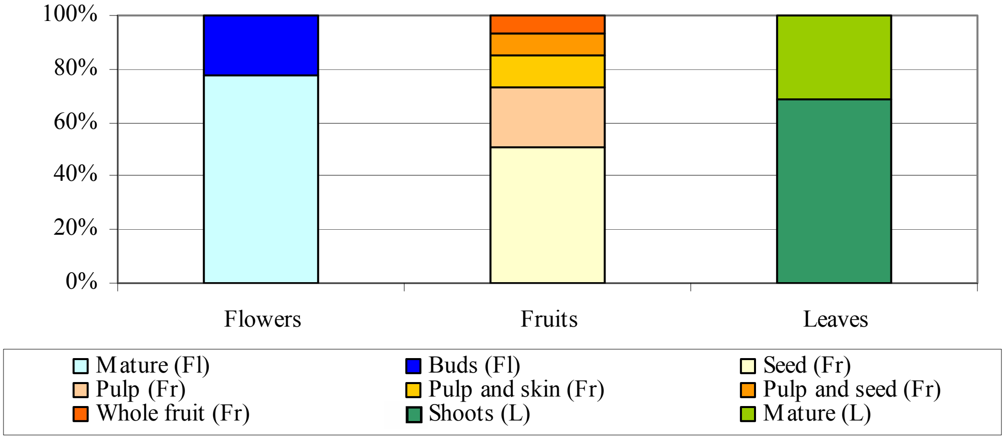


Figure 4.4. Percentage of different parts eaten for flowers, fruits and leaves. Fl: flowers, Fr: fruits, L: leaves.

4.4.2 ‘*Food*’ availability and its effect on dietary composition and energy balance

The availability of fruits and flowers fluctuates from month to month. The impact of changes in ‘*food*’ availability on diet will be investigated, together with the effect of these fluctuations on orang-utan health, measured by the amount of ketones in the urine which is an indicator of changes in energy balance.

Monthly variations in diet

The amount of different food-types in the diet varies and was closely related to ‘*food’* availability (Figure 4.5 and 4.6).

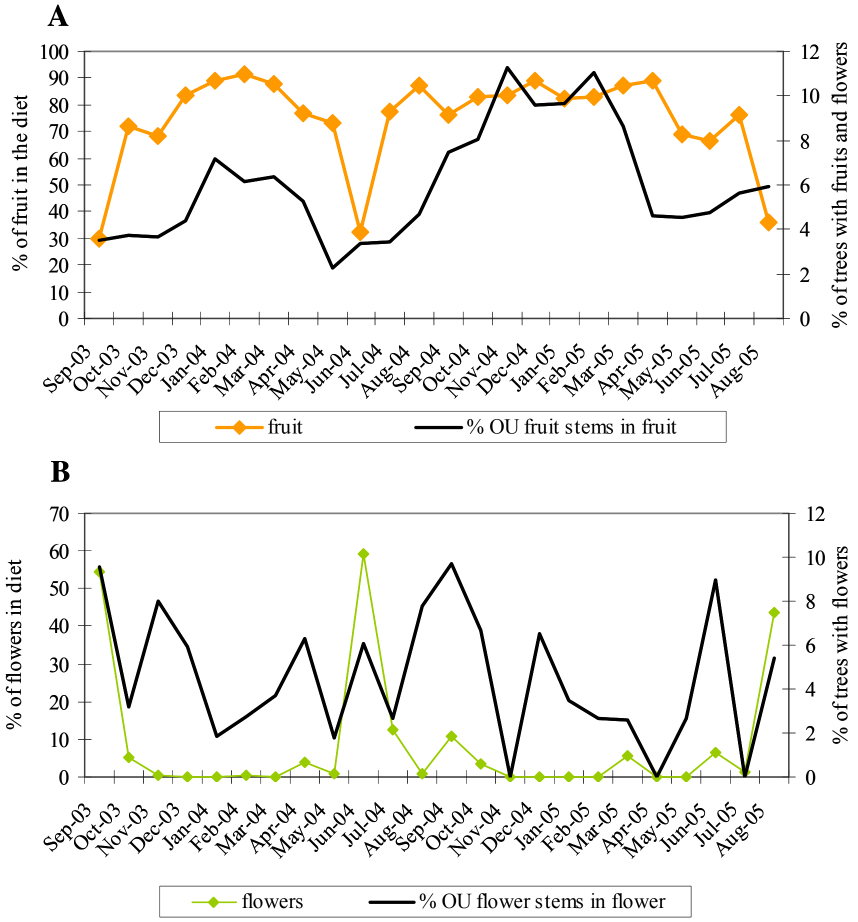


Figure 4.5 Percentage of fruits (A) and flowers (B) in the diet compared to their availability from species orang-utans ate.

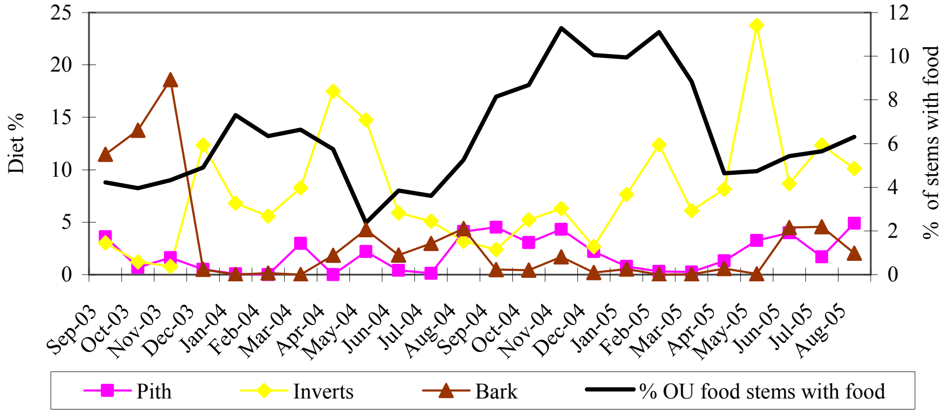


Figure 4.6 Percentage of pith, invertebrates and bark in the diet compared to *'food'* availability.

The percentage of fruits and flowers in the diet was significantly correlated with the availability of fruits and flowers in the forest (Table 4.3). When orang-utans favourite flower species were available (Figure 4.5b), flowers formed the major part of the diet, but at all other times fruits formed the majority of the diet (Figure 4.5a). No correlation with '*food*' availability was found for the amount of leaves, pith or invertebrates, but there was a significant negative correlation between '*food*' availability and the amount of bark in the diet (Table 4.3). Orang-utans ate more bark when '*food'* availability was low (Figure 4.7).

Table 4.3 Food-types in the diet against '*food*' availability.

Correlation	**r^2**	**Number**	**p**
*Fruits in diet *vs* fruit availability	0.186	24	0.035
*Flowers in diet *vs* flower availability	0.169	24	0.047
Leaves in diet *vs* '*food*' availability	-0.000	24	0.939 (ns)
Pith in diet *vs* '*food'* availability	0.012	24	0.605 (ns)
Invertebrates in diet *vs* '*food'* availability	0.002	24	0.828 (ns)
Bark in diet *vs* '*food*' availability	0.451	24	<0.001

Pearson correlation. *Using species orang-utans feed from only. ns: not significant

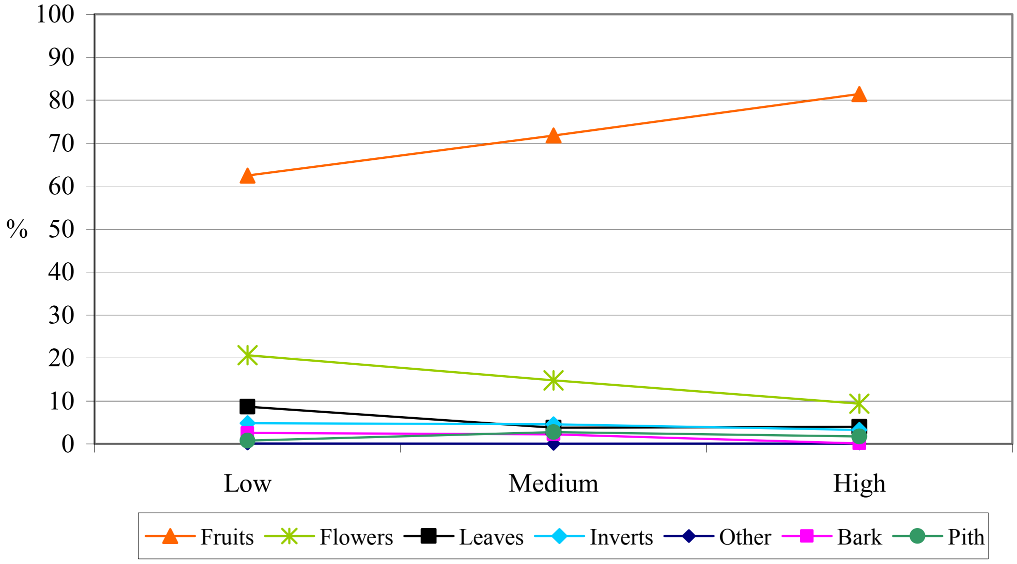


Figure 4.7 Percentages of different food-types in the diet during different periods of '*food'* availability**.** Inverts is an abbreviation for Invertebrates.

Productivity levels and diet

The above correlations show trends but do not indicate any differences between varying levels of '*food'* availability or control for age/sex differences. Thus an ordinary least squares (OLS) regression, incorporating '*food*' availability (high, medium and low) and age/sex class was performed. Age/sex class was incorporated as there are differences in diet between them (Table 4.2). Table 4.4 shows how dietary composition differs between different levels of *'food'* availability, with fruit making up more of the diet when '*food'* availability is high and everything else, especially flowers, forming more of the diet when low (Figure 4.7).

Table 4.4 Orang-utan diet (%) during three different levels of '*food*' availability.

***Food'* levels**	**Age/sex**	**N**	**Fruit**	***sd***	**Fl**	***sd***	**Le**	***sd***	**Inv**	***sd***	**Bark**	***sd***	**Pith**	***sd***
High	FM	5	84.81	*7.69*	2.38	*1.46*	3.91	*2.32*	5.61	*4.49*	0.18	*0.41*	3.01	*1.95*
Medium	FM	6	77.61	*14.95*	0.02	*0.04*	6.16	*6.03*	7.06	*8.01*	2.15	*3.52*	7.00	*8.66*
Low	FM	2	56.54	*1.99*	40.08	*0.64*	1.81	*0.41*	1.47	*2.07*	0.00	*0.00*	0.10	*0.14*
High	NSAF	2	87.88	*7.16*	2.15	*3.04*	4.77	*1.44*	4.53	*4.66*	0.11	*0.16*	0.51	*0.72*
Medium	NSAF	3	56.16	*35.12*	32.10	*39.13*	4.78	*2.61*	3.74	*4.65*	2.47	*1.97*	0.73	*0.77*
Low	NSAF	2	63.30	*0.97*	10.51	*2.55*	10.51	*7.42*	10.89	*8.58*	3.07	*0.79*	1.24	*0.96*
High	SAF	2	84.47	*0.96*	3.88	*0.19*	6.57	*2.19*	3.11	*0.82*	0.18	*0.26*	1.42	*0.58*
Medium	SAF	3	72.80	*7.64*	8.06	*6.98*	4.49	*1.86*	7.25	*4.08*	6.10	*4.38*	1.23	*1.46*
Low	SAF	2	74.47	*3.50*	13.53	*14.29*	2.08	*0.81*	1.22	*1.47*	8.18	*11.03*	0.41	*0.58*
High	UFM	3	90.63	*8.82*	5.23	*9.06*	0.68	*1.18*	1.97	*3.09*	0.00	*0.00*	1.48	*0.52*
Medium	UFM	5	82.79	*16.42*	8.56	*10.89*	2.02	*2.00*	3.75	*7.16*	1.21	*1.88*	1.48	*1.80*
Low	UFM	2	54.71	*46.99*	36.53	*50.54*	4.47	*5.68*	3.29	*2.91*	0.00	*0.00*	0.97	*0.73*
High	Mean	12	**86.95**	*2.90*	3.41	*1.44*	3.98	*2.46*	3.81	*1.59*	0.12	*0.17*	1.60	*1.04*
Medium	Mean	17	72.34	*11.53*	12.18	*13.84*	4.36	*1.72*	**5.45**	*1.97*	**2.98**	*1.22*	**2.61**	*2.94*
Low	Mean	8	62.26	*8.94*	**25.16**	*15.29*	**4.72**	*4.04*	4.22	*4.55*	2.81	*5.40*	0.68	*0.52*

* Number of individuals; ** Number of follows. NSAF=non-sexually active females including 1 nulliparous female; SAF=sexually active females; FM=flanged males; UFM=Unflanged males. Fl=flowers; Le=leaves; Inv=invertebrates. Individual means were averaged to calculate the mean for each age/sex class for each productivity level, then age/sex class means were averaged to calculate an overall mean for each productivity level.

From Table 4.4, food-types in the diet appear to differ between different *'food'* availability classes, with orang-utans eating more fruit when '*food*' availability was high, and more flowers and leaves when '*food*' availability was low. For bark and pith, they were eaten more when '*food*' availability was low and medium compared to high, where as invertebrates were eaten more in high and medium compared to low. To test if there was a difference in food-types eaten during different '*food*' availability classes when age/sex class was controlled for, a GLM model was used in which a repeated measures ANOVA with regression model was run. The mean scores for the different types of foods eaten during different *'food'* availability classes was found to be significant ($F_{10, 137} = 4.41$, p <0.001). See Table 4.5 for pair-wise comparisons.

Table 4.5 Pair-wise comparisons for food-types in the diet against food availability.

Diet	Food class	t	df	P
Fruit	high > Low	5.45	137	< 0.001
Fruit	High > Medium	3.3	137	< 0.001
Fruit	Medium > Low	2.95	137	< 0.004
Flowers	Low > High	5.22	137	<0.001
Flowers	High - Medium	1.68	137	0.095 (ns)
Flowers	Low > Medium	4.12	137	< 0.001
Leaves	High - Low	0.11	137	0.913 (ns)
Leaves	High - Medium	0.2	137	0.844 (ns)
Leaves	Low - Medium	0.05	137	0.960 (ns)
Inverts	High - Low	0.05	137	0.957 (ns)
Inverts	High - Medium	0.42	137	0.675 (ns)
Inverts	Low - Medium	0.42	137	0.675 (ns)
Bark	high - Low	0.42	137	0.675 (ns)
Bark	High - Medium	0.66	137	0.510 (ns)
Bark	Low - Medium	0.13	137	0.897 (ns)
Pith	High - Low	0.25	137	0.803 (ns)
Pith	High - Medium	0.36	137	0.719 (ns)
Pith	Low - Medium	0.58	137	0.563 (ns)

The only significant pair-wise comparison was for fruits and flowers (Table 4.5). Orang-utans were found to eat significantly more fruit in periods of high '*food*' availability compared to medium or low, and they were found to eat significantly more flowers during periods of low '*food*' availability compared to medium or high. No other significant pair-wise comparison was found, although bark appears to be eaten more in medium and high than in low (ca. 25 times more) (Table 4.4), but no significant difference was found. This is probably due to the high standard deviations for those foods which made up a small proportion of the diet, and the small sample size.

Orang-utan health (Energy Balance)

From October 2003 - July 2005, 162 urine samples were tested for the presence of ketones. Samples were collected each month from as many individuals as possible. Fewer than half of all samples (67) were found to have ketones present.

Table 4.6 Number of individuals sampled each month.

Month	**Number of individuals**	**Number of samples**
Oct-03	1	3
Nov-03	1	3
Dec-03	1	1
Feb-04	2	4
April-04	1	2
May-04	1	1
Aug-04	8	21
Sep-04	5	17
Oct-04	6	30
Nov-04	7	14
Dec-04	4	7
Jan-05	5	18
Feb-05	5	6
Mar-05	3	9
Apr-05	5	9
May-05	2	4
Jun-05	4	8
Jul-05	1	5
Total	66	162

Ketone scores were compared against *'food'* availability , from September 2003 – July 2005, although there are no data for 5 months of this period (Figure 4.8). From this graph it is apparent that the level of ketones varies according to '*food*' availability. Ketones were first detected in August 2004. For 3 months prior to this (May, June and July 2004) *'food'* availability had dropped to low levels - the only time food availability fell to such low levels during the study period. When ketones were first detected, however, '*food*' availability had risen to medium. The percentage of samples with ketones present, and the amount of ketones present, then gradually reduced as *'food'* availability increased to high levels. Thus there appears to be a lag period during which ketones are still expressed even though '*food*' availability has increased. Although '*food*' availability increased, ketones were not absent until January 2004, when presumably orang-utans had regained their fitness. When testing ketone scores against *'food'* availability, it was not found to be significant (Pearson correlation: $r^2 = -0.016$, $p = 0.689$, (ns)).

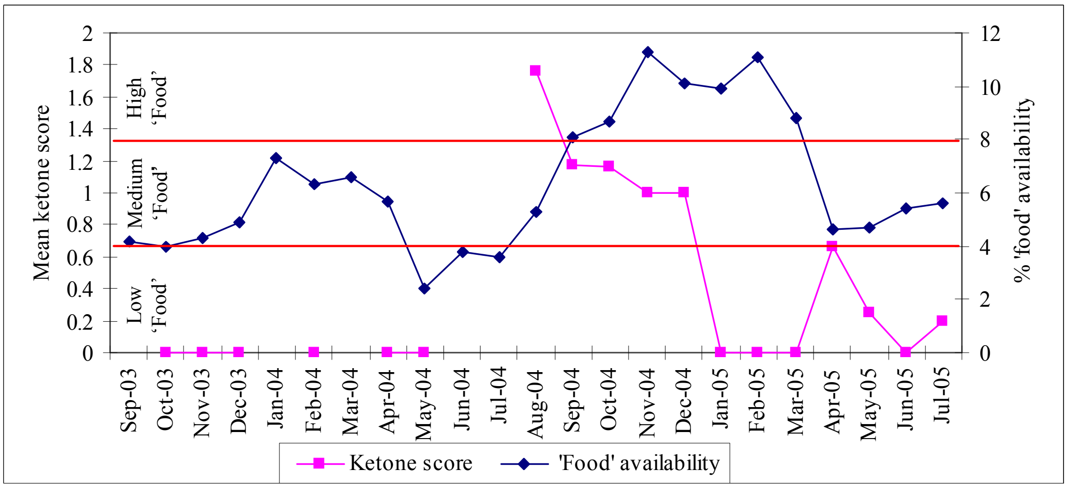


Figure 4.8 Ketone scores against *'food'* availability from September 2003 – July 2005.

4.4.3 Site differences in diet

Table 4.7 is adapted from Morrogh-Bernard *et al.* (2009), showing the percentage of food-types in the diet from nine different sites. Because researchers have used different ways of presenting data, an attempt was made to present data from all sites in as similar a way as possible, by using means, monthly ranges, trimester ranges and low-fruit:high-fruit measurements for comparison. No statistical analysis could be performed as the raw data was not available for these sites.

i. Fruit

The mean percentage of fruit in the diet was above 60 % for all sites except Mentoko and Ulu Segama where it was nearer 50 %. Sabangau has the highest percentage at 74 %, followed by Gunung Palung at 70 %. Those sites where the average was below 60 % had a monthly range where fruit eating fluctuated greatly from as low as 10 % to greater than 90%. The site that had the smallest monthly range was Ketambe (58-72 %) indicating that fruit availability at this site is much more stable.

ii. Flowers

The mean value for flowers at most sites was below 6 %, with the clear exception of Sabangau where it was 9 %. At some sites where flower eating was very low, flowers were included with leaves or other (Suaq Balimbing, Mentoko, and Ulu Segama). Kinabatangan had the lowest proportion of flowers in the diet - 1.3 %. Although most sites had little flower eating, monthly maximums at Tanjung Puting and Gunung Palung were 41% and 50% respectively, indicating that flowers are important during certain periods of the year at these sites, together with Sabangau which has the highest maximum of 61 %, and Tuanan having the lowest maximum of only 5.1 %.

iii. Leaves

The mean value for leaves was 13 % or above for all sites except Sabangau where it was less than 6 %. At the sites with *P.p.morio* (Kinabatangan, Mentoko and Ulu Segama) leaf eating was above 20 %. The monthly maximum at Sabangau was 18 %, and the highest trimester value was 13 %, which were lower than at all other sites thus indicating that leaves are less important in the diet in Sabangau than elsewhere.

iv. Bark

Bark eating was below 3 % at Suaq Balimbing, Ketambe, Tuanan and Sabangau, and was above 10 % at Tanjung Puting, Mentoko and Ulu Segama. Although Gunung Palung's mean was not above 10 %, the monthly maximum was high at 31%, and 3 sites had monthly or trimester maximums greater than 40 % (Tanjung Puting, Mentoko and Kinabatangan). This indicates that bark is much more dominant in the diet at certain sites than others.

v. Invertebrates

The mean value for invertebrates was below 10 % for all sites except Suaq Balimbing (13%), and sites with 2 % or less were those with *P.p.morio* (Kinabatangan, Mentoko, and Ulu Segama).

Table 4.7 Orang-utan diet at eight sites, expressed as percentage of total feeding time.

Site and Habitat	Fruits	Flowers	Leaves	Bark	Inverts	Other
Suaq Balimbing [1] PSF (*Pa*)						
mean	**66.2**	**-**	**15.5**	**1.1**	**13.4**	**3.8** (inc. fl)
monthly range						
trimester range						
low fruit - high fruit	*62.7- 69.6*	-	*18.3 - 12.7*	*0.8 -1.4*	*14.6- 12.2*	*3.6 - 4.1*
Ketambe [2] MD (*Pa*)						
mean	**67.5**	**3.5**	**16.4**	**2.7**	**8.8**	**1.3**
monthly range	*57.5- 71.5*	-	*10.6 - 20.1*	*2.2 - 3.3*	*5.7 - 11.7*	-
trimester range						
low fruit - high fruit	*64.2- 70.7*	*5.6 - 1.5*	*17.5 - 15.2*	*3.0 - 2.5*	*8.7 - 8.8*	*1.1 - 1.5*
Sabangau PSF (*Ppw*)						
mean	**74.2**	**8.8**	**5.6**	**1.5**	**7.7**	**2.2**
monthly range	*30.1-91.7*	*0.0-61.3*	*0.5-18.3*	*0.0-10.5*	*0.7-22.6*	*0.2-6.1*
trimester range	*56.4-88.1*	*0.02-24.9*	*2.0-12.5*	*0.1-7.4*	*1.6-12.01*	*0.3-3.6*
low fruit - high fruit	*68.8-80.5*	*11.5-5.6*	*6.5-4.6*	*2.2-0.2*	*8.3-6.9*	*2.2-2.2*
Tuanan [3] PSF (*Ppw*)						
mean	**68.6**	**5.9**	**17.2**	**1.0**	**6.3**	**0.6**
monthly range	*26.3- 88.0*	*0.0 - 5.1*	*4.5 - 49.5*	*0.0 - 5.9*	*0.3 - 24.1*	*0.0 -2.5*
trimester range						
low fruit - high fruit						
Tanjung Puting [4] PSF^{D}/MD (*Ppw*)						
mean	**60.9**	**3.9**	**14.7**	**11.4**	**4.3**	**4.0**
monthly range	*16.4- 96.1*	*0.0-41.1*	*0.0 - 39.6*	*0.0 - 47.2*	*0.0 - 27.2*	*0.0 - 21*
trimester range						
low fruit - high fruit						
Gunung Palung [3] MD^{D}/PSF (*Ppw*)						
mean	**70.0**	**5.1**	**13.4**	**4.9**	**3.7**	**2.9**
monthly range	*25.8- 99.0*	*0.0 - 49.6*	*0.1 - 41.1*	*0.0 - 30.9*	*0.0 - 14.0*	*0.0 - 9.2*
trimester range	*53.2- 98.3*	*0.10-24.2*	*0.3 - 27.7*	*0.0 - 16.2*	*0.5 - 6.1*	*0.3 - 5.0*
low fruit - high fruit	*60.7- 98.3*	*4.3 - 5.9*	*9.8 - 7.5*	*8.2 - 1.9*	*3.7 - 3.7*	*3.4 - 2.3*
Kinabatangan [3] MD^{D}/PSF (*Ppm*)						
mean	**68.0**	**1.3**	**22.9**	**6.7**	**1.2**	**-**
monthly range						
trimester range	*20.2- 97.2*	*0.0 - 7.2*	*2.8 - 76.8*	*0.0 - 40.0*	*0.0 - 4.8*	-
low fruit - high fruit						
Mentoko[5] MD (*Ppm*)						
mean	**53.8**	**-**	**29.0**	**14.2**	**0.8**	**2.2**(inc. fl)
monthly range	*25.7- 89.0*	-	*5.3 - 55.6*	*0.0 - 66.6*	*0.0 - 11.1*	*0.0- 2.5*
trimester range						
low fruit - high fruit						
Ulu Segama[6] MD (*Ppm*)						
mean	**51.5**	**-**	**35.6** (inc. fl)	**11.2**	**2.1**	**-**
monthly range	*10.0- 90.0*	-	*8.3 - 75.0*	*0.0 - 36.7*	*0.0 - 8.3*	-
trimester range	*17.2- 78.3*	-	*20.3 - 52.2*	*0.0 - 29.4*	*1.1 - 3.1*	-
low fruit - high fruit	*26.9- 75.3*	-	*49.3 - 21.9*	*21.0 - 1.4*	*2.8 - 1.4*	

Habitat types: PSF=Peat swamp forest; MD=Mixed dipterocarp forest; ^{D} = Dominant habitat; *Pa =Pongo abelii; Ppw= Pongo pygmaeus wurmbii*; *Ppm = Pongo pygmaeus morio*; Values for Sabangau used all follows >2 hr and was based on monthly means rather than individual means as in figure 4.1. Values for low-fruit are the mean value of all months classed as low fruit, ditto for high-fruit. Three studies have combined flowers with other categories, marked as (inc. fl) in the table. [1]Fox *et al.* (2004); [2]Wich *et al.* (2006a); [3]Morrogh-Bernard *et al.* (2009); [4]Galdikas (1988); [5]Rodman (1988); [6]estimated from Figure 19 in MacKinnon (1974).

4.4.4 Species eaten

Over 289 species of plant have been identified in the Sabangau mixed-swamp forest, of which 154 species were eaten by orang-utans during this study. (see Appendix VII for a full list and Table 4.8 for a summary).

Table 4.8 Number of plant families, genera and species eaten by orang-utans.

Plants	Total	Identified taxonomic level
Families	50	50
Genus	86	80
Species	154	95
Average Genera per family	1.7	
Average Species per family	3.1	
Average Species per Genus	1.8	

Of these 154 different species of plants, 110 were trees, 26 climbers, 7 figs, 6 epiphytes, 2 parasites and 3 herbs. In addition to foliage orang-utans also ate invertebrates, fungi, moss, and tree roots. When dividing the species up by parts eaten; fruits had the largest number (111) followed by leaves (Table 4.9).

Table 4.9 Number of species fed on by food parts.

Food parts	Fruit	Flowers	Leaves	Bark	Pith	Roots	Total
Number of species	111	32	78	24	12	1	154
% of species eaten	72	21	51	16	8	1	100

Important food species eaten

Over 70% of all feeding time was on just twenty species (Table 4.10). One of these species is in fact a group of species, -termites - which are ranked 4th, and is the only non-plant item in this list. The plant species in this list are from 12 families: Annonaceae, Apocynaceae, Clusiaceae, Ebenaceae, Euphorbiaceae, Fagaceae, Linaceae, Moraceae, Myrtaceae, Pandanaceae, Sapotaceae and Tetrameristaceae, and 5 off these families are classed as dominant and 1 as eudominant in the forest (Chapter 3 Table 2.3), indicating that a majority of the species in the diet come from the forest's dominant families.

Table 4.10 The most important species eaten by orang-utans ranked by percentage of time feeding (>1.5 %).

Ranking	Family	Latin Name	Local name	Percent of total feeding time, weighted by follow effort / month
1	Annonaceae	*Mezzetia leptopoda / parviflora*	Pisang Pisang Besar	8.52
2	Sapotaceae	*Madhuca mottleyana*	Katiau	6.94
3	Ebenaceae	*Diospyros bantamensis*	Malam Malam	6.79
4	Termitidae	Termites "spp indet."	Rayap	6.54
5	Apocynaceae	*Dyera lowii*	Jelutong	5.52
6	Annonaceae	*Polyalthia hypoleuca*	Alulup	4.98
7	Ebenaceae	*Diospyros siamang*	Ehang	4.35
8	Euphorbiaceae	*Blumeodendron elateriospermum / kurzii*	Kenari	3.84
9	Clusiaceae	*Garcinia bancana*	Manggis	3.47
10	Tetrameristaceae	*Tetramerista glabra*	Ponak	2.89
11	Annonaceae	*Mezzetia umbellata*	Pisang Pisang Kecil	2.25
12	Annonaceae	*Xylopia fusca*	Jangkang Kuning	2.10
13	Linaceae	*Ctenolophon parvifolius*	Kayu Cahang	2.06
14	Moraceae	*Parartocarpus venenosus*	Lilin Lilin	2.05
15	Clusiaceae	*Calophyllum hosei*	Mentangor	2.02
16	Pandanaceae	*Pandanus* sp. *1*	Pandan	2.00
17	Apocynaceae	*Willughbeia* sp. *1*	Bajakah Dango	1.93
18	Fagaceae	*Lithocarpus cf. dasystachys*	Pampaning Bitik	1.80
19	Sapotaceae	*Palaquium cochlearifolium*	Nyatoh Gagas	1.63
20	Myrtaceae	*Syzygium havilandii*	Tatumbu	1.60

Percentage of time spent feeding is on all food items – fruit, leaves, bark etc.

Mezzetia leptopoda was the species eaten for the most time, followed by *Madhuca mottleyana, Diospyros bantamensis,* termites and *Dyera lowii*. Additionally, there were species which did not form a large part of the diet overall, but were important at certain times of the year (seasonally-important species). To identify these, the 3 most-eaten species in each of the 24 months were recorded (Table 4.11). These species include nearly all of species in Table 4.10 (except for *Pandanus sp.* and *Palaquium cochlearifolium*), with 7 additional species, and 1 non-plant group of caterpillars. These species were only available for limited periods during the study, but were popular when in season, e.g. caterpillars - highly selected, but available for a limited time. These species are thus seasonally-important foods in the diet even though they are not the dominant species.

Table 4.11 A list of seasonally-important species eaten by orang-utans, based on the number of months a species was in the top three for a particular month.

Family	**Latin Name**	**Local Name**	**Overall Rank**	**Number of Months (out of 24) in Top Three**
Clusiaceae	*Callophyllum hosei*	Mentangor	15	1
Myrtaceae	*Syzigium sp. 15*	Hampuak galaget	36	1
Annonaceae	*Artobotrys suaveolins*	Bajakah Balayan	21	1
Fagaceae	*Lithocarpus sp. 4*	Pampaning Suling	45	1
Sapotaceae	*Palaquium ridleyii/xanthochymum*	Nyatoh Burung	26	1
Annonaceae	*Artobotrys cf. roseus*	Bajakah Kalalawit	40	1
Lepidoptera (Order)	Caterpillars “spp. indet.”		28	1
Meliaceae	*Sandoricum beccanarium*	Papong	42	1
Moraceae	*Parartocarpus venenosus*	Lilin Lilin	14	2
Tetrameristaceae	*Tetramerista glabra*	Ponak	10	2
Apocynaceae	*Willughbeia sp. 1*	Bajakah Dango	17	2
Fagaceae	*Lithocarpus cf. dasystachys*	Pampaning Bitik	18	2
Linaceae	*Ctenolophon parvifolius*	Kayu Cahang	13	2
Myrtaceae	*Syzygium havilandii*	Tatumbu	20	2
Sapotaceae	*Madhuca mottleyana*	Katiau	2	3
Annonaceae	*Mezzetia umbellata*	Pisang^2 Kecil	11	3
Annonaceae	*Xylopia fusca*	Jangkang Kuning	12	3
Euphorbiaceae	*Blumeodendron elateriospermum / kurzii*	Kenari	8	4
Clusiaceae	*Garcinia bancana*	Manggis	9	4
Annonaceae	*Polyalthia hypoleuca*	Alulup	6	4
Ebenaceae	*Diospyros siamang*	Ehang	7	5
Termitidae	Termites ”spp. indet.”	Rayap	4	5
Apocynaceae	*Dyera lowii*	Jelutong	5	5
Ebenaceae	*Diospyros bantamensis*	Malam Malam	3	6
Annonaceae	*Mezzetia leptopoda / parviflora*	Pisang^2 Besar	1	6

Species not in top 20 overall, but which are seasonally important are highlighted.

Species at the bottom of this list include many important species such as *Diospyros bantamensis, Mezzetia leptopoda, Diospyros siamang*, termites and *Dyera lowii*. These species were important in the diet for 5 or 6 months of my study, indicating that the parts eaten from these species are available for many months of the year (see Chapter 3 for discussion of fruiting cycles) e.g. termites were available in the forest all year round, and *Dyera lowii* was available all year round because bark from this species was also eaten when fruits were not available.

Preferred foods eaten (highly selected)

Those species that are most important in the diet are identified in the previous section. To work out which species are most preferred, a Preference Score (see methods section 4.3.4) was calculated which identifies the most preferred species by food-type (Table 4.12).

The top 20 highest ranked food-types in the preference table include 3 additional species: *Polyalthia glauca, Licania splendens* and *Litsea resinosa*, which were not included as '**Important Species'** in table 10 or 11. Species in Table 4.12 are divided by part eaten, so that, for example, *Parartocarpus venenosus* fruit and flowers are two separate entries. Thus, parts of the same species scored differently, e.g. *Madhuca mottleyana* flowers had the highest score of 22.24, compared to their fruits which scored 0.31; *Dyera lowii* fruits (4.34) scored much higher than flowers (<0.001). Thus, food-type (e.g. fruit or flowers) has a great influence on species preference.

The top 5 preferred food-types are *Madhuca mottleyana* flowers, *Parartocarpus venenosus* fruits, *Polyalthia glauca* fruits, *Parartocarpus venenosus* flowers and *Licania splendens* fruits. The Preference Index strongly favours those species that are rare in the forest, hence *Mezzetia leptopoda,* which is relatively common and is the most Important species, gained a score of 6.35, indicating that although it appeared in the diet the most, it was only the 12th most preferred species.

Table 4.12 Fruit and flower species eaten by orang-utans ranked in descending order of preference.

Family	Species	Local name	Part eaten	Ps
Sapotaceae	***Madhuca mottleyana***	**Katiau**	**FLOWER**	**22.24**
Moraceae	***Parartocarpus venenosus***	**Lilin lilin**	**FRUIT**	**21.36**
Annonaceae	*Polyalthia glauca*	Kayu bulan	FRUIT	20.49
Moraceae	***Parartocarpus venenosus***	**Lilin lilin**	**FLOWER**	**19.56**
Chrysobalanaceae	*Licania splendens*	Bintan	FRUIT	15.85
Annonaceae	***Mezzetia umbellata***	**Pisang^2 kecil**	**FRUIT**	**14.40**
Sapotaceae	***Palaquium ridleyii / xanthochymum***	**Nyatoh burung**	**FRUIT**	**9.86**
Ebenaceae	***Diospyros siamang***	**Ehang**	**FRUIT**	**8.64**
Ebenaceae	***Diospyros bantamensis***	**Malam malam**	**FRUIT**	**8.03**
Annonaceae	***Polyalthia hypoleuca***	**Alulup**	**FRUIT**	**7.73**
Sapotaceae	***Palaquium cochlearifolium***	**Nyatoh gagas**	**FRUIT**	**6.89**
Annonaceae	***Mezzetia leptopoda / parviflora***	**Pisang^2 besar**	**FRUIT**	**6.59**
Tetrameristaceae	***Tetramerista glabra***	**Ponak**	**FRUIT**	**6.35**
Euphorbiaceae	***Blumeodendron elateriospermum / kurzii***	**Kenari**	**FRUIT**	**5.11**
Sapotaceae	***Palaquium cochlearifolium***	**Nyatoh gagas**	**FLOWER**	**4.67**
Apocynaceae	***Dyera lowii***	**Jelutong**	**FRUIT**	**4.34**
Meliaceae	***Sandoricum beccanarium***	**Papong**	**FRUIT**	**3.87**
Lauraceae	*Litsea sp. 1 cf. resinosa*	Medang	FRUIT	3.70
Clusiaceae	***Garcinia bancana***	**Manggis**	**FRUIT**	**3.24**
Linaceae	***Ctenolophon parvifolius***	**Kayu cahang**	**FRUIT**	**2.64**
Ebenaceae	*Diospyros confertiflora*	Kayu arang	FRUIT	2.52
Sapotaceae	*Isonandra lanceolata*	Nyatoh palanduk	FRUIT	2.49
Annonaceae	*Xylopia cf. malayana*	Tagula	FRUIT	2.29
Fagaceae	***Lithocarpus cf. dasystachys***	**Pampaning bitik**	**FRUIT**	**2.13**
Clusiaceae	*Calophyllum sclerophyllum*	Kapur naga	FRUIT	1.65
Fagaceae	*Castanopsis foxworthyii*	Takurak	FRUIT	1.43
Myrtaceae	***Syzygium havilandii***	**Tatumbu**	**FRUIT**	**1.31**
Sapindaceae	*Xerospermum laevigatum*	Kelumun	FRUIT	1.29
Annonaceae	***Xylopia fusca***	**Jangkang kuning**	**FRUIT**	**0.91**
Clusiaceae	*Calophyllum soulattri*	Takal	FRUIT	0.84
Myrtaceae	*Syzygium garcinifolia*	Jambu burung	FRUIT	0.60
Sapotaceae	*Palaquium pseudorostratum*	Nyatoh babi	FLOWER	0.56
Annonaceae	*Cyathocalyx biovulatus*	Kerandau	FRUIT	0.46
Anacardiaceae	*Campnosperma coriaceum*	Terontang	FRUIT	0.44
Magnoliaceae	*Magnolia bintulensis*	Medang limo	FRUIT	0.41
Sapindaceae	*Nephellium maingayi*	Rambutan	FRUIT	0.38
Sapotaceae	***Madhuca mottleyana***	**Katiau**	**FRUIT**	**0.31**
Clusiaceae	***Calophyllum hosei***	**Mentangor**	**FRUIT**	**0.25**
Tiliaceae	*Microcos sp. 1*	Brania himba	FRUIT	0.24
Sapotaceae	***Palaquium ridleyii / xanthochymum***	**Nyatoh burung**	**FLOWER**	**0.16**
Sapindaceae	*Nephellium lappaceum*	Rambutan gundul	FRUIT	0.14
Anacardiaceae	*Campnosperma squamatum*	Teras nyating	FRUIT	0.11
Elaeocarpaceae	*Elaeocarpus mastersii*	Mangkinang	FRUIT	0.10
Sapotaceae	*Isonandra lanceolata*	Nyatoh palanduk	FLOWER	0.08
Anisophyllaceae	*Combretocarpus rotundus*	Tumi	FRUIT	0.07
Clusiaceae	*Calophyllum sclerophyllum*	Kapur naga	FLOWER	0.06
Myrtaceae	*Tristaniopsis sp. 3 cf. merguensis*	Blawan	FRUIT	0.05

Family	Species	Local name	Part eaten	Ps
Sapotaceae	*Palaquium leiocarpum*	Hangkang	FRUIT	0.05
Myristicaceae	*Horsfieldia crassifolia*	Mahadarah	FRUIT	0.05
Sapotaceae	*Palaquium pseudorostratum*	Nyatoh babi	FRUIT	0.05
Linaceae	***Ctenolophon parvifolius***	**Kayu cahang**	**FLOWER**	**0.03**
Magnoliaceae	*Magnolia bintulensis*	Medang limo	FLOWER	0.03
Tetrameristaceae	***Tetramerista glabra***	**Ponak**	**FLOWER**	**0.02**
Annonaceae	***Polyalthia hypoleuca***	**Alulup**	**FLOWER**	**0.01**
Euphorbiaceae	*Neoschortechinia kingii*	Pupu palanduk	FRUIT	0.01
Annonaceae	*Xylopia coriifolia*	Nonang	FRUIT	0.01
Lauraceae	*Litsea cf. rufo-fusca*	Tampang	FRUIT	0.01
Dipterocarpaceae	*Shorea teysmanniana*	Meranti sumut	FRUIT	0.01
Elaeocarpaceae	*Elaeocarpus mastersii*	Mangkinang	FLOWER	0.01
Icacinaceae	*Stemonorus scorpiodes*	Tabaras	FRUIT	0.01
Lauraceae	*Litsea cf. elliptica*	Medang sp.	FRUIT	<0.001
Apocynaceae	***Dyera lowii***	**Jelutong**	**FLOWER**	**<0.01**
Euphorbiaceae	*Neoscortechinia kingii*	Pupu palanduk	FLOWER	<0.01
Ebenaceae	***Diospyros bantamensis***	**Malam malam**	**FLOWER**	**<0.01**
Crypteroniaceae	*Dactylocladus stenstachys*	Mertibu	FLOWER	<0.01
Sapotaceae	*Palaquium leiocarpum*	Hangkang	FLOWER	<0.01
Myristicaceae	*Horsfieldia crassifolia*	Mahadarah	FLOWER	<0.001
Annonaceae	***Xylopia fusca***	**Jangkang kuning**	**FLOWER**	**<0.001**

Only species that appear in the phenology plots were assessed for preference. Species in bold are species which appear in the 'Important Species' table or the 'Seasonally Important table.

4.5 DISCUSSION

4.5.1 Dietary composition and site comparisons

Fruits and flowers are the preferred food-types in Sabangau, followed by invertebrates, leaves, pith and then bark. This differs from most other sites where leaves are usually the second most fed-upon food-type after fruit (e.g. at Ketambe, Tuanan, Tanjung Puting, Gunung Palung and Kinabatangan) and are considered a main fallback food, along with bark. Of all 154 species, flowers were eaten from 32, although 1 species in particular was clearly favoured, accounting for 76% of all time feeding on flowers (*Madhuca mottleyana*). Flowers from this species are only available for short-periods, but were identified as the most preferred food item in the diet. Flower eating makes sense as flowers are nutritionally rich (Harrison, 2009), albeit rarely available due to seasonality (McConkey *et al.,* 2003). The absence or low density of this species at other sites may explain why flowers elsewhere feature so little in the diet. For example at Tuanan a similar peat-swamp forest, the density of *Madhuca mottleyana* was 3.5 stems/ha compared to 10 stems/ha in Sabangau and formed a much smaller component of the diet there (Wich *et al.,* in prep). Thus, habitat type and species density clearly influence the choice of foods. Part eaten can also influence species selection. Although fruits are the preferred food-type, seeds were the preferred part. Over 50% of all feeding time on fruit in Sabangau was on seeds. Leighton (1993) found that orang-utans preferred to eat both seeds and pulp from non-fig fruits, and that energy content rather than protein was important in food selection. Social learning and cultural behaviours may also play a part in food selection. Russon *et al.* (2009) found that certain species that were present at multiple sites were not eaten at all sites, suggesting that social learning rather than just species diversity was an influencing factor on food-types and species eaten.

Taylor (2006) found that ecological factors influenced jaw morphology, as the eastern Borneo sub-species *P.p. morio* has a strong jaw which is better adapted for feeding on tougher food-types such as barks and leaves, the main fallback foods. This morphological adaptation appears to have come about because of their diet. In this comparative study orang-utans from Mentoko, Ulu Segama and Kinabatangan had the lowest percentage of flowers and termites in their diet, but a higher percentage of barks and leaves than orang-utans from non-*P.p.morio* sites. Marshall and Wrangham (2007) suggest that the evolutionary importance of fallback foods applies more to adaptations for processing than for harvesting foods, and that fallback foods are typically abundant and easy to locate but hard to process, and therefore provide low rates of energy gain when compared to preferred foods.

4.5.2 '*Food*' availability and energy budgets

Differences in diet between age/sex classes

Although significant differences between age/sex classes were not found for the amount of each food-type eaten, trends showed that flanged males had more pith and invertebrates in their diet than the other age/sex classes. This is probably due to the amount of time they spend on the ground, which is more than any other age/sex class (unpublished data). The main source of pith is *Pandanus* which grows on the forest floor (APPENDIX VIII); and the main source of termites, is fallen dead trees which have rotted away. Flanged males are strong enough to also push over dead standing trees to access termites. Trends also show females as the sex class with the greatest percentage of flowers in their diet, which could be due to their high nutritional value compared to other food-types.

Diet and 'food' availability

Primate diet changes as '*food'* availability changes, because most primates prefer to eat fruits when it is available (van Schaik and Pfannes, 2005). In the Sabangau, changes in '*food'* availability influenced diet, similar to findings by Knott (1998, 1999b) and contrary to Wich *et al*. (2006a) where diet was not influenced by fruit availability. In Sabangau fruit and flower feeding was highly correlated with the availability of these food-types. When looking at differences between '*food'* availability levels, orang-utans ate more fruit when its availability was medium or high compared to low, and more flowers when *'food'* availability was low compared to medium or high. Thus flowers appear to be eaten when food availability is low probable due to the flowering and fruiting cycles, which accure at different times. Although there was no significant difference in the amount of bark or leaves in the diet between different periods of '*food'* availability, orang-utans did eat more of these food-types when '*food*' availability was low or medium compared to high thus indicating that bark and leaves are a fallback food, similar to findings from other sites (Mackinnon, 1974; Galdikas, 1988; Rodman, 1988; Knott, 1998; Lackman-Ancrenaz and Ancrenaz, 2006). Unlike other sites, flowers seem to play a more imporant role in the diet of orang-utans in the Sabangau, and are thus selected for when fruits are low.

Ketones

Ketones are produced when fats are metabolised, and testing for these in the urine is an efficient way of examining if animals are in a negative or positive energy balance. Ketones were found in the urine after periods of low *'food'* availability had ended, eventually disappearing when '*food*' availability remained high for a period of time, indicating a time lag before ketones stopped being produced by the orang-utan's metabolism. This lag appears to work in one direction only, for example. when '*food*' availability decreased, ketones were produced soon after, whereas Knott's (1999b) study in Gunung Palung found there to be a lag of one month in ketone production after fruit availability decreased to low levels, and she explains this by the amount of fat stored, which meant that orang-utans bodies was not stressed enough to produce ketones, until one month into the low fruit period. A possible reason why ketones were detected soon after '*food*' availability decreased in Sabangau, may be due to the different amounts of fat stored between the different populations, as Knott's study took place in a masting forest during the mast, thus production levels would have been much higher than that found in the peat-swamp forests in Sabangau. Also Knott makes no mention of a lag effect before entering a fruit high period, whereby ketones were still detected, and this is because her study was started in the middle of the mast, and ended while fruit availability was low. Thus, these findings of a lag in the disappearance of ketones, but not in the appearance, as Knott (1999b) found, may be due to the different productivity levels between the different forests, which will affect the amount of fat orang-utans can be store. In a study in Ketambe, Wich *et al.* (2006a) found no ketones present, thus suggesting that fluctuations in fruit availability are far less severe in Sumatra, due to the high abundance of figs, which are the main fallback food there, rather than bark, invertebrates or leaves. Thus orang-utans in Ketambe can maintain a positive energy balance all year round, without having to maximise their fat reserves for use when non-fig fruits are low, as the Bornean orang-utans must do.

4.5.3 Species importance and preference

The most up-to-date comparative study on diet by Russon *et al.* (2009) found that orang-utans feed from a wider range of taxa than African apes, and that orang-utans living in swamp habitats ate from more taxa than did orang-utans in dryland forest types. In the Sabangau 154 different species of plant were eaten from 50 families. Of all species eaten, the majority of feeding time (72%) was concentrated on 20 species, of which 3 were non-tree species, including termites ranked 4th, pandan (*Pandanus* spp.), ranked 16th, and one liana (*Willughbeia sp.*), ranked 17th. The top species eaten by percentage of time was *Mezzetia leptopoda* (APPENDIX IX), which was considered the most **'Important Species'** in the diet. **'Important Species'** were species which appeared in the diet the most due to either their frequent and long fruiting cycles, or, in the case of termites, constant availability all year round. *Mezzetia leptopoda* and *Diospyros bantamensis* were identified as having an asynchronous reproductive cycle (Chapter 3), i.e. different individuals produce fruit at different times of the year and hence there is nearly always a tree somewhere in fruit. Additionally, some species provided more than one food-type e.g. *Dyera lowii* bark was eaten when fruits were not available, and thus appear high in the list of '**Important Species'**.

In addition, there are species which do not form a large part of the diet overall, but were important at certain times of the year and are referred to as '**Seasonally-Important Species'**. These species included nearly all the top twenty '**Important Species'** with several additional tree species, and caterpillars, which were favoured when they were available. Therefore seasonal variation must be taken into account when assessing which food species are important for orang-utans, as they may not figure highly in terms of overall annual percentage in the diet, but are important and selected for when they come into season.

The species which appear in the diet regularly (i.e. most months of the year) can be referred to as '*Staples*'. '**Preferred Species**' in contrast are highly selected for when available. The flowers of *Madhuca mottleyana* was the top ranked food for preference, even though it only produced flowers for a very limited period. Many of the top **'Preferred Species'** appear to have precise flowering or fruiting seasons and/or have lower density (e.g. *Madhuca mottleyana* 12.2 stems/ha; *Parartocarpus venenosus* 2.2 stems/ha), compared to the top '**Important Species'** (e.g. *Mezzetia leptopoda* 58 stems/ha or *Diospyros bantamensis* 51 stems/ha), which appear in the diet most months of the year and have higher densities. Species dominance, however, did not influence overall selection as the most dominant species *Palaquium leiocarpum* (268 stems/ha) was rarely eaten. Thus, dominance seems to plays a less important role in selection, than other influencing factors such as fruiting cycles, palatability, nutrient value and phenolic content. For example the energy value of *Palaquium leiocarpum* fruit was less than average (Harrison, 2009). Thus, when assessing the most important species for orang-utans, a combination of '**Important Species'** and **'Seasonally-Important Species'** must be considered. This knowledge is important when writing management plans or conservation strategies for habitat containing orang-utans.

4.6 CONCLUSION

The main food-types in the diet were fruits and flowers, contrary to finding from other sites where flowers were rarely eaten. In Sabangau, *Madhuca mottleyana* flowers were identified as the most preferred food item. The major fallback foods were bark, similar to other sites, and invertebrates, but not leaves, although they were eaten as a fallback food by three of the four age/sex classes. Diet differed between age/sex classes, is probably due to different energetic requirements as smaller individuals will find accessing some food-types harder than others, and adult females will expend more energy when lactating and carrying around an infant. Seasonal fluctuations in '*food'* availability affected nutrient intake, as the proportion of samples with ketones was negatively correlated with '*food'* availability. Thus if '*food'* availability was low for extended periods of time, perhaps during years with severe El Niño events this could increase mortality rates, due to starvation.

Orang-utans' diet in the Sabangau is dominated by 20 species, but 30 species were identified as **Overall Important Species**, by combining the top 20 species on the **'Important Species' Seasonally-Important Species'** and **'Preferred Species'** lists. This includes 28 species of plant and 2 types of invertebrate (termites and caterpillars). Out of all plant species identified in the diet, *Mezzetia leptopoda* was identified as the most dominant species in the diet and can be considered a '*staple*' as it appears in the diet in most months.

Knowing which species are eaten and which are either **'Important', 'Seasonally-Important'** or **'Preferred'**, is essential if management plans for orang-utans are going to be successful, as most orang-utan populations occur in production forests, that are being logged. This information is thus important for government officials, who liaise with logging companies on management issues. Previous species lists have not indicated importance, but this is vital, as these lists can also be used for assessing habitat suitability for orang-utan reintroduction programmes. This knowledge is also of great consequence for comparative studies in terms of the species' evolutionary ecology and adaptations.

4.7 SUMMARY

- Fruit was the main food-type eaten followed by flowers, leaves, invertebrates, bark and pith.
- Other food-types which were eaten included moss, fungi and tree roots.
- Fruit seeds were the most popular food part eaten.
- Age/sex differences were not found when *'food'* availability was controlled for.
- Diet was influenced by *'food'* availability, with fruit feeding increasing when *'food'* availability increased, and flower feeding increasing when *'food'* availability decreased. Although they were eaten more during this time, feeding on flowers was positively correlated with flower production, indicating that they were selected.
- Bark and leaves were eaten more when *'food'* availability was low, and thus were the main fallback food-types, as they are available in the forest most of the time, but were eaten more when *'food'* availability was low or medium.
- Fruit availability affects energy budgets, with periods of low *'food'* availability sending orang-utans into a negative energy balance.
- The disappearance of ketones from the urine, when food availability increases, is delayed while orang-utans gain fitness, whereas the appearance of ketones was more immediate.
- 154 species of plant were identified as orang-utan food.
- **'Important Species'** were identified, by incorporating both dominant species in the diet together with '**Seasonally-Important Species**'.
- *Mezzetia leptopoda* was the most dominant species of fruit in the diet, and was eaten all year round, thus it was referred to as a '*staple*'.
- *Madhuca mottleyana* flowers were the most preferred food, as it was the most highly selected food-type.

CHAPTER 5

ORANG-UTAN ACTIVITY PATTERNS

5.1 INTRODUCTION

This chapter is an overview of orang-utan activity budgets and the impact of seasonal *'food'* (fruit and flower) availability on these in the Sabangau peat-swamp forest. It will also add to our current knowledge about orang-utan behaviour by comparing orang-utans in the Sabangau with those in other sites and investigating differences between orang-utan species and habitat types. Previously-unpublished data collected by several different researchers are used in this analysis, which I standardised and analysed for a collaborative study (Morrogh-Bernard *et al.,* 2009).

5.1.1 Activities

An animal's main daily activities are feeding, resting, travelling and socialising (Williams and Dunbar, 1999). The percentage of time taken up by each activity forms the overall *activity budget.* These activities take place during the *active period*, defined for orang-utans as starting when they sit up in their nest in the morning, and ending when they lie down in their nest at night (Morrogh-Bernard *et al.,* 2002).

There are many variables that can influence active period length (within and between sites), ranging from environmental conditions (food availability) to social organisation and status (Chivers, 1974, 1980; Ahsan, 2001). Lodwick *et al.* (2004) found that the active period length in individual female chimpanzees (*Pan troglodytes schweinfurthii)* varied according to their reproductive status and dominance ranking. In the hoolock gibbon (*Hoolock hoolock*) Ahsan (2001) found that the start and end of the active period was highly correlated with sunrise and sunset, but was also influenced by the weather. Hoolocks delayed the start of their active period until late dawn during the winter due to fog, but began earlier in the summer when it was warmer. Similar results have been found for the siamang (*Symphalangus syndactylus*) and lar gibbon (*Hylobates lar*). Chivers (1974, 1980) reported that the day ended earlier than normal for siamangs and lar gibbons when food availability was low, thereby demonstrating how different variables can influence the active period and thus the distribution of activities within it.

An important influence on primate activity is the availability of food. Knott (1998) found that orang-utans were not maintaining their body weight during periods of low food availability even though they were spending the same amount of time feeding as in the fruit- rich period; this was due to lower food quality. Most frugivorous primates increase the proportion of low-quality food in their diet during fruit-scarce periods (Doran, 1997; Strier, 2000), and thus also alter their activity, ranging and social groupings (Strier, 2000). Northern muriquis (*Brachyteles hypoxan*) were found to switch their ranging patterns along with their diet during fruit-scarce periods; they were found to travel shorter distances when they ate abundant, but low-quality leaves, or high-quality fruits which occurred in larger patches (Strier, 1987). In wetter conditions, when fruit availability was higher, they would range further to maintain a more frugivorous diet (Strier, 2000). How food availability in peat-swamp forests, in particular, is influencing orang-utan activity budgets will be investigated.

5.1.2 Comparative studies

Most inter-population comparison studies have been on the African great apes, particularly gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*), which have highlighted interesting variation in diet, behavioural ecology and culture (McGrew, 1992, 1998; Boesch and Boesch-Achermann, 2000; McNeilage, 2001; Doran *et al.*, 2002a, 2002b; Goldsmith, 2003; Rogers *et al.*, 2004; Lehmann *et al.*, 2008). The first study to compare populations of orang-utans was John MacKinnon's (1974) research on populations at Ulu Segama in Sabah, Borneo and Ranun in Sumatra. Since then several reviews of orang-utan behavioural ecology have been published, using previously-analysed data for their comparisons or summaries (Rodman, 1988; Knott, 1999a; Rijksen and Meijaard, 1999; Delgado and van Schaik, 2000; Fox *et al.*, 2004; Wich *et al.*, 2006a); but these data were not strictly comparable, as different methods were used and different computation methods can influence the results (Harrison *et al.,* 2008).

More recently, there have been more comparative studies on orang-utans, focusing mainly on cultural traits (van Schaik and Knott, 2001; van Schaik *et al.*, 2003), morphology

(Groves, 1999; Taylor, 2006), life history (Wich *et al.*, 2004a) and population densities (Singleton *et al.*, 2004), all of which indicate that orang-utans, like the African apes, show considerable inter-population variation, especially between the Bornean and Sumatran species. The Bornean orang-utan (*P. pygmaeus*) has been found to have morphological differences which indicate that they rely more heavily on bark and relatively tough vegetation than does the Sumatran species (*P. abelii*) (Taylor, 2006). Within Borneo, the northern sub-species (*P.p. morio)* exhibit structural features of the mandible that provide greater load resistance than any of the other sub-species, thus they are better suited to eating tougher foods such as bark (Taylor, 2006). Other comparative studies found cultural differences; for example tool use has been observed only in Sumatran orang-utans (van Schaik *et al.*, 2003), whereas fur-rubbing as a form of self-medication has been witnessed only in the Bornean orang-utans in Sabangau (Morrogh-Bernard, 2008). Another difference is the inter-birth interval which is longer in Sumatra than Borneo (Wich *et al.,* 2004a). Thus, many inter-specific differences have been found, but as yet there has been no standardised comparison of activity budgets.

The aim in this chapter is to add to the current literature by comparing orang-utan activity budgets across sites, using a standardised method, in order to understand better why orang-utans differ between sites, species and habitat type, with special emphasis on the Sabangau population.

5.2 OBJECTIVES

I will describe orang-utan active periods and activity budgets in the Sabangau and compare these to '*food'* availability. I will also carry out the first standardised analysis comparing activity budgets between a number of locations, and highlight and explain the possible reasons for these observed differences. Thus I will address the question of what foraging strategies orang-utans use to cope with different environmental conditions.

The questions addressed for this chapter are in three parts: (i) activity budgets for Sabangau orang-utans; (ii) the effects of '*food*' availability on the activity budget and (iii) a comparison of activity budgets between sites and habitat types.

Active period

- When do orang-utans start and finish their day?
- What is the active period length, and is there a difference between each age-sex classes?
- What influences the active period start time and length?

Activity budget

- What are the activity budgets for the Sabangau orang-utans, and is there a difference between individuals in the same age/sex class?
- What are the activity budgets for each age/sex class in the Sabangau and is there a difference between them?
- Are orang-utan activity budgets affected by *'food'* availability?

Comparison with other sites

- Are there differences in activity budgets between habitat type, and if so what is influencing these differences?

5.3 METHODS AND ANALYSIS

5.3.1 Active period and activities

An orang-utan's active period starts when it sits up in the night-nest and ends when it lies down in their new night-nest. The total amount of time spent performing each activity within the active period forms the activity budget. Primary activities were defined as feeding (including co-feeding, food search and food sharing), resting, travelling, social (mating, playing, fighting and calling), nest building and a number of other activities including aggression to observers, aggression to other people, self-play, allo-grooming and self-medication. Mean party size (the number of independent individuals, including the focal, within 50 m of each other) is used in some analyses as a proxy for social, rather than minutes spent performing social activities (grooming, food sharing, mating, playing), as orang-utans can be in party with another individual but not actively interacting e.g. feeding in the same tree,

For most analyses the normal age/sex classes defined in Chapter 2 applied, but when analysing party size, NSAM (non-sexually-active males) and NLF (nulliparous female) were used as separate categories, rather than the usual UFM and NSAF as described in Chapter 2.

5.3.2 Sabangau

Data were collected using standard focal-animal sampling techniques, which were standardised between research sites (Morrogh-Bernard *et al.,* 2002). Data were collected instantaneously at 5-minute intervals in the Sabangau. Data collection started when the orang-utan was found and continued until it went to sleep in its nest. The orang-utan would then be followed the next day until it nested again. The maximum number of days an individual was followed before being abandoned was 10 days, unless it was lost or exited the grid beforehand (see Chapter 2, section 2.2 onwards, for a full description of methods and protocol used).

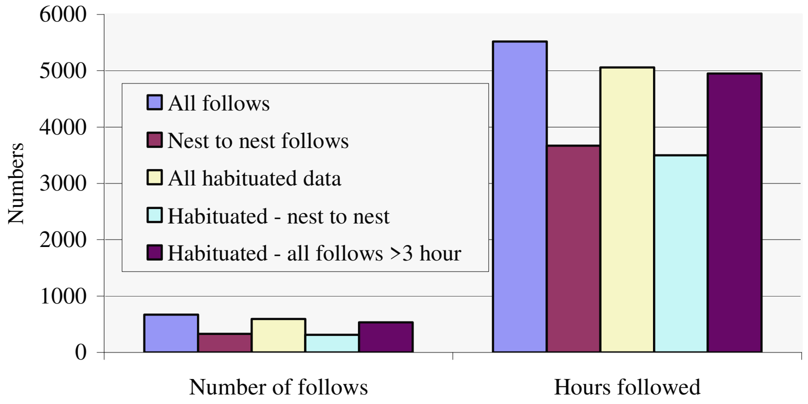


Figure 5.1 Number of hours followed in Sabangau using different data sets.

The total number of follow hours in the Sabangau was 5519. All habituated data, including follows greater than 3 hours, total 4954 hours (Figure 5.1). Habituated data, using full-day follows (nest to nest) will be the main dataset used for analysing activity budgets for Sabangau, as this is considered the most accurate data set (Harrison *et al.,* 2008). In some analyses, party size is used as a proxy for social activity, rather than time performing social activities. Overall means, presented in all tables, were calculated using a mean of age/sex classes, and means for age/sex classes were calculated using individual means (see Chapter 2, section 2.4.2). Individuals for which there are less than 50 hours of data were excluded, as it was considered insufficient time in which to obtain an accurate representation for those individuals. For statistical analysis, individual follow days were used as individual data points (see Chapter 2, section 2.4.2) unless otherwise stated. Monthly means or yearly means were used for inter-site comparisons.

Because the active period was found to differ between age/sex classes (see results), activity-budget data had to be standardised in order to compare between age-sex classes accurately. Thus, individual activity budgets were converted from percentages to actual minutes, with the cumulative mean daily-activity budget equalling 12 hours (720 minutes), and daily budgets were converted in the same way, but to a cumulative time of 24 hours (1440 minutes), because some daily active periods were longer than 12 hours.

Food availability

When comparing food availability with activity budgets for Sabangau, I used the availability of both flowers and fruits and defined them as *'food'* (see Chapter 3) for Sabangau. '*Food'* availability was then divided into 3 productivity classes: low, medium and high (Chapter 3) and compared to activity budgets for Sabangau. Studies elsewhere have just used edible-fruit availability to compare with behaviour, and have called this food. I refer to *'food'* in italics to distinguish this measure from all other food (which includes termites, leaves and other vegetative parts which are continuously available).

5.3.3 Comparison with other sites

Data from the nine sites compared (Table 5.1) were either collated from published papers or were unpublished and kindly made available for this analysis by the following people: Cheryl Knott (Gunung Palung), Serge Wich (Ketambe), Carel van Schaik (Tuanan), Maria van Noordwijk (Suaq Balimbing), Isabelle Lackman-Ancrenaz (Kinabatangan) and Tanamori Kanamori and Noko Kuze (Danum Valley). The full comparison is published as Morrogh-Bernard *et al.* (2009).

Data used in the analysis were standardised as much as possible. Data from non-habituated individuals and from all follows less than 3 hours long were excluded. The length of time taken up by each activity is typically presented as a percentage of the active period. In order to standardise activity patterns between sites, I present all figures here in minutes out of a 12-hour day. To convert activity budgets presented as percentages of active period into minutes/day, I multiplied the percentage of time spent in each activity by the mean active period length of the age-sex class under investigation. As mean active periods were all less than 12 hours, the difference was added to the total time resting (sleeping). I used annual means of age/sex classes as independent data points for inter-site comparisons, whereas monthly means were used for intra-site comparisons (for which all months with less than 15 hours of data/month were excluded). Overall, figures presented were means of the respective figures of the four age-sex classes. Thus, figures presented for Sabangau in the inter-site comparison tables will differ from the figures presented just for Sabangau where individual means were used.

Table 5.1 Data from the following sites were used in the comparison.

Site	Research dates	No. of hours	Species	Habitat type	Disturbance
Suaq Balimbing	1994 - 1999	17084	*P. abelii*	Peat swamp	unlogged
Ketambe	1976 - 2002	17109	*P. abelii*	Mixed dipterocarp	unlogged
Sabangau	2003 - 2005	5519	*P. p. wurmbii*	Peat swamp	logged
Tuanan	2003 - 2005	8300	*P. p. wurmbii*	Peat swamp	logged
Tanjung Puting[1]	1971 - 1975	6804	*P. p. wurmbii*	Peat swamp (main) / Mixed dipterocarp	unlogged
Gunung Palung	1994 - 1996	5615	*P. p. wurmbii*	Mixed dipterocarp (main) / Peat swamp	unlogged
Mentoko[2]	1981 - 1983	3900	*P. p. morio*	Mixed dipterocarp	unlogged
Danum Valley	2004 - 2006	977	*P. p. morio*	Mixed dipterocarp	unlogged
Ulu Segama[3]	1968 - 1979	-	*P. p. morio*	Mixed dipterocarp	unlogged
Kinabatangan	1998 - 2006	-	*P. p. morio*	Mixed dipterocarp (main) / freshwater swamp	logged

All data unpublished except: [1]Galdikas (1988); [2]Mitani (1989); [3]MacKinnon (1974).

Fruit availability

The only site where fruit availability was measured was Ketambe, where data were adapted from data already published in Wich *et al.* (2006a), in which 4 levels of fruit availability were compressed into two levels (level 1 and 2 were low fruit availability and level 3 and 4 were high fruit availability). Fig density per hectare was recorded for stems >10 cm dbh for Ketambe and for Kinabatangan.

5.3.4 Analysis

Pearson's test was used for all correlations. For normally-distributed data t-tests or ANOVA's, with Tukey *post-hoc* comparisons to determine significant pairwise differences, and where data did not conform to the normal distribution, or where Levene's Test for Homogeneity of Variance produced a significant result, I used a Mann-Whitney test or a Kruskal-Wallis test followed by a Dunn's *post-hoc* test (Siegel and Castallan, 1988), in lieu of t-tests/ANOVA.

To test differences in the activity budget between age/sex classes and between different *'food'* availability classes, I used a GLM (General Linear Model) with repeated measures, incorporating both *'food'* availability and age/sex class. The time spent carrying out each major activity were compared between the three *'food'* availability classes. The GLM was considered the most robust test for this data set which incorporated both continuous and categorical data.

For analyses where quantitative raw data was not available, descriptive statistics were used.

5.4 RESULTS

5.4.1 Active period start and finish time

Sabangau

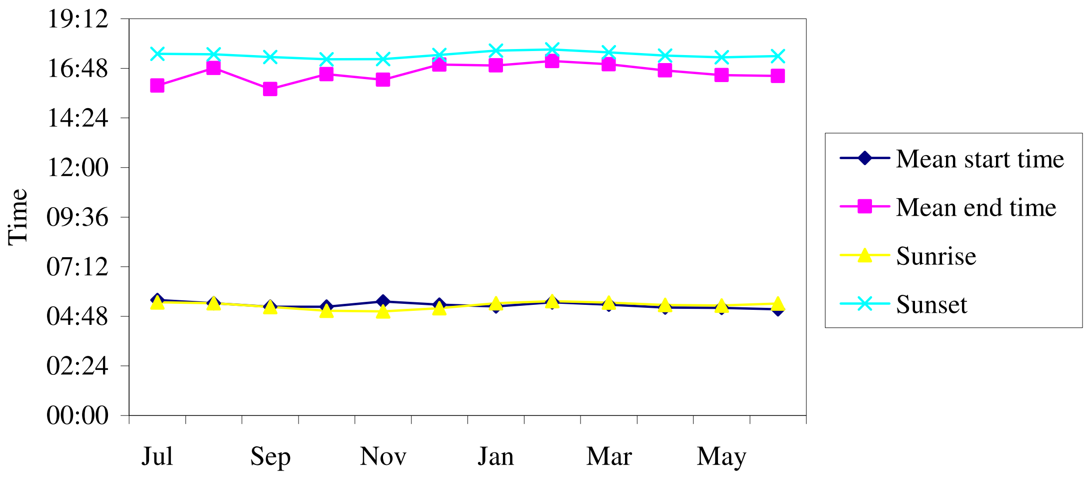


Figure 5.2 Mean start and end time in relation to sunrise and sunset (monthly means).

Orang-utans in Sabangau get up at sunrise and end their day before sunset (Figure 5.2). The mean start time is 0520 h, 1 minute after sunrise (range of monthly means -17 to +29 minutes before/after sunrise). The mean end time is 1635 h, 53 minutes before sunset (range of monthly means 29 to 94 minutes before sunset). Only once did the researchers abandon an orang-utan before it nested, because the individual was still feeding after dark (1921 h), and the researchers were far from base-camp.

To see what was influencing start time, I tested correlations with sunrise and *'food'* availability, but no significant correlation was found between start-time and either sunrise or *'food'* availability (sunrise: r^2 =0.0020,n=23, p=0.840 (ns); *'food'* availability: r^2 = 0.000036, n = 23, p=0.979 (ns)).

There was no real difference in the start time between age/sex classes. The average rising times for NSAF and UFM was 0510 h, next were SAF which rose at 0517 h, and last to rise were FM which rose at 0529 h on average.

Inter-site comparison

Table 5.2 Mean start time.

Site	**Species**	**Mean Start Time**	**Minutes after sunrise (range of monthly means)**	**Mean End Time**	**Minutes before sunset (range of monthly means)**
Suaq Balimbing	*P. abelii*	0628	+ 2 (-5 to +19)	1738	55 (44 to 68)
Ketambe	*P. abelii*	0631	+ 6 (-5 to +23)	1730	62 (42 to 82)
Sabangau	*P.p. wurmbii*	0520	+ 1 (-17 to +29)	1635	53 (29 to 94)
Tuanan	*P.p. wurmbii*	0524	+ 6 (-9 to +16)	1620	65 (41 to 77)
Gunung Palung	*P.p. wurmbii*	0557	+ 14 (-30 to +107)	1637	64 (-16 to 101)
Danum Valley	*P.p. morio*	0631	+ 31 (-16 to +62)	1741	33 (5 to 72)
Ulu Segama[1]	*P.p. morio*	0630	+ 26 (mean only)	1746	30 (mean only)
Kinabatangan	*P.p. morio*	0745	+ 101 (54 to 158)	1808	1 (-7 to 9)

[1] MacKinnon (1974)

Orang-utans at most sites were found to start their day around sunrise and end their day about an hour before sunset (Table 5.2). In contrast to this general pattern, orang-utans in north-eastern Borneo (Ulu Segama, Danum Valley and Kinabatangan in Sabah), rose 0.5–1.5 hours after sunrise. Apart from Sabangau, correlations with sunrise and fruit availability were also tested for Ketambe, the only site where data were available. A significant positive correlation with sunrise (r^2 =0.07, n=60, p=0.04) and negative correlation with fruit availability (r^2=0.15, n= 60, p=0.002) was found, but a multiple regression showed that fruit availability was the most important predictor of start time (sunrise: z-score=0.174, t-test=1.399, p=0.17 (ns); fruit availability: z-score =-0.347, t-test =-2.797, p=0.007). Thus, at Ketambe orang-utans started the day earlier when fruit availability was high.

5.4.2 Active period length

Sabangau

The mean active period length was 676 minutes (Table 5.3). For individuals, this ranged from a mean of 633 minutes for the flanged male Jupiter to 721 minutes for Einstein, a non-sexually-active male (Appendix X). This was mirrored in the general trend in the length of active period between age/sex classes using individual means; UFM have the longest active period, followed in order by SAF, NSAF and FM (Table 5.3). When active period was compared between age/sex classes, however, no significant difference was found ($F_{3,11} = 3.035$, $p = 0.075$ (ns)).

Table 5.3 Mean active period length for each age-sex class.

Active period		
Age/sex class	**N**	**Mean AP length (minutes)**
UFM	4	703
SAF	2	676
NSAF	4	667
FM	5	659
Mean	**15**	**676**

Numbers in brackets show rank order from (1) the longest to (4) the shortest. N = number of individuals

To determine what was influencing active period length, *'food'* availability and sociality were tested. A significant correlation between active period and *'food'* availability was not found ($r^2=0.093$, $n=22$, $p=0.168$ (ns)), but a significant result was found for sociality (i.e. party size >1). An individual's active period was significantly longer on days when they were in party with another individual for at least part of the day (Wilcoxon matched pairs: not social: m=658, sd=28.2; social: m=688, sd=28.3, w=0.004, ($p<0.01$)). Thus, being social increased the active period.

Inter-site comparison

The mean active period (Table 5.4) ranged from 630 minutes in Kinabatangan to 684 minutes in Mentoko. At most sites UFM were active the longest, followed by NSAF, SAF and FM. The only exceptions were Sabangau, Gunung Palung and Tanjung Puting, in each of which one adjacent pair were swapped, i.e. rank 2 and rank 3 (Sabangau), rank 3 and rank 4 (Gunung Palung), and rank 1 and rank 2 (Tanjung Puting). In the latter case NSAF were found to have the longest active period with UFM coming second.

Table 5.4 Mean Length of Active Period (AP) in minutes at each site, overall and by age-sex class.

Site	**Mean Length of AP (min)**	**UFM**		**FM**		**SAF**		**NSAF**	
Suaq Balimbing	673	682	*(1)*	655	*(4)*	674	*(3)*	679	*(2)*
Ketambe	664	684	*(1)*	637	*(4)*	673	*(3)*	660	*(2)*
Sabangau	676	703	*(1)*	658	*(4)*	676	*(2)*	667	*(3)*
Tuanan	661	686	*(1)*	642	*(4)*	647	*(3)*	669	*(2)*
Tanjung Puting[1]	640	647	*(2)*	598	*(4)*	643	*(3)*	671	*(1)*
Gunung Palung	656	675	*(1)*	641	*(3)*	639	*(4)*	670	*(2)*
Mentoko[2]	684	-		-		-		-	
Danum Valley	676	-		-		-		-	
Ulu Segama[3]	676	-		-		-		-	
Kinabatangan	630	648	*(1)*	611	*(4)*	628	*(3)*	634	*(2)*

Numbers in brackets are ranking from longest (1) to shortest (4). [1]Galdikas (1988); [2]Mitani (1989); [3]MacKinnon (1974).

To determine what was influencing active period at these sites, fruit availability and time spent socialising were again tested, although these data were available only for Ketambe. The active period length was positively correlated with fruit availability (r^2=0.07, n=477, p<0.001: consistent with the significantly earlier start time attributed to higher fruit availability, as described above). This correlation was found for SAF (r^2=0.04, n= 296, p<0.0005) and for FM (r^2=0.06, n=156, p=0.003), but not for UFM (r^2=0.06, n=25, p=0.238 (ns), but these relationships are relatively weak (i.e. very low r^2 values), thus fruit availability explains little of the variance in active period.

When investigating time being social, at Ketambe the duration of the active period was found to correlate positively with minutes spent socialising (r^2=0.08, n=108, p=0.004). Thus, in common with Sabangau, being social increased the active period at Ketambe.

5.4.3 Activity budgets

Sabangau

The active period was found to be significantly longer for UFM compared to FM in the previous section, thus minutes in a 12-hour day were used instead of percentages (Figure 5.3).

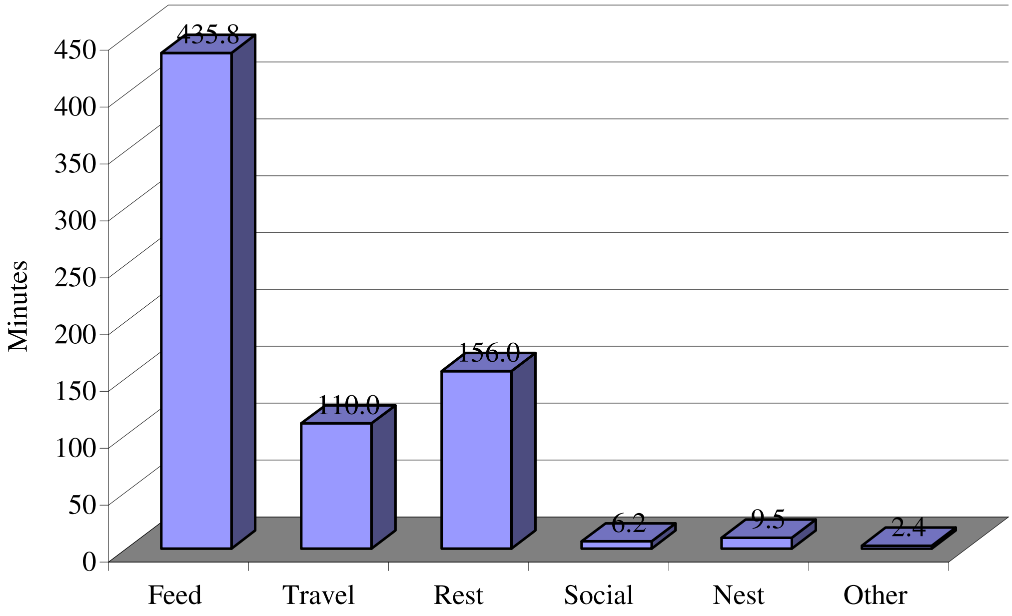


Figure 5.3 The overall activity budget for orang-utans in the Sabangau expressed in minutes in a 12-hour day.

Feeding was found to dominate the active period, followed by resting then travelling, with social, nesting and other taking up a very small percentage of the active period (2.5%).

Individual differences

Table 5.5 shows the means and standard deviations for the main primary activities (feeding, travel and resting) for each individual. There were high standard deviations found within individuals for most activities. The individual who fed the most was Beethoven, Einstein was found to travel the most, and Romeo was found to rest the most. To see individual variation in the other activities - social, nesting and other - see Appendix XI.

Table 5.5 Individual means and standard deviations for feeding, travelling and resting.

Primary Activity Name	**Age/sex Class**	**Feed**			**Travel**			**Rest**		
		Mean	**N**	***sd***	**Mean**	**N**	***sd***	**Mean**	**N**	***sd***
Ella	NSAF	465	15	*58.8*	133	15	*42.2*	114	15	*60.7*
Feb	NSAF	440	43	*67.1*	128	43	*34.6*	121	43	*62.1*
Shima	NSAF	469	15	*49.4*	86	15	*22.8*	158	15	*53.3*
Viola[1]	NSAF	349	14	*83.5*	111	14	*36.1*	244	14	*87.6*
Cleo	SAF	481	28	*67.4*	89	28	*33.5*	127	28	*57.7*
Indah	SAF	429	81	*103.1*	101	81	*38.3*	152	81	*75.9*
B'hoven	FM	**496**	26	*52.7*	107	26	*32*	103	26	*49.7*
Franky	FM	405	3	*126.3*	106	3	*59.2*	197	3	*186.3*
Hengky	FM	418	41	*130.1*	74	41	*46.8*	205	41	*127.1*
Jupiter	FM	422	10	*82.3*	66	10	*22.8*	219	10	*79.7*
Wallace	FM	476	11	*85.6*	92	11	*32.9*	137	11	*75.3*
Darwin	UFM	383	2	*106.8*	106	2	*28.6*	140	2	*14.6*
Mozart	UFM	455	3	*95.8*	133	3	*19*	120	3	*116.1*
Romeo	UFM	336	4	*167.5*	78	4	*36.5*	**265**	4	*130.3*
Einstein[2]	UFM	386	8	*69.6*	**151**	8	*41.4*	151	8	*66*
Total	**All**	**427**	304	*48.4*	**104**	304	*24.3*	**163**	304	*50.3*

Presented as minutes in a 12 hour day. Figures in bold are the individual with the highest value for that activity. N= number of full day follows. NSAF: non-sexually-active females; SAF: sexually-active females; FM: Flanged males; UFM: unflanged males. Viola is a NLF (nulliparous female) but has been included with the NSAF; Einstein is a NSAM (non-sexually-active male) but has been included as UFM.

I ran a series of statistical tests to test for differences between individuals in each age/sex class. The types of test and results are presented in Table 5.6. Viola was included here as a NSAF, fed significantly less but rested more than Ella, Feb and Shima. Shima fed less than Ella or Feb. The only significant difference between the two SAF was for feeding, Cleo fed more than Indah. This may be due to Cleo having a very small dependent baby, whilst Indah's infant was much older (around 3-4 years old). Within the FM Beethoven fed and travelled significantly more than Hengky, and rested less than Hengky and Jupiter. The differences between Beethoven and Hengky may be due to Hengky's injured leg, which may have caused him to rest more and travel less (Chapter 7). For the UFM, Romeo travelled the least, significantly less than Einstein, who travelled the most. This may be due to his sociality with Indah, during which he travelled less in order to stay with her.

Table 5.6 Individual differences in feeding, resting and travelling within each age-sex class.

Age/sex	Activity	Value	df	P-value	Post-hoc
NSAF	Feed - daily minutes /24hr [1]	10.323	3, 83	<0.001	Viola < Ella, Feb, Shima
NSAF	Rest - daily minutes /24hr [1]	14.071	3, 83	<0.001	Viola > Ella, Feb, Shima
NSAF	Travel - daily minutes /24hr [1]	6.751	3, 83	<0.001	Shima < Ella, Feb
SAF	Feed - daily minutes /24hr [2]	2.492	105	0.014	Cleo > Indah
SAF	Rest - daily minutes /24hr [2]	-1.959	61	0.055 (ns)	
SAF	Travel - daily minutes /24hr [2]	-1.716	105	0.089 (ns)	
FM	Feed - daily minutes /24hr [3]	10.934	4	0.027	Beethoven > Hengky
FM	Rest - daily minutes /24hr [3]	20.612	4	<0.001	Beethoven < Hengky & Jupiter
FM	Travel - daily minutes /24hr [1]	3.533	4, 85	0.010	Beethoven > Hengky
UFM	Feed - daily minutes /24hr [3]	2.057	3	0.561 (ns)	
UFM	Rest - daily minutes /24hr [1]	1.926	3, 13	0.175 (ns)	
UFM	Travel - daily minutes /24hr [1]	3.776	3, 13	0.038	Romeo < Einstein

[1]ANOVA ‘F’ value reported, with Tukey post-hoc; [2] Independent t-test ‘t’ value reported; [3] Kruskal-Wallis ‘X^{2}’ value reported, with Dunn’s post-hoc test; ns = not significant at a 0.05 level. Full-day follows only.

Between age/sex classes

When comparing the primary activities (feeding, travelling and resting), SAF fed the most, UFM travelled the most and FM rested the most (Table 5.7).

Table 5.7 Mean activity budget for feeding, travelling and resting for each age-sex class, (presented as minutes in a 12 hour day).

Age-sex	N	Feed	*Sd*	Travel	*sd*	Rest	*sd*
NSAF	4	427	*56.2*	120	*24.9*	159	*63.0*
SAF	2	**462**	*25.0*	99	*8.9*	141	*19.7*
FM	5	442	*34.1*	92	*17.4*	**171**	*45.6*
UFM	4	412	*35.9*	**129**	*31.0*	153	*51.0*
Total	**15**	**439**	***37.8***	**110**	***20.6***	**156**	***44.8***

Figures in bold are the age/sex class with the highest value for that activity; N=Number of individuals.

In order to see if there were differences in activity budget between age/sex classes, I conducted a General Linear Model (GLM) with repeated measures, controlling for *food’* availability, but no significant difference was found (F 6, 45 = 1.90, p = 0.101 (ns)).

Party size

Orang-utans spent 82% of time on their own (Table 5.8). FM were the least social of all age/sex classes, spending on average 96% of their time on their own, with a mean party size of 1.04, where as UFM were the most social, spending 67% of time on their own. However, SAF had the largest mean party size of 1.3 (Table 5.9). The average party size overall was 1.2, with party sizes greater than 2 rarely being seen. The largest party recorded was 6, which was only witnessed on one occasion. The time spent socialising was found to be weakly significantly between the different age/sex classes (X^2 (3) = 7.860, p = 0.049), with FM socialising more than UFM. No other significant pair-wise comparison was found.

Table 5.8 Percentage of time in different party sizes.

Age/sex	**N**	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
FM	5	95.17	4.40	0.43	0.00	0.00	0.00	100
SAF	2	82.70	14.32	2.64	0.18	0.13	0.04	100
NSAF	3	80.62	15.91	3.12	0.16	0.18	0.00	100
UFM	4	67.69	27.78	4.53	0.00	0.00	0.00	100
Mean	14	81.54	15.60	2.68	0.09	0.08	0.01	100
sd		*11.25*	*9.58*	*1.70*	*0.10*	*0.09*	*0.02*	

Table 5.9 Mean party size for each age/sex class.

Age-sex	**Party size**	***Sd***	**N**
SAF	**1.3**	*0.3*	2
NSAF	1.2	*0.2*	3
UFM	1.2	*0.2*	4
FM	1.04	*0.03*	5
Total	**1.2**	***0.1***	**15**

All follows >3hr were used to calculate party size. N=Number of individuals. NLF and NSAM were included in the normal age/sex classes. Figure in bold is the age/sex class with the largest mean party size.

When investigating how much individuals from each age/sex class were socialised with individuals from each other age/sex class, I separated NLF and NSAM from the usual classes. SAF were found to spend the least time socialising with other SAF, and the most time socialising with NSAF and *vice versa*. FM socialised most with NLF and *vice versa*, whereas UFM socialised most with SAF (Table 5.10). Thus, each age/sex class spent different amounts of time with other age/sex classes.

Table 5.10 Percentage of time different age/sex classes spent in a party with another age/sex class.

Age-sex class	**SAF**	**NLF**	**NSAF**	**FM**	**UFM**	**NSAM**
SAF	0.2	2.7	**9.8**	0.9	**13.2**	1.3
NLF	0.4	0	0	**1.4**	0	0
NSAF	**15.6**	1.8	0	1	7	**30.5**
FM	1.6	**29.6**	0.3	0.2	0.4	1.3
UFM	6	10.2	2.8	0	6.8	10.8
NSAM	1.3	0	1.2	0	0	0
Unknown	0.3	0	0.4	0.4	0.7	0.5

Figures in bold are the age/sex class that the focal age/sex class spend most of the time with.

5.4.4 Changes in activity budgets in response to changes in '*food*' availability

Sabangau

Activity budgets were compared with '*food'* availability to see if there was a relationship (Table 5.11). Overall, orang-utans appear to feed more when '*food'* is low, and travel, rest and socialise more in periods when '*food'* availability is high (Figure 5.4).

Table 5.11 Activity budgets at different levels of *'food'* availability

'*Food*' availability	N^*	Activity Age-sex class	Feed		Travel		Rest		Party size		
			mean	*sd*	Mean	*sd*	mean	*sd*	mean	*sd*	N^{***}
Low	2	NSAF	460	*13.9*	**108**	*32.0*	865	*19.5*	1.05	*0.17*	3
Low	2	SAF	**532**	*20.5*	81	*6.1*	819	*22.1*	1.06	*0.10*	2
Low	2	FM	512	*21.1*	67	*1.3*	849	*21.2*	1.02	*0.02*	4
Low	1	UFM	506	-	30	-	**894**	-	**1.44**	*0.55*	2
Medium	4	NSAF	471	*108.3*	116	*20.8*	841	*94.4*	1.25	*0.08*	4
Medium	2	SAF	455	*24.0*	103	*4.3*	865	*24.9*	**1.35**	*1.35*	4
Medium	5	FM	**501**	*51.3*	95	*51.0*	829	*85.8*	1.03	*0.03*	7
Medium	5	UFM	415	*39.1*	**121**	*19.4*	**867**	*19.3*	1.20	*0.31*	7
High	2	NSAF	398	*57.1*	117	*18.0*	896	*90.8*	**1.34**	*0.33*	3
High	2	SAF	**466**	*14.1*	96	*10.3*	856	*8.9*	1.19	*0.22*	2
High	5	FM	419	*66.7*	82	*10.0*	923	*74.2*	1.05	*0.09*	6
High	1	UFM	397	-	**153**	-	866	-	1.23	*0.32*	6
Low	7	Overall	**502**	*30.9*	72	*32.5*	857	*31.4*	1.14	*0.20*	12
Medium	16	Overall	461	*35.8*	109	*11.8*	850	*18.5*	**1.21**	*0.13*	22
High	10	Overall	420	*32.4*	**112**	*31.0*	**885**	*30.0*	1.20	*0.12*	17

Figures in bold are the highest value for that activity for each productivity level, except for the overall results, where they are the highest value for that activity overall. Full nest to nest follows were used to calculate activity budgets (in minutes totalling 24 hours) except for party size where all follows > 3 hours were used. Individual means were used to calculate means for each age/sex class and the overall mean was the mean of all age/sex classes.*The number of individuals; ** The number of individuals used to calculate party size (all follows >3 hr were used). NSAF=non-sexually-active females; SAF=sexually active females; FM=flanged males; UFM=Unflanged males.

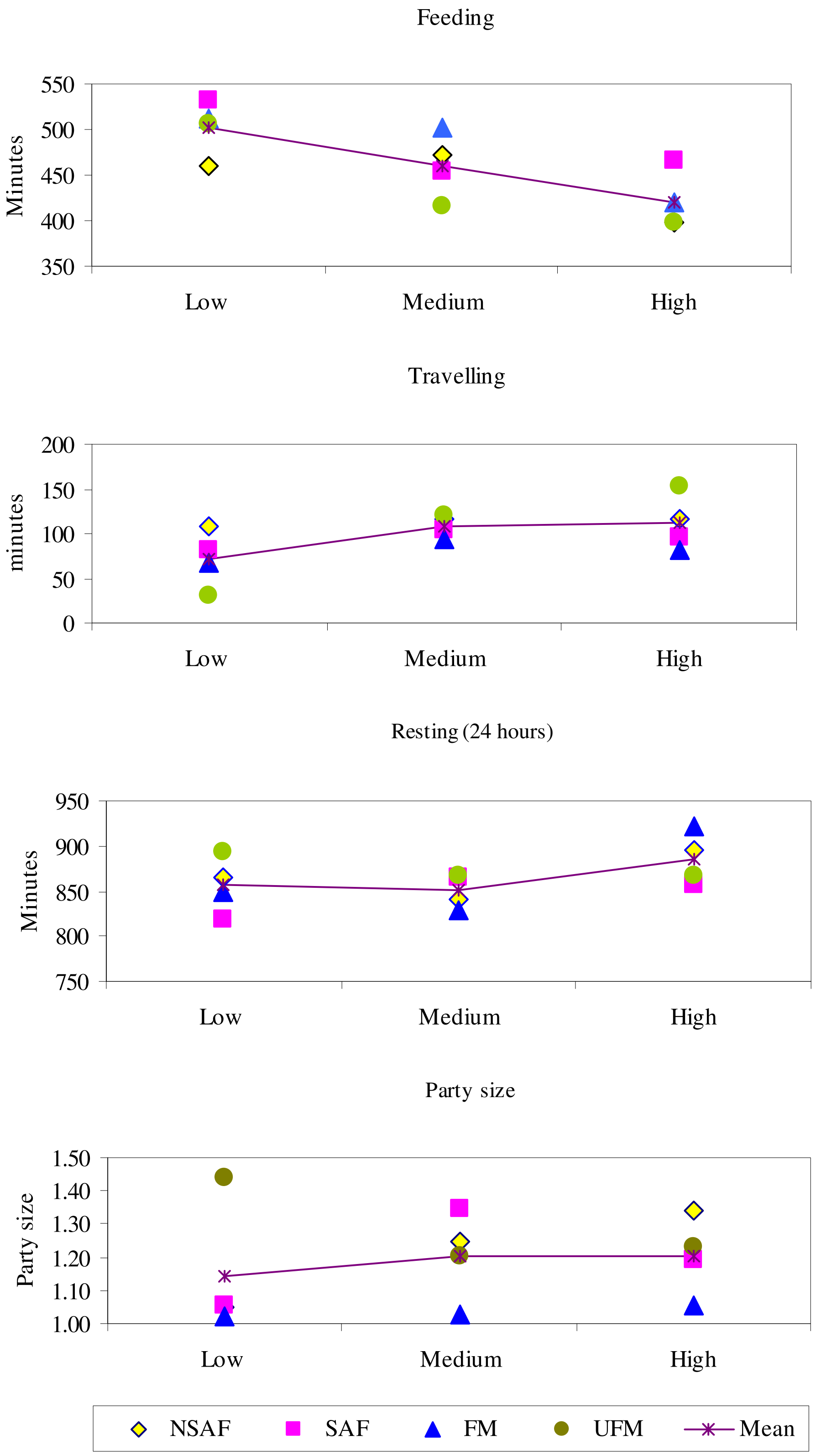


Figure 5.4 The amount of time spent feeding, travelling and resting and mean party size at different levels of '*food*' availability.

In order to test if these findings were significant, a GLM with repeated measures ANOVA was used, controlling for age/sex classes, in which a significant difference in activity budgets between periods of different *'food'* availability was found ($F_{4, 45} = 4.16$, $p = 0.006$). Orang-utans were found to feed significantly more during periods of low and medium '*food*' availability compared to high (Table 5.12), but no other significant pair-wise comparison was found.

Table 5.12 Results of post-hoc t-tests from a GLM with repeated measures ANOVA comparing activity budgets between periods of different '*food*' availability.

Activity	***Food'* class**	**t**	**df**	**P**
Feed	High < Low	3.35	45	0.002
Feed	High - Medium	1.54	45	0.131 (ns)
Feed	Medium < Low	2.23	45	0.031
Travel	High - Low	1.49	45	0.143 (ns)
Travel	High - Medium	0.03	45	0.976 (ns)
Travel	Low - Medium	1.64	45	0.108 (ns)
Rest	High - Low	1.38	45	0.174 (ns)
Rest	High - Medium	1.51	45	0.138 (ns)
Rest	Low - Medium	0.13	45	0.897 (ns)

Other sites

Data on fruit availability were available for Ketambe. Fruit availability was tested against the main activity categories using Pearson's test for correlations. The length of time spent feeding (r^2=0.82, n=133, p=0.484 (ns)), resting (r^2=0.0324, n=133, p=0.890 (ns)), and socialising (r^2=0.0196, n=133, p=0.279 (ns)) did not change significantly, but the time spent travelling did (r^2=0.110, n=133, p=0.009). Travelling was found to be positively correlated with fruit availability. Thus, the observed increase in active period in Ketambe when fruit availability was high (section 5.4.2), appears to be due to a larger amount of time spent travelling.

5.4.5 Comparing activity budgets between sites

The overall activity budgets from nine sites are shown in Figure 5.5. In the graph, the sites have been ordered by the amount of time spent feeding, the thick vertical line divides the sites into those where orang-utans fed for more than 50% of a 12-hour activity budget, and those where orang-utans fed for less than 50% of the time. The same line is also the divide between sites where feeding time exceeds resting time and those where resting exceeds feeding. All of the sites where orang-utans fed for less than 50% are predominantly mixed-dipterocarp forests where masting occurs, and all sites where orang-utans fed for more than 50% of the time are predominantly peat-swamp forests where masting events do not occur. The only exception here is Ketambe, a mixed-dipterocarp forest, where feeding is > 50%.

Significant differences were found between sites in time spent feeding ($F_{4,98} = 25.52$, $p < 0.001$), travelling ($F_{4, 96} = 20.39$, $p = < 0.001$) and resting ($X^2_4 = 57.87$, $p < 0.001$). *Post-hoc* tests revealed that orang-utans in peat-swamp forest (Sabangau and Tuanan) spent more time feeding and travelled for longer periods of time than orang-utans from most mixed-dipterocarp forests (Gunung Palung and Kinabatangan). An exception to this was found at Ketambe, another mixed-dipterocarp forest, where orang-utans exhibited similar activity patterns to those in peat-swamp forests, although they did rest significantly more than orang-utans from Sabangau (but not Tuanan).

Differences found between sites may be due to fruiting patterns or productivity levels. Figure 5.6 shows seasonal changes in diet between two sites, a mixed-dipterocarp forest and a peat-swamp forest. Diet is an indicator of food availability and thus productivity, as more fruit in the diet generally means more fruit is available. Fruit seems to be regularly available in the peat-swamp forest compared to the mixed dipterocarp forest.

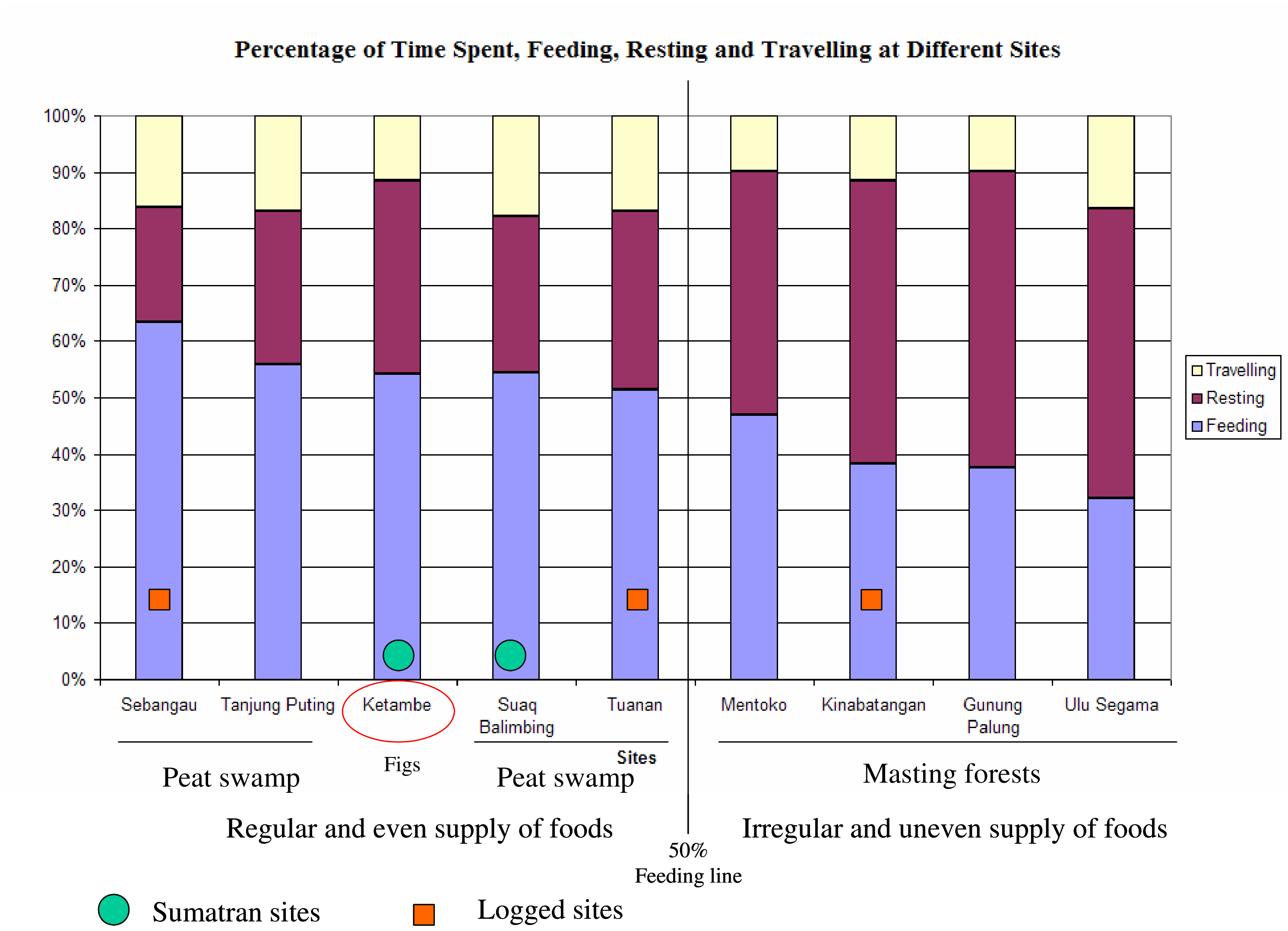
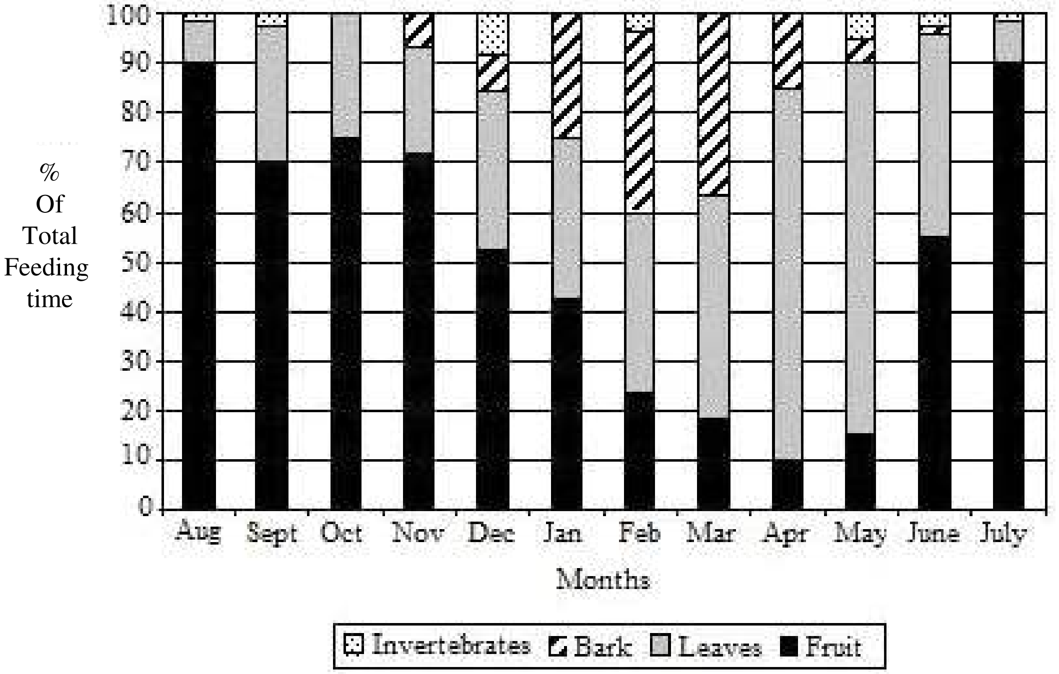


Figure 5.5 Comparison of activity budgets between sites. Data presented as minutes of a 12 hour activity budget, and presented in order of decreasing feeding time. The site circled in red is a mast-fruiting dipterocarp dominated forest, not a peat-swamp forest.

A. Monthly diet at Ulu Segama. Figure adapted from Figure 19 MacKinnon (1974)



B. Monthly diet at Sabangau (Sept – Aug 2005)

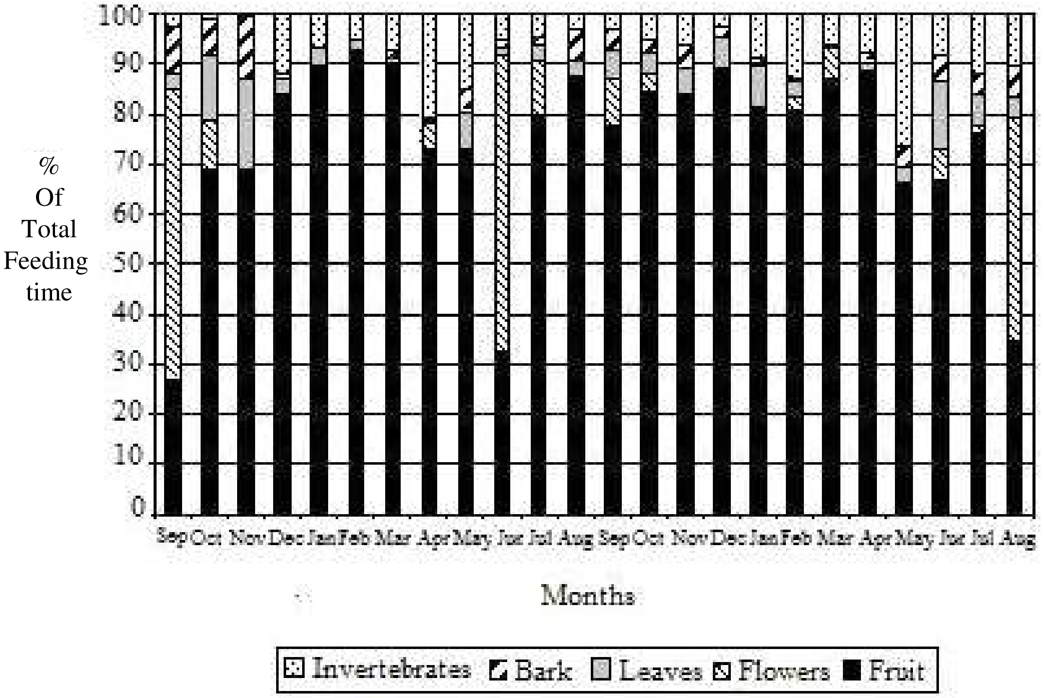


Figure 5.6 Seasonal changes in diet in an irregular fruiting forest (A), and a regular fruiting forest (B).

5.5 DISCUSSION

5.5.1 Active period

Start of the active period

In Sabangau and most other sites orang-utans were found to rise at sunrise and end the day before sunset. Although start time is clearly influenced by sunrise, no correlation was found between changes in sunrise time and changes in start time. Fruit availability was found to correlate with start-time at Ketambe (higher fruit availability led to earlier rise), but this finding was not replicated at Sabangau, probably due to more regular non-fig fruiting in Sabangau compared to Ketambe, a difference between peat-swamp forests and mixed-dipterocarp forests that is discussed at length later. In the east Bornean sites (Ulu Segama, Danum Valley and Kinabatangan), by contrast, orang-utans were found to rise 30 minutes to 1 ½ hours after sunrise. At one of the sites (Kinabatangan) the forest is heavily logged and fragmented, where 100% of the emergent trees and 80% of the original canopy have been destroyed (Ancrenaz *et al.,* 2004b; Lackman-Ancrenaz and Ancrenaz, 2006). Here their diet is heavily dominated by leaves and inner bark (see diet in Chapter 4). Orang-utans at the other east Bornean sites also have a diet heavily dominated by leaves and bark, however, so logging is unlikely to be the reason for this (Chapter 4 Table 4.7). Van Schaik (pers. comm.) notes that orang-utans in Sumatra nested earlier if they had eaten a large proportion of leaves the previous day. The increased fibrous component of the diet may lead to longer digestion times, which may be facilitated by increasing the time spent resting, as Mitani and Rodman, (1979) found that an increase in leaf eating correlated with less travel. Similarly, Dasilva (1992) found that in colobus monkeys a diet containing a substantial proportion of leaves was related to low activity levels.

All orang-utans in the east Bornean sites were found to extend the time that they went to bed, thereby shifting their active period towards dusk rather than dawn. This shift in active period may be a geographical difference between populations, rather than purely a diet difference, although diet may be a contributing factor.

Length of active period

With regard to age/sex differences, in Sabangau and at all other sites unflanged males had much longer active periods than flanged males, who usually had the shortest. This is probably due to their social status and structure. Unflanged males are more opportunistic in their mating strategy compared to flanged males (Chapter 9) and therefore travel widely in search of females (Chapter 9; MacKinnon, 1974; Rijksen, 1978; Singleton and van Schaik, 2002). They are more gregarious than flanged males and thus spend more time socialising. Active period length was found to be greatly affected by time socialising; thus, the more social an individual the longer the active period. MacKinnon (1974) and Horr (1975) hypothesised that group-living orang-utans would need to travel longer distances and visit more food sources daily than lone individuals. Flanged males increased their time spent travelling when with adult females, compared to when travelling alone (Mitani, 1989). The socio-ecological hypothesis, that suggests that various time-budget components increase with group size (Dunbar, 2002), is also supported. Thus, if orang-utans are more social, their active period will increase.

The length of the active period was similar between sites, although Kinabatangan had the shortest. This may be a result of low fruit availability due to the heavily-logged state of the forest (Lackman-Ancrenaz and Ancrenaz, 2006), causing orang-utans to rest more and thus have shorter active periods. Sub-species and habitat-type differences are excluded as explanations because orang-utans at Mentoko, an unlogged mixed dipterocarp forest in east Borneo, had the longest active period. Thus logging seems to increase resting time (decreasing search effort), presumably because logging reduces fruit availability. This theory is supported by data from Ketambe (section 5.4.2), where the active period increased when fruit availability increased.

5.5.2 Differences in activity budgets between age/sex classes

In Sabangau no significant difference in activity budget was found between the age/sex classes, but the trend shows that sexually-active females feed the most, unflanged males travel the most and flanged males rest the most. The reason why unflanged males travelled more is likely due to their gregarious nature, as they were found to be the most social, significantly so compared to flanged males. They also have longer day ranges than the other age/sex classes (Chapter 7). Thus, if individuals are spending more time socialising, they will need to travel further in search of other orang-utans, as orang-utans are widely dispersed.

In comparison, flanged males had the shortest travel time. This is probably due to their larger body size compared to the other age/sex classes. In Sabangau (Chapter 7), Kinabatangan (Lackman-Ancrenaz and Ancrenaz, 2006) and Ketambe (Rijksen, 1978), flanged males have the shortest day ranges of all age/sex classes, although at Tanjung Puting, Galdikas (1988) found that flanged males travelled much further than adult females, and implied that the reason for this may be that flanged males routinely travel on the ground and can thus travel faster. Sabangau flanged males travel on the ground more than any other age/sex class (Morrogh-Bernard, unpublished data), but this did not increase their travel time, possibly due to the thick undergrowth which prevents rapid or extensive ground travel. Trees in the Sabangau are small, which means that the most popular mode of travel is clambering, as orang-utans have evolved distinct locomotion modes to solve a variety of complex habitat problems (Thorpe and Crompton, 2005). Thus, habitat structure dictates locomotion type (Chapter 6), and the size of individual affects the type of locomotion used in Sabangau. Flanged males were found to travel by quadrupedal walking significantly more than females, whereas non-sexually active females were found to brachiate significantly more than sexually-active females or flanged males (Morrogh-Bernard, unpublished data).

Another reason why flanged males may travel for the least amount of time may be social status. Unlike unflanged males, dominant flanged males should attract cycling females (Chapter 9), so once they become resident in an area where there are cycling females, they will concentrate their movement in and around that area and wait for the females to come to them (Chapter 9). This is in contrast to unflanged males who spent more time searching for, and attempting to guard, females. Only one flanged male (Beethoven) travelled extensively in an apparent search for females, during which time a forced mating was witnessed (Chapter 9). He also had the longest day range of all flanged males and travelled further each hour compared to all other flanged males (Chapter 7); thus, his travel profile was more similar to an unflanged male than a dominant flanged male. An individual's social status may affect time spent travelling, so that dominant resident flanged males will spend less time searching for females by concentrating their movement around cycling females (Chapter 9), but this hypothesis is still to be tested.

5.5.3 Impact of '*food*' availability on activity

In Sabangau orang-utans were found to feed for significantly shorter periods of time during high and medium '*food'* availability periods compared to low. This is probably because more nutritionally-valuable fruits and flowers were available during high and medium `*food*` availability periods, thus allowing orang-utans to feed for less time, although no difference in feeding time between fruit-poor and fruit-rich periods was found for Ketambe. At Gunung Palung, Knott (1998) also found that the time spent feeding in fruit-rich compared to fruit-poor periods remained similar, but the nutrient value of the foods was vastly different: 376 kcal/100g for *Dipterocarpus sublamellatus,* a commonly-eaten food during the mast, compared to 110 kcal/100g for *Polyalthia sumatrana* and under 200 kcal/100g for bark and leaves, commonly-eaten non-masting foods. Although a significant difference for travel was not found, the trend showed that travel time increased when *'food'* availability was high, this suggests that orang-utans may travel more at this time in search of the most preferred energy-rich foods. Although I do not have nutritional data for this period, the number of individuals expressing ketones in their urine decreased as *'food'* availability increased (Chapter 4), suggesting that energy intake was higher during high *'food'* periods. Knott (1998) found that orang-utan diet during fruit-poor periods in Gunung Palung mainly contained nutrient-poor foods, such as cambium and leaves, and they lost weight as a result, with high levels of ketones detected in their urine.

Similar results were obtained at Ketambe and Suaq Balimbing (Fox *et al.,* 2004), in which time feeding did not increase during high fruit periods, but time spent travelling did. Thus the increase in the length of the active period during the high fruit period in Ketambe was probably due to orang-utans getting up early to search for the most preferred foods. In Sabangau and these other sites it seems that the increase in travel time and day range, but not feeding, during periods of high *'food'* availability is because orang-utans travel further in search of more-preferred and thus energy rich fruits.

5.5.4 Impact of habitat on activity

When comparing activity budgets between all sites, orang-utans from habitats that are predominantly peat-swamp forest (Sabangau, Tuanan, Tanjung Puting, Suaq Balimbing) spent more time feeding, less time resting and travelled for longer periods than orang-utans from most mixed-dipterocarp forests (Gunung Palung, Mentoko, Ulu Segama, Kinabatangan) with the exception of Ketambe, where the activity budget was more similar to orang-utans from peat-swamp forest. Thus differences in the activity profile due to habitat type are far more apparent than geographic location and species differences (Borneo vs. Sumatra).

Fruit production in mixed-dipterocarp forest is highly-seasonal, compared to peat-swamp forest, due to supra-annual mast-fruiting events (Cannon *et al.,* 2007a) during which the majority of trees will fruit in synchrony for short intervals followed by extended periods of low-fruit availability (van Schaik, 1986; Ashton *et al.,* 1988; Knott, 1998; Wich and van Schaik, 2000). This means that fruit availability in masting habitats is very irregular throughout the year. Non-masting peat-swamp forest has a more regular supply of fruit (Cannon *et al*., 2007a) due to the temporal segregation of synchronised species, together with the presence of many asynchronous-fruiting species (Chapter 3).

The reason why orang-utans in Ketambe, a masting forest, have an activity pattern similar to those in peat-swamp forest may be due to the high density of strangling figs in Ketambe. Figs are a common genus, representing 3.1% of all tree species in Ketambe (Rijksen, 1978). In comparison, strangler-fig density in mixed-dipterocarp forests in Borneo is much lower (0.33 stems/ha in Kinabatangan compared to 2.7 stems/ha in Ketambe: (Ancrenaz, unpublished data; Wich, unpublished data), so figs are largely replaced by leaves, piths and cambium as fall-back foods at these sites (Galdikas, 1988; Knott, 1998; Lackman-Ancrenaz and Ancrenaz, 2006; Chapter 4). Figs produce fruit year round, and thus are eaten by orang-utans constantly throughout the year, compared to non-fig fruits which have more circumscribed fruiting periods (Sugardjito *et al.,* 1987). Figs are a fall-back food (compared to leaves, piths and cambium) that can be relied on when non-fig fruits are low (Wich *et al.,* 2006a). Thus overall fruit production (fig and non-fig combined) at Ketambe is more regular and more similar to seasonal patterns in peat-swamp forest than other mixed-dipterocarp forests in Borneo, which have low strangler fig densities.

Optimality models, which consider trade-offs between costs and benefits in foraging decisions (Dunbar, 2002), suggest that orang-utans will respond to reduced food availability either by expanding their diet to include lesser-quality foods or by travelling further to include more preferred foods. Thus, one would expect different foraging strategies to be adopted, depending on whether the habitat has a regular or irregular fruiting pattern.

Knott (1998) found that energy intake in orang-utans at Gunung Palung was much higher during the mast as at that time there is a surplus of food, including many species with oil-rich seeds, thereby enabling them to store fat reserves for the fruit-poor period. Wheatley (1982) found that orang-utans are very efficient at storing adipose tissue, due to their large body mass and ability to subsist on low-quality foods. The diets at Kinabatangan, Ulu Segama, Mentoko and Gunung Palung (all mixed-dipterocarp forests) are very similar, with very high leaf- and bark-eating in some months. The poorer the foraging quality, the further an individual would have to forage and the more time they would need to spend feeding to ingest the same quantity of nutrients (Bean, 1999; Williams and Dunbar, 1999). Instead, these orang-utans rest more and travel less, probably in order to conserve energy as they have to subsist off low quality foods for long periods of time. In contrast, orang-utans in regular fruiting forests spend more time feeding and travelling between food sources in order to meet their metabolic needs. Because fruits in peat-swamp forests are distributed more evenly spatially and temporally, orang-utans can continuously search for fruits, as there is a high likelihood that they will find them. Thus, it appears that there are two foraging strategies being adopted by orang-utans, depending on the fruiting pattern that occurs in the habitat in which they live:

1. Sit-and-wait - conserve energy by resting (and digesting low-quality food) as much as possible during periods of low fruit and waiting for times of high fruit - this strategy applies to orang-utans in seasonal dipterocarp forests in Borneo e.g. Gunung Palung.

2. Search-and-find – continuously feed and move in search of food, in order to maintain daily metabolic requirements - this strategy applies to orang-utans who live in forest where fruit availability is more regular (even if of lower quality), e.g. peat-swamp forest in Sabangau.

The adoption of different feeding strategies as food availability alters has been found in other species. Western gorillas (*Gorilla gorilla gorilla* and *G. g. diehli*) adopt a low-energy strategy by decreasing day range and feeding more on low-quality foods (herbs and fibrous fruits), when fruit abundance is low, but when fruit was available they would travel further to add it to their diet, rather than subsist on a lower-quality diet (Doran *et al.,* 2002a; Rogers *et al.,* 2004). Dasilva (1992) described colobus monkeys (*Colobus polykomos*) as time minimisers who rest more and travel less when high-energy foods are not available; and Milton (1980) described howler monkeys as time-minimising folivores, due to the high percentage of leaves in their diet. A similar result was found for the siamang when high-energy foods were not available (Chivers, 1974). Importantly in the case of the orang-utan, however, the major difference in activity patterns, and hence foraging strategy, occur between populations in different habitat-types. Orang-utans adopt an activity budget based on the seasonal fruit production of the habitat type they live in, with the temporal availability of fruit the driving force for which strategy is adopted.

5.6 CONCLUSION

Differences in orang-utan activity budgets were found between periods of different '*food*' availability levels and sites. Orang-utans were found to start the day at sunrise and end the day before sunset at most sites, and the length of the active period was found to increase when orang-utans were more social. Trends between age/sex classes were found, including unflanged males having the longest active period and flanged males travelling the least. These differences are thought to be due to both social and energetic constraints. Orang-utans in Sabangau were found to decrease their time spent feeding during periods of high and medium '*food*' availability, thus suggesting an increase in the nutrient value of the foods available during these times.

Habitat type was found to be the major influencing factor driving inter-site differences. It seems that there are two distinct foraging strategies adopted depending on the habitat type and thus fruiting patterns, which I propose as: (1) **Sit-and-Wait**, where orang-utans limit their energy expenditure during low fruit periods; (2) **Search-and-Find**, where orang-utans are constantly feeding or moving in search of food. In those sites where high-quality fruit are only available for a limited period of time, the first strategy is adopted. This is characteristic of orang-utans living in mixed-dipterocarp forests that exhibit high fruiting seasonality and mast-fruiting and where peaks of high-quality fruit production are followed by extended periods of low-fruit availability. During low-fruit periods orang-utans in those habitats feed mainly on low-quality food and partly subsist off fat reserves. By contrast, orang-utans living in sites where a regular supply of fruit is present follow the second strategy. This is typical of orang-utans living in peat-swamp forests where fruit availability is more regular, together with orang-utans from forests which have a high density of strangling-figs, which provide a year-round supply of fruit. Thus, the determining factor for which strategy is adopted appears to be the temporal availability of fruit, largely determined by habitat-type, rather than any species- or sub-species difference. The only variable for which possible sub-specific differences occur is in the active period start and finish time, as orang-utans in Eastern Borneo have shifted their active period towards getting up and going to sleep later. Indicating that these findings have important implications in regards to orang-utan behavioural ecology.

5.7 SUMMARY

- Orang-utans in Sabangau start their day at sunrise and end their day nearly 1 hour before sunset. This trend was true for most sites except for those in east Borneo and Sabah where they got up and went to sleep later.
- Although changes in sunrise time and '*food*' availability did not affect start time in Sabangau, fruit availability was found to be a strong predictor of start time in Ketambe.
- The age/sex class with the longest active period is unflanged males, with flanged males having the shortest. This was mirrored at nearly all sites. The length of the active period was shortest at Kinabatangan and longest at Mentoko, both east Bornean sites.
- The activity budget at Sabangau was dominated by feeding, followed by resting and travel, and there were differences between age/sex classes for travelling and party size (socialising).
- *'Food'* availability affected activity budgets at Ketambe and the trend at Sabangau shows a similar pattern of increased travel when '*food'* (or fruit) availability increased, and in Sabangau they fed longer during times of low *'food'* availability, although this did not happen at Ketambe.
- There were differences in activity budgets between sites, in which annual fruiting patterns were the major influencing factor: regular fruiting habitats *vs*. irregular fruiting habitats.
- Orang-utans from regular fruiting sites fed for over 50% of a 12 hour active period and travelled more, compared to orang-utans from irregular fruiting habitats which fed for less than 50% of the time and rested more. From these findings I propose two different foraging strategies for orang-utans depending on fruiting patterns: 'sit-and-wait' or 'search and find'.

CHAPTER 6

FOREST STRUCTURE AND ANTHROPOGENIC DISTURBANCE: ON ORANG-UTAN HABITAT USE AND BEHAVIOUR

6.1 INTRODUCTION

6.1.1 Selective logging

There are many different views in regards to the effects habitat disturbance has on primates. Plumptre and Reynolds (1994) state that primates appear to be fairly flexible in their response to disturbance and therefore are not a good indicator of disturbance, although Plumptre and Johns (2001) showed that responses vary depending on the level of damage and, in areas where logging was relatively heavy, primate densities declined the most. Wilson and Wilson (1975), in their study of primates in East Kalimantan, highlighted two species of primate that were adversely affected by selective logging; the orang-utan and the proboscis monkey (*Nasalis larvatus*). Orang-utan densities were found to be higher in unlogged forest compared to logged forest in many subsequent studies (MacKinnon, 1971; Rijksen, 1978; Davies and Payne, 1982; van Schaik *et al.,* 1995; Russon, *et al.*, 2001; Morrogh-Bernard *et al.*, 2003; Felton *et al.,* 2003; Johnson *et al.,* 2005; Husson *et al.*, 2009). Orang-utans typically respond to logging by moving away from affected areas, but will return once the disturbance has ended, although at lower densities (MacKinnon, 1974; Morrogh-Bernard *et al.*, 2003). Knop *et al.* (2004) found that densities in a forest which was logged 22 years ago were not significantly lower than those in an unlogged forest nearby, thus suggesting that if an area is left for an extended period of time, densities will recover to pre-logging levels.

Much of the forests in lowland Borneo have already been converted to agriculture and those that have not have been selectively or illegally logged for timber production (Meijaard and Sheil, 2008), thus nearly all lowland forests in the orang-utans range have been degraded to a certain extent. Even National Parks, such as Tanjung Puting and

Gunung Palung, have been subject to illegal logging. Although most lowland forests have been selectively or illegally logged, it is the intensity and degree of damage and the ability of animals to cope with this that ultimately dictates if animals can continue to survive there.

Johns (1988) found that selective logging was much more destructive than was otherwise thought, resulting in over 50% of forest stands being destroyed when removing just a few selected species. Cannon *et al.* (1994) found that 45% of the forest canopy was damaged and Asner *et al.* (2004) noted that gaps up to 50 m in radius were produced around each felled tree. The density and basal area of trees >35 cm in diameter were significantly lower in logged areas compared to unlogged areas (Felton *et al.,* 2003). The most profound ecological effect of logging is the reduction in the number of woody species in the regeneration cohort (Ganzhorn *et al.,* 1990). Heydon and Bulloh (1997) described the areas where logging skids had been constructed as a food resource ‘desert’ for mouse deer (*Tragulus* spp.) and other frugivores, as these areas contained few mature trees and were dominated by pioneer species, species which are rarely eaten by a majority of frugivores (Chivers, 1980). Thus, selective logging not only affects the structure of a forest, but species composition as well.

Although most primates can continue to survive in logged forest (Wilson and Wilson, 1975; Plumptre and Johns, 2001; Ancrenaz *et al.*, 2004a; Marshall *et al.*, 2006), it depends on their ability to adapt, especially their degree of dietary flexibility (Johns, 1997; Meijaard *et al.,* 2005; 2008). The effect of disturbance on orang-utan behaviour is little understood because most studies have used orang-utan densities, rather than behaviour, to determine responses to logging on a population scale (Morrogh-Bernard *et al.,* 2003; Felton *et al.*, 2003; Husson *et al.*, 2009). The lone study in which this question was addressed was carried out by Rao and van Schaik (1997). They showed that in logged forest, orang-utans became more folivorous and travelled more, although their sample size was small and the duration of study short.

6.1.2 Effects of logging on orang-utans and other species

Many studies on birds, invertebrates and other mammals have investigated their responses to logging, in which they have mainly compared behaviour in logged forest to that in unlogged forests (e.g. Wilson and Wilson, 1975; Johns, 1986; Johns and Skorupa, 1987; Plumptre and Reynolds, 1994; Decker, 1994; Spitzer *et al.*, 1997; Heydon and Bulloh, 1997; Aleixo, 1999; Fairgrieve and Muhumuza, 2003; Cleary, 2003; Ganzhorn *et al.,* 1990; Nijman, 2004; Brady, 2005; Meijaard *et al.,* 2006; Cleary *et al.,* 2007).

Most studies have focused on selectively logged forests, a method of logging widely used in the tropics which involves the removal of large trees, and results in openings in the canopy (Cannon *et al.,* 1994) and a patchy distribution of many tree species, including important food resources for many animals. This potentially can lead to changes in an animal’s foraging behaviour. The destruction of large trees also decreases the availability of arboreal travel routes, nesting and sleeping places (Cannon and Leighton, 1994; Felton *et al.,* 2003; Thompson, 2007). Bornean orang-utans have generally persisted quite well in logged areas because most of the trees selected for extraction by timber companies in Asia are species that are mainly unused by orang-utans for food (Chivers, 1980; Russon *et al.,* 2009; Chapter 4), including many species from the *Dipterocarpaceae* family of trees (Cannon *et al.,* 1994; Meijaard and Sheil, 2008). This has changed more recently, however, as many areas which had already been legally logged have now been illegally logged two or three times over (Commitante *et al.,* 2003; pers. obs.), in which medium to large trees of many more species, including important orang-utan food species, have become valuable for loggers and removed (Chapter 3).

The degree of damage to forest structure increases if the logging operation was unplanned (no structure to the operation) (Johns *et al.*, 1996) or illegal (Husson *et al.*, 2008). Illegal logging causes increased damage as it is indiscriminate and uncontrolled (Felton *et al.*, 2003; pers. obs.). In Chapman *et al.*’s 2000 study of the long-term effects of logging it was shown that primates could persist better in areas where low-intensity selective logging was conducted, as opposed to areas of high-intensity logging, similar to findings for orang-utans, for which densities have been found to be lower in more disturbed areas (Husson *et al.,* 2009).

With regard to food availability, if there is a major loss of important food sources this can have devastating results, as witnessed during the 1991 forest fires in Kutai National Park, East Kalimantan, after which orang-utans survived by mainly eating bark (Suzuki, 1991). Rode *et al.* (2006) found that the nutritional value of the redtailed monkey's (*Cercopithecus ascanius*) diet was significantly reduced in heavily logged forest, emphasising the implications that logging can have on animal health (Gillespie *et al.,* 2005). Sumatran orang-utans are found to avoid logged forest when they have a choice, and become more folivorous when in logged forest (Rao and van Schaik, 1997). The lar gibbon (*Hylobates lar*) and banded langur (*Presbytis melalophos*) switched from a largely frugivorous diet to a more folivorous one following logging (Plumptre and Johns, 2001). Mouse deer (*Tragulus* spp.) home ranges were found to be more than twice as large in logged forest compared to primary forest (Ahmad, 1994), due to loss of feeding sources (fallen fruits). Golden-cheeked gibbons (*Nomascus gabriellae*) living in recently-disturbed evergreen forest had smaller ranges than gibbons in old disturbed semi-evergreen forest, with species diversity being the most important factor determining home range size (Kenyon, 2008). In orang-utans, females are particular vulnerable to disturbance (Felton *et al.,* 2003) as they have high nutritional requirements (Knott, 1998), and do not leave their home range when disturbance occurs, instead making biased use of their ranges in an attempt to avoid the disturbance (van Schaik *et al.*, 2001; Singleton *et al.*, 2009).

With regard to habitat structure, this has a great influence on activity patterns, especially travel for arboreal species (Johns, 1986; Cannon and Leighton, 1994; Thorpe and Crompton, 2005; Thompson, 2007). In selectively-logged forest, lar gibbons concentrated most of their activities in areas which were less affected by logging, and were found to use the lower-canopy more than the upper-canopy; the same was found for the banded langur in logged forest (Johns, 1986). This is due to the removal of many large trees and disruption of the upper-canopy structure and hence travel routes, meaning that arboreal species in logged areas are forced to descend to lower levels or even travel on the ground to cross gaps (Johns, 1986), which can increase predation risks in orang-utans from tigers, clouded leopards and snakes (reticulated python). Plumptre and Johns (2001) report that the density of L'Hoest's monkey (*Cercopithecus hosei)* may decline in logged forest because it forages mostly on the ground. Activity patterns in the Sumatran orang-utan were different in logged forest compared to primary forest, as they travelled more, rested less and used more energetically expensive locomotion (Rao and van Schaik, 1997). In contrast, the lar gibbon and banded langur increased their time resting and decreased their time feeding or travelling in logged forest (Johns, 1986). Thus, changes in behaviour due to disturbance affects species differently, and can have profound effects on some. Sterck (1998) found that habitat disturbance upset the social system in langurs (*Presbytis* spp.), causing incidents of infanticide to increase due to habitat saturation.

Different species respond to habitat disturbance in different ways, and thus one cannot generalise. The forest composition and structure before and after logging plays an important part in an animal's response to disturbance (Wilson and Wilson, 1975; Plumptre and Johns, 2001; Kenyon, 2008; Meijaard and Sheil, 2008). Two tolerance levels for animals have been identified by Meijaard and Sheil (2008): (1) intolerant animals - those which tend to have narrow ecological niches and are mainly frugivorous, carnivorous or insectivorous – and are specialists using a particular forest strata, and (2) tolerant animals – mainly herbivorous or more omnivorous animals. Thus, dietary flexibility is important, so, although orang-utans are mainly frugivorous, they do have a flexible diet which includes bark, leaves and invertebrates as well as fruit, and thus are able to cope with light logging disturbance (Rao and van Schaik, 1997). Meijaard *et al.* (2008) found that Phylogenetic age was a key variable in determining species sensitivity to logging, and this was associated with the degree of endemism and dietary specialisation; thus older species (>5 million years old) were found to be less tolerant to habitat changes.

The habitat structure within the Sabangau today is a mosaic of primary and logged forest (with various degrees of damage, at various stages of re-growth). Although we know that orang-utans, particularly the Bornean species, are able to persist in logged habitat (Russon *et al.,* 2001; Felton *et al.,* 2003; Morrogh-Bernard *et al.*, 2003; Ancrenaz *et al.*, 2004a; Johnson *et al.*, 2005; Husson *et al.*, 2008), little is known about their behavioural response to logging, in particular in regard to fine-scale habitat use.

6.1.3 Impact of direct human disturbance

There are many forms of human disturbance which do not cause gross destruction of the habitat (Marsh *et al.,* 1987), including the collection of wild fruit, honey, rubber, bark, rattan and the hunting of animals for meat or the pet trade (pers. obs.). For these activities to occur access into the forest is needed, and this is usually by road, or in the case of the

Sabangau, along canals which were constructed for extracting timber from the forest (Husson *et al.,* 2002b). Hunting of orang-utans in the Sabangau occurred in the past (pers. obs.), and hunting is the most destructive of all human activities for orang-utans, with the potential to cause local extinctions (Singleton *et al.,* 2004). A recent study in East Kalimantan showed that the distance from the nearest hunting village was a better predictor of orang-utan density than logging intensity (Marshall *et al.,* 2006). Poaching can readily result in the local extermination of orang-utans because of their slow life history, with an inter-birth interval of 6-9 years (Singleton *et al.,* 2004; Wich *et al.,* 2004a).

Immediate changes in orang-utan behaviour in response to the presence of humans has not yet been explicitly investigated, although we do know that orang-utans and other primates change their behaviour in the presence of scientists when first followed, before they become habituated (Setiawan *et al.,* 1996; Williamson and Feistner, 2003; Chapter 2), but not much is known about their response to other people in the forest. Most animals will respond to human presence by avoiding them in the same way they would avoid predators; but this behaviour is usually found in animals which have been hunted as there are many accounts of birds not fleeing in areas where they have not been hunted. Thus, the experience of past hunting may have resulted in more vigilant and cryptic behaviour in many animals. Johns (1986) found that during active logging, lar gibbons kept as far away from the foci of logging activity as possible, by either restricting their activities to parts which had not yet been logged, or by moving behind the logging front to areas of their range which had already been logged. Marsh *et al.* (1987) reported that lar gibbons ceased calling during logging and became very agitated, but remained within their territory, whereas banded langurs escaped from the advancing logging front by moving several hundred metres away from their former ranges into areas not yet logged. Direct avoidance of humans was also found in the long tailed macaque (*Macaca fascicularis*), the pig tailed macaque (*M. nemestrina*), and the slow loris (*Nycticebus coucang*) (Johns, 1986). Thus many animals are faced with trade-offs: either stay and increase the chances of being found and possibly hunted, or leave and enter unfamiliar territory. Even primates which had been habituated to researchers show behavioural changes when the number of people increased or unknown people were present (Williamson and Feistner, 2003). Studying changes in orang-utans behaviour and activity patterns will give us a better understanding of orang-utans response to active human presence.

6.2 OBJECTIVES

Orang-utan habitat-use will be investigated in relation to various levels of logging and anthropogenic disturbance, and I will try to identify at what level disturbance becomes sub-optimal for orang-utans, in which their natural behaviour is changed or compromised. This is the first investigation of fine-scale habitat disturbance on orang-utans, and the first examination of the effects of human presence in the forest on the behaviour of fully-habituated orang-utans.

Questions addressed in this chapter are in two parts:

Section 1 - Habitat quality and logging damage

- How many different habitat classes (classes of differing habitat quality) were present?
- What was the proportion of each habitat class in the study area?
- Were orang-utans using the habitat randomly, or were they showing preference for certain habitat classes?
- Were there changes in orang-utan activity patterns between the different habitat classes?
- Were orang-utans preferentially selecting different habitat classes for different activities (feeding, resting, travelling, nesting and social)?
- At what level would logging disturbance become critical for the continued survival of orang-utans in an area?

Section 2 – Human disturbance (human activity in the forest)

- What kinds of human disturbance occurred in the forest?
- What was the intensity of these disturbances?
- What was the reaction of orang-utans to these disturbances?

6.3 METHODS

6.3.1 Habitat classification

Estimating canopy height and completeness was a simple method for assessing forest structure visually, instead of measuring habitat variables while following the orang-utans, which would have been impossible. Seven discrete habitat structure classes were defined (Table 6.1; Figure 6.1) and were assessed by eye, using tree height and completeness (% cover) of the canopy in a 10 m radius round the central point (the focal orang-utan) (representing the immediate area surrounding the focal). During focal-animal follows I recorded habitat quality every 5 minutes, together with the normal behaviour data. This was a quick and efficient way to assess the habitat while on the move. These classes were used to assess the quality of habitat used by orang-utans, and these were later measured to prove that there were differences between each class. To determine the proportion of each habitat class present in the study area, transects within the grid were assessed visually every 50 m in the same way as on the follows.

Table 6.1 Habitat classes used to describe forest quality when following orang-utans.

Class	Habitat classes	Canopy height (m)	% Canopy cover (≥20m)
TCA	Tall complete A	>20 - 35	75 – 100
TCB	Tall complete B	>20 - 35	50 – 75
TIC	Tall Incomplete	>20 - 35	<50
MC	Medium Complete	>15 - ≤20	50 – 100
MIC	Medium Incomplete	>15 - ≤20	<50
LMS	Low Mixed Secondary	>10 - ≤15	0
S	*Secondary	>2 - ≤10	0
Cl	Clearings	0 - ≤2	0

* Secondary refers to the first successional stage after logging.

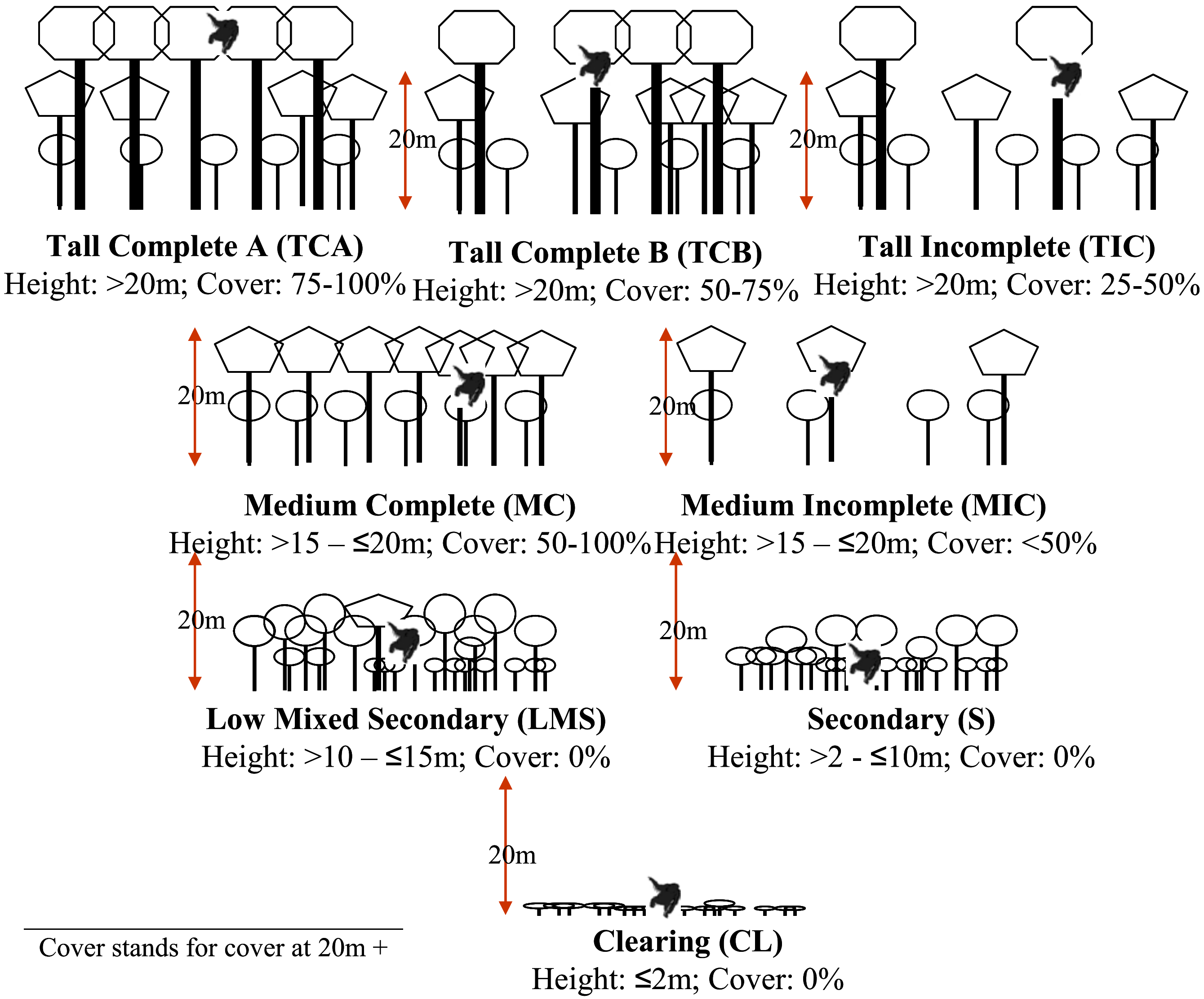


Figure 6.1 Illustration of habitat classes.

My assistants and I trained to estimate tree height accurately to classify habitat quality. We used the phenology plots, where all trees had already been numbered and measured for training. We would practise estimating the height of trees which had already been measured. All researchers had to score over 70% in each test. If they failed to do this they had to continue until they passed. Tree height tests were performed every 3 months on different trees to maintain consistency and quality of data. In order to test inter-observer differences in classifying the different habitat quality classes, all observers walked the same transects and then their results were compared with mine. Results from the repeated transects were only 50% - 63% similar to mine. Thus, I decided to use only my focal follow data, which included habitat quality data, for these analyses, as I considered inter-observer differences to be too great. I also performed intra-observer reliability tests, and thus was confident in using my data.

Measured plots

I classified habitat quality when following orang-utans using visual determinants of habitat structure – tree height and canopy cover (Table 6.1; Figure 6.1). In order to prove that these classes were different from each other, and were accurately describing what I was estimating visually, I chose a selection of locations within the study site that covered the full range of habitat-quality classes, and measured a number of habitat variables there. In total, 193 plots were measured within the 9 km^2 study area.

Each of these 193 plots was given a visual habitat quality classification (Table 6.1) before any measurements were taken. All habitat quality classifications were done by me in order to remove problems of inter-observer reliability. Transects were walked and assessed every 50 m for habitat quality, within the grid system. In cases where a habitat class was only represented by a few plots, I purposefully selected plots which represented those habitat classes. In all, 19 plots were tall complete A; 61 tall complete B; 29 tall incomplete; 33 medium complete; 17 medium incomplete; 21 low-mixed secondary; and 13 secondary. Secondary was the least represented habitat type within the grid, as it was mainly found along used and disused railway lines and in disused bat-hunting areas.

I measured the following variables in each plot:

- Density of large trees >20 cm diameter at breast height (dbh)
- Density of medium-sized trees >10 – ≤20 cm dbh
- Size of trees, using diameter at breast height
- % Canopy cover at 10 m
- % Canopy cover at 20 m (top canopy)
- Number of cut stumps – a measure of logging disturbance
- Number of fallen trees – a measure of canopy incompleteness
- % ground cover occupied by saplings – a measure of forest re-growth

Tree Density

I used the point-centred quarter method (Sutherland, 1996) to estimate the density of trees >10 - ≤20 cm dbh and trees >20 cm dbh. In this method, each plot is divided into four sub-plots (Figure 6.2). In each sub-plot the distance from the centre of the plot to both the nearest tree >20 cm dbh and the nearest tree >10 – ≤20 cm dbh was measured. To calculate tree density, the average distance for all four trees of the selected size class was calculated, and the mean of these averages over all plots = D_2, so that; *Tree Density per Hectare* = 1000 / $(D_2)^2$ (Sutherland, 1996).

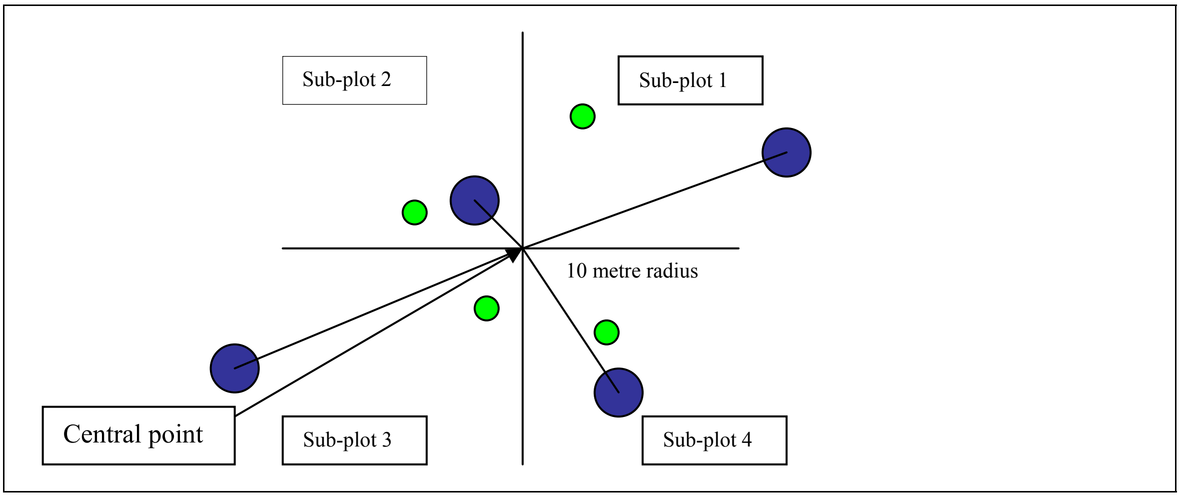


Figure 6.2 Point-centred quarter method. The large blue circles are trees >20 cm dbh, and the small green circles are trees ≤20 cm dbh.

Tree size

The diameter of each of the eight trees was measured. Although all eight trees were measured, an overall value for each plot was obtained by taking the average of the four nearest trees > 10 - ≤20 cm dbh, and the four nearest trees >20 cm dbh, as long as each tree was within 10 m of the centre point. If one or more of the nearest trees was further than 10 m from the centre point, the measurements for those trees were not included.

Canopy cover

Canopy cover at 10 m and 20 m was recorded using a spherical densitometer at the central point of each plot. Percentage cover using the spherical densitometer (4 x 4 cm grid squared) was estimated. The percentages from each plot were then averaged to give an overall percentage for each habitat class.

Logging disturbance

For indices of disturbance, the number of cut stumps with a dbh >10 cm and the number of tree falls (defined as a tree with a dbh ≥ 10 cm leaning at an angle greater than 45^o to the vertical (using 45^o meant that the crown was nearer the ground than the canopy)) were counted within a 10 m radius from the centre of the plot. The percentage of ground occupied by saplings (trees <5 cm dbh and <5 m in height) was also estimated using 6 classes (<1 %, 1-5 %, 6-25 %, 26-50 %, 51-75 %, 76-100 %). These figures were averaged across plots to give a figure for each habitat class.

6.3.2 Habitat scores

To enable me to compare habitat quality between classes, I decided to calculate a relative score for each habitat class based on these measurements. In order to do this I designed a method which weighted each variable onto the same scale – although, because certain variables were considered more important than others when assessing habitat quality, I double-weighted variables which I considered to be most important when assessing habitat quality (density of large trees and canopy cover at 20 m). These are the two variables that I predicted to be most important for orang-utans i.e. the presence of large fruit-bearing trees and unbroken travel routes. Some variables were scored positively and some negatively. Those variables which were considered indicators of good-quality forest were scored positively i.e. large (>20 cm dbh) and medium (>10 - ≤20 cm dbh)-sized tree density, mean diameter and canopy cover (at 10 m and at 20 m), and those considered indicators of disturbed forest, were scored negatively, i.e. tree stumps, tree falls, and saplings, thus they were given high scores for low values.

Convert measured variables into scores

For each positively-scored variable, the habitat class with the highest value was given a score of 100 (200 for the double-weighted variables), and a value of 0 was given a score of 0. Thus, for example, a score of 0 for tree density could only be achieved in a clearing or burnt area, i.e. an area with no trees. Each remaining habitat class was given a score based on this scale, using the following formula:

$$\frac{X}{X_1} * 100 \ (or\ 200)$$

where: X = measured value to be converted; X_1 = highest value

For each negatively-scored variable, the habitat class with the highest value was given a score of 0, and a value of 0 was given a score of 100. Each remaining habitat class was given a score based on this scale, using the following formula:

$$[1-(X / (X_1)] * 100$$

The highest score should represent the most complete forest and the best habitat quality, and the lowest score should represent the worst habitat quality, with the greatest disturbance.

This scoring method for habitat classification was used to confirm the classification made by eye when following orang-utans. Because there is general agreement between the measurements and visual-estimation (see Results section), I was confident, therefore, to use my visual determination of habitat classes as a means for classifying habitat quality whilst following orang-utans.

Habitat quality classes

To test whether the habitat classes defined were significantly different to each other, I used a multinomial logistic regression.

Proportion of each habitat class in the study area

To assess the proportion of different habitat quality classes present in the study area, I walked 15 transects within the grid system (both east to west and north to south) which totalled 522 data points. At 50 m intervals the habitat was classified using the seven classes defined in Table 6.1. In December 2004 two big storms caused many tree-falls and noticeably changed the appearance of large parts of the forest. Because of this I re-assessed habitat quality to see how the quality of the forest had changed after the storm by re-walking 6 of the transects (T0, T0.4, T1B, T1.3, T1.6, T2 = 261 data points) from east to west from the main walkway, (excluding those that run north-south as there was obviously more storm damage the nearer one was to the main walkway (the old railway) in the east – whereas when one walked further into the forest (west) damage appeared to decrease.

In order to compare the different habitat classes used by orang-utans by with the proportion of each habitat quality class present in the study area, I used a mean of the before and after storm proportions because I had behavioural data from both before and after the storm. I also performed a one-tailed Chi-square Test to see if the forest composition had become significantly more disturbed.

6.3.3 Habitat preference

I calculated orang-utans preference for the different habitat classes using Jacob's D value (Jacobs, 1974), which is calculated by the formula:

$$D= (r-p) / (r+p-2rp)$$

Where:

r = frequency of use (number of counts from behavioural data) for each habitat quality class.

p = relative availability of each habitat quality class (a count of each habitat class).

These values are bounded between -1 and 1 with 0 being neutral (neither disproportionate selection nor avoidance). Positive values indicate preference and negative values indicate avoidance. A chi-squared test was used to examine whether orang-utans use the different habitat-quality classes for significantly different periods of time relative to their availability. Secondly, each habitat class was collapsed into a 2 x 2 contingency table and a chi-squared test carried out to see whether orang-utans significantly preferred or avoided that particular habitat class. Due to an unequal number of data points for each age/sex class, most analyses were done on the combined dataset (all age/sex classes combined).

6.3.4 Direct human disturbance

For identifying the level of disturbance within the research area during the study period (from August 2003 to September 2005), the percentage of follow days with disturbance was used.

Effect of disturbance on orang-utans activity budgets

The impacts of direct human disturbance on orang-utan behaviour were recorded. For this analysis all habituated follows and follows >3 hr were used, including data from all assistants. Researchers following the orang-utan were not considered to be human disturbance, as the presence of researchers was consistent throughout the study, and the additional effect of this disturbance could not be quantified. The presence of all other people, including hunters, loggers and other scientists was recorded as human disturbance and the disturbance noted as either human presence or logging Table 6.2.

Table 6.2 Activities recorded as disturbance.

Disturbance	Activities
Human presence	Talking, shouting, singing, the sighting of a person, the sound of tree being tapped, and the sound of dogs barking (hunters).
Logging	Sound of chainsaws, axes or tree falls.

The activity budgets (feeding, resting and travelling) of orang-utans were compared between periods when disturbance was recorded and periods when no disturbance was recorded. In order to see if there were any associations between disturbance and activity budgets, a Pearson Chi-Squared test was used.

For analysis of human disturbance, a count of observations was used as the dependent variable.

6.4 RESULTS

6.4.1 Habitat

Habitat classification

193 plots were measured in the study area for habitat quality characteristics. The mean values for each variable for each habitat class are shown in Table 6.3. These were then converted into scores using two weighting methods (called A and B), and the scores for each variable combined to give a total score for each habitat quality class (Tables 6.4 A and B). Although the *standard deviations* in Table 6.3 are high, a multinomial logistic regression (with classifications) confirms that these habitat classes can be separated.

The highest score in Table 6.4 referred to the best-quality forest habitat and the lowest score the worst quality habitat. Classes with a high score had a relatively high density of large trees, complete canopy, few tree falls, few cut stumps and fewer saplings, compared to classes with low scores. Both methods produced the same rank order, which matched with the predicted rank order from visual estimation of habitat quality, i.e. TCA was the best quality habitat and S was the worst (Table 6.5).

Table 6.3 Mean values for each measured habitat variable for each habitat quality class.

Habitat class	Density /ha Trees >10-≤ 20 cm dbh	*sd*	Density /ha Trees>20 cm dbh	*sd*	Mean dbh (cm)	*sd*	% Cover at 10m	*sd*	% Cover at 20m	*sd*	No. Tree falls /leaning	*sd*	No. Stumps >10cm dbh	*sd*	% sapling < 5m tall	*sd*
TCA (19)	85	*39.8*	34	*18.1*	21	*2.4*	79	*15.6*	63	*21.2*	1.8	*2.0*	0.4	*0.8*	38.2	*12.3*
TCB (61)	92	*81.8*	27	*25.0*	20	*2.1*	73	*18.3*	38	*24.7*	3.5	*3.0*	0.7	*1.1*	40.2	*14.0*
TIC (29)	38	*46.9*	17	*8.1*	20	*1.8*	59	*22.6*	14	*29.6*	6.7	*3.9*	1.4	*1.8*	35.8	*13.4*
MC (30)	98	*50.8*	21	*11.7*	18	*1.8*	68	*26.3*	41	*24.4*	3.7	*4.3*	0.7	*0.8*	50.0	*12.6*
MIC (20)	50	*101.3*	14	*15.7*	18	*2.3*	68	*23.0*	18	*31.1*	5.8	*2.7*	1.2	*1.6*	56.3	*16.0*
LMS (21)	47	*107.1*	4	*9.6*	17	*3.2*	67	*20.8*	2	*9.8*	2.6	*2.8*	2.7	*2.2*	65.5	*16.7*
S (13)	19	*29.8*	2	*1.4*	14	*2.7*	56	*23.1*	0	*0*	0.4	*1.0*	5.23	*2.4*	73.1	*19.0*

Table 6.4 Habitat quality scores (**Trees >10 - ≤ 20 cm dbh = Medium size trees; Trees >20cm dbh = Large trees**).

Method A - Scores

Habitat class	Medium tree density	Large tree density	Mean diameter	% Cover at 10 m	% Cover at 20 m	No. Tree falls /leaning	No. Stumps > 10 cm dbh	% sapling < 5 m tall	Overall
TCA	83	200	100	100	200	78	100	94	954
TCB	92	155	86	72	122	52	94	89	761
MC	100	118	60	53	44	48	94	100	617
TIC	24	97	83	12	131	0	80	62	489
MIC	39	77	56	50	57	14	85	45	421
LMS	36	14	33	46	7	65	54	20	275
S	0	0	0	0	0	100	0	0	100

Method B - Scores

Habitat class	Medium tree density	Large tree density	Mean diameter	% Cover at 10m	% Cover at 20 m	No. Tree falls /leaning	No. Stumps > 10 cm dbh	% sapling < 5 m tall	Overall
TCA	86	200	100	100	200	73	92	48	899
TCB	94	158	95	92	122	48	87	45	740
MC	100	123	87	86	44	45	87	51	623
TIC	38	103	94	75	131	0	74	32	546
MIC	51	84	85	86	57	13	78	23	475
LMS	48	25	78	84	7	61	49	10	363
S	19	11	66	71	0	94	0	0	262

Table 6.5 Description of habitat classes in order of forest quality and structure (based on the measurements from Table 6.3).

Order	**Forest type**	**Description**
Complete	**TCA**	**Tall complete A –** Density of large trees (>20 cm dbh) is high (34 stems /ha), with complete canopy. Tree-falls (1.8 stems/plot) and stumps (0.4 stems/plot) are extremely low.
Complete	**TCB**	**Tall complete B –** Density of large trees is high (27 stems/ha), some gaps due to some tree-falls, but minimal damage from tree falls or logging.
Complete	**MC**	**Medium complete** – Lower complete canopy, all trees at the same level (≤20 m in height). High density of medium size trees (>10-≤20cm dbh - 98 stems/ha). May naturally occur like this, due to differences in peat depth and water table, or may be maturing secondary forest due to past logging in the 1980s.
Incomplete	**TIC**	**Tall incomplete** – Low density of large trees (17 stems/ha), Uneven canopy with large gaps and lots of tree-falls from recent logging activity. Gaps create isolation of trees with no connecting canopy.
Incomplete	**MIC**	**Medium incomplete –** Lower version of TIC, with a low density of medium size trees (50 stems/ha); an uneven canopy with large gaps, and denser understorey than TIC due to secondary growth (sapling cover - 73%) .
Secondary	**LMS**	**Lower mixed secondary** – Uneven lower canopy with high density of saplings (65%) and stumps (2.7 stems). Very low density of large trees (4 stems/ha), thus not many tree-falls.
Secondary	**S**	**Secondary (**first successional stage) – high proportion of small trees and saplings (73%) so very dense. Many old and rotting stumps. Density of large trees extremely low (2 stems/ha).
Clearing	**Cl**	**Clearing -** no trees standing. High density of saplings with many stumps and fallen trees within a 10 x 10 m area.

Large trees = trees > 20cm dbh; Medium trees = trees >10 - ≤ 20 cm dbh.

A multinomial logistic regression was used to test if the different habitat classes were significantly different. Using 9 variables (the 8 listed in Table 6.3, plus average tree height) they explained 87.2% (Nagelkerke $r^{2;}$ very high variance) of the variation between the different habitat classes; with 69.3% of classes classified correctly (Appendix XII). Overall, there was a significant difference between habitat classes (X^2=357.124, df=72, p<0.001). The most significant predictors were cover at 20 m (X^2=38.474, df=6, p<0.001), average height (X^2=29.131, df=6, p<0.001) and tree falls (X^2=26.199, df=6, p<0.001) (see Appendix XIII-for likelihood ratio test).

I also tested differences in the mean diameter of trees >20 cm dbh for classes TCA, TCB, TIC, MIC and MC. A one-way ANOVA shows the size of large trees to be significantly larger in the tall classes compared to the medium size-classes ($F_{4,154}$ = 10.37, p<0.001;

TCA, TCB & TIC > MC & MIC). Thus, different habitat classes can clearly be distinguished from each other, justifying the use of these seven classes for visual determination of habitat quality, and their integrity as structurally different classes of habitat quality. These seven habitat classes are used in all further analyses in this chapter.

Table 6.6 Average size of trees >20 cm dbh between complete and incomplete habitat classes

Habitat description	Habitat classes	Mean DBH (cm)
Complete	**TCA**	28.8
Complete	**TCB**	28.0
Incomplete	**TIC**	28.7
Complete	**MC**	24.2
Incomplete	**MIC**	24.9

6.4.2 Forest quality within the research area

26 km of transect were walked within the 9 km^2 study area, during which 522 habitat classifications were assigned.

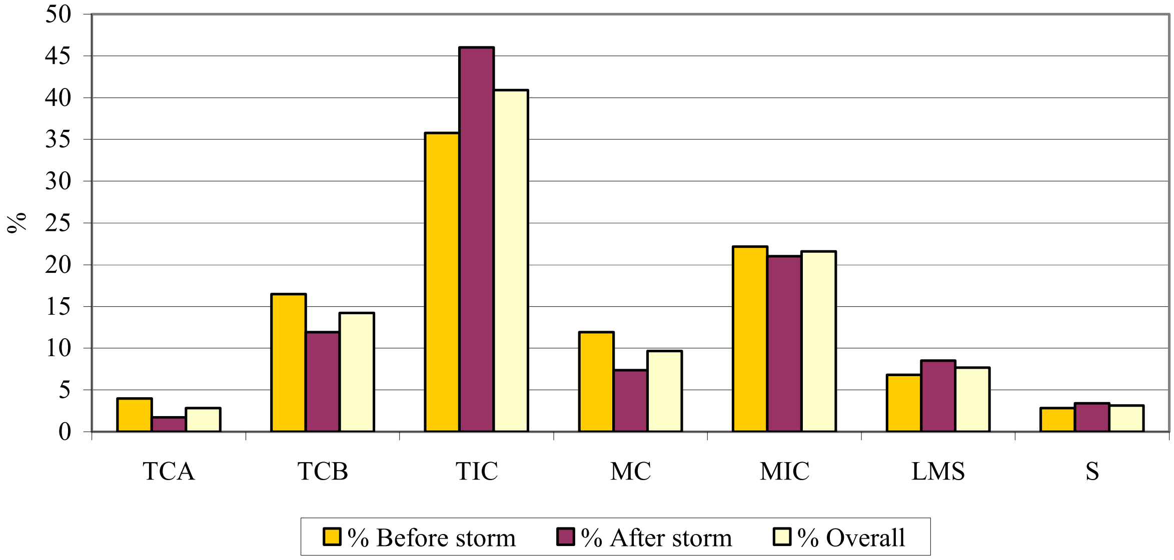


Figure 6.3 Proportion of each habitat class within the study area (% overall = a mean of before storm and after storm, using just those transects which were walked both before and after the storm).

Figure 6.3 shows the proportion of each habitat class in the forest both before and after the December 2004 storm, and an average. The habitat that dominated the forest overall was

TIC, which represented 41% of the forest, followed by MIC. S and TCA were the rarest habitat types, with only 3.5% and 3% respectively.

The proportion of complete habitat classes (TCA, TCB and MC) decreased after the storm, whereas the proportion of the incomplete and secondary habitats increased (TIC, LMS, S, but not MIC). Using a Chi-squared test I tested to see if this change was significant, resulting in more incomplete classes and less complete classes, but no significant result was found ($X^2 = 7.489$, df = 6, 1-tailed $p = 0.139$). When testing just the tall habitat classes (those more likely to be affected by the storm) the result was not significant either ($X^2 = 7.015$, df = 4, 1-tailed $p = 0.068$).

To compare orang-utan forest use with the proportion of different forest quality classes, I used the mean of the before and after figures.

6.4.3 Orang-utan habitat preference

Overall preference

The Jacob's D Value was used to test habitat preference by orang-utans. Values were calculated using all age/sex classes, and then for each age/sex class individually. Additionally, habitat-quality preference was assessed separately for feeding, resting and nesting.

The overall Jacob's D Value (Figure 6.4) for preference shows orang-utans were actively choosing and avoiding certain habitat-quality classes. Orang-utans were positively choosing the tall habitat classes (TCA, TCB and TIC) and avoiding the smaller habitat classes (MC, MIC, LMS and S), regardless of canopy cover.

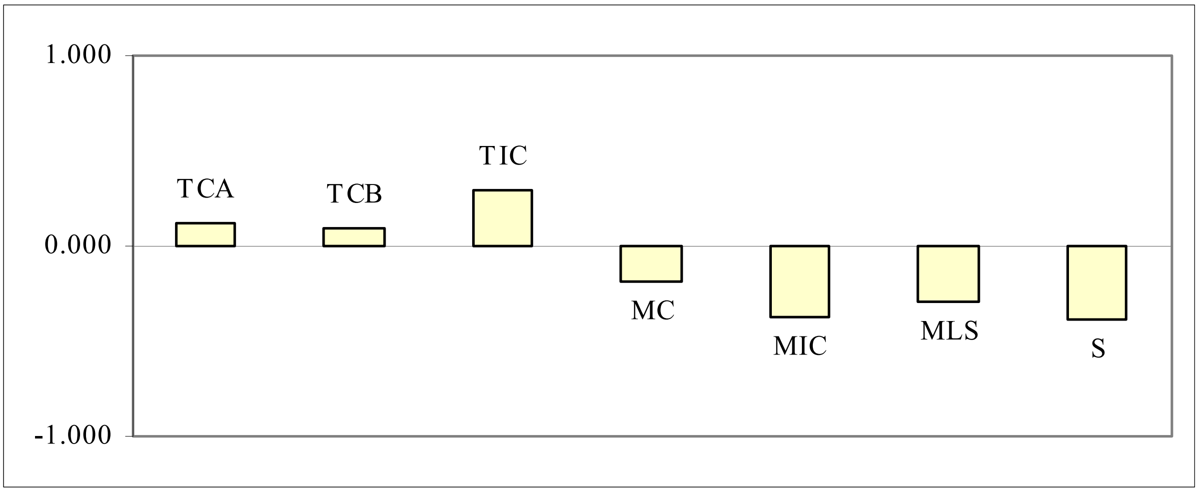


Figure 6.4 The Jacob's D preference values for each habitat class. Positive values indicate preference and negative values indicate avoidance.

Age/sex class preference

When assessing the preferences of each age-sex class separately (again using Jacob's D values), all age/sex classes – with the exception of flanged males (FM) - followed the overall pattern by actively choosing the taller habitat classes (TCA, TCB and TIC) and avoiding the smaller habitat classes (MC, MIC, LMS and S).

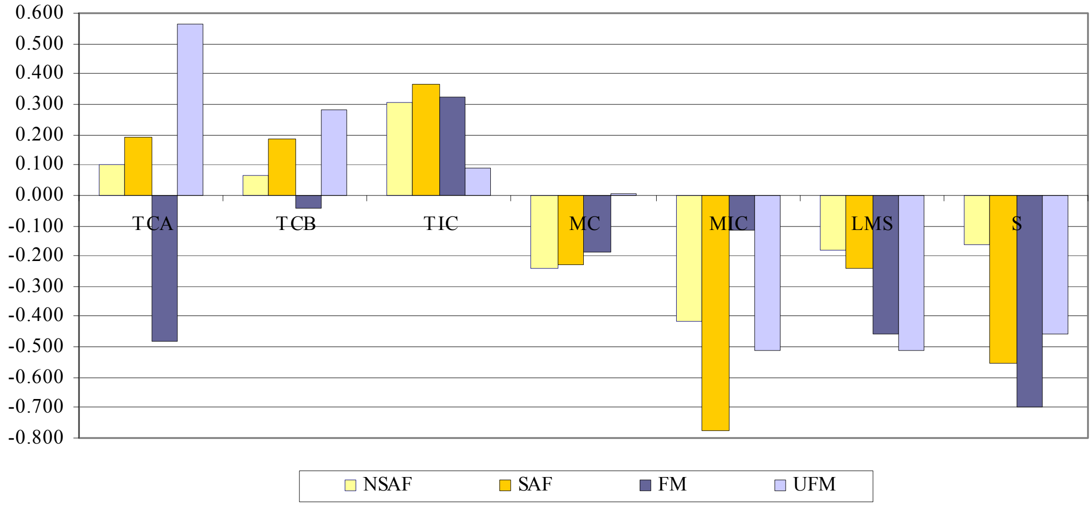


Figure 6.5 The Jacob's D preference values for each habitat quality class by age/sex class.

Positive values indicate preference and negative values indicate avoidance.

For the following analyses, however, I decided to use all age-sex classes combined, due to small and uneven sample sizes for each age/sex class on their own.

6.4.4 Habitat preference for activities

Feeding

The Jacob's D values show that orang-utans were preferentially choosing the tall habitat classes TCB and TIC for feeding, and actively avoiding the medium height (MC and MIC) and secondary (LMS and S) habitat classes (Figure 6.6). The degree of canopy completeness appears unimportant, as complete and incomplete habitats were both positively and negatively selected. This indicates that there was no preference for complete habitat; that more food is available in areas with big trees (Chapter 3), and that completeness of canopy cover has little effect on this.

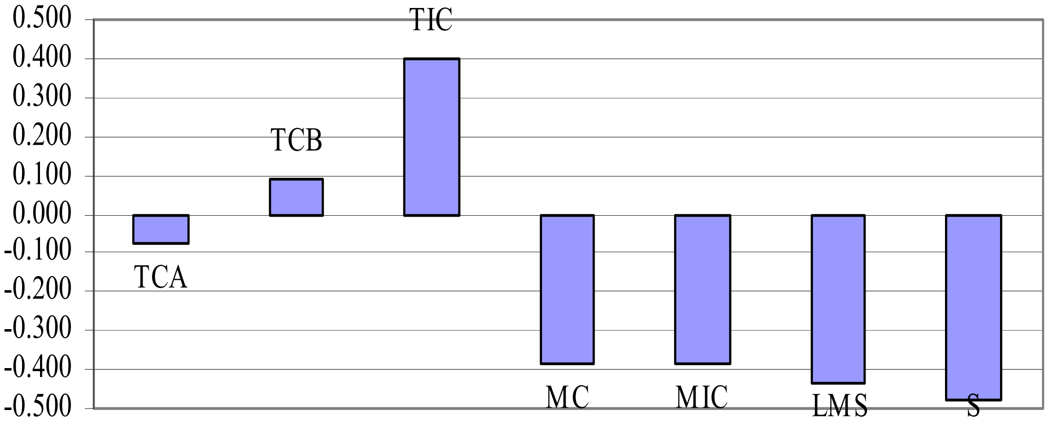


Figure 6.6 Jacob's D preference value for feeding. Positive values indicate preference while negative values indicate avoidance.

Resting and nesting

The Jacob's D values show that habitats that were either tall or complete were actively preferred for resting, where as the lower incomplete habitats (MIC, LMS and S) were actively avoided for both resting and nesting (Figure 6.7A).

There was a positive preference for nesting in the most complete habitats, regardless of height as TCA, TCB and MC were selected. The habitats with incomplete canopies (TIC, MIC) and the secondary habitats (LMS and S) were all avoided (Figure 6.7B). No nests were built in habitat class S. This result suggests that canopy completeness is more important than canopy height when choosing nesting sites.

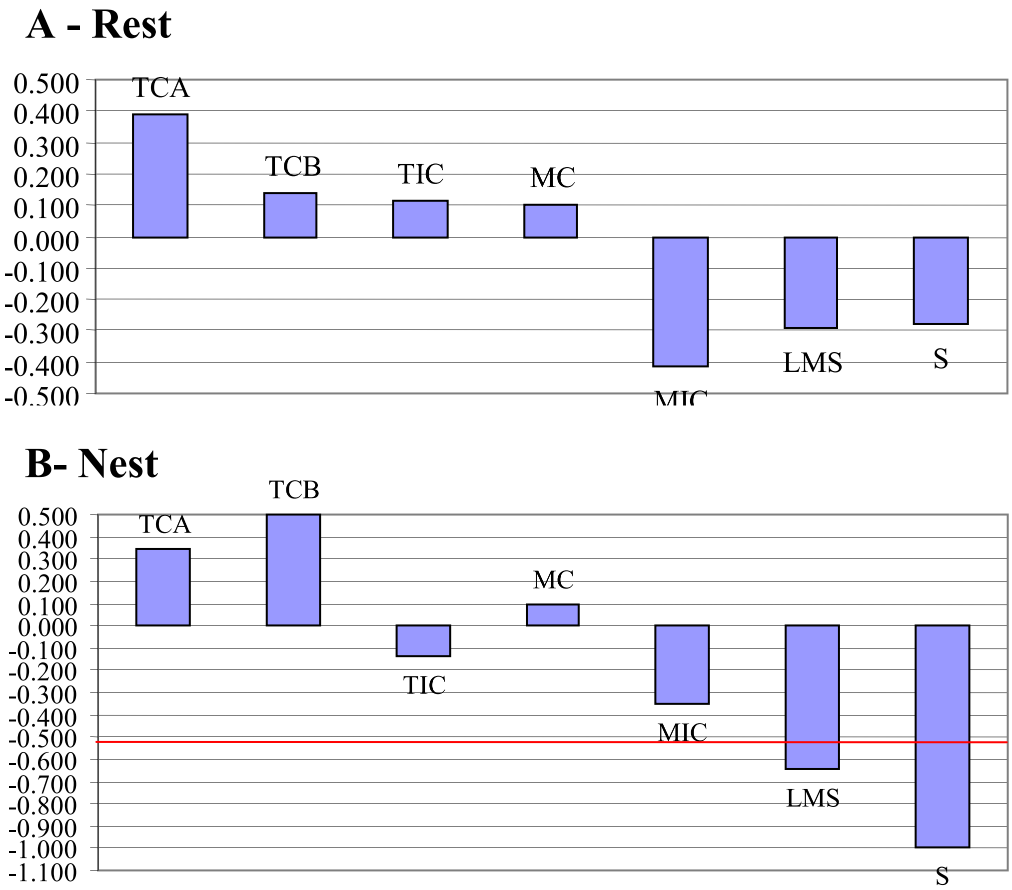


Figure 6.7 Jacob's D preference value for resting (A) and nesting (B). Positive values indicate preference while negative values indicate avoidance. Redline is the -0.500 scale axis.

Travel

It can be argued that orang-utans would not 'choose' to travel in any particular habitat, for if they did they would have to travel through other habitats to get to the preferred habitat, which is paradoxical. Avoidance of certain habitat classes may be expected, on the other hand. The Jacob's D values mostly show no obvious preference or avoidance, as expected, apart from MIC and S which are avoided (Figure 6.8). This may be because MIC is the only habitat class with both large gaps AND no big trees, and thus may be the hardest (and thus most energetically expensive) habitat to travel in.

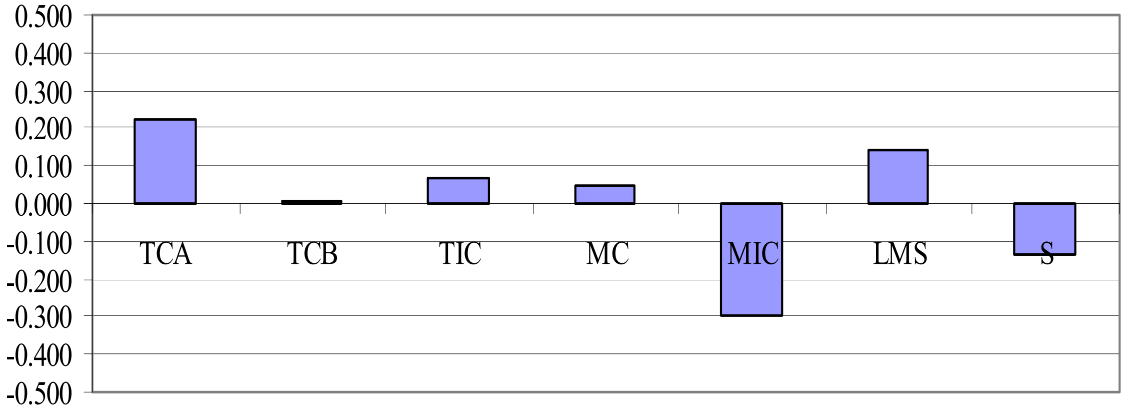


Figure 6.8 Jacob’s D preference value for travel. Positive values indicate preference while negative values indicate avoidance.

6.4.5 Orang-utan activities in different habitat classes

The activity budget of orang-utans differs depending on the habitat class they were in (Table 6.7), with a clear distinction between the complete, incomplete and secondary habitats. The ratio of time spent feeding compared to time spent resting was much higher in the most open, incomplete-canopy habitats of TIC (ca. 5.5:1) and MIC (ca. 4.4:1) compared to the complete-canopy habitats of TCA and MC (both ca. 1.6:1), where they preferred to socialise (biggest party sizes, Table 6.7). TCB, which has a canopy completeness half way between TCA and TIC, also had a feeding:resting ratio half way between (ca. 3.5:1). The Jacob’s D values above (Figures 6.6 and 6.7) suggest that this relationship is found because orang-utans prefer to rest (and nest) in complete-canopy habitat, and not because of any preference to feed in incomplete-canopy habitat, instead they appear to prefer tall forest in which to feed. In the secondary habitat classes (LMS and S), neither feeding nor resting is high – and the Jacob’s D values for these activities is strongly negative for both secondary classes. Instead they spend between a quarter and a third of their time in secondary habitat travelling, more than in the taller habitat classes. For travel, different modes of locomotion were used in the different habitat classes (Table 6.8), with quadrupedal walking occurring more in the complete habitat classes TCB and MC, whereas climbing occurred more in the tall incomplete forest and tree swaying more in the low (LMS) and incomplete classes (TIC and MIC) (Table 6.8).

Table 6.7 Activity budgets in each habitat class.

Forest quality	% Feed	% Travel	% *Rest	Total	Mean party size
TCA	50	19	31	100	1.57
TCB	69	13	18	100	1.36
TIC	74	11	16	100	1.29
MC	48	24	28	100	1.38
MIC	67	18	15	100	1.23
LMS	50	34	16	100	1.14
S	54	25	21	100	1.25

Figures highlighted in yellow are the highest values for that activity. *Resting includes nesting. Mean party size is an indication of social activity.

Table 6.8 Modes of travel in the different habitat classes.

Mode of travel %	TCA	TCB	TIC	MC	MIC	LMS	S
Branchiate	5	6	4	8	1	6	5
Clamber	85	70	66	67	72	62	86
Climb	3	4	8	3	4	3	-
Quadrupedal walk*	-	4	1	2	1	1	-
Tree sway	8	16	22	19	22	28	9
Total	100	100	100	100	100	100	100

Figures highlighted in yellow are the highest values for that mode of travel. *Quadrapedal walking was walking on the ground.

Orang-utan diet in the different habitat classes also differs (Table 6.9) with fruit and flowers (combined) forming a much larger part of the diet in the tall habitats (TCA, TCB and TIC) than in the low and secondary (LMS and S) forest, whereas these classes have a much larger proportion of invertebrates and leaves in the diet compared to the taller classes.

Table 6.9 Percentage of each food item in the diet in the different habitat classes.

Food Types %	TCA	TCB	TIC	MC	MIC	LMS	S
Bark	0.8	1.1	2.2	0	1.3	0.6	0
Flowers	28.3	1.2	2.5	1.0	0.9	0	0
Fruit	56.2	87.8	82.5	71.7	70.8	54.5	61.7
Invertebrates	8.3	4.0	4.5	13.8	18.1	25.6	8.5
Leaves	6.0	5.3	6.7	12.1	6.2	15.4	21.3
Pandan and other piths	0.4	0.5	1.3	1.0	1.7	0.6	8.5
Other (roots, sap, water)	0	0.2	0.3	0.3	1.1	3.2	0
Total	100	100	100	100	100	100	100

Figures highlighted in yellow are the highest values for that food type.

6.4.6 Impact of active human disturbance

Disturbance at the research site

There were six major types of human disturbances recorded in the forest throughout the study period (Table 6.10). The most destructive was bat hunting, which involved the hunters clearing areas of 30 x 30 m of forest for their nets. Twelve of these areas were used during the study. Additionally, there were three regularly-used pondoks (temporary accommodation huts) in the study area, which were occupied by latex collectors and hunters (of pigs), although the hunters were not permanent.

Table 6.10 Types of human disturbance identified.

Activity within the research site	Dates
Illegal logging for big timber	November 2003 – March 2004
Illegal logging for small timber (scaffolding etc.)	December 2003 – January 2005
Bat hunting	February – April, September – November each year
Other forms of hunting (pigs, birds)	All year round
Jelutong collecting	May – November each year
Gemur collecting	All year round

Illegal logging for large trees was stopped in March 2004 by the efforts of the CIMTROP patrol team. Other forms of disturbance continued at low levels. Out of all follows 22% experienced some form of disturbance; humans other than the researchers came close in 15% of follows and nearby logging disturbance was recorded on 7% of follows. Despite 22% of follows experiencing some disturbance this was generally for short periods of time, with only 1.5% of all behavioural counts (using habituated data only and follows > 3 hr) having disturbance recorded.

Effect of disturbance on orang-utan behaviour

Figure 6.9 shows orang-utan activity budgets for times when there was (a) no human disturbance and (b) human disturbance (either human presence or nearby logging). Orang-utans clearly seem to change their behaviour in response to disturbance. Their activity pattern changed to a budget with more feeding and resting and their time travelling decreased.

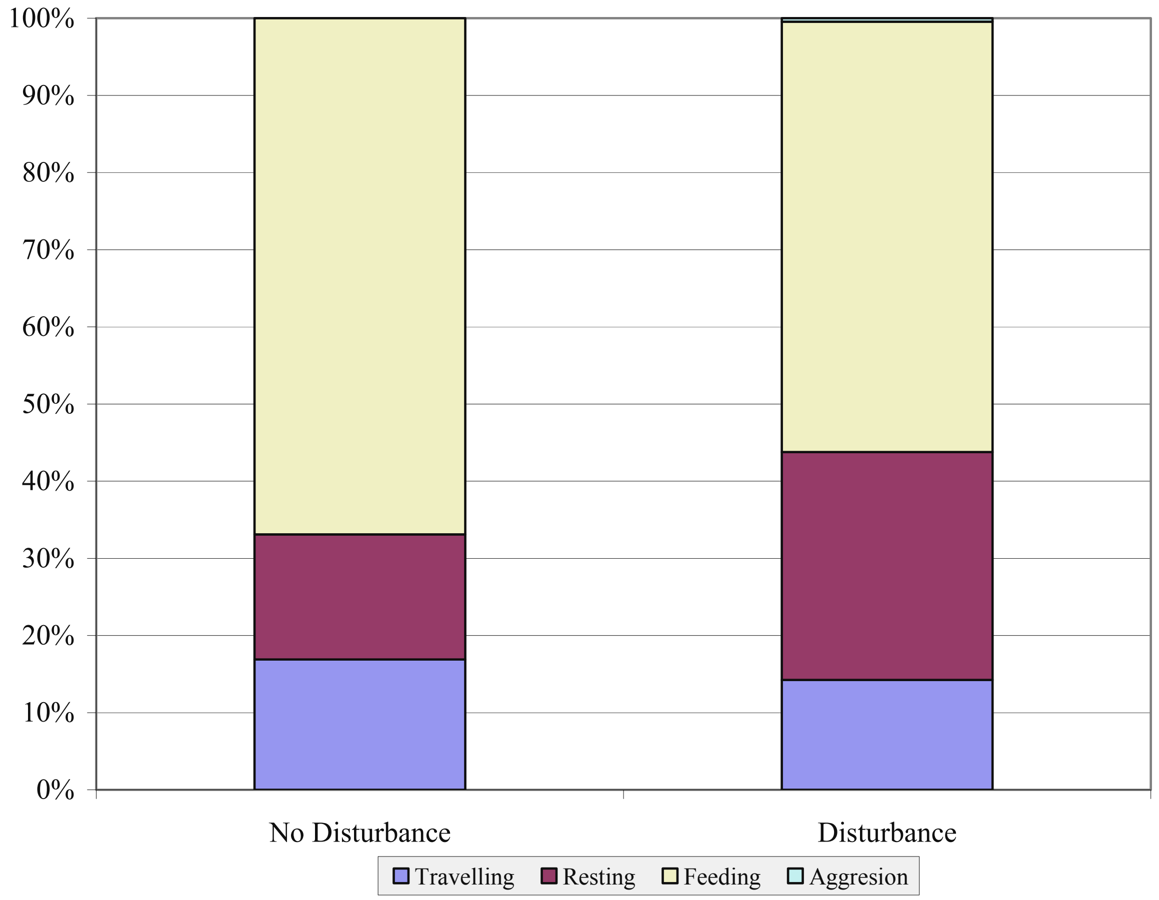


Figure 6.9 Orang-utans activity budget when there was no disturbance in the forest compared to when there was disturbance. A count of all follows >3hr was used.

Figure 6.10 shows the activity budgets when disturbance is split up into direct human presence and active logging disturbance. Orang-utans react to human presence by decreasing their time feeding and travelling, and increasing their time resting. Their reaction to logging (i.e. the sound of chainsaws), also resulted in them decreasing their time feeding and resting. Direct aggression towards humans was minimal, but occurred for human presence but absent for logging disturbance. The effect of both disturbances combined was a reduction in feeding time by 11% compared to when there was no disturbance.

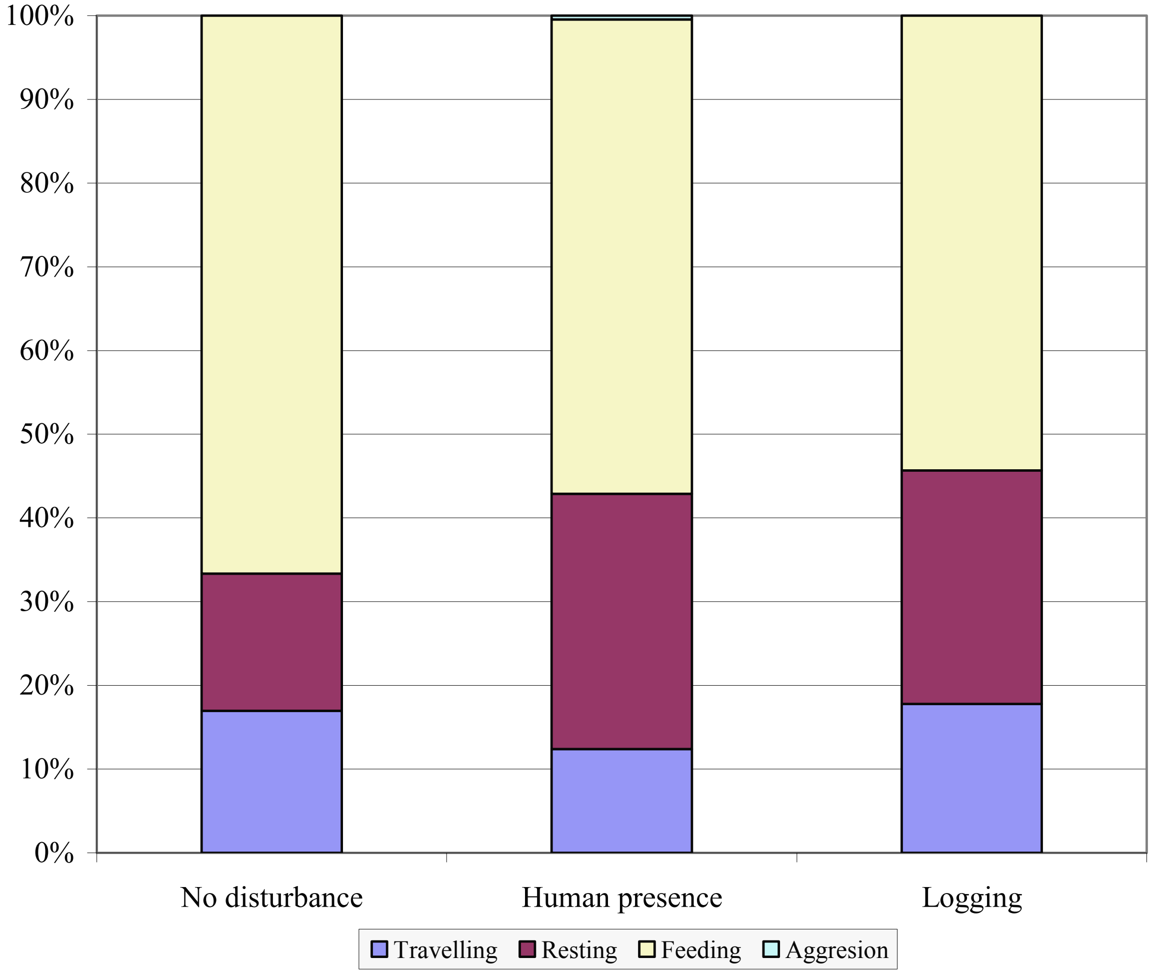


Figure 6.10 Orang-utans activity budgets in situations where there was (i) no disturbance, (ii) human presence and (iii) active logging.

6.5 DISCUSSION

6.5.1 Habitat classes

The forest in the Sabangau is dominated by the tall- and medium-incomplete (TIC and MIC) habitat classes, which make up 60% of the forest area. This is due to past-logging in the area, resulting in patches of different habitat quality and areas of secondary growth. The forest is thus in many different successional stages, in which large gaps become significantly smaller with time as the canopy of logged forest re-grows (Cannon *et al.,* 1994). The standing biomass in the study area has decreased by 20% since 1993 or by about 2% per year (Husson *et al.,* 2008), due to intense illegal logging since 1996 when the legal logging concession ended. As a result, less than 20% of the forest is now in – or close to – the primary state - tall complete forest (TCA and TCB). Cannon *et al.* (1994) found that a period of 8 years was required for severely-disturbed areas to recover any canopy structure beyond the short-stature stand which is formed by pioneer species. The Sabangau forest is in the middle of this period, with patches of old-logged and patches of recently-logged forest. If logging in the area is stopped now and the forest is left alone, it should recover to resemble its original state, although species diversity may be different.

6.5.2 Orang-utan habitat preference

Overall preference

Felton *et al.* (2003) found that unlogged sites had a greater proportion of orang-utan food trees in the larger size classes than logged sites, although stem density was significantly higher in logged areas. The heterogeneous structure of logged forest, however, tends to force primates to search more intensively through the remaining patches of vegetation, resulting in more dispersed foraging (Johns, 1986). That ability to adjust foraging strategies to cope with variations in habitat and food supply probably accounts for the continued survival of primate populations in logged forest (Johns, 1986). So the orang-utans ability to adapt and alter its activity patterns and diet (Knott, 1998, 1999b; Morrogh-Bernard *et al.,* 2009) has allowed it to persist in logged habitat, albeit at lower densities (Morrogh-Bernard *et al.,* 2003). In spite of this, when orang-utans have a choice they choose unlogged forest over logged (Rao and van Schaik, 1997), and thus the intensity of logging is extremely important, as I have found in this study.

In the Sabangau, where orang-utans do not have an explicit choice of logged or unlogged forest, all seven habitat quality classes defined by me were used, and orang-utans did show a positive preference for the taller – and, thus, by extension, the less-logged habitats - over the medium-height and secondary classes, which were all significantly avoided. The only age/sex class not to prefer the tall complete TCA was flanged males. A possible reason why they significantly avoided this forest class may be their size and energetic requirements, as flanged males weigh twice as much as adult females (Cant, 1987) and have larger home ranges in comparison to all other age/sex classes (see Chapter 6), so it may be more energetically expensive for them to actively search out this habitat, when the tall-incomplete forest (TIC) is so dominant.

Overall, the tall forest classes, regardless of completeness, were preferred over the medium and secondary classes, suggesting that the presence of large trees out-weighs a more complete but smaller forest, even though there are more intact arboreal pathways in the latter. The preference for the tall habitat classes is presumably because large trees are more likely to fruit (Chapter 3) and have larger crop sizes, thereby supporting the theory that orang-utans deliberately search out habitat patches with large trees.

Preference for activities

When habitat preference was broken down between activities, orang-utans preferred to feed in the tallest forest classes, regardless of canopy completeness, whereas for nesting orang-utans preferred the complete-canopy forest classes (TCA, TCB and MC) and avoided the incomplete and secondary classes. The complete-canopy classes also had larger party sizes, indicating that these habitat classes were preferred for social activities, such as play. This finding is important as it shows that orang-utans are actively choosing and avoiding certain habitat classes over others for different activities. The reason why orang-utans prefer large trees is probably due to large crop sizes, as already discussed, but competition with sympatric primate species may also play a part, as one study found orang-utans fed mainly on the largest fruiting trees, largely ignoring the smaller fruit-bearing trees which were instead fed upon by other species (Wich *et al.,* 2002).

In regards to nesting, many studies have implied that orang-utans select open habitat (e.g. slopes and vegetation breaks) for nesting, as this gives them a good look-out for predator detection (Harrisson, 1969; MacKinnon, 1974; Rijksen, 1978). Previous studies on nest selection in the Sabangau (which does not have slopes) came to the same conclusion - that orang-utans were selecting nesting sites on the edge of clearings for predator detection (Hearn, 2002; Gibson, 2005). This seems not to be the case from this study, however, as I found that orang-utans actively chose the more complete-canopy habitat classes for resting and nesting. This is probably because they are choosing cover, perhaps for protection. Sugardjito (1983) states that orang-utans do not seem to be alert in their nest and instead rely on camouflage and concealment for protection. Increasing safety by reducing detectability by predators and exposure to the natural elements has been found to be a strong influencing factor in nest-site location (Anderson, 1998). Ancrenaz *et al.* (2004b) found that in logged forest, tall trees were preferred for nesting sites, and most nests were in the upper part of the tree crown where more leaves were available and where the apes were not directly exposed to sunlight or rain. They also suggest that large trees provide more relaxing sleeping opportunities during the night, as tree falls in Kinabatangan are common.

The reason why previous researchers in the Sabangau concluded that orang-utans were choosing to nest in open forest was probably because the incomplete habitat classes are by far the most dominant classes in the forest and, therefore, more nests will inevitably be found there, regardless of whether orang-utans actively choose to nest there or not. I tend to agree with Ancrenaz's (2004b) explanation as to why orang-utans nest in tall overlooking trees in disturbed habitat, which is to minimise risk from tree falls, rather than as an anti-predator measure. Trees regularly fall down in storms, particularly in a logged peat-swamp forest such as the Sabangau, and the danger to orang-utans is that a tree falls on top of them whilst they are sleeping. Thus, although most nests are found in the incomplete habitat classes, when you assess preference the complete-canopy classes were preferred over the incomplete-canopy classes, and thus nest location for orang-utans in Sabangau seem to be connected with concealment (from predators, wind and rain).

6.5.3 Effects of habitat disturbance on secondary activities

Arboreal primates that remain in an area after logging are faced with the loss of food resources, i.e. large fruiting trees. In these cases there are two options available to them: (1) increase search time, hence increasing energetic costs, or (2) reduce selectivity of food items, hence minimising cost at the expense of quality (Marsh *et al.*, 1987). Both strategies were adopted in a Sumatran forest where orang-utans became more folivorous and were also found to expend more energy by travelling more and using more energetically expensive locomotion in logged forest (Rao and van Schaik, 1997).

In the Sabangau, orang-utans could not completely avoid the worst habitat classes, as the forest is an irregular mosaic in which certain habitats can probably not be avoided. Therefore, all classes were used, but preferences were apparent. When orang-utan diet was compared between habitat classes, they were found to feed on flowers and fruits mostly in the tall complete forest classes, whereas invertebrates, leaves and pandan pith were eaten more in the secondary-forest classes. Thus, a change in diet to a more insectivorous and folivorous diet in the secondary habitat classes is apparent, as these resources are more abundant in these habitat classes compared to fruits as there are virtually no large trees. More dead wood in the secondary classes means more termites and more small saplings means more young leaves. Thus, orang-utans in the Sabangau may be reducing their selectivity for preferred food items when in disturbed habitat classes.

Travel and type of locomotion was also affected by habitat quality. The proportion of time spent travelling was highest in the secondary habitat classes. Clambering was more common in the secondary habitat classes, whereas climbing was more common in the incomplete habitat classes, as orang-utans could only enter and leave large feeding trees by ascending and descending via the trunk (pers. obs.), thus expending more energy that would be needed in a continuous canopy forest due to increasing path length (Cant, 1992; Rao and van Schaik, 1997). Although many studies have found that locomotion costs account for less than a fifth of the total daily activity costs of mammals (Karasov, 1981), large body size and larger daily travel distances have been found to increase these costs (Warren and Crompton, 1998).

Thus, this demonstrates that differences in habitat structure not only affect food selection, but also energetics (energy intake and expenditure), as the costs from ascending and descending are very expensive (Thorpe *et al.,* 2007).

6.5.4 Implications for conservation

The results from this study indicate orang-utans do show a preference for different habitat classes, with the quality of the habitat affecting their behaviour greatly; ranging from diet and nesting sites to modes of locomotion and, by implication, their energy balance. The patchy distribution of different habitat classes means that orang-utans have to spend more time searching for certain habitat classes in order to perform certain activities. Food availability and, thus, energy balance is a major influencing factor with regard to activity budgets and habitat use. Large amounts of ketones are found in orang-utans urine at times of low fruit availability (Knott, 1998; Chapter 4), indicating that orang-utans cannot exist on little or no fruit for extended periods of time. Thus, if secondary habitat (as described in this chapter) were the only habitat type available to orang-utans, fruit would be a rare commodity. As a result, orang-utan diet would become more insectivorous and folivorous, as invertebrates, leaves and pandans would dominate their diet. Leaves are less energy-rich compared to flowers and leaves (Knott, 1998, 1999b; Harrison, 2009), thus it is likely that orang-utans will lose weight.

Thus, if medium incomplete and secondary habitat classes (as defined in this chapter) were to be the dominant habitat classes within a forest, this would have a huge impact on energy intake and expenditure, and would result in a density decrease through probable starvation, disease and emigration, as some individuals try to find better habitat. Unsurprisingly, therefore, fruit availability is highly correlated with orang-utan density (Knop *et al.*, 2004; Wich *et al.,* 2004b) and, thus, carrying capacity. A highly-disturbed forest also has a lower availability of nesting sites, which could cause stress and illness on vulnerable age/sex classes by increasing parasite load by re-using old nests. The prevalence and richness of gastrointestinal parasites has been found to be higher in heavily logged areas, suggesting that nutrition and disease may interact in affecting infant and or adult mortality (Gillespie *et al.,* 2005). Overcrowding can also become an issue, with a distinct localisation of activities in areas less affected by logging witnessed for the lar gibbon, as well as a significant difference in activity budgets (Johns, 1986). Thus, forest structure and species diversity are extremely important factors to consider when assessing forest suitability for orang-utans.

These data indicate that the effects of habitat modification on orang-utan behaviour and survival are heavily scale-dependent, in which a high proportion of the tall habitat classes (complete and incomplete) are likely to be needed if orang-utans are to continue to thrive in an area. Thus, the intensity of logging in an area where orang-utans are found must be controlled and managed, so that the forest does not become dominated by medium and secondary habitats. Thus, selectively-logged areas with a high percentage of tall habitat classes remaining - so-called '*relic primary*' forests - are most likely to hold viable populations of orang-utans. Thus, well managed timber concessions could potentially be important orang-utans strong holds if they are retained.

6.5.5 Response to active human disturbance

Not only is habitat quality reduced through logging, but human presence interferes with orang-utans natural behaviour. When predators are around primates will engage in predator avoidance behaviour, including vigilant scanning, hiding, retreating, fleeing or forming groups (Setiawan *et al.,* 1996). Unhabituated orang-utans will respond to humans in the same way that they would respond to a threat ((Setiawan *et al.,* 1996), and humans can be a direct threat to orang-utans (MacKinnon, 1974; Rijksen and Meijaard, 1999; Marshall *et al.*, 2006), so it is only normal for orang-utans to adopt more cryptic behaviours when humans are present. Wilson and Wilson (1975) described orang-utans as slow, methodical brachiators, who tend to escape detection through immobility rather than by flight. Results from this study showed that orang-utans reduced their feeding time and increased resting, thus making use of their cryptic nature. Thorpe (pers comm), on the other hand, has found orang-utans to also make a rapid retreat when human presence is near, during which a number of very rare locomotory behaviours were witnessed. This can be interpreted as a flight response when feeling threatened. In order to reduce detection, however, orang-utans will be more cryptic, which could result in reduced feeding time.

Not only were behavioural changes found in relation to disturbance from other forest users, but behavioural changes in habituated orang-utans were also found when more researchers were present. When more than two observers joined the follow, orang-utans seemed more agitated and would flee or increase aggressive displays, particularly if the observers were unknown to the orang-utan. This is similar to findings by Williamson and Feistner (2003). Thus even habituated orang-utans are sensitive to researchers, especially new people.

6.6 CONCLUSION

Although many authors say that orang-utans can survive and tolerate logged habitat, it depends on the extent and intensity of logging, and on the species and sub-species of orang-utan. In the Sabangau, although orang-utans utilised all habitat classes, they selected certain forest classes over others for certain activities. The tall forest classes were preferred over all other habitat classes, which has important implications when considering secondary forest as a suitable habitat for orang-utans. The Bornean orang-utan appears to be able to cope with a certain amount of disturbance, and can persist in logged forest, but this may be scale dependent as it is unlikely that a forest dominated by the secondary classes as described in this chapter (LMS and S) could sustain orang-utans over the long term. This is mainly due to the limited number of large trees within these habitat classes, as large trees are required for feeding. Thus, this study into habitat use by orang-utans has highlighted the need for patches of original habitat to be retained, as orang-utans, when given the choice, will select certain habitats for certain activities, i.e. the tall habitat classes were chosen for feeding and the complete habitat classes were chosen for resting and nesting.

With regard to human disturbance on orang-utan behaviour, orang-utans appear to become more cryptic and vigilant when encountering human disturbance, by decreasing their feeding and increasing their resting time. This may have important implications if the intensity of disturbance in the forest is very high or continuous, as orang-utans may reduce their foraging time to spend more time hiding.

Recommendations

Selective-logging operations should not completely destroy the original forest structure, but try and retain a large number of large trees and a degree of continuity in the canopy (leaving sizeable areas of habitat classes TCA, TCB and TIC), if it is going to be compatible with orang-utan survival. Thus a well-managed selective-logging operation should allow orang-utans to persist, although at lower densities, as long as the degree of destruction does not result in a habitat being dominated by low canopy and secondary habitat classes. Thus, as more habitat is gazetted for clearance, and the global population of this endangered ape continues to decline (Singleton *et al.,* 2004), retaining previously-logged forest within former logging concessions is a viable option for conserving orang-utans (Chapman *et al.,* 2000; Husson *et al.,* 2009).

The presence of people in the forest causes changes in orang-utan behaviour, so the number of people entering and using the forest should be controlled, so that there are not continuously high numbers of people in the forest all the time. If eco-tourism is introduced to an area with orang-utans, the number of visitors and their behaviour must be carefully monitored as the presence of strangers could decrease orang-utan foraging time, which in turn could affect their general health. Careful guidelines on the number of visitors into the forest, and numbers of people in a group visiting an orang-utan, must be monitored, as orang-utans show sensitivity to increased numbers, especially if the people following are new. No orang-utan should be singled out for continuous visits from tourists. There is also an increased likelihood of disease transmission (Homsy, 1999; Kondgen *et al.*, 2008). Thus, any eco-tourism project should be well managed and carefully planned and monitored with the welfare of the orang-utan taken into consideration first and foremost.

6.7 SUMMARY

- The forest habitat classes which dominated the study area were the tall and medium-incomplete habitat classes (TIC and MIC), with the tall-complete (TCA and TCB) forest classes (the habitat classes nearest to the primary state of the forest) representing less than 20%.

- Overall, orang-utans showed a positive preference for the tall habitat classes (TCA, TCB and TIC) regardless of canopy completeness, and a negative preference for all other habitat classes. When broken down by activities, the tall forest classes (TCB and TIC) were favoured for feeding, whereas the classes with complete canopy (TCA, TCB and MC) were favoured for nesting and socialising. The tall forest classes offer more food, whereas the complete forest classes probably offer concealment and safety from rain and wind-induced tree falls.

- Activities such as feeding and travel were influenced by forest structure. Although fruit was the dominant food type and eaten in all habitat classes, fruit and flowers were eaten more in the tall forest classes (TCA, TCB), whereas invertebrates, leaves and pandan pith dominated the diet when in the secondary habitat classes (LMS and S).

- When in the secondary habitat classes, travel made up a larger proportion of the activity budget compared to travel in the other classes, with modes of travel altering between classes. Climbing occurred more in the tall incomplete (TIC) forest, whereas clambering occurred more in the secondary (S) forest class.

- Orang-utans activity budgets changed when there was increased human disturbance, so that feeding decreased and resting increased, as they become more cryptic and vigilant.

CHAPTER 7

RANGING

7.1 INTRODUCTION

7.1.1 Home ranges

Home ranges are defined as the area occupied by an individual, within which it enacts its day-to-day activities (food gathering, mating, caring for young) (Burt, 1943), and unlike territories they are not defended (Powell, 2000). In primates, the location and size of home ranges are influenced by resources, especially food availability, mates and distribution of different habitats (Clutton–Brock, 1977; Johns, 1986; Cowlishaw and Dunbar, 2000; Powell, 2000). The key reason why animals establish and maintain fixed home ranges are if the benefits of maintaining a home range exceed the cost (Stamps, 1995); but if the costs are greater than the benefits then the animal can not survive using local resources, and it must go to another location where resources are sufficient, or be nomadic and not show site fidelity (Powell, 2000). In mammals, the location of male ranges is usually explained in terms of mating opportunities, and those of females in terms of food resources (Williams *et al.,* 2004). The density of females has also been found to be a strong influencing factor on the spatial distribution of males, in which ranges were found to get smaller and become more exclusive when female densities increased (Nelson, 1995). Thus when female density decreased, ranges were bigger with more overlap.

In orang-utans, both male and females have large overlapping home ranges. Female ranges are smaller and established near or overlapping their mother’s range; whereas male ranges are much larger and change over time (Singleton, 2001, 2002). Males disperse away from their natal ranges once they are flanged adults (Chapter 8) and their location and size is dictated not only by food availability but also by the availability of cycling females, whereas female ranges are influenced by food availability only (MacKinnon, 1974; Galdikas, 1988; Mitani, 1991; Rijksen and Meijaard, 1999; Singleton and van Schaik, 2001, 2002). There is much confusion with regards to home range stability in terms of residence and non-residence (Singleton and van Schaik, 2001). Rijksen and Meijaard (1999) described three kinds of ranging patterns which can co-exist in a population:

resident (individual found in one place for many years), commuters (individual seen regularly for several weeks or months each year) and wanderers (individual seen very infrequently and may never return). Singleton and van Schaik, (2001), however, found no evidence for commuters with only some unflanged males possibly being transient or wanderers without a stable home range. In their study they defined resident individuals as those with a stable home range, or those who are regularly observed, and thus use a presence index to categorise individuals as either rare, occasional, regular or frequent visitors.

Because the spatial distribution of males and females are influenced by different needs (i.e. mating opportunities for males, and food availability for females), range size differs due to the different spatial and temporal distribution of these important resources. In orang-utans home range size varies between age/sex class, dominance and location (MacKinnon, 1974; Galdikas, 1988; Rijksen and Meijaard, 1999; Singleton and van Schaik, 2001). Adult males have large overlapping ranges which encompass the ranges of several adult females and adolescents of both sexes (MacKinnon, 1974; Horr, 1975; Rijksen, 1978; van Hooff, 1995; Singleton and van Schaik, 2002). In Sumatra, Singleton and van Schaik (2002) found that both adult males and adolescent males have a minimum home range of 2,500 ha, whereas the dominant adult males had a smaller minimum home range of 1,500 ha. This smaller range is due to the local abundance of receptive females (Singleton and van Schaik, 2002). Galdikas (pers. comm.) estimated that male home ranges at Tanjung Puting were very large (up to 10,000 ha), as certain males left her study area, only to return years later. Similar findings have been found in Suaq Balimbing where adult male ranges are estimated to be between 1,500 and 10,000 ha (Singleton, 2000; Singleton and van Schaik, 2002).

Home range size is thus influenced by a number of factors including resource availability (food or females for orang-utans) and density. In a recent comparative study by Singleton *et al.* (2009), the sites with the largest female home ranges were those with the highest densities, and this apparent anomaly can only be explained by the spatial ‘grain’ (distances between food patches) of sites with a mosaic of habitat types. Thus, areas with a mosaic of different habitat types e.g. Tanjung Puting, Gunung Palung (Borneo) and Suaq Balimbing (Sumatra), can support high densities because the different habitat types provide abundant food resources at different times of the year. Thus, because orang-utans move between these different habitat-types, they necessarily have larger ranges than those from homogeneous habitat types (Table 7.1).

Table 7.1 Mean home range size estimated at eight research sites using the minimum area polygon method.

Study Site	Habitat	Species	Home Range Size (ha)	
			Female	**Male**
Gunung Palung [1]	*Mixed dipterocarp (hetero)	*P. p wurmbii*	500-600	>600
Tanjung Puting [2]	**Mixed peat- swamp (hetero)	*P. p wurmbii*	350-600	
Tuanan [3]	Peat swamp forest (homo)	*P. p wurmbii*	250-300	
Kinabatangan [4]	*Mixed dipterocarp (homo)	*P. p morio*	170	224 FM, 175 UFM
Kutai [5,6]	*Mixed dipterocarp (homo)	*P. p morio*	> 150	400-800
Lokan [7]	*Mixed dipterocarp (homo)	*P. p morio*	65	520– 780
Ketambe [3,8]	*Mixed dipterocarp (homo)	*P. abelii*	100– 400	600 – 1,000
Suaq Balimbing [9,10]	**Mixed peat swamp (hetero)	*P. abelii*	850 - 950	1,500-10,000

*Mixed dipterocarp means dipterocarp forest dominated; **Mixed peat-swamp means peat-swamp forest dominated; hetero: heterogeneous; Homo: homogeneous. Male refers to both FM and UFM unless otherwise stated. [1]Knott *et al.* (2008); [2]Galdikas (1988); [3]Singleton *et al.* (2009); [4]Lackman-Ancrenaz and Ancrenaz (2006); [5]Mitani (1989); [6]Suzuki (1992); [7]Horr (1975); [8]Rijksen (1978); [9]Singleton and van Schaik (2001). [10] Singleton, 2000.

Females, by contrast, live in more stable home ranges (Singleton and van Schaik, 2001). In Sumatra, female ranges overlap with those of other related females, forming distinct social clusters (Singleton and van Schaik, 2002). Females do not use their range equally, but instead spend most of their time inside a core-area. These are particularly exclusive and hardly overlap at all with other females' core-areas (Knott *et al.*, 2008; Chapter 8).

7.1.2 Day ranges

The day range is the distance travelled by an individual from when they wake in the morning to the time they settle for the night at the end of their active period. Day ranges differ between age/sex classes and can be affected by a number of variables, especially food availability. In most frugivorous primates, fruit abundance and distribution are the main determinants of home range use (Di Bitetti, 2001), and this generally correlates positively with time spent travelling, day range and home range size (Strier, 2000).

In orang-utans, day range appears longer in peat-swamp forest compared to dipterocarp forests, with the largest day ranges found at Suaq Balimbing in Sumatra, and the smallest in north and east Borneo (Kinabatangan and Kutai) (Table 7.2).

Table 7.2 Mean day ranges for different sites.

Study Site	Habitat	Species	Day Range (metres)			
			Female	FM	UFM	Mean
Gunung Palung [1]	*Mixed dipterocarp (hetero)	*P.p. wurmbii*	818			
Tanjung Puting [2,3]	**Mixed peat swamp (hetero)	*P.p. wurmbii*	710	850		
Tuanan [4]	Peat swamp forest (homo)	*P.p. wurmbii*	766-1025			
Kinabatangan [5]	*Mixed dipterocarp (homo)	*P.p. morio*	250	180	430	
Kutai [6]	*Mixed dipterocarp (homo)	*P.p. morio*				305
Ketambe [4, 7]	Mixed dipterocarp (homo)	*P. abelii*	550- 722	480	890	
Suaq Balimbing [4]	**Mixed peat swamp (hetero)	*P. abelii*	833-1077			

*Mixed dipterocarp means dipterocarp forest dominated; **Mixed peat-swamp means peat-swamp forest dominated; hetero: heterogeneous; Homo: homogeneous. Male refers to both FM and UFM unless otherwise stated.[1]Knott *et al.* (2008); [2]Galdikas (1988); [3]Singleton *et al.* (2009); [4]Lackman-Ancrenaz and Ancrenaz (2006); [5]Mitani (1989); [6]Suzuki (1992); [7]Rijksen (1978).

Unflanged males range further at Kinabatangan and Ketambe compared to flanged males or females, whereas flanged males at Tanjung Puting range further than females and also further than flanged males from all other sites (Table 7.2). Day ranges are more sensitive than home range size to the way in which food is distributed (lsbell, 1991). An increase in leaves in the diet is correlated with less travel (Mitani and Rodman, 1979; Strier, 2000). In some female primates that have strong dominance hierarchies, day ranges increase when there is an increase in group size, but not in those species that do not, and thus intra-group competition is determined by food distribution, and inter-group competition by food abundance (Isbell, 1991). Di Bitetti (2001) found that capuchin monkeys (*Cebus apella*) concentrated their activities within their core area when fruit abundance was high. Thus the availability of food must be an important variable in day range length.

7.2 OBJECTIVES

Home range and day range may be affected by resource availability. In this chapter I will examine differences in home range size and day range length between age/sex classes and periods of different *'food'* (fruits and flowers) availability, in order to understand better how resources affect ranging in Sabangau. Home ranges and day ranges are assessed separately.

Questions to be addressed in this chapter are:

Home ranges

- What orang-utans were resident or visitors to the study area?
- What was the average home range size for each age/sex class?
- What were the core-areas for females and how big were they?
- What was the range overlap between female individuals?

Day ranges

- What was the mean day range for each individual and each age/sex class?
- What age/sex class had the longest day range?
- Did *'food'* availability affect day range length?

7.3 METHODS AND ANALYSIS

7.3.1 Residency

Resident status

Residence status was estimated by the number of times an individual was seen within the study area, using monthly sightings. Individuals were recorded as present when seen at least once within a single calendar month.

A presence index (Kj) was calculated by dividing the number of months an individual was present by the length of the study, expressed as a percentage (Singleton and van Schaik., 2001).

Individuals were classified as either (i) Frequent visitors - those individuals which spend most of their time in the area: Kj ≥50%; (ii) Regular visitor - those individuals which spend a lot of their time in the area: Kj ≥ 25 <50%; (iii) Occasional visitors - those individuals which occasionally enter the area, perhaps because the area is on the outer edges of their range: Kj >4 <25% or (iv) Rare visitors - those individuals who visit the area very infrequently and may never return, these individuals are more nomadic: Kj ≤ 4%. The different classifications for visitors were based on the Kj values assigned by Singleton and van Schaik (2001). A Presence Index of 4% equates to being seen during only 1 month of the study period. For the purpose of distinguishing which individuals were resident, all frequent visitors will be considered to be resident individuals.

7.3.2 Ranging

Range data were collected on all age/sex classes from September 2003 to August 2005. Orang-utans were followed within the grid system. If an individual left the grid they were followed as far as was practical, until being eventually abandoned.

On each individual follow the travel route was drawn on a grid map, aided by use of a compass. Distance was estimated and checked against distance markers on the transects, particularly at each crossing point, which also verified the accuracy of our estimations. Day range length was estimated from full day follows only, and values for each age/sex class taken by averaging the means for each individual.

GPS positions were taken every 30 minutes and each time the orang-utan stopped to feed. Positions were not taken more frequently, as orang-utan day ranges are usually no more than 1 km, and orang-utans rarely moved far in 30 minutes without stopping to feed. It was also not feasible to take this more often due to the logistics in taking this data, which required one person to remain stationary in order to a obtain a signal. All GPS points were downloaded into the GIS software package ArcView 3.2 and plotted onto the grid map. Each hand drawn range map was laid under a laminate sheet and copied. This was done separately for each individual. The laminates were overlaid on to the GPS range points for each individual separately, to identify range boundaries for that individual.

Home range size estimates

In order to estimate accurately home range size, three methods were used: (i) the polygon, (ii) the circle and (iii) the kernel method. I did this because they all measure different things; the first measures the minimum area, the second measures the maximum area (Singleton and van Schaik, 2001), and the third identifies and measures the core areas. Arc View 3.2 was used for analysis with the home range extension pack downloaded from the internet.

i. Minimum area polygon method (Hayne, 1949). This is the oldest and most commonly used method for estimating an animal's home range, and has been used by most orang-utan researchers. This method links the peripheral data points by straight lines, giving a minimum area convex polygon for the animal's home range. Thus, there are a few problems with it as it also only provides a crude outline of the home range, and ignores all information provided by interior data points, thus assuming that animals use their home range evenly which is clearly not the case (Powell, 2000). In order to estimate the size of an orang-utan's home range, it is only accurate if one has many data points over a long period of time (Singleton and van Schaik, 2001). Thus, home range estimates produced in this way will be treated as minimum values.

ii. Circle method (Hayne, 1949; Trevor-Deutsch and Hackett, 1980). This assumes that animals use space in a fashion conforming to an underlying bivariate normal distribution, and assumes that an animal has a single centre of activity, the very centre of the range (Powell, 2000). This method assigns the distance between the widest points as the diameter of a circle, thus enabling the area of that circle to be calculated. This means that areas within that circle but where orang-utans were not followed are included within the home range estimate. This method is good for predicting the ‘real’ home range size if data are limited, and is commonly used for estimating maximum home range size for orang-utans (Singleton and van Schaik, 2001; Lackman-Ancrenaz and Ancrenaz, 2006). In common with the minimum-area polygon method, this method also assumes even use of the home range.

iii. Kernel home range analysis (Worton, 1989) is an accurate method for analysing range use (Seaman and Powell, 1996), and produces an unbiased density estimate directly from GPS data points and is not influenced by grid size or placement (Silverman, 1986). The kernel density estimator uses non-parametric methods for estimating probability density. Because it is non-parametric it has the potential to accurately estimate densities of any shape, provided that the level of smoothness is selected appropriately. The kernel method consists of placing a kernel (probability density) over each observation point in the sample. A rectangular grid is superimposed on the data, and an estimate of density is obtained at each grid intersection, using information from the entire sample. The density at any location is an estimate of the amount of time spent there, so the density will be higher in areas with many observations, and lower in areas with few observations, thus this method is appropriate for analysing habitat use.

Determining the band width of the kernel is important. Narrow band widths allow nearby observations to have greater influence on the density estimator, where as wider band kernels allow more influence of distant observations. The bands can be held constant. For this analysis I used the fixed kernal home range estimator in ArcView GIS 3.2 – using 50%, 75% and 95% density probability contours – i.e. contours within which the orang-utan was present 50/75/95% of the time. I used this method to locate core-area use (50%) for the main resident females, the same percentage that was used by Knott *et al.* (2008). Core areas were not worked out for males, as their ranges were much larger than the grid system and hence I did not have complete range boundaries for them.

In most studies where home ranges have been estimated in orang-utans, the polygon method was used (Horr, 1975; Rodman, 1988; Mitani, 1988; Suzuki, 1992; Rijksen, 1978; Galdikas, 1988; Singleton and van Schaik, 2001), thus results from the polygon method will be used for site comparison analysis.

7.3.3 ‘*Food*’ availability

‘Food’ availability (the availability of ‘seasonally-limited foods’, i.e. fruits and flowers) was calculated in Chapter 3). This was tested against day range length to see if there were any differences in day ranges between periods of low, medium and high *‘food’* availability.

Because differences in daily travel distance between age/sex classes was found, an ordinary least squares (OLS) regression was used to test if there were differences in day ranges between periods of different ‘*food’* availability once age/sex class was controlled for.

7.4 RESULTS

7.4.1 Residence status

A Presence score (Kj) (Singleton and van Schaik, 2001) was worked out for each individual (Table 7.3), classing each as either a frequent, regular, occasional or rare visitor. In total, 7 individuals were classified as frequent visitors and they include 2 SAF, 1 NSAF, 3 FM and 1 UFM; 7 were classed as regular visitors and they include 1 NLF, 1 SAF, 1 FM and 4 UFM (Table 7.3).All others were classified as either occasional or rare visitors. The only individuals who were considered residents during the study period were those who were classed as frequent visitors.

Table 7.3 Classification of individuals as either frequent, regular, occasional or rare visitors to the study site, ranked in descending order of Presence Index (Kj).

Name	**Age/sex**	**Kj**	**Status**
Indah	SAF	83	Frequent visitor (resident)
Feb	NSAF	67	Frequent visitor (resident)
Cleo	SAF	50	Frequent visitor (resident)
Beethoven	FM	63	Frequent visitor (resident)
Hengky	FM	63	Frequent visitor (resident)
Franky	FM	54	Frequent visitor (resident)
Kay	UFM	50	Frequent visitor (resident)
Wallace	FM	33	Regular visitor
Viola	NLF	33	Regular visitor
Teresia	SAF	29	Regular visitor
Mozart	UFM	29	Regular visitor
Leonardo	UFM	29	Regular visitor
Shogun	UFM	25	Regular visitor
Romeo	UFM	25	Regular visitor
Willow	SAF	20	Occasional visitor
Qu	UFM	20	Occasional visitor
Potret	SAF	17	Occasional visitor
Jupiter	FM	17	Occasional visitor
Einstein	NSAM	17	Occasional visitor
Shima	NSAF	13	Occasional visitor
Archimedes	UFM	13	Occasional visitor
Drake	FM	4	Rare visitor
Fenser	FM	4	Rare visitor
Benjy	NSAM	4	Rare visitor
Galileo	UFM	4	Rare visitor
Newton	UFM	4	Rare visitor
Oscar	UFM	4	Rare visitor
Zeus	UFM	4	Rare visitor

NSAF: non-sexually-active females; SAF: sexually-active females; NLF: nulliparous female; FM: flanged males; UFM; unflanged males; NSAM: non-sexually-active male (adolescent).

7.4.2 Home ranges

Table 7.4 Individual estimates for home range size using both minimum convex polygon and circle methods.

Orang-utan Name	Polygon / ha	Circle / ha	Number of days followed
Wallace	237	340	36
Beethoven (resident)	552	710	55
Franky (resident)	271	610	30
Hengky (resident)	283	430	90
Jupiter	286	430	16
Average FM	**326**	**504**	**227**
sd	***128***	***151***	
Romeo	264	420	12
Kay (resident)	306	720	12
Mozart	184	510	12
*Einstein	248	390	16
Average UFM	**251**	**550**	**52**
sd	***51***	***149***	
Indah (resident)	249	360	118
Cleo (resident)	172	210	58
Average SAF	**211**	**285**	**176**
sd	***54***	***106***	
Feb (resident)	295	540	76
Shema	111	240	20
**Viola	334	530	22
Average NSAF	**246**	**436**	**118**
sd	***102***	***144***	
All females (SAF and NSAF)	**232**	**376**	**294**
sd	***83***	***139***	
All males (FM and UFM)	**292**	**507**	**279**
sd	***104***	***141***	

*Einstein, a non-sexually active male (NSAM) was included as an UFM for the purposes of this analysis; **Viola, a nulliparous female (NLF) was included as a NSAF (non-sexually active female) for the purposes of this analysis.

Home ranges were estimated for all age/sex classes using both the polygon and circle methods (Table 7.4). Using the polygon method, FM have the largest home range of all age/sex classes (325 ha) followed by UFM (251 ha), NSAF (246 ha) and SAF (211 ha) with the smallest. In contrast, the Circle method has UFM (550 ha) with the largest, followed by FM (504 ha), then NSAF (436 ha) and once again SAF with the smallest (285 ha) (Table 7.4). Beethoven had the biggest range of all followed animals (552-710 ha depending on the method used), which encompassed most of the study area and which overlapped with all other followed males' ranges (Figure 7.1). In order to discount the number of days each individual was followed as an influencing factor on range size, I performed a correlation and found that the number of days followed was not a significant influence on range size (Pearson's correlation: $r^2=0.020$, n=14, p=0.628). Although ranges are presented in two different ways, and male ranges are bigger than females, they are expected to be an underestimate of their true range size, as males travelled out of the study area further than we were able to follow, and in some circumstances did not return for months at a time. Figure 7.1 shows both FM and UFM range overlap.

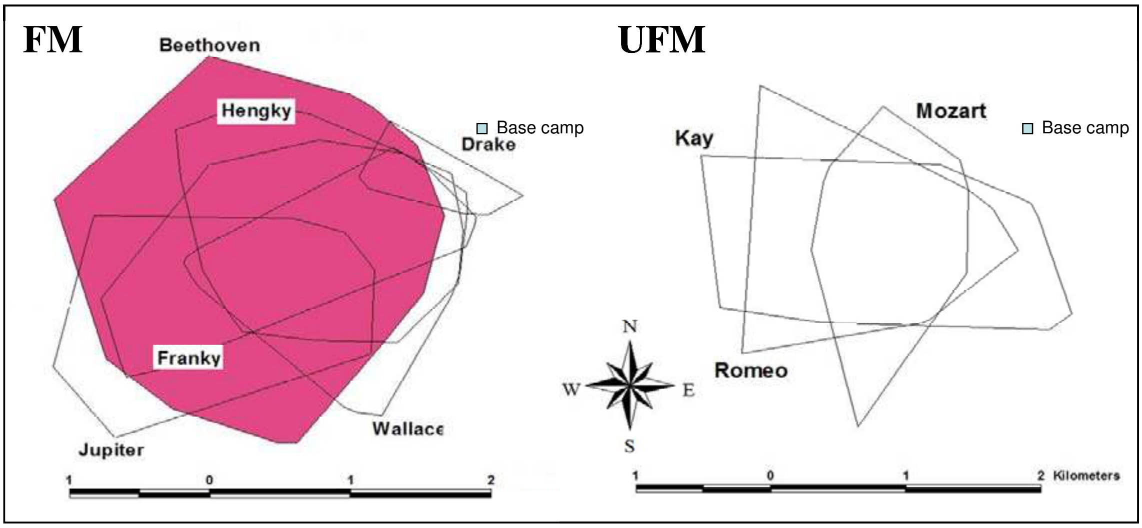


Figure 7.1 FM and UFM home ranges using the polygon method. Beethoven's range is coloured pink as he has the largest home range.

The best known female home range is Indah's, as her home range is situated in the centre of the study area. Her home range was estimated to be between 249 ha (polygon) and 360 ha (circle) (Table 7.4). Cleo's range was on the edge of the grid and thus I believe that the size of her home range is underestimated by the polygon method. (Figure 7.2) The largest female home range was Viola's if using the polygon method (334 ha), and Feb's if using the circle method (540 ha). All females had overlapping ranges (Figure 7.3), which in turn overlapped with all male ranges.

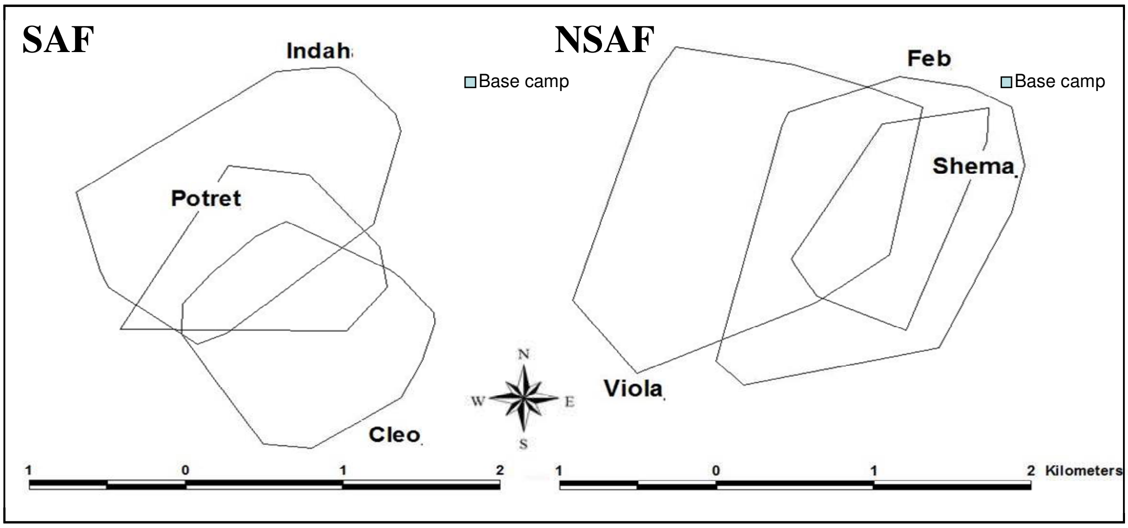


Figure 7.2 SAF and NSAF home ranges using polygon method. Viola the nulliparous female was included with the NSAF.

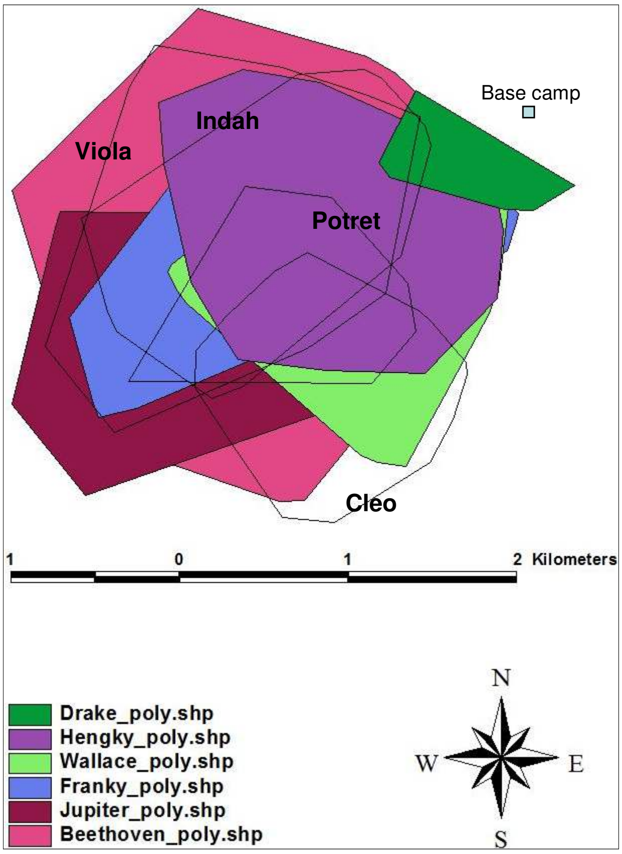


Figure 7.3 Overlap between adult male and adult female ranges.

7.4.3 Female range overlap

All females ranges overlapped, with the highest number of adult females overlapping each other at any single point being four (Figure 7.4).

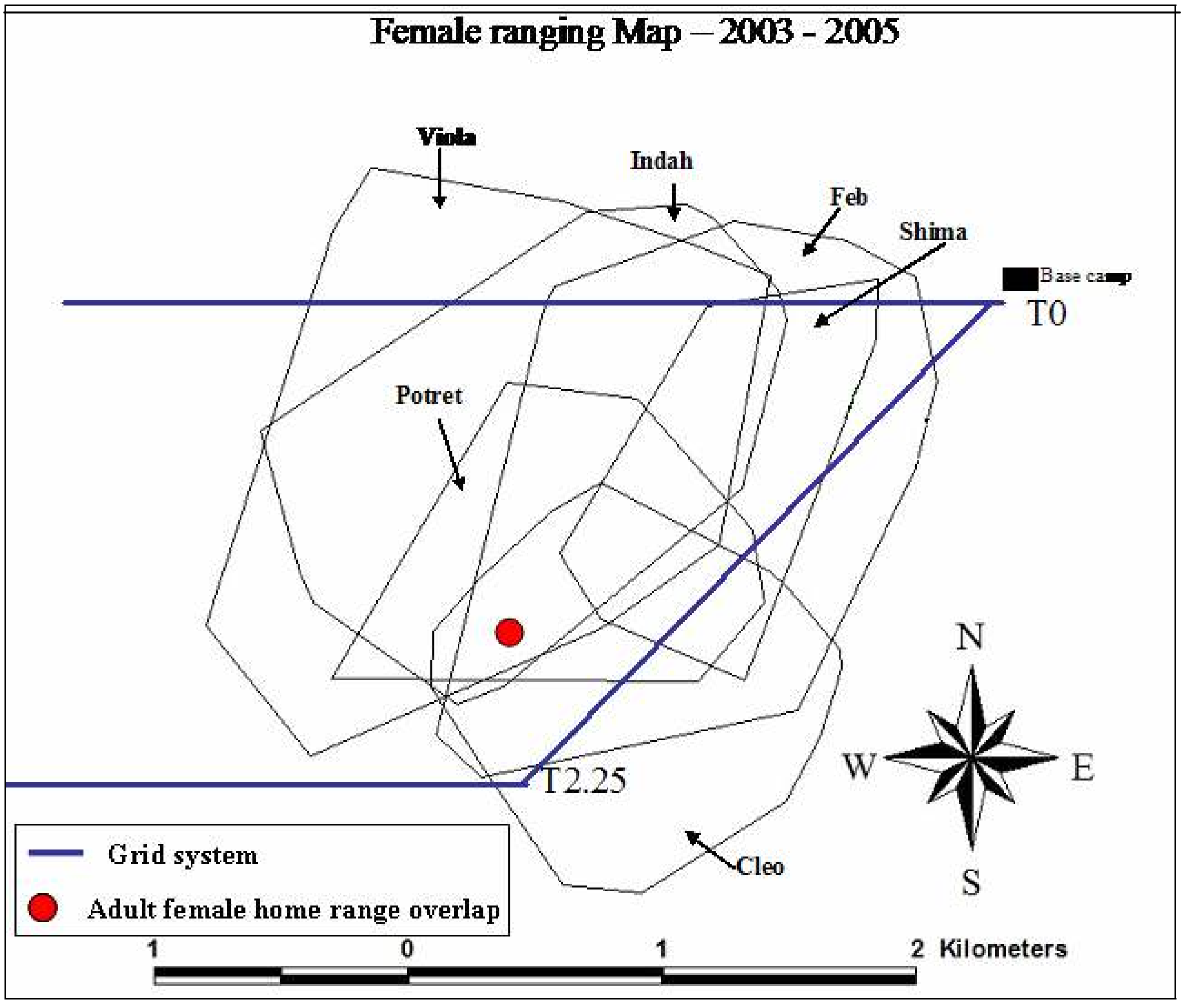


Figure 7.4 Female range overlap.
The red spot indicates where the greatest number of adult female home ranges overlap (Viola, Indah, Potret and Cleo).

7.4.4 Core area

Using the fixed kernel method, the four females with the most amount of data were analysed in order to identify their core areas of use (three resident females Cleo, Indah and Feb) and one regular visiting female (Viola). The density bands used were 50%, 75% and 95%, in which the 50% density band was used to delineate core-area (Figure 7.4).

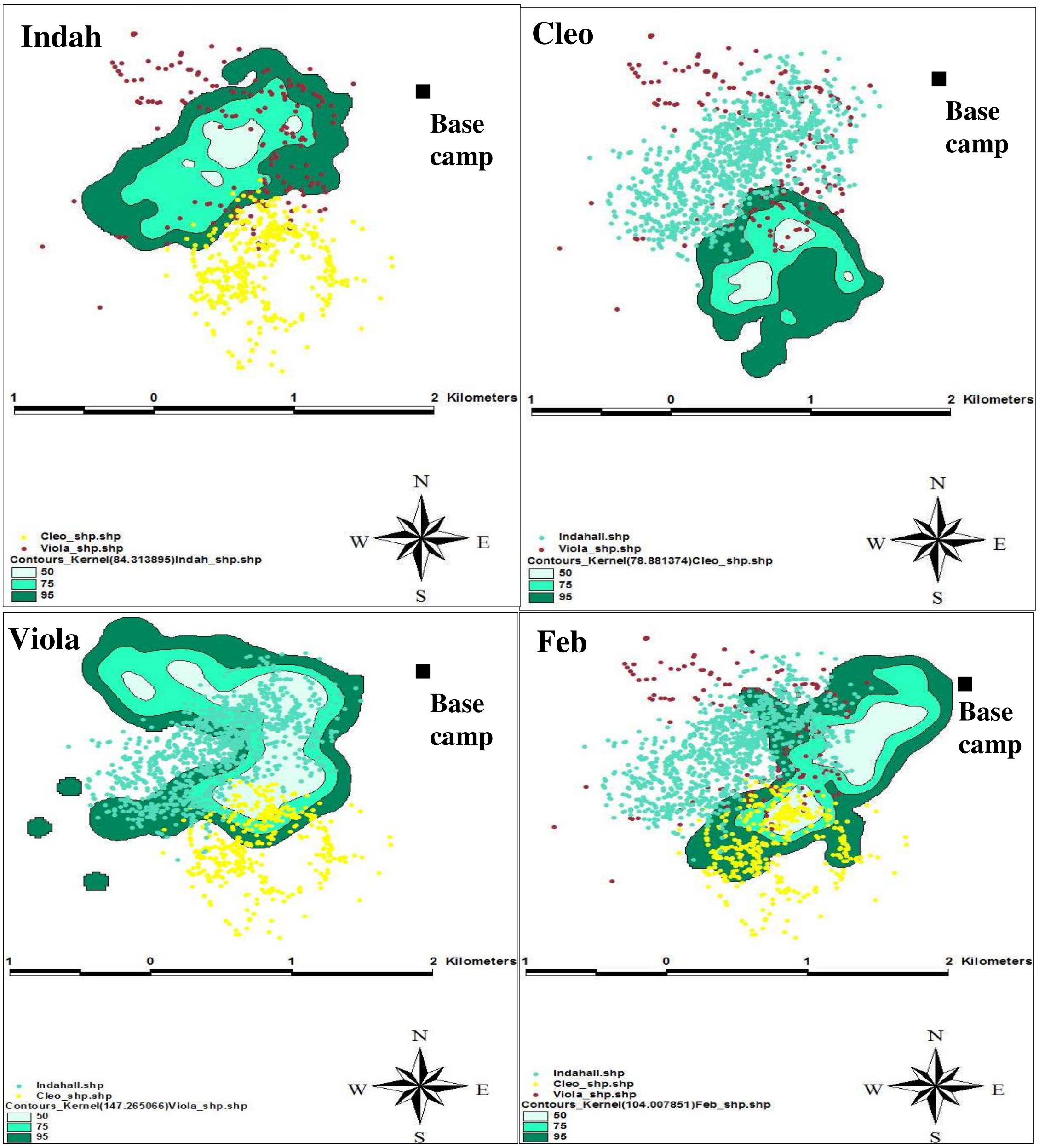


Figure 7.5 Fixed kernel estimates of female ranges using 50, 75 and 95 % contours of home range use. The different coloured dots are different individuals (Yellow = Cleo, Blue = Indah; Red = Viola).

Core area use was only calculated for Indah, as her range was considered the most accurate as it was completely within the study area, and had the most number of follows. Using the fixed kernel method and the 50% density band, Indah's core area was calculated to be 20 ha, thus representing 6% of her home range.

7.4.5 Day ranges

Daily ranges for individuals

The individual with the largest day range was Mozart (UFM) and the individual with the shortest day range was Wallace (FM) (Table 7.5), although when Hengky was injured, his day range was the shortest covering a mean distance of only 186 m, and his mean hourly travel distance decreased from 56 m/h to only 19 m/h, as travel through the canopy proved difficult. Thus, for further analysis between age/sex classes, Hengky was excluded when he was injured. The individual with the largest distance travelled per hour was again Mozart (UFM), with Wallace (FM) having the shortest (Table 7.5).

Table 7.5 Mean daily travel distances and rates of travel for each individual

Age-sex class	Orang-utan	N	Mean	*sd*	Distance /hr (m)
FM	Beethoven	26	1098	*406*	96
	Franky	2	783	*135*	71
	Fencer	3	775	*226*	66
	Hengky	41	601	*371*	56
	Jupiter	10	658	*205*	62
	Wallace	11	585	*233*	53
UFM	Mozart	3	1340	*275*	113
	Einstein	8	1133	*183*	94
	Shogun	2	953	*53*	82
	Darwin	2	853	*182*	73
	Romeo	4	755	*297*	67
NSAF	Feb	43	954	*318*	83
	Viola	14	821	*367*	75
	Shima	15	731	*183*	68
SAF	Cleo	26	783	*383*	68
	Indah	81	756	*298*	68

Age/sex class differences in day range

The overall mean day range was 834 m (range: 750-1007 m), and the age/sex class with the longest mean day range was UFM, followed by NSAF, SAF and then FM with the shortest day ranges (Table 7.6).

Table 7.6 Average distance travelled each day in metres for each age/sex class.

Age/sex	N*	N**	Mean Day Range (m)	*sd*	Distance /hr	*sd*
UFM	5	19	**1007**	*233*	86	*19*
Range			*755-1340*			
NSAF	5	87	**809**	*106*	73	*8*
Range			*731-954*			
SAF	2	102	**769**	*19*	68	
Range			*756-783*			
FM	6	93	**750**	*190*	67	*16*
Range			*585-1098*			
Overall mean	**18**	**301**	**834**	***118***	**82**	***14***

Individual means using full day follows only. Viola was included with NSAF and Einstein was included with UFM. Overall mean was worked out by averaging the means for each age/sex class. *Number of individuals, **Number of days.

When a statistical test was preformed with *'food'* availability controlled, no significant differences was found ($F_{3, 27} = 6.514$, $p = 0.072$) between the different age/sex classes.

Effect of 'food' *availability on day range*

The mean distance travelled during different *'food'* availability periods is shown in Table 7.7. NSAF had the longest day range when *'food'* availability was low and UFM had the longest day range when *'food'* availability was either medium or high. FM had the shortest day ranges for each *'food'* availability level.

Table 7.7 Distance travelled in different periods of '*food'* availability.

Food availability	Age/sex	Mean	*sd*	N*	N**
low	NSAF	**695**	*50.8*	2	26
low	SAF	649	*261.6*	2	9
low	UFM	522	*173.2*	1	2
low	FM	513	*93.5*	2	9
Mean	**All**	**595**	***91.3***	**7**	**46**
medium	UFM	**1026**	*184.3*	5	12
medium	SAF	900	*194.0*	2	55
medium	NSAF	878	*220.1*	4	31
medium	FM	801	*243.6*	5	32
Mean	**All**	**901**	***93.6***	**16**	**130**
high	UFM	**1213**	*94.2*	1	5
high	NSAF	848	*147.1*	2	30
high	SAF	757	*60.0*	2	43
high	FM	717	*122.0*	5	52
Mean	**All**	**884**	***226.2***	**10**	**130**

Individual means. *Number of individuals, **Number of days. Figures in bold, are the age/sex class with the longest day range in each *'food'* availability class.

Overall, orang-utans travelled longer distances when '*food'* availability was medium, and travelled the shortest distances when '*food'* availability was low. When distance travelled was tested against *'food'* availability, it was found to be significant ($F_{2, 28} = 6.514$, p=0.005), with orang-utans travelling significantly shorter distances when '*food*' availability was low compared to medium (p= 0.003). Although orang-utans also travel less in low compared high, this was not significant. No other pair-wise differences were found.

7.5 DISCUSSION

7.5.1 Home range

Home ranges were estimated for all age/sex classes, although estimates made using the minimum-area convex polygon method are likely to be underestimates of the true home range size. This is likely to be a more severe underestimate for males because their ranges are larger and thus more of their range is outside the study grid where they were not followed. Because of this I consider the circle method the best method for estimating minimum home range size for males, and maximum home range size for females. Thus female home range size is estimated to be between 232 and 376 ha, whereas the males are estimated to have a minimum home range size of 507 ha.

When comparing female home range size estimates (using the polygon method) with those from other sites, they are similar to those found at the only other peat-swamp forest site in Borneo, Tuanan, and also to that at Ketambe in Sumatra, but smaller than all other Bornean sites (Table 7.1). Singleton *et al.* (2009) state that habitat heterogeneity influences range size, with those areas which have a number of different habitat types having larger home ranges. Sabangau, Tuanan and Ketambe are all homogenous sites, and ranges were found to be smaller than at either Tanjung Puting or Gunung Palung (Table 7.1) when comparing estimates using the polygon method. Suaq Balimbing in Sumatra, which has large areas of both peat-swamp forest and dry forest in foothills, has the largest home ranges recorded, with female ranges larger than 800 ha and males larger than 2,500 ha (Singleton and van Schaik, 2001). This is presumably because the orang-utans here regularly commute between the two habitats.

With regards to flanged male ranges in Sabangau, they are much larger than female ranges, as expected and in agreement with findings from other sites (MacKinnon, 1974; Galdikas, 1988; Singleton and van Schaik, 2001; Lackman-Ancrenaz and Ancrenaz, 2006). Beethoven, a frequent visitor, had the largest home range and Hengky, another frequent visitor, had the smallest. Although the Presence Indices for these two males was the same, dominance shifted between them over the course of this study (Chapter 9), and Hengky's residency was more continuous. Thus whether a male is dominant or not may affect home range size, for example in Sumatra dominant males had a smaller home range than non-dominant males (Singleton and van Schaik, 2002). Amongst the females, the nulliparous female Viola had the largest home range. This may be because she regularly associated with FM and followed them around.

Core area

At Suaq Balimbing females have a core area (using 50% density bands) of 44-80 ha (5-9%) out of a minimum home range size of 850 ha (Singleton and van Schaik, 2001; Singleton *et al.,* 2009). In Gunung Palung Knott *et al.* (2008) found females used a core area comprising 68 ha (13.5%) of their home range and found that these areas were maintained and had little overlap with other female core areas, compared to their home ranges overall, which had a high degree of overlap. In Sabangau core areas were found to be smaller at 20 ha (6%) with little overlap (Chapter 8). Thus habitat heterogeneity seems to influence core area size, with more homogeneous sites having smaller core areas. Core area data for the Sabangau are only presented for one individual, however, and thus must be treated as preliminary.

7.5.2 Day ranges and '*food'* availability

Although there was no significant differences in day range size between age/sex classes, the trend showed unflanged males to have the longest day range (1007 m), with flanged males having the shortest day range (750 m). This may be due to body size and thus energetics, as unflanged males do not have infants to carry round and are much smaller than flanged males, so it may not be as energetically expensive to travel. Social status must also play a part, as unflanged males are subordinate to, and flee from, flanged males (Utami *et al.,* 1997). In Sabangau, unflanged males have been observed fleeing feeding trees when flanged males approach, thus they will need to travel further to search for another feeding tree; they also travel widely in search of cycling females (MacKinnon, 1974; Rijksen, 1978; Singleton and van Schaik, 2002; Chapter 9). The overall hourly distance covered (Appendix XV) by UFM was further than any other age/sex class, showing they travel more often and for longer periods.

Effects of ‘food’ *availability on day range*

When comparing day ranges and *‘food’* availability, orang-utans in Sabangau were found to have significantly longer day ranges when resources were medium compared to low, and although there was no significant difference between low and high periods, the trend shows that they had longer day ranges when resources were high compared to low. Thus orang-utans increase their travel distance when there is more *‘food’* available. This may be due to increased effort to find more preferred fruits when they are available, similar to findings from Gunung Palung (Knott, 1998).

When comparing these findings to those other sites where data are available, Sabangau females had similar day ranges to females in Ketambe, but larger day ranges than females in Kinabatangan, and shorter day ranges than females in Suaq Balimbing (Table 7.2). Mitani and Rodman (1979) found day range in primates (from reviewed literature and primary sources for 33 different primate species) to be negatively related to the proportion of foliage in the diet. Thus day ranges should get shorter the more folivorous their diet. This may explain why female day ranges are longest in Suaq Balimbing and shortest in north and east Borneo (Kinabatangan and Kutai). Orang-utans in Sumatra are known to be more frugivorous, while the eastern Bornean orang-utan (*P.p. morio*) is known to be the most folivorous (Taylor, 2006; Morrogh-Bernard *et al.,* 2009). Doran-Sheehy *et al.* (2004) showed that western lowland gorillas (*Gorilla gorilla gorilla*) have longer day ranges than mountain gorillas (*G. g. beringei*), because they have more fruit in their diet. Thus, the more frugivorous the diet, the longer the day ranges will be.

7.6 CONCLUSION

Male ranges, although they are underestimated, are large and overlap with many other males and females. Females had smaller ranges than males, which overlapped each other and had small core-areas.

‘*Food*’ availability affected day range length, in which orang-utans were found to travel further when ‘*food*’ availability increased, as they were probably increasing their search effort for more preferred fruits. When comparing between sites, the more frugivorous the diet, the larger the day ranges.

7.7 SUMMARY

Home Ranging and day ranges

- Seven individuals were identified as resident in my study area (3 females, 3 flanged males and 1 unflanged male).
- Both the polygon and circle methods were used for estimating range size. If using the polygon method flanged males had the largest home range, followed by unflanged males, non-sexually-active females and sexually-active females with the smallest, whereas the unflanged males had the largest ranges if using the circle method.
- UFM had the largest day range and FM had the shortest.
- '*Food*' availability affected day range with individuals travelling further when '*food'* availability was high.

CHAPTER 8

UNDERSTANDING ORANG-UTAN SOCIAL ORGANISATION - GENETIC DIVERSITY AND DISPERSAL PATTERNS

8.1 INTRODUCTION

The principal factors shaping primate social behaviour and grouping are the distribution and abundance of food resources and reproductive potential (van Schaik, 1996; Cowlishaw and Dunbar, 2000; Kappeler and van Schaik, 2002). Observed primate social systems may not be similar to those they evolved from, and selection pressures that led to the evolution of those social systems may not be present anymore. Researchers have theorised that orang-utans have evolved from a group living ancestor, whose males could monopolise access to females (MacKinnon, 1971; Utami and van Hooff, 2004; Harrison and Chivers, 2007). Harrison and Chivers (2007) suggested that the orang-utan's ancestors had a social structure more similar to gorillas, with one dominant male guarding a harem of females. Under their theory, climate change, in particular the onset of El Niño cycles, resulted in more severe periods of low food availability, which meant that females had to disperse more widely in search of food and males were no longer able to guard the females effectively. Thus, a non-group living lifestyle arose, which is more suitable for habitats where resources are limited and patchily distributed.

Both species of orang-utan are commonly described as 'solitary' or 'semi-solitary' (as the mother-infant relationship is strong) (Galdikas, 1979; Sugardjito *et al.,* 1987; Mitani *et al.,* 1991), but recently they have been described as a individual-based fission-fusion species (van Schaik, 1999) as they form groups or travel parties when food availability is high, particularly in Sumatra (MacKinnon, 1974; Sugardjito *et al.,* 1987; Utami *et al.,* 1997; Knott, 1999a; Singleton and van Schaik, 2002; Morrogh-Bernard *et al.,* 2009). Mitani *et al.* (1991) found that orang-utans were attracted to common resources, either food trees or, for adult males, potential mates, and emphasised that longer studies are needed to understand the more complex social network linking individuals. One aspect of orang-utan socioecology that is little understood is dispersal, for which knowledge of relatedness between individuals within a study population is required. This kind of information can take years to gather from observations alone, owing to the orang-utan's solitary nature and long inter-birth interval of 6-9 years (Wich *et al.,* 2004a; van Noordwijk and van Schaik, 2005). Thus, genetic analysis is needed to help clarify our understanding of social organisation of a predominantly solitary species; as Kappeler and van Schaik (2002) have emphasised.

Dispersal patterns

Knowledge of genetic diversity and relatedness within a population is vital for understanding dispersal patterns and, hence, a population's social organisation, when long-term observational data are not available. Primate dispersal patterns involve either both sexes dispersing, both sexes exhibiting philopatry (the tendency of an individual to return to, or stay in, its natal area) or one sex dispersing and one sex remaining. Most animal species show some degree of philopatry, and one sex tends to show it to a greater degree than the other, e.g. male birds and female mammals tend to be more philopatric than those of the opposite sex, which will disperse from their natal group or breeding site (Greenwood, 1980). Sex differences in potential reproductive success affects the balance between local resource competition and local mate competition (Perrin and Mazalov, 2000), thus sex-biased dispersal is influenced by resources and mating strategy. No bias is expected when the local competition equally affects both males and females, such as in monogamous systems and also in polygynous or promiscuous ones, as long as female fitness is limited by extrinsic factors such as breeding resources (Perrin and Mazalov, 2000). Within the great apes, male chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are philopatric (Pusey and Packer, 1987; Gerloff *et al*., 1999), while females of those two species disperse and join other groups, usually permanently. In gorillas (*Gorilla gorilla*), both males and females may be philopatric or both may disperse (Tutin, 1996), but natal emigration is female-biased in mountain gorillas (Pusey and Packer, 1987).

The dispersal patterns of orang-utans, particularly the Bornean species, are less well known compared to other apes, probably due to their very low density, solitary lifestyle, long-life history and lack of long-term studies. Observations at several sites have proposed female philopatry and male dispersal (Rodman, 1973; MacKinnon, 1974; Galdikas, 1985a; van Schaik and van Hooff, 1996; Singleton and van Schaik, 2001, 2002; Knott *et al.,* 2008). In

Sumatra female ranges overlap with other related females, forming distinct social clusters, in which a group of females occupy similar home ranges, show philopatric tendencies, and express reproductive synchrony. Offspring also set up their home range within or near their maternal range (Singleton and van Schaik, 2002). Within their home range, adult females spend most of their time in a core-area. In female Bornean orang-utans, Knott *et al.* (2008), found passive range exclusion through mutual avoidance, presumably to minimise resource competition, and thus there is a relative non-overlap of adult female core-areas. This avoidance is suggested to be the reason why there is a much lower adult female encounter rate in the Bornean species than in the Sumatran.

Males have much larger ranges than females and are thus more difficult to follow in order to determine their dispersal (Singleton and van Schaik, 2001). They also undergo major morphological changes between adolescence and adulthood. This makes it hard to identify adult males as the same individuals followed as infants and juveniles. Thus, determining dispersal patterns and degree of philopatry in males is difficult. On the whole, however, field observations suggest that males are more nomadic than females, and disperse away from their natal range (Rijksen, 1978; Galdikas, 1988; van Schaik and van Hooff, 1996).

Using genetic data, however, Goossens *et al.* (2006a) found that both females and males at a site in Sabah (Kinabatangan) were highly-related, thus implying philopatry in both sexes. It is suggested that orang-utans at this site tend to live in ‘family units’ with a very small dispersal range (Lackman-Ancrenaz and Ancrenaz, 2006), although this may be due to the highly disturbed and fragmented forests in this region preventing dispersal. Only one other study of genetic diversity in an orang-utan population has been carried out, by Utami *et al.* (2002) in Ketambe, Sumatra. Their data have been interpreted to suggest that both males and females disperse away from their natal range. Released ex-captives are present at this site, however, making any interpretation of genetic data problematic. Thus no definite pattern of dispersal has been identified to date.

Dispersal patterns, relatedness and range overlap are all important for understanding the social organisation of orang-utans. As this study is only based on 2 years of data collection, trying to attempt to answer these questions will be impossible without genetic analysis, which has been found to be successful in confirming sex biased dispersal in both mammals and birds (Mossman and Waser, 1999). Thus, DNA samples were collected from faeces and analysed, together with observations of ranging patterns and social interactions, in order to determine dispersal patterns and degree of philopatry in the Sabangau population.

8.2 OBJECTIVES

In this chapter I will examine genetic diversity within the population in order to interpret dispersal patterns. Relatedness between individuals, together with home range overlap and social interactions, will be used to help explain social organisation in the Bornean orang-utan. Genetic analysis was necessary as long-term data on demographics were not available.

Questions to be addressed in this chapter are:

8.2.1 Genetic diversity

- What is the genetic diversity of the Sabangau population?
- What is the genetic diversity within each sex class, and can the degree of philopatry or dispersal exhibited by each sex class be identified?
- What is the pedigree (family tree and maternal lines) of each related individual, and can the dispersal and ranging distribution of close relatives be interpreted?
- How frequently do related and non-related females meet?

8.2.2 Range overlap

- What is the range overlap and number of encounters between individuals, and are these individuals related?
- What is the range overlap between a mother and her female offspring, and do offspring show site fidelity?

8.3 METHODS AND ANALYSIS

8.3.1 Relatedness

In order to answer a number of questions, genetic analysis of DNA samples was necessary. To achieve this, I established a collaboration with Dr. Benoit Goossens and Dr. Mike Bruford from Cardiff University and Dr. Michael Krützen from Zürich University in 2000, in which they analysed my samples and carried out the essential genetic analysis for answering my questions.

Genetic analysis was carried out to identify relatedness between all individual, and thus identify dispersal patterns. To test relatedness faecal samples were collected from each individual orang-utan which visited the grid in the main study site (see detailed field methods in Chapter 2), as well as from a number of satellite study sites within the Sabangau forest (Figure 8.1). Pairwise-relatedness estimation methods based on genetic data are used extensively as a substitute for pedigrees when there are no long term data regarding pedigree (Csillery *et al.*, 2006), and were thus used for this analysis.

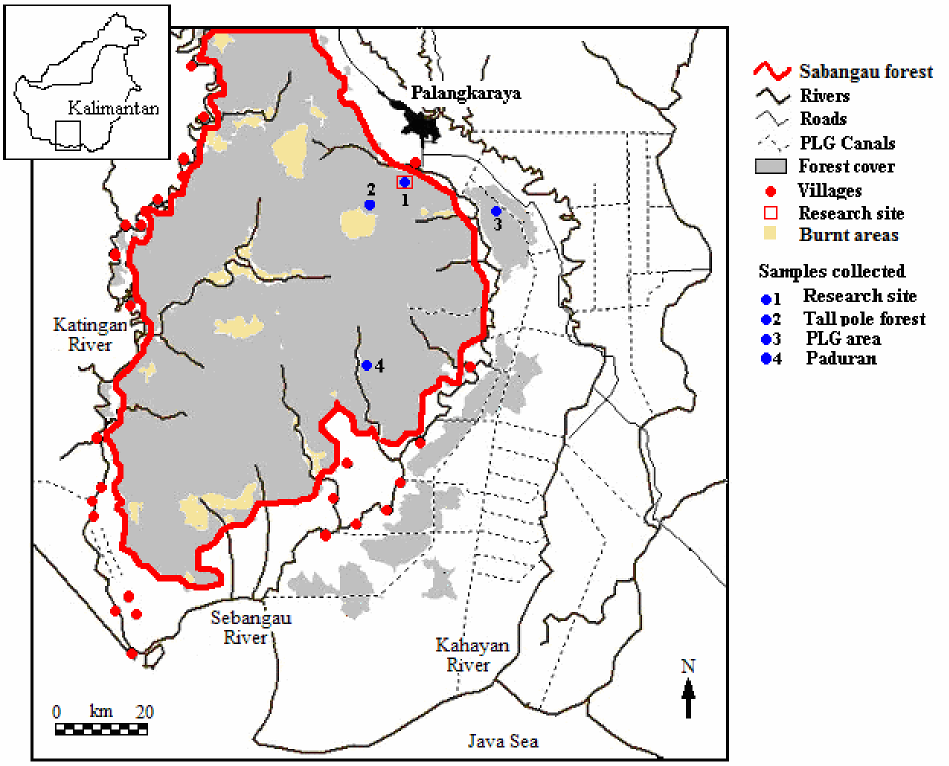


Figure 8.1 Areas where samples were collected. Samples from location 3 (PLG) were not included in this analysis, as they were separated from the research area by the Sabangau river. Location 1 was the study site where most samples were collected, and interpretation of results was based on these samples.

DNA extraction

DNA was extracted using the QIAamp DNA stool Mini Kit (QIAGEN). Total DNA concentration was measured using the photo spectrometer NanoDrop® - 1000 (Software v3.3) (see Morf, 2008, for detailed methods on DNA extraction.)

Genetic analysis

The data were analysed by Nadja Morf, MSc student from the University of Zürich. The method used was a real time polymerase chain reaction assay that allows quantification of target DNA. To estimate relatedness multi-locus genotypes from all polymorphic microsatellites were used. A panel of 19 microsatellite markers (loci) were used to genotype 16 out of 35 individuals (6 females and 10 males which account for 68% of all samples being successfully genotyped. The ones that were not successfully genotyped were because of the low quality of the samples (Morf, 2008). The SPAGeDi programme (Hardy and Vekemans, 2002) was used to calculate differences in relatedness indices. Data on the genetic markers were then compared by Monte Carlo simulations (generate paired multi-locus genotypes conditional on the allele frequencies and the actual relationship), which determined the proportion of time that the randomised pairwise relatedness estimates yielded a higher difference between mean female relatedness and mean male relatedness than observed. Four different relatedness indices were used for estimating relatedness between these 16 individuals. Queller and Goodnight (1989) was the earliest estimator, followed by Lynch and Ritland (1999), which assumes that the allele frequency of a population is known and estimates across loci; whereas Li e*t al.,* (1993) and Wang (2002) use a similarity index (SIM) at a single locus. The Wang estimate has been found to be robust for small sample sizes, where the number of alleles per locus is large. It is also robust when unknown relatives are included in samples for estimating allele frequency, compared to previous estimators (Wang, 2002), which assume that the allele frequencies are known without error (Anderson and Weir, 2007).

Rarefaction analysis (which aims to determine how many loci are needed to generate an appropriate level of the standard deviation for the relatedness values) with 5000 simulations of parent-offspring relationships did not differ more than 0.5% from each other. This indicates that the mean pairwise relatedness (Queller and Goodnight, 1989) simulated for r=0.5, and the differences following the mean r-values and standard deviations, stabilised after approximately 13 loci, which in turn indicates that the 19 loci used in the study for assessing relatedness were sufficient, with the standard deviation of the mean r-value being 0.1. Due to this, discriminating between relatedness categories such as half-siblings r=0.250 and cousins r=0.125 may be difficult. For this study attempts will be made to identify full sibling and mother offspring (0.50) and half siblings (0.250) only; thus, individuals which have an expected r-value greater than 0.250 will be considered to be a close relative, and all samples with an r-value less than this will be considered distant relatives. Any r-values of 0 or below are assumed to come from another gene pool and are thus unrelated. Although marker-based estimates are commonly used now, in situations where breeding systems suggest low variance in relatedness across a population this method may often have low power in addressing research questions of interest (Csillery *et al.,* 2006).

In order to attempt to identify these relationships, a demographic knowledge of the population was needed for this analysis. Indah and Indy is a known mother-offspring pair, but the relatedness of these two individuals was misclassified, thought to be a result of the high standard deviation revealed by the rarefaction analysis, in which one mismatch in the genotype has resulted in a lower classification than the other mother-offspring pair (Cleo and Feb). Because no adoptions by wild orang-utans have ever been witnessed, I believe that Indy is the true offspring of Indah. For pairwise relatedness, I used the Wang (2002) estimator, as it had the highest r-values (relatedness value) for the known mother-offspring pairs (closest to the expected value of 0.5), and is known to be robust with small sample sizes.

Maternal line

ARLEQUIN v.3.0 (Excoffier *et al.,* 2005) was used to estimate haplotype diversity, and thus enabled me to identify maternal lines through MtDNA.

Paternity

For paternity, the programme CERVUS 1.0 (Marshall *et al.,* 1998; Kalinowski *et al.,* 2007) was used to assess the possible occurrence of null (non-amplifying) alleles that could result in false paternity discrepancies, and to identify the most likely father. Paternity was based on the statistical likelihood that a specific male was the father, given the genotype of a known mother-offspring pair. It uses a simulation approach based on all the allele frequencies observed in the population to a set of critical values for Delta, which is the difference between the LOD score, which evaluates the likelihood of paternity of each male. An individual with a positive LOD score is more likely to be the father, and the male with the highest score is the father. A significance level of 95% was used.

8.3.2 Range overlap and social encounters

Female range overlap

Range overlap was calculated using range estimates from the minimum area polygon method (Hayne, 1949; Chapter 7). Range overlap for females was calculated for each individual against each other individual; because the size of each individual's range was different, range overlap as a percentage of range size was not the same for each individual. Core-area was calculated using the fixed kernel home range analysis, where 50% density contours bounded the core-area (see Chapter 7 for detailed ranging methods). All follows were used to identify home ranges (Table 8.1).

Table 8.1 Number of follows for each female who was successfully genotyped.

Female orang-utans	**Number of follows**
Indah	118
Feb	76
Cleo	58
Viola	22
Potret	6
Total	312

Social encounters

Associations between two individuals should be proportional to the degree to which their home ranges overlap (Singleton and van Schaik, 2002). Thus encounters (when two individuals were <50 m apart from each other) were calculated based on the observed degree of home range overlap. A numerical value for the frequency of interaction between females was calculated by dividing the proportion of home range overlap between those two individuals by the number of times those individuals were seen together, divided by the number of hours followed for both individual. Both focal and non-focal data were used; the number of hours followed was used to control for the number of encounters.

$$\frac{\text{Number of meetings}}{\text{(hours following individual 1 + hours following individual 2)}} \Big/ \text{\% overlap}$$

8.4 RESULTS

8.4.1 Genetic diversity and pedigree

Genetic diversity

Individuals from a number of locations within the Sabangau forest were genotyped, of which 16 were from the study area (Table 8.2). These individuals were used in order to identify dispersal patterns within Sabangau, and identify parentage and pedigree within the research area.

Table 8.2 Names and age/sex of individuals who were successfully genotyped.

Age/sex class	Name
Dependent infant	Indy (Female)
Adolescent	Feb (Female), Einstein (Male)
SAF	Cleo, Indah, Potret
NLF	Viola
FM	Beethoven, Hengky, Fencer, Drake
UFM	Archimedes (Archi), Romeo, Darwin, Zeus, Mozart

SAF: sexually-active female; NLF: nulliparous female; FM: flanged male; UFM: unflanged male.

Regardless of which estimator was used, mean relatedness among all females and among all males was significantly different from each other, with the mean relatedness (r-value) among females being higher than males (Table 8.3, Appendix XIV).

Table 8.3 Mean relatedness values (r) among females (FF) and males (MM) with standard errors (estimated by jackknifing over all loci) and different Δ between mean relatedness among females and among males. P-values (Monte Carlo resampling simulation) indicate possible differences between sexes.

Sex	r Lynch and Ritland, 1999	r Queller and Goodnight, 1989	r Wang, 2002	r *Li *et al.,* 1993
FF	-0.0074 (0.0306)	0.0463 (0.0523)	0.1664 (0.0672)	0.1904
MM	-0.0806 (0.0068)	-0.1146 (0.0235)	-0.0857 (0.0317)	-0.0686
Δ FF, MM	0.0732	0.1609	0.2521	0.2589
p (FF *vs*. MM) (15 *vs*. 45)	0.022	<0.001	<0.001	<0.001
p (FF *vs*. MM) (15 *vs*. 15)	0.043	0.012	<0.001	<0.001

*Standard errors were not calculated for the Li *et al.,* 1993 estimator, probably due to a putative error in the SPAGeDi software.

These results indicate that females are more related to each other than are the males to each other, indicating philopatric tendencies in females and dispersal in males.

Differences in the distributions between male and female pair-wise relatedness for each estimator are shown in Figure 8.2; in which the estimators which show the mother-offspring pairs closest to the expected values of 0.5, were the Wang (2002) and the Li *et al.* (1993) estimators. This suggests that these two estimators perform better in high-relationship categories than the Queller and Goodnight (1989) or Lynch and Ritland (1999) estimators.

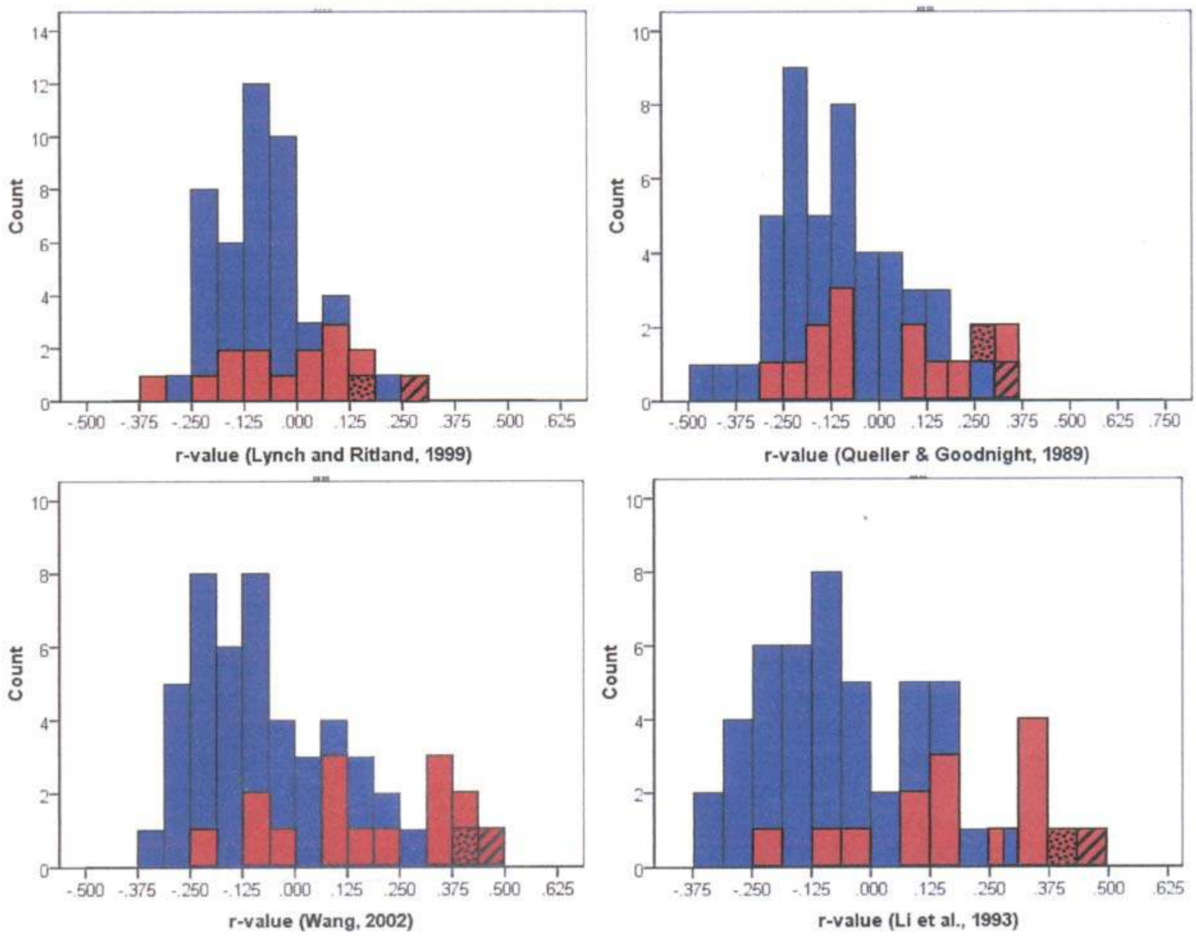
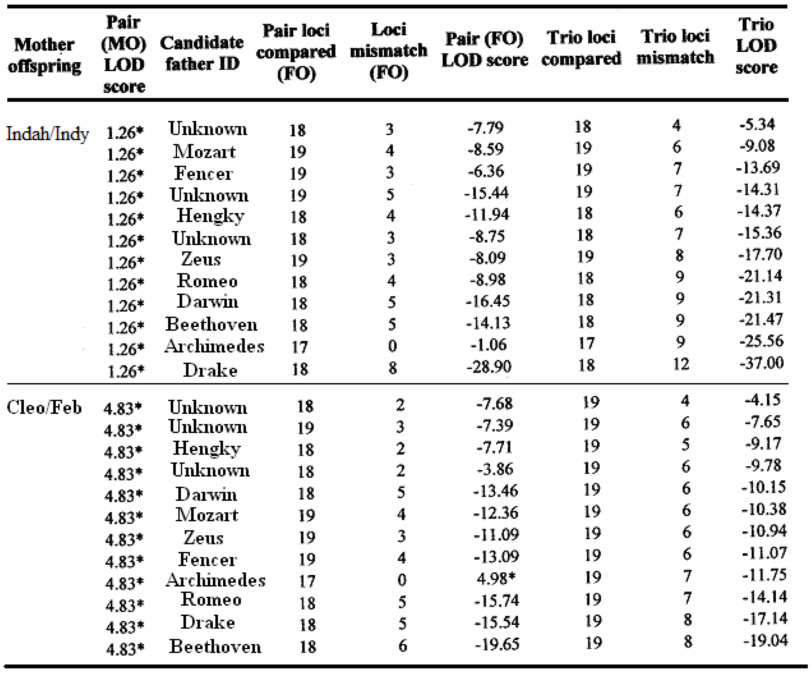


Figure 8.2 Histograms of the different relatedness indices.
Pairwise relatedness values within males are in blue and for females in red. Known mother offspring pairs with an expected r-value of 0.5 are indicated by black dots for Indah and Indy and by black stripes for Cleo and Feb.

Paternity

All males (including unknown males) that were successfully genotyped were tested to see if they were the fathers of either Feb or Indy. For each candidate father-offspring pair (FO) and mother-father-offspring trio, a 95% confidence level was needed, but no candidate father could be assigned to either mother-offspring pair (Table 8.2), although Archimedes does share a high r-value with Feb, indicating that they are very closely related – but are not father-daughter.

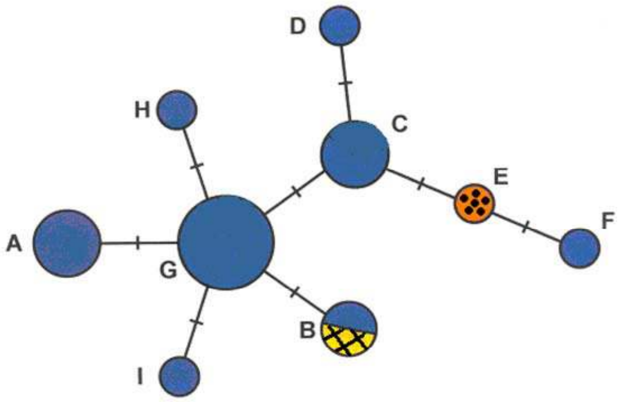
Table 8.4 Summary of the parental assignment between the mother-offspring pairs and its candidate father. (CERVUS paternity assessment). Pair or trio confidences with 95% confidence levels are indicated with an asterisk.



Mother offspring	Pair (MO) LOD score	Candidate father ID	Pair loci compared (FO)	Loci mismatch (FO)	Pair (FO) LOD score	Trio loci compared	Trio loci mismatch	Trio LOD score
Indah/Indy	1.26*	Unknown	18	3	-7.79	18	4	-5.34
	1.26*	Mozart	19	4	-8.59	19	6	-9.08
	1.26*	Fencer	19	3	-6.36	19	7	-13.69
	1.26*	Unknown	19	5	-15.44	19	7	-14.31
	1.26*	Hengky	18	4	-11.94	18	6	-14.37
	1.26*	Unknown	18	3	-8.75	18	7	-15.36
	1.26*	Zeus	19	3	-8.09	19	8	-17.70
	1.26*	Romeo	18	4	-8.98	18	9	-21.14
	1.26*	Darwin	18	5	-16.45	18	9	-21.31
	1.26*	Beethoven	18	5	-14.13	18	9	-21.47
	1.26*	Archimedes	17	0	-1.06	17	9	-25.56
	1.26*	Drake	18	8	-28.90	18	12	-37.00
Cleo/Feb	4.83*	Unknown	18	2	-7.68	19	4	-4.15
	4.83*	Unknown	19	3	-7.39	19	6	-7.65
	4.83*	Hengky	18	2	-7.71	19	5	-9.17
	4.83*	Unknown	18	2	-3.86	19	6	-9.78
	4.83*	Darwin	18	5	-13.46	19	6	-10.15
	4.83*	Mozart	19	4	-12.36	19	6	-10.38
	4.83*	Zeus	19	3	-11.09	19	6	-10.94
	4.83*	Fencer	19	4	-13.09	19	6	-11.07
	4.83*	Archimedes	17	0	4.98*	19	7	-11.75
	4.83*	Romeo	18	5	-15.74	19	7	-14.14
	4.83*	Drake	18	5	-15.54	19	8	-17.14
	4.83*	Beethoven	18	6	-19.65	19	8	-19.04

MtDNA

Haplotype diversity of 0.8713-+0.0547 and a nucleotide diversity (Nei, 1987) of 0.003841-+0.002680 were estimated for the Sabangau population. To visualise the relationship between the haplotypes a minimum spanning network (Rohlf, 1973) was generated with (ARLEQUIN v.3.0) (Excoffier *et al.*, 2005).



Individual used for the mtDNA analysis
and their appropriate haplotype (no contraction).

mtDNA (haplotypes)	**Indiviuals**
A	Cleo; Indah; Archimedes; Feb; Indy; Chivers.
B	Fencer
C	Einstein; Viola
D	Potret
E	-
F	Gracier
G	Beethoven; Drake; Romeo; Zeus; Mozart.
H	Hengky
I	-

Figure 8.3 Minimum spanning network (ARLEQUIN V.3.0) of 9 haplotypes (indicating 9 maternal lines). Blue (or solid) indicates individuals from the study site; Orange (or dots) is an individual from Paduran; and Yellow (or chequered) is from an unknown individual in the study site.

Figure 8.3 is an indication of the many different maternal lines (nine) found in the study site, and thus a signal that the population is diverse with many different breeding lines.

Pedigree

I used the pairwise relatedness indices (Appendix XIV; Wang, 2002) and mtDNA to compile a pedigree for those individuals within the study area. All pairs of individuals that had a pairwise r-value greater than 0.250 are shown in Table 8.5 and Figure 8.4. These values indicate that these pairs are related as parent-offspring, full siblings or half siblings. Only pairs of individuals with an r-value greater than 0.250 were included, as the error rating was too high to distinguish different levels of cousins.

Table 8.5 Pairwise relatedness based on the Wang estimates for highly-related pairs only.

All Loci	Feb	Einstein	Cleo	Indah	Viola	Indy	Potret	Drake
Feb								
Einstein	0.290							
Cleo	0.499	0.141						
Indah	0.075	-0.031	0.324					
Viola	0.207	0.072	0.327	0.064				
Indy	0.319	0.088	0.408	0.396	-0.191			
Archimedes	0.526	0.139	0.813	0.472	0.267	0.331		
Potret	-0.094	0.014	0.157	-0.001	0.064	0.090		
Drake	-0.117	-0.095	-0.241	-0.15	0.098	-0.363	-0.058	
Fenser	0.031	0.097	0.135	0.155	0.062	0.286	0.267	0.274

All the adult females except Potret appear to be closely related to each other, as mother-offspring, full siblings or half siblings (Table 8.5). Indah is Indy's mother, but due to a mismatch in the genotypes between these two the r-values are lower than expected. Using the pairwise related values and mtDNA, there seem to be two possible family trees to explain this pedigree (option 1 and option 2) which are shown in Figure 8.4.

In Option 1, Indah may be the half sibling of Cleo and Archimedes, whereas for Option 2 Indah may be the mother of both Cleo and Archimedes. Feb is closely related to Einstein as half sibling, indicating that the two of them must share the same father as they have different mtDNA lines. Potret and Indy are the only females who are closely related ($r>0.250$) to a flanged male (Fenser), and Fenser is the only flanged male who is closely related to another flanged male (Drake) although only 4 flanged males were genotyped.

Possible reasons why Potret and Indy have such low r-values with Drake include potential errors in the analysis or the inheritance of different genetic material during each meiosis. Until further analysis can be done to confirm these hypotheses, no concrete conclusions can be made. For home range overlap analysis, option 1 (Indah and Cleo as half siblings) was used to explain social organisation and range placement, as it is more likely that Indah is the sister of Cleo, rather than the mother as no interactions between the two were ever witnessed, and there was very little range overlap between the two.

Unfortunately, not all males could be genotyped, but out of those that were, 4 were flanged males and 6 were unflanged males. Archimedes, unflanged, was the only male to come from the same maternal line as 2 adult females. His relationship with these two individuals are either as a full sibling to Cleo (option 1 and 2) and half sibling to Indah (option 1) or as a mother-offspring pair with Indah (option 2), as Cleo is not old enough for Archimedes to be her son.

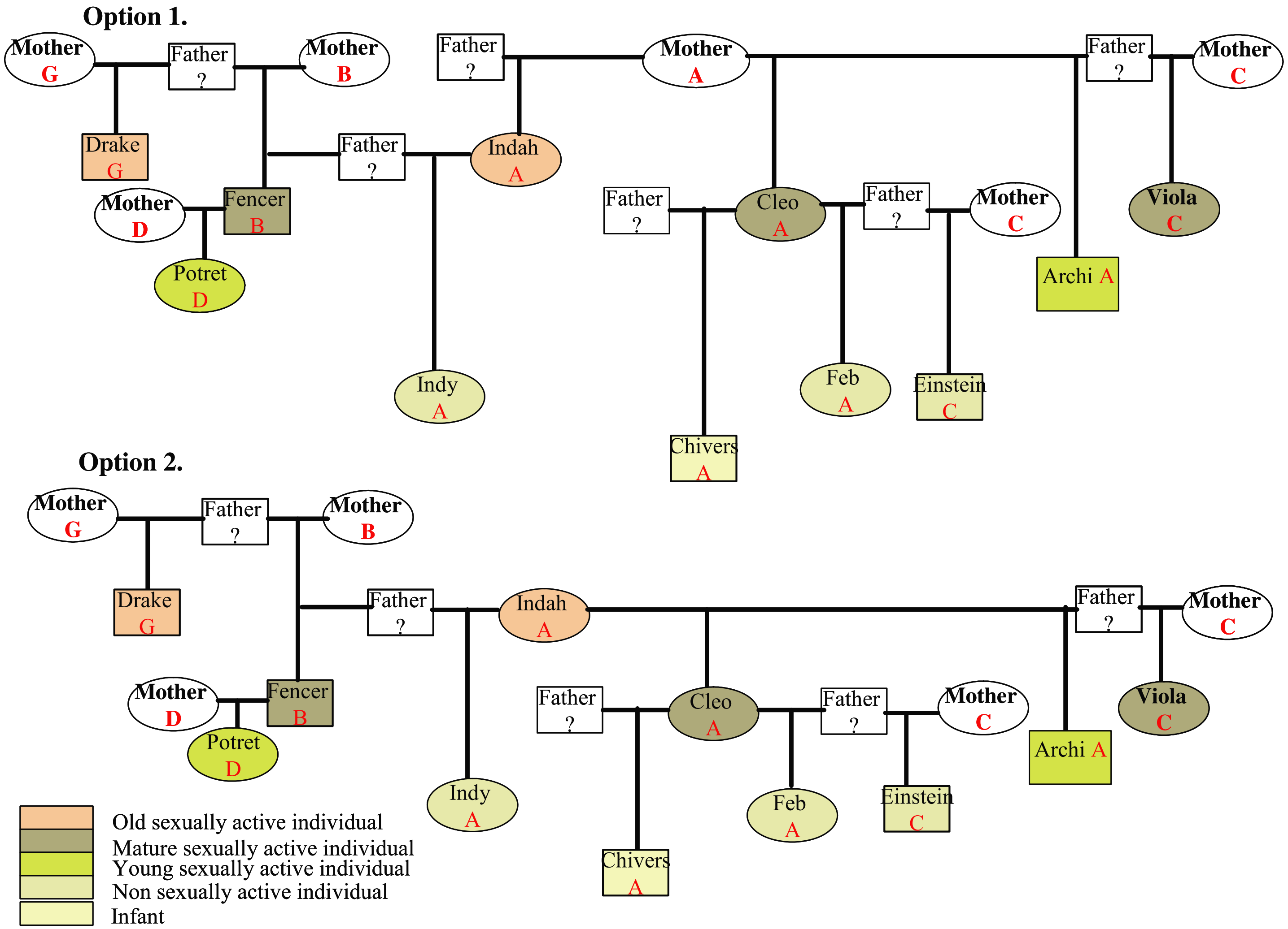


Figure 8.4 Pedigree of related individuals using pairwise relatedness with mtDNA for all individuals with an r-value > 0.250. Option 1 and option 2 are two hypothesised relatedness pedigrees. Red letters refer to the mtDNA group.

8.4.2 Female range overlap and encounters

Using the genetic data I was able to identify related individuals and thus calculate percentage range overlap for those with the same and with different maternal lines (Table 8.6). I only considered females, as most males were unrelated to each other or to the females.

Table 8.6 Overlap of related female ranges.

Individuals	**Indah %**	**Cleo %**	**Potret %**	**Viola %**	**Feb %**
Indah		19	72	**71**	**44**
Cleo	17		51	13	38
Potret	39	33		32	35
Viola	**95**	20	**79**		44
Feb	53	**53**	76	39	
Total range (ha)	*249*	*210*	*134*	*334*	*295*

Values highlighted in yellow are individuals who were from the same maternal line; values in orange are mother-offspring pairs; values in bold are the largest overlaps for each individual.

Out of all the female ranges, only one individual’s range (Potret) overlaps more than 50% with all the other females and she happens to be the only female who is only very distantly related or not related to the other females, and comes from a different maternal line to all the others. None of the closely-related adult females via the maternal line have large proportions of their home ranges overlapping each other (Table 8.6, Figure 8.5). Thus no clusters of close adult relatives from the same maternal line were found (e.g. possible half-siblings, Indah and Cleo), but clusters of females from different maternal lines were, for example Indah’s range overlaps greatly with Viola’s (Table 8.6, Figure 8.5).

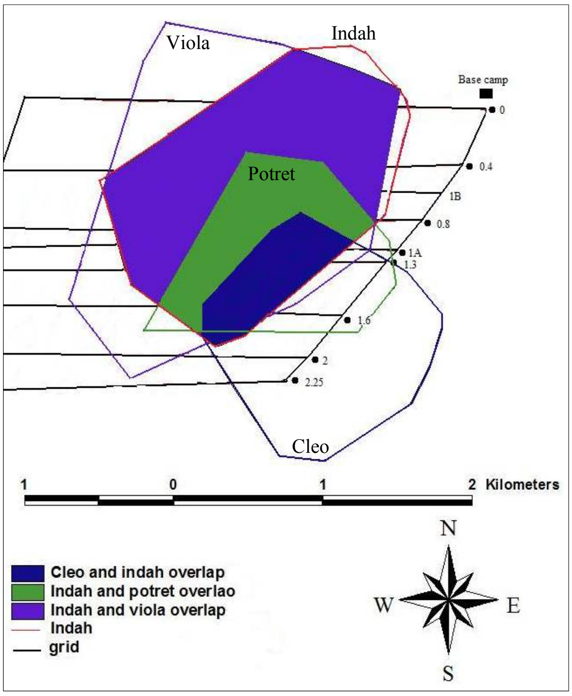


Figure 8.5 Indah's range overlap with adult females (Cleo, Viola and Potret).

The adolescent female Feb had a range which range overlapped with her mother Cleo's range and with her aunt / grandmother Indah's range by about the same amount – ca. 40% (Table 8.6; Figure 8.6). This suggests that, although members of the same maternal line do share some areas of their range, there is by no means complete overlap.

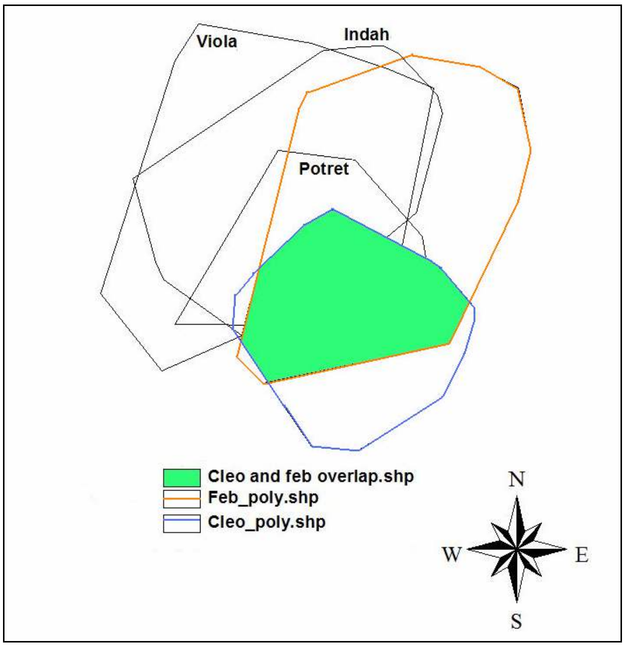


Figure 8.6 Cleo's range overlap with her daughter Feb.

Core-area overlap

For the two resident adult females that share the same maternal line (Indah and Cleo), little range overlap (Figure 8.5) and no core-area overlap was found (Figure 8.7 A). There appears to be a clear separation between the ranges of these two closely-related individuals. On the other hand, part of Feb's core-area clearly overlaps part of her mother's (Figure 8.7 B), but not that of Indah's. Viola, who is from a different maternal line, has a core-area which is larger than the others, and overlaps both Indah's and Cleo's core-area.

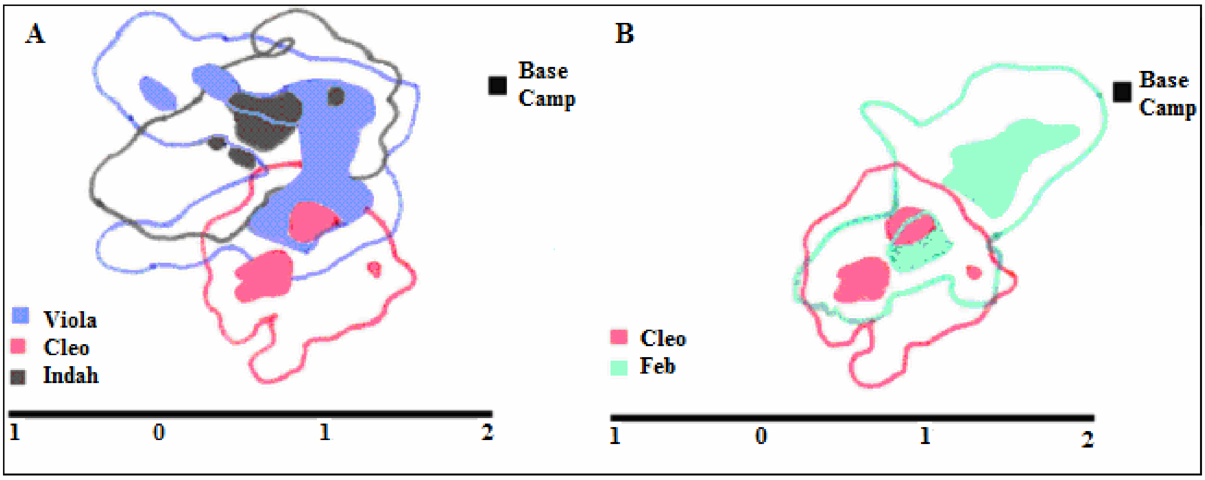


Figure 8.7 Female core-area overlap. A: Adult female overlap; B: Mother and offspring overlap. Blue is Viola; Red is Cleo; Black is Indah; Green is Feb.

Encounters

Numerical values representing the frequency of female/female encounters are presented in Figure 8.8. Most encounters were between females from different maternal lines (Indah and Viola; Indah and Potret; Viola and Feb), except between mother and offspring (Cleo and Feb). The amount of time Feb spent with other individuals including her mother is shown in Table 8.7. She spent three-quarters of her social time with her mother, indicating that the mother-offspring relationship remains very strong at this stage of Feb's development. Associations between possible half siblings from the same maternal line (Cleo and Indah) were not witnessed, but associations between more distant relatives (e.g. Feb and Indah) were.

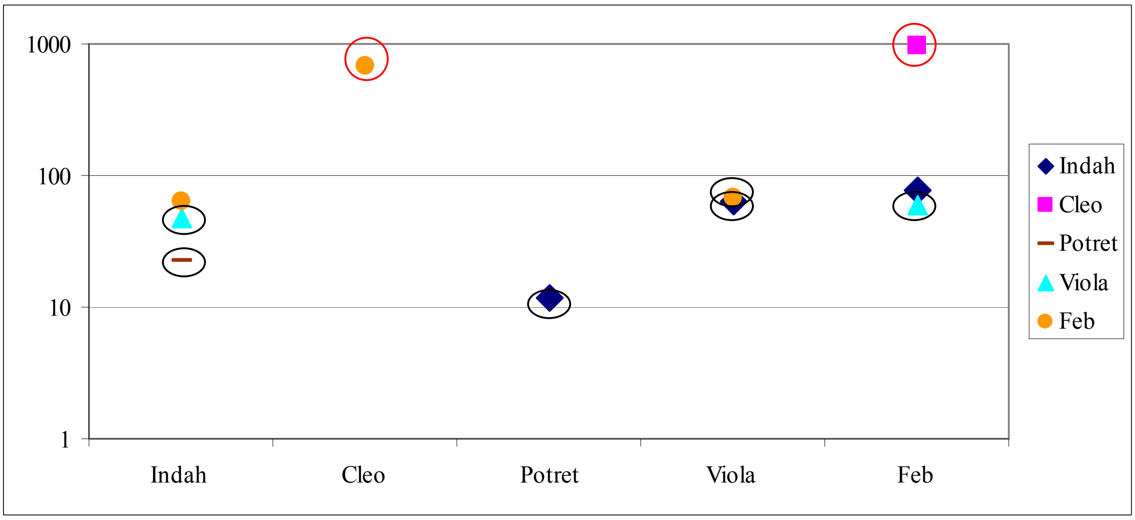


Figure 8.8 Female encounters (Log graph). Encounters circled in red are mother-offspring; encounters circled in black are different maternal lines (different mtDNA groups).

Table 8.7 Percentage of time an adolescent female (Feb) spent with other age/sex classes including her mother (Cleo)

Orang-utan	% alone	% mother	% mother & others	% others
Feb (NSAF)	82.9	8.5	4.1	4.6

8.5 DISCUSSION

8.5.1 Genetic diversity and dispersal patterns

Diversity

Within the Sabangau orang-utan population there is a high genetic diversity as the mean relatedness among females and among males was significantly different from each other, with many different maternal lines. Thus there is a healthy population which does not appear to have suffered from excessive in-breeding or out-breeding; compared to the Kinabatangan region in northern Borneo, where there is strong evidence for a recent demographic collapse, independent of mutation (Goossens *et al.,* 2006b). This is believed to have resulted from recent human-induced deforestation and habitat fragmentation, in which between 33 and 50% of the original forest area has been cleared in the last 30 years. The effect of habitat fragmentation on genetic diversity over a relatively short period of time is evident. Thus, large areas of forest are necessary if inbreeding depression (reduced fitness as a result of breeding between related individuals) is to be avoided.

Dispersal patterns

Investigating the relatedness between individuals is important in order to identify natural dispersal patterns in orang-utans (in forests for which fragmentation is not an issue). Females were found to be more closely related to each other than to males; thus supporting the hypothesis from field observations that females are philopatric and males disperse (Rodman, 1973; Rijksen, 1978; Galdikas, 1988; van Schaik and van Hooff, 1996). This is contrary to Goossens *et al.* (2006a), who found that both sexes were philopatric in Kinabatangan, or Utami *et al.* (2002), who suggest that both sexes dispersed in Ketambe. In both cases an unnatural situation had occurred: plantations and forest conversion have fragmented the Kinabatangan forest and thus prevented males from dispersing naturally, whereas ex-captive orang-utans have been released at Ketambe, thus giving the impression that females had dispersed here (Utami *et al.'s* research was primarily to assess paternity, not dispersal). The results of the genetic analyses that I present here are the first to provide conclusive evidence for the widely-held hypothesis that females stay within their natal range and males disperse to other areas, and thus a male-biased dispersal system is operating. Inbreeding avoidance would seem the most obvious reason for this difference between the sexes. Males will disperse to take advantage of mating opportunities elsewhere, as male-biased dispersal is predicted when local mate competition exceeds local resource competition, usually under polygynous or promiscuity systems (Clutton-Brock, 1989; Gandon, 1999; Perrin and Mazalov, 2000; Chapter 9). Females benefit from philopatry, as they can form long-term associations with other female kin (Wrangham, 1980), thus decreasing hostility between individuals. Living with kin has also been shown to increase reproductive success (Pusey, 1987; Pusenius *et al.,* 1997). Females benefit from remaining in their natal range, as they can access known and valuable resources. Perrin and Mazalov (2000) draw parallels with the sex-ratio theory, which predicts biases towards the sex that suffers less from local competition. In orang-utans, which have a polygynous breeding system and much male-male competition (Chapter 9), it is more advantageous for males to depart in regards to reproductive strategy, as females are widely distributed and thus a limited resource (adult sex ratio: male/females 2.7:1 in Sabangau).

Site fidelity

In Kinabatangan, Goossens *et al.,* (2006a) were able to identify the mothers for 3 unflanged males, and suggested that males were delaying dispersal until they were large unflanged adults ready to flange, but also suggested that their presence may be due to the fragmented state of the Kinabatangan forest. One unflanged male in Sabangau (Archimedes) came from the same maternal line as two of the adult females (Indah and Cleo), indicating that he is yet to leave, or is revisiting, his natal area, and thus mature unflanged males may incorporate some of their mothers range into theirs, and may show some degree of site fidelity, before they disperse more widely when flanged. No flanged males were found to come from the same maternal line as the adult females. In chimpanzees, Murray *et al.* (2008) found that when males were on their own, they concentrated their range use near the area where their mother ranged when they were dependent. Murray *et al.* (2008) explains this solitary ranging as a way for males to avoid direct competition from conspecifics; and that foraging in familiar areas maximised foraging efficiency. The same may be true for adult unflanged male orang-utans, as aggression from relatives is likely to be lower, so returning to their natal range when food resources are low makes sense. Once flanged, however, returning to one's natal range when resources are low may not be worthwhile because of fewer mating opportunities. More data, however, are still needed on adult male ranging before one can make predictions of whether mature flanged males show any signs of site fidelity.

Paternity

In Sabangau, unlike findings from Ketambe and Kinabatangan, no fathers could be identified for any infants or adolescent from the 9 males sampled. This may imply that there is a high turn-over of males within the area and thus high male-male competition, or alternatively could simply be due to limited sampling, as DNA could not be extracted from 2 of the regularly-seen flanged males. Only 3 flanged males were classed as resident (DNA extracted from two of them), and their dominance was not stable over the course of this study. Instead it appeared to shift between individuals as they entered and exited the study area (Chapter 9), indicating high male-male competition.

8.5.2 Range overlap

Out of the 7 identified females only 3 were resided in the centre of the grid (Cleo, Indah and Feb), and all of their ranges overlapped with each other. The maximum number of adult females whose ranges overlap each other was 4 (Chapter 7), and not all of these individuals were closely related to each other, compared to 16 overlapping closely related females observed at Suaq Balimbing, Sumatra (Singleton and van Schaik, 2001, 2002). Distinct clusters of related females with overlapping ranges have also been found in Gunung Palung, (Knott *et al.,* 2008). Females in Suaq Balimbing share similar range boundaries with considerable range overlap (Singleton and van Schaik, 2002). The high overlap of related individuals at these sites is contrary to the findings in this study, where the most closely related adult females (r-value > 0.250 – Cleo and Indah) from the same maternal line only shared a small proportion of their ranges (20% and 17%), compared to females from a different maternal line which had a higher range overlap, i.e. Indah and Viola (area of range shared: 95%). At Gunung Palung 76% overlap was found between sisters and 65% for non-relatives (Knott *et al.,* 2008). In Sabangau there is more overlap between adults who are from a different maternal line, than between close relatives who share the same mtDNA. Even mother-offspring overlap is much less than expected (< 40% overlap between Feb and Cleo), compared to 80% at Gunung Palung (Knott *et al.,* 2008), but one must be careful in interpreting these findings as they are based only on 2 years of data. Data collected over a longer period are needed to confirm these results.

Chimpanzee females spend more time alone than males, but occupy distinct yet overlapping core-areas to which they show high site fidelity (Williams *et al.,* 2002; Murray *et al.,* 2007). Knott *et al.* (2008) hypothesised that female orang-utans occupy core-areas to optimise food intake and thus counteract the effects of scramble competition, and proposed that core-areas may function as territories in which females focus their foraging efforts on relatively exclusive resources. They found preliminary evidence for core-area defence (as adult females were more likely to win fights in their core-area than elsewhere) and passive range exclusion (Knott *et al.,* 2008). Mutual avoidance of aggressive contests creates range exclusion without active defence (Kaufmann, 1983). This explains the relative non-overlap of adult female core-areas in Gunung Palung, also similar to findings in Kinabatangan, where there was also little core-area overlap (Lackman-Ancrenaz and Ancrenaz, 2006). Williams *et al.* (2002) propose that familiarity with food resources is the reason why female chimpanzees maintain core-areas. In Sabangau the two resident females had exclusive non-overlapping core ranges, but this was not true for mother-offspring pairs, as Cleo shared one of her core-areas with Feb, thus sharing important resources with her offspring. Feb's main core-area was outside Cleo's range, however, and did not overlap with any other female's core-area. Overall, Knott *et al.*'s (2008) finding that females have exclusive core-areas, seems to be apparent in the Sabangau population, although more research is needed to find out whether these areas are defended by mutual avoidance.

Moses and Millar (1994) describe spatial patterns between parent and philopatric offspring in non-territorial systems as 'spatial clustering of families'. Thus each female is surrounded by their female offspring. Regarding interactions between related individuals, little interaction was observed between closely-related individuals such as Indah and Cleo, and the only regular female-female interactions were between a mother and her adolescent daughter, or between unrelated adults from different maternal lines, i.e. Indah and Viola. Galdikas (1985a) described orang-utans as living in open 'societies' with overlapping ranges, where individuals become increasingly less familiar with each other the further apart are the core-areas of these home ranges. I had similar results, with individuals that have little overlap and no core-area overlap, having little or no contact with each other. Adult females on the whole had less social contact with each other than with any other age/sex class (Appendix XV), and this is most likely due to passive exclusion through mutual avoidance as Knott *et al.* (2008) hypothesised, and thus very different from the social structure of female Sumatran orang-utans (Singleton and van Schaik, 2002).

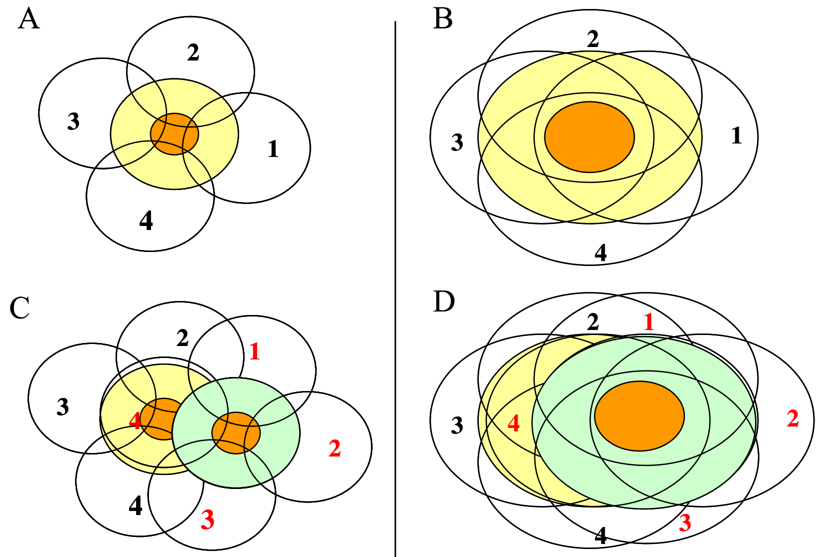
In Suaq Balimbing, where there is a mosaic of different habitat types compared to the Sabangau (homogenous habitat), home ranges are larger (Singleton and van Schaik, 2001, Singleton *et al.,* 2009), and densities are higher (Husson *et al.,* 2009). Singleton *et al.* (2009) found that areas with large home ranges also had large overlap between individuals, as might be expected, with more social interactions between related individuals. Range overlap between related individuals is to some degree also affected by the density of females, which is itself affected by resource availability, both temporal and spatial. As females are philopatric (at least at Sabangau), there will be range overlap between mothers and their female offspring. In Suaq Balimbing which is a high density area with large ranges, there is higher overlap and more associations between related individuals who have shared borders (Singleton and van Schaik, 2002) than in Sabangau, a low density area with small female home ranges and not much border sharing. Thus females are more spread out in the Sabangau. The most likely reason for this difference between Sabangau and Suaq Balimbing seems to be the spatio-temporal distribution of resources. In heterogeneous forests in Sumatra, it is more advantageous for offspring to stay in and share their mothers range, as resources are unevenly distributed in both space and time, thus offspring need to learn where (and when) important resources are; whereas in a homogenous habitat such as Sabangau, resources are more evenly distributed, thus it is more advantageous for offspring to move away and avoid direct competition for food resources with their mother and siblings. Thus more exclusive ranges and core-areas have developed in Sabangau.

I propose the ‘Petal Hypothesis’ for explaining partial range overlap in Sabangau, in which the centre of the flower is the mother’s range, and the petals are the female offspring (Figure 8.9). Females living in a homogenous habitat will have a range map resembling models A and C, with little range overlap between mother, daughter and siblings, whereas females from a heterogeneous area will have a range map resembling models B and D, with more overlap between a mother and her daughters and other close relatives.

‘Petal Hypothesis’

The ‘Petal Hypothesis’ is proposed to explain the spatial distribution of closely-related females (r-value > 0.250) from the same maternal line within the Sabangau peat-swamp forest.

In areas where productivity is high, but resources are spatially and temporally distributed due to habitat heterogeneity, Singleton and van Schaik. (2002) found that females showed tendencies towards simultaneous presence or absence in particular areas and explains this as convergence on particular food resources. Thus, large ranges and high overlap between assumedly-related individuals was found. From genetic evidence in the Sabangau, a daughter incorporated <50% of her mothers range into hers, and there was very little overlap between close relatives from the same maternal line. Female offspring in Sabangau set up ranges which do not completely overlap their mother’s range. I theorise that the pattern of a mother’s range with her offspring’s ranges resembles that of a flower, with the offspring’s ranges the petals (Figure 8.8 A); hence, I call this my ‘Petal Hypothesis’, which is dictated by habitat type, productivity and female density. In the Sabangau, a homogenous habitat, ranges are small compared to heterogeneous habitats (Singleton *et al.,* 2009), and resources are more evenly distributed (Marshall *et al.,* 2009b). Thus, home ranges are more exclusive, especially core-areas, as the mother will encourage her siblings to set up ranges beside each other, rather than top of each other. Thus, range placement is predicted to be affected by resource distribution.



Model A (1st generation) **and C** (2nd generation).
Homogenous habitat:
- Small ranges
- Less overlap between related individual except mother and daughter
- Almost exclusive core area

Low productive areas = low density area

Model B (1 generation) **and D** (2nd generation).
Heterogeneous habitat:
- Larger ranges
- Large overlap between related individual with shared borders
- High overlapping core areas

High productivity area = high density areas

NB. In areas which are heterogeneous but productivity is lower eg. Gunung Palung in Borneo, core areas are more exclusive.

Figure 8.9 ‘Petal Hypothesis’ for related female offspring: Model A – homogenous habitat; Model B – Heterogeneous habitat. Model A and B first generation of female offspring; Model C and D – Second generation of female offspring. Yellow circles = first generation mother; Blue circle = second generation mother; Orange circles = mother’s core-area.

8.6 CONCLUSION

Genetic diversity in the Sabangau was found to be high, with several different maternal lines. Genetic data confirms field observations that females are philopatric, whereas males disperse, although one unflanged male was found to visit his maternal area, as he came from the same matriarchal line as two adult females, indicating that unflanged males may show some degree of site fidelity until they become flanged. The reason why they may show site fidelity is probably due to accessing known food resources and less intra-specific competition for unflanged males. No fathers could be found and those males that were identified were mainly unrelated.

More range overlap was found between females from different maternal lines than between close relatives, as no more than half a mother's range was incorporated into her daughter's range, and sometimes very small overlap between close relatives was found. This small degree of overlap between close relatives, including almost complete exclusivity of core-areas, is very different from that found in Sumatra, where there is large home range and core-area overlap. This arrangement in which the mother places her female offspring side by side, with only partial overlap with her range resembles the petals of a flower, hence the 'Petal Hypothesis'. In areas that are more productive and have a mosaic of different habitat types for orang-utans to use, such as in Suaq Balimbing, ranges are larger with more overlap between mother and daughter, but the general arrangement will stay the same.

Thus, in the peat-swamp forest in Sabangau, orang-utans seem to live in open 'societies', similar to that described by Galdikas (1985a), in which individuals become increasingly less familiar with each other the further apart the core-areas of their home ranges are. More interaction was found between individuals from different maternal lines, which had overlapping ranges, than between close related individuals, which is the case in Sumatra.

Overall, it appears that orang-utans in Sabangau have a male-biased dispersal pattern to avoid inbreeding. Female social organisation appears to be influenced by the spatial distribution and productivity of a forest. Thus, habitat types are major influencing factors on the social organisation of orang-utans.

8.7 SUMMARY

Genetic diversity

- Genetic diversity was high, and females were more closely related to each other than males, implying philopatry in females and dispersal in males.
- The high number of different haplotypes indicated many different maternal lines.
- No fathers were found indicating a high turn-over of males and thus high male-male competition.

Range overlap and site fidelity

- There was more female range overlap between females from different maternal lines, than close relatives from the same maternal lines, except for mother and daughter.
- The 'Petal Hypothesis' as proposed in this chapter, illustrates social organisation, in which spatial distribution of resources influences social organisation in females.
- UFM may show a small degree of site fidelity right up until they become flanged. Thus, inbreeding avoidance by males is a good explanation for explaining male-biased dispersal in orang-utans.

CHAPTER 9

REPRODUCTIVE STRATEGIES AND MALE DOMINANCE

9.1 INTRODUCTION

9.1.1 Mating strategies.

As discussed in Chapter 8, many factors influence an animal population's dispersal patterns, of which mating strategy is one. If dispersal is costly, for example by travelling through unknown and unsuitable habitat, then natural selection will favour philopatry (Perrin and Mazalov, 2000), which in orang-utans was female-biased in Sabangau (Chapter 8). Polygynous and promiscuous species usually display a male-biased dispersal, whereas in monogamous species (e.g. gibbons), both sexes disperse (Perrin and Mazalov, 2000). Thus, reproductive strategies are highly associated with dispersal patterns. The Bornean orang-utan, unlike the Sumatran orang-utan or other great apes are mainly solitary, with males roaming large areas in search of cycling females, thus having large home ranges which overlap many female ranges (Wich *et al.*, 1999; van Schaik, 1999).

Male strategies

Male orang-utans of both species exhibit extreme sexual dimorphism and, unlike most other primates, possess two distinct adult morphs; the fully-developed male with flanged cheek pads and large throat sac, and unflanged males without these secondary sexual characteristics. Both morphs are capable of siring offspring (Utami *et al.,* 2002). Flanged males of both species are predominantly solitary and will only actively socialise during courtship when females are fertile. There is a distinct difference in mating strategies between the two species, with Sumatran males courting for weeks, and Bornean's only for a few days (Delgado and van Schaik, 2000). Female orang-utans, unlike female chimpanzees, do not have sexual swellings to advertise ovulation; thus males generally have to search for cycling females and thus their social organisation is influenced by the distribution of fertile females (Mitani *et al.,* 1991; van Hooff and van Schaik, 1994). As a result there is much intra-male competition for females (Utami and Mitra-Setia, 1995; Utami *et al.,* 2002).

Although unflanged males rarely emit long calls, they are usually quite successful at locating females and will often attempt to mate with one even if she is not cycling. Such matings are typically forced and often referred to as 'sneak rape' tactics (Galdikas, 1985b). In a study by Utami *et al.* (2002) in Ketambe, Sumatra, over half the offspring at the study site were sired by unflanged males and a similar result was found in Borneo at Kinabatangan, Sabah (Goossens *et al.,* 2006a). The 'arrested' state of unflanged males is thought to be a strategy to avoid stress, as arrested adult males are fertile but their appearance allows them to be tolerated by mature flanged males, who are not tolerated by other flanged males (Galdikas, 1985b; Maggioncalda *et al.,* 2002). Utami *et al.* (2002), however, suggested that this 'arrested' state is also an alternative reproductive strategy, described as the 'going, searching and finding' strategy *versus* the 'sitting, calling and waiting' strategy adopted by flanged males. Delgado and van Schaik (2000) support this theory that remaining unflanged is an alternative mating strategy in Sumatra; they theorise that, because dominant flanged males monopolise females, remaining unflanged must give non-dominant males more chance of being reproductively successful. In Borneo, where densities are much lower (Husson *et al.*, 2009), the proportion of flanged males is higher and sneak/rape tactics are common amongst both unflanged and non-dominant flanged males (Galdikas, 1985b; van Schaik and van Hooff, 1996; Delgado and van Schaik, 2000). These differences have resulted in two different male mating strategies: (i) roving male promiscuity in Borneo, where it is harder to defend access to females and females do not congregate in predictable areas; and (ii) socially-dispersed dominant males in socially-distinct communities in Sumatra (van Schaik and van Hooff, 1996; Delgado and van Schaik, 2000).

Female strategies

Female orang-utans prefer to consort with flanged males rather than unflanged males (Galdikas, 1985a) and prefer dominant over non-dominant flanged males (van Hooff, 1995; Singleton and van Schaik, 2002; Utami *et al.,* 2002). As a result, non-dominant flanged males obtain virtually no mating success in Sumatra (Singleton and van Schaik, 2002). Females will also actively try and avoid interactions with unflanged males

(Singleton and van Schaik, 2002; Fox, 2002). Thus female preference has been described as the mating strategy (Rijksen, 1978; van Hooff, 1995). In Sumatra, courtship is usually initiated by females as they can locate males easily by their long calls (Mitani, 1985; Utami and Mitra-Setia, 1995).

9.2 OBJECTIVES

The focus in this chapter will be on mating and male dominance within the study area, in order to identify mating strategies.

Questions to be addressed in this chapter are:

- Which age/sex classes were interacting with each other?
- What was the social status of individual flanged males and did it change?
- Were resident flanged males dominant over other flanged males?
- What reproductive strategy were males and females adopting?

9.3 METHODS

All habituated follows with more than 3 hours were used. For this analysis nulliparous females (NLF) were considered separately, and thus were not included in the usual age/sex class (NSAF) as described in Chapter 2. A nulliparous female was a female with no dependent offspring; whereas a sexually-active female (SAF) was a female with dependent offspring. Social data was collected on agonistic behaviour (submission and aggression).

Associations

An association was recorded whenever an individual who was less than 50 m away from another individual. The party size was defined as the number of independent individuals within 50 m from the focal. The number of encounters between individuals was used to see which individuals were associating with whom. For calculating individual associations only the 15 individuals on which more than 50 hours of follow data had been collected were used (Chapter 2). Associations and party size were only recorded for the focal individual, thus some age/sex classes may show up as not having an association with another age/sex class when in fact an association did occur.

Dominance

Flanged male dominance was assessed whenever there was an encounter between two flanged males. Data on who approached and who fled were recorded, thus enabling me to assess which male was dominant in each encounter. The male who approached another male was considered the aggressor (directional approach); the male that retreated was considered the less dominant individual as he had been displaced (fast departure of an individual when another individual approached within 50 m); the male that stayed and did not flee was the dominant male (Utami *et al.,* 1997). Although many contests were not witnessed, they clearly occurred, as new injuries were observed and recorded throughout the study period (e.g. presence of blood, lameness, scars, particularly on the face, and broken or missing digits).

Individuals were recorded as resident if they were present in the study area for more than 50% of the study period (Presence Index - see methods in Chapter 7).

Mating

The number of matings witnessed was counted for each individual. Females were noted to either approach or try and flee from males. Whether she attempted to resist or not once mating began was also recorded, in order to classify whether the mating attempt was forced (the female usually bit, hit and punched the male) or not (Fox, 2002). Consortship was when the male and female travelled in a party for more than one day.

9.4 RESULTS

9.4.1 Associations

The number of individuals with which each orang-utan associated over the course of this study is shown in Figure 1. Feb (NSAF), Indah and Cleo (both SAF) were seen more often with other individuals, associating with a number of different individuals from all age/sex classes, particularly UFM and FM, rather than other females. Figure 1 is not an indication of which individuals were more social, because it is not corrected for the length of time an individual was observed.

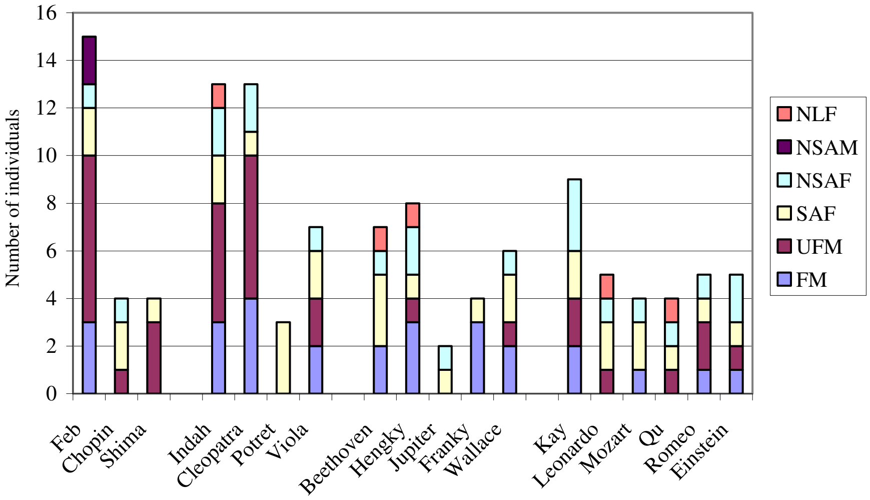


Figure 9.1 Number of different individuals with which each orang-utan associated.
NLF: nulliparous female; NSAM: adolescent male; NSAF: non-sexually-active female; SAF: sexually-active female; UFM: unflanged male; FM: flanged male.

The percentages of time that different individuals interacted with different age/sex classes are shown in Table 1. For males, most of their time in a party was spent interacting with either adult or adolescent females. For flanged males, a small percentage was with other flanged males, but these associations were usually aggressive encounters and lasted for short periods. No encounters between flanged and unflanged males in which they were within 50 m of each other were witnessed, as the unflanged male always fled before the flanged male got too close.

Table 9.1 Social encounters and percentage of time an individual spent with any other age-sex class (using focal data).

Name	Age/sex	Mean party size	% time alone	% time in a party	% with SAF	% with NLF	% with NSAF	% with FM	% with UFM	% with NSAM	% with unknown
Indah	SAF	1.1	91.7	8.3	0.1	0.7	0.4	0.3	7.7	0	0.3
Cleopatra	SAF	1.5	66.4	33.6	0.3	0	30.7	2.9	4.4	2.6	0.2
Viola	NLF	1.5	56.5	43.5	2.7	N/A	1.8	29.6	10.2	0	0
Feb	NSAF	1.3	82.5	17.5	12.4	0	0	1	7.4	3.5	0.4
Shima	NSAF	1.0	97.3	2.7	1.4	0	0	0	0.8	0	0.5
Hengky	FM	1.0	96.0	4.0	1.4	0	2.5	0.3	0	0	0.8
Beethoven	FM	1.1	90.6	9.4	1.0	7.0	0.6	0.2	0	0	0.7
Wallace	FM	1.0	97.1	2.9	1.8	0	0.4	0.1	0	0	0.6
Franky	FM	1.0	98.6	1.4	0	0	1.1	0.2	0	0	0.1
Jupiter	FM	1.0	99.4	0.6	0.4	0	0.2	0	0	0	0
Kay	UFM	1.3	74.2	25.8	9.1	0	14.7	0.4	6	0	1.3
Romeo	UFM	1.3	73.0	27.0	21.5	0	0.7	0.3	14.4	0	0.9
Mozart	UFM	1.1	85.0	15.0	9.1	0	5.5	0.4	0	0	0
Einstein	NSAF	1.5	57.9	42.1	1.3	0	30.5	1.3	10.8	0	0.5

Data on those 15 individuals that had more than 50 hours of observations are presented. The total does not add up to 100% because party sizes of more than 2 were recorded. These figures are based on the focal animal only; thus, for example, Viola (the only NLF) is recorded as being in a party with unflanged males, but no unflanged male was recorded as being in party with Viola, as Viola was always the focal individual when these interactions took place.

9.4.2 Male-male encounters

Table 9.2 Flanged male encounters.

Encounters	Focal	Party 2	Ind. Chasing	Ind. Fleeing
04/12/2003	Hengky - Injured	UNFM	UNFM	Hengky
06/02/2004	Franky	Beethoven	Beethoven	Franky
28/03/2004	Franky	Beethoven	Beethoven	Franky
07/07/2004	Wallace	UNFM	UNFM	Wallace
14/07/2004	Hengky	Franky	Franky	Hengky
18/07/2004	Hengky	Franky	Franky	Hengky
20/07/2004	Hengky	Franky	Franky	Hengky
11/08/2004	Beethoven	Franky	Franky	Beethoven
11/09/2004	Hengky	Franky	- No chase	Hengky
15/09/2004	Franky	Jupiter	Jupiter	Franky
07/10/2004	Hengky	UNFM	- No chase	UNFM
08/11/2004	Beethoven	Hengky	Hengky	Beethoven
10/11/2004	Hengky	Wallace	Hengky	Wallace
04/12/2004	Beethoven	Hengky	Hengky	Beethoven
05/12/2004	Hengky	UNFM	UNFM	Hengky
08/01/2005	Wallace	Hengky	- No chase	Wallace
27/02/2005	Franky	Hengky	Hengky	Franky

UNFM: unidentified flanged male

In all, 17 encounters were witnessed between 5 known flanged males, of which none were physical, and not all were aggressive (chase) (Table 9.2). Most encounters were between flanged males that were resident in the area for prolonged periods: Beethoven, Hengky and Franky (Figure 9.2). Jupiter was an occasional visitor (Chapter 7) and was only witnessed once having an encounter with Franky who fled (Figure 9.2), even though Franky was believed to be the resident dominant male at the time. Thus Jupiter must have been dominant over Franky, although Franky was dominant over Beethoven and Hengky who he had displaced the previous month. Thus dominance was not stable, with no one individual being dominant over all others during the study period (Table 9.3).

Table 9.3 Displacement between flanged males.

	Winners						
Losers	**Hengky**	**Beethoven**	**Franky**	**Wallace**	**Jupiter**	**Unknown**	**Total**
Hengky	■		4			2	6
Beethoven	2	■	1				3
Franky	1	2	■		1		4
Wallace	2			■		1	3
Jupiter					■		0
UNFM	1					■	1
Total	6	2	5	0	1	3	

Winners = the individual who displaced the other individual; Losers = the individual who lost and was thus displaced.

Table 9.4 Timetable of change in resident flanged males and dominance.

	2003				2004												2005							
Mo	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**
B	D			D		D	D		D			S		🟦	🟦	🟦			D?	D?	D	D	D	🟦
F		🟨		🟨	🟨	🟨	🟨	🟨		🟨	D	D	D	🟨	🟨			🟨						
H			🟩	Inj						🟩	🟩	🟩	🟩	D	D	D	D	D	D?	D?	🟩			🟩

Mo: Month; B: Beethoven; F: Franky; H: Hengky; Coloured blocks indicates presence; D: Dominant individual (the individual who was dominant in the study area). Inj: injury (which may have resulted from a contest); S: New scars (result of a contest); D?: Dominance not confirmed

The three resident flanged males in the grid: Beethoven, Franky and Hengky were present for more than 50% of the time, although they were not observed every month and may have left the study area during these times (Table 9.4). Based on interactions between these males, including observations on which male approached and which fled, Beethoven was the resident dominant male at the start of the study from September 2003 to May 2004, then Franky (believed to be the youngest of these three) took over as resident dominant male until October 2004 when Hengky became dominant. When Beethoven reappeared in August 2004 he had new scars on his face, implying that he had been in a fight, which may have been the event that cost him his dominance in May 2004. His cheekpads were deflated and his physical condition had deteriorated. In March 2005 when we encountered Beethoven again, he was in good physical condition compared to May 2004; his cheekpads were visibly larger and he had a large throat sac and made many long calls to assert his authority. Unfortunately, no encounters between Beethoven and Hengky were witnessed during the rest of the study, so it is not clear who was the dominant resident, but Hengky disappeared from the grid in May 2005 for 2 months and Beethoven remained, so I tentatively assume that Beethoven re-established himself as the resident dominant at this time (Table 9.4).

All interactions between flanged and unflanged males (8 encounters) resulted in the unflanged males fleeing from the flanged males. Only once did a flanged male (Hengky) aggressively chase an unflanged male away. This male was starting to developing flanges and had a large throat sac.

Out of the 14 unflanged-unflanged male encounters, five resulted in chases, in which the one being chased fled, except on one occasion when the aggressor fled. No physical contact was observed.

9.4.3 Matings

Only 2 females were witnessed mating over the 24-month study period (Table 9.5). Indah (SAF) was mated 12 times by unflanged males and once by a flanged male (Beethoven). All matings with Indah were forced (Table 9.5). Viola (NLF) was mated twice by the same flanged male (Beethoven), who may have been the dominant male at the time (March 2005). Both these matings were initiated by Viola (she approached him). She also spent a long time in apparent consortship with another FM (Hengky, in January 2005 for 5 ½ days), who was the dominant flanged male at the time, but no attempts to mate were witnessed during this time, even though he was in consort with her and much grooming took place between them. After this they just drifted apart.

Table 9.5 Observed matings.

Individual	FM	UFM	Notes
Indah (SAF with dependent infant)	1 (forced)	12 (forced - 5 different UFM)	1 with FM (Beethoven –who was in consort with Viola at that time). 7 with UFM in consort - coercive). 5 with UFM not in consort.
Viola (NLF)	2 (not forced) No mating witnessed.		Consort with Beethoven (cooperative) Consort with Hengky (cooperative)

9.5 DISCUSSION

9.5.1 Male-male encounters

The time flanged males spent in a party was usually short, except if the interaction was with an adult female, both sexually-active and nulliparous females. Interactions between adult males were always very short, and resulted in either unflanged males fleeing from flanged males; non-dominant flanged males fleeing from a dominant flanged male or after a contest in which the loser fled (physical fights have since been witnessed after the end of this study in 2005). This implies that there must be high flanged male competition in Sabangau, similar to findings from other sites (Rijksen, 1978; Galdikas, 1985a; Mitani, 1985), and also between unflanged males as 35% of encounters resulted in an aggressive chase (no physical contact ever witnessed). Singleton and van Schaik (2002) used sex ratios of adult as an indication of male/male competition in Suaq Balimbing, where the sex ratio of adult females was 4.9:1 females:adult males, believed to have arisen because of high adult-male mortality. The sex ratio in Sabangau, in stark contrast, is male biased with an adult male:female ratio of 2.7:1 and a flanged male to unflanged male ratio of 0.6:1 (Chapter 2). Thus there are nearly 3 times as many males as females, with more unflanged males than flanged males.

The number of resident flanged males present within the grid fluctuated, as they would enter and exit the area; thus, dominance shifted between the three resident flanged males Beethoven, Franky and Hengky. Thus the ‘roving male promiscuity’ strategy, which states that males cannot defend access to females and females do not congregate in predictable areas, proposed for orang-utans by van Schaik and van Hooff (1996), seems to fit, as cycling females were mated by a number of males, as opposed to socially-dispersed dominant males in socially-distinct communities that is found in Sumatra (Delgado and van Schaik, 2000; Singleton and van Schaik, 2002). In Sumatra one male was the dominant resident male for 18 years before being defeated (Utami and Mitra Setia, 1995). Galdikas (1988) found that residency was not permanent at her site in Borneo, as regularly-observed males left the study area after resident females gave birth, thus shifting their location in response to the reproductive condition of different females. In Sabangau, the resident male at the time of conception for two different females was Hengky, and he left the area a few months prior to one of the females giving birth, and has not been seen since.

9.5.2 Mating strategies

Male strategies

Interactions between sexually-active females and unflanged males were usually coerced. In the case of Indah (SAF), when she was cycling her interactions with unflanged males were usually long and even though she tried to escape, she could not because they were usually persistent and she had a large infant who slowed her down. Indah was regularly chased by unflanged males and forced to mate, whereas the same behaviour was not witnessed with Cleo, another resident sexually-active female, who was not cycling due to having a young baby. Whilst Indah was being pursued she adopted submissive behaviour, including not leaving her nest in the morning for long periods of time; coming down to the ground to hide; and in some instances following behind submissively; in these circumstances she did not attempt to flee as the male would usually chase after her. These counter actions were probable used to reduce sexual harassment and possible injury to her infant.

Interactions between sexually-active females and flanged males were rare, similar to findings by Galdikas (1988) who found that females usually avoided close contact with flanged males. On a number of occasions flanged males would approach females, but if they had young babies and were thus not cycling (e.g. Cleo) they would leave. Indah, whose infant was nearly weaned at the time, approached a flanged male when she was being harassed by an unflanged male, thus using the presence of the flanged male as a protective service (Fox, 2002); this behaviour was only witnessed once. Thus, **'sneak-rape tactics'** (Galdikas, 1985b) by unflanged males were common, but focused on individuals who were soon to be or already cycling, and thus were potentially able to conceive.

This tactic was not only used by unflanged males, but also by one flanged male, Beethoven, who, at the time of the 'sneak-rape' was not the dominant male, although he is assumed to have become the resident dominant male shortly after. On this occasion, the female (Indah) had already nested for the night when Beethoven approached and pulled her out of her nest. This flanged male was in consortship with a nulliparous female (Viola) at the time (in consortship for 4 days before they left the study area), and all matings with Viola were cooperative. The reason for this behaviour towards Indah is unclear, as later we found out that Indah was already pregnant at this time. Due to this male's absence from the study area for the previous few months, he may have been hopeful that she was still cycling. Similar behaviour has been reported at other sites by flanged males when in consortship (Utami *et al.,* 2009).

Forced mating by unflanged males and flanged males has been witnessed at other sites (MacKinnon, 1974; Galdikas, 1985b; Mitani, 1985; Schurmann and van Hooff, 1986; Utami *et al.,* 2009), although forced matings by flanged males have only been witnessed in Borneo and usually by non-dominant individuals (Delgado and van Schaik, 2000). Forced matings probably arise because mating opportunities for non-dominant flanged males are low and because females preferentially choose to mate with dominant flanged males, especially in Sumatra (Utami and Mitra Setia, 1995; Utami *et al.,* 2009). The same seems to be true in Sabangau, in which the resident male is preferred by females over visitors. Visitors in turn will try to mate with cycling females if they have the chance, especially unflanged males.

The size of dependent offspring seems to play a large part with regard to which females are pursued. Indah's daughter Indy was 4 years old and nearly weaned when first followed. Her size may give an indication to males that Indah was already, or soon to start cycling, whereas Cleo, who had just had a baby (Chivers) at the start of my research period and was evidently not cycling, was left alone, although males did regularly approach to check. In 2007, when Chivers was 4 years old, the behaviour by unflanged males towards Cleo was similar to their behaviour towards Indah in 2004 (Appendix XVI). Thus, males appear to take a straightforward cue from the age of the offspring to assess whether a female is cycling or not. Orang-utans, unlike a lot of other primates, do not show any external signs when they are cycling, thus these simple observations must help to indicate to them whether a female is cycling or not.

There appear to be two mating strategies adopted by male orang-utans (i) **'going, searching and finding'** (looking for cycling females), in which **'sneak rape tactics'** are used (Galdikas, 1985b; Utami *et al.,* 2002), and (ii**) 'sitting, calling and waiting'** (Utami *et al.,* 2002), adopted by dominant resident males. The nulliparous female, Viola, who had no offspring, was seen pursuing a flanged male, rather than him pursuing her. Thus, unflanged males and non-resident flanged males adopt strategy (i), and resident dominant flanged males adopt strategy (ii). As an overall male reproductive strategy, the **'roving male promiscuity'** model (Clutton-Brock, 1989), as proposed for orang-utans by van Schaik and van Hooff (1996), appears to be adopted here.

Female strategies

Cycling females with offspring usually tried to avoid interactions with males if possible, by either (a) fleeing when they hear a male approaching or (b) hiding (staying very quiet, not moving or eating) until they knew the identity of the individual or the individual had passed by. Cycling females without offspring (i.e. Viola) used different tactics. Instead of hiding, this individual was found to seek flanged males out and initiate consortship, similar to findings for adolescent females in Tanjung Puting (Galdikas, 1995).

Thus, mating strategies adopted by females are more complicated, as adult females in Sabangau responded to the presence of males in a number of ways. They respond by either (i) using flanged males as a shield to keep unflanged males away; (ii) hiding from both unflanged males and flanged males if they are cycling but have an infant; or (iii) if they are cycling but do not have an infant, will follow and solicit the dominant resident flanged male. Thus, different strategies are adopted, in which an important influencing factor in '**female preference'** is the presence of dependent offspring for cycling females, and not just social states and morph of males, which is considered to be the main factor behind female choice in orang-utans (Utami *et al.,* 2009).

9.5.3 Overall reproductive strategy

The *'scramble competition polygyny'* mating system in which both sexes typically mate with several partners (Kappeler, 1997), is evident in the Sabangau population. In this system males roam widely in search of receptive females, which they desert soon after mating in search of additional mates, but there are several different strategies adopted depending on gender. **'female preference'** is evident, although van Schaik and van Hooff (1996) state that if **'female preference**' is the strategy adopted, then the **'roving male promiscuity'** model must be rejected, but from these findings it appears that both strategies can be used; although the presence of dependent offspring of cycling females seems to play a large part in the **'female preference'** model. Utami *et al.* (2009) found that the reproductive condition of females affects **'female preference'** and male-male competition. The high turnover of resident males, and the number of different males mating with cycling females, is evident for the **'roving male promiscuity'** model. Thus, both strategies are present in Sabangau.

9.6 CONCLUSION

There was high male-male competition, particularly between flanged males, and a high turnover of resident dominant flanged males, which exited and entered the study area regularly. This may be due to contests with other males or the presence of cycling females somewhere else. With regard to mating strategies, both the **'roving male promiscuity'** and **'female preference'** models were strategies seen in the Sabangau, in which the presence of dependent offspring for cycling females influenced the **'female preference'** model greatly. Cycling females with infants avoided males (both unflanged and flanged males), whereas cycling females with no infants were attracted to the resident flanged male.

A key indicator to males to whether a female is cycling or not seems to be the age of their offspring, as well as changes in her behaviour or olfactory signals (Schurmann, 1982). Fox (2002) and Mitani (1985) both found that mating attempts on females with unweaned infants were rare, thus emphasising that age of offspring is a good sign of whether a female may be cycling. In the Sabangau, although the sample size is small, this appears to occur when the infant is around 4 years old.

9.7 SUMMARY

- Flanged male dominance within the study area changed regularly between the three resident males. Aggressive encounters between unflanged males also took place, thus suggesting high male-male competition, particularly within flanged males.
- Unflanged males used **'sneak rape tactics'**; whereas flanged males used both **'sneak rape tactics'** and **'sitting, calling and waiting',** depending on whether they were dominant or not.
- Both the' **'roving male promiscuity'** strategy and **'female preference'** strategy are adopted, but the presence of dependent offspring for cycling females seems to be of great importance in the **'female preference'** strategy.
- Overall, the reproductive strategy in action in Sabangau seems to be a *'scramble competition polygyny'* strategy.

CHAPTER 10

CONCLUSIONS

I carried out my research in the Sabangau Forest, an extremely important tropical peatland which holds the largest population of orang-utans in the world, but was subject to intense illegal logging until 2004. The objectives of my research were to understand the behavioural ecology of orang-utans in this important ombrogenous peat-swamp forest, a population which had never been studied before; to identify the effects of habitat disturbance on their behaviour in order to help with management plans for the area; and to compare my findings to those from other habitats; in order to further the understanding of orang-utans.

10.1 MAJOR RESULTS

In order to address my questions, I collected over 5,500 hours of observational data from September 2003 – August 2005. I used instantaneous focal sampling methods, and collected data on 27 different individuals from five different age/sex classes: non-sexually active females (adolescents), sexually-active females (adults), adolescent males, unflanged adult males and flanged adult males, all of which needed to be habituated to my presence first, thus allowing me to follow without the orang-utan fleeing or being aggressive towards me. This research was the beginning of what is now a long-term study on orang-utan behaviour and ecology in peat-swamp forest. The presence of researchers also helps in protecting the forest, as the area was being illegally logged before this study started, but this ceased in January 2004.

10.1.1 Behaviour in Sabangau

I have discovered a number of important aspects of orang-utan behaviour in this study. A standardised inter-site comparison of orang-utan activity budgets (Chapter 5), revealed clear differences between orang-utans in peat-swamp forest and those in dipterocarp-dominated dryland forests, in particular the use of two different foraging strategies to cope with different fruiting seasonality in the different habitat-types. This is the first study where genetic evidence for the theory that female orang-utans are philopatric and males disperse is provided (Chapter 8) and the first where fine-scale logging damage was investigated, which showed how orang-utans make biased use of their home range, either choosing or avoiding areas of different habitat quality (Chapter 6).

10.1.2 Differences between Sabangau and other research sites

There are both differences and similarities between Sabangau and other sites. The main differences seem to be the seasonal distribution of resources which vary between peat-swamp forest and dipterocarp-dominated forests, and the spatial distribution of resources which vary between sites with heterogeneous and homogeneous habitat. These differences influence orang-utan behaviour (Chapters 3, 5 and 8). Sabangau is a true ombrotrophic peat-swamp forest, which means that it gets all its nutrients from rainfall and aerial deposition, and it is truly homogeneous with no other habitat types present. The other sites compared here include those that are dipterocarp-dominated masting forests (Ketambe, Gunung Palung, Mentoko, Ulu Segama and Kinabatangan) or heterogeneous combinations of peat-swamp, freshwater and dry forest habitats (Suaq Balimbing and Tanjung Puting).

Fruiting patterns

The fruiting patterns of dipterocarp forest are better known, with well-documented community-wide masting events occurring every 4-10 years, during which fruit availability is elevated to very high levels for a period of 3 to 4 months, and then drop down to their normal, low background levels. Fruiting patterns in peat-swamp forest differ greatly as there is no mast, instead there is a regular pattern of fruiting peaks and troughs which are rarely extreme. From this study, it appears that trees in peat-swamp forest generally have asynchronous fruiting patterns, both at the species and community level (Chapter 3), thus allowing fruits and flowers to be available all year round, unlike in dipterocarp-dominated forests where a high percentage of trees fruit in synchrony. Thus fruit production is more regular in peat-swamp forests, which means orang-utans have a more regular supply of fruits.

10.1.3 Impact of these differences on orang-utan behaviour

Diet and Activities

Although differences between peat-swamp forest and dipterocarp forest are apparent in regards to fruiting patterns, overall fruit availability in Sumatra is generally higher and more constant than in Borneo (Chapters 3 and 4). Orang-utans from Sabangau and Gunung Palung in Borneo both expressed ketones (the result of fat-metabolism) in their urine during periods of low fruit and flower availability (Chapter 4) unlike orang-utans from Ketambe in Sumatra. This appears to be due to the high density of large strangler figs in Sumatra which act as the main fallback food when non-fig fruit availability is low. Thus orang-utans in Ketambe are able to maintain a neutral energy balance, unlike orang-utans from Borneo who rely more on leaves, barks and invertebrates as fallback foods, no matter what habitat type they live in. When variation in fruit and flower (‘*food’*) availability was assessed in Sabangau, orang-utans decreased their time travelling when ‘*food*’ availability was low and increased feeding, presumably because they were feeding on less energy-rich fallback foods (Chapter 5). In contrast, orang-utans from a dipterocarp forest in Borneo did not increase their feeding time during periods of low fruit availability, which suggests that different foraging strategies were adopted in different habitat types.

Activity budgets were found to differ between sites (Chapter 5). Orang-utans from the peat-swamp dominated forests and the dipterocarp forest with a high fig density, fed and travelled significantly more than orang-utans from dipterocarp-dominated forests in Borneo where they rest more and travel and feed less. This difference appears clearly linked to differences in seasonal availability of fruit, resulting in two different foraging strategies being adopted: (i) ‘search-and-find’ where orang-utans are continuously feeding or moving in search of food, in habitats where fruits are available most times of the year, even if less nutritious; and (ii) ‘sit-and-wait’ where orang-utans limit their energy expenditure and build large fat reserves to cope with extended periods of very low fruit availability (Chapter 5).

Ranging and dispersal

Although the Sabangau had been subject to many years of logging, both legal and illegal, it is still relatively intact and not fragmented. Analysis of DNA samples from Sabangau confirmed the hypothesis that male orang-utans disperse away from their natal range whereas females remain philopatric (Chapter 8), confirming field observations elsewhere but contrary to other genetic analyses from both Sumatra (Ketambe) and Borneo (Kinabatangan).

Habitat heterogeneity was found to be an important factor affecting behaviour, particularly influencing the size of home ranges and the degree of overlap between related females (Chapter 8). Related females from heterogeneous habitat in both islands (Gunung Palung and Suaq Balimbing) had high range overlap and bigger ranges than orang-utans in Sabangau (Chapter 7). In Sabangau, related females via the maternal line had more overlap with unrelated individuals than with close relatives. Thus females from a homogeneous forest have smaller and more dispersed ranges, than those from heterogeneous habitats (Chapter 8). Homogenous peat-swamp forest has resources which are dispersed more evenly, thus orang-utans can set up independent ranges with little overlap with their mothers, compared to female orang-utans in masting forests which are more heterogeneous, as fruits are more spatially dispersed (i.e. larger fig trees). Thus, orang-utans need to range longer distances to make use of the different habitats at different times of the year. I proposed the 'Petal Theory' to describe range placement in female offspring in the Sabangau (Chapter 8). Differences here are not just due to differences between peat-swamp and dipterocarp-dominated forests, but due to the distribution of resources within the forest (homogeneous *vs*. heterogeneous habitats).

Overall, these results highlight differences in behaviour between orang-utans in Sabangau and those in other sites, which are the result of the effects of different fruiting patterns and the degree of heterogeneity within a site. Our current knowledge of orang-utans has been expanded in this study, as there were previously few data from peat-swamp forest.

10.2 IMPACTS OF DISTURBANCE AND IMPLICATIONS FOR CONSERVATION

10.2.1 Impact of disturbance

Data on the impact of human disturbances are extremely important, especially for improving management efforts for the Sabangau population, one of the highest priority populations for conservation, and also for those populations outside protected areas in logging concessions, as habitat disturbance is a major issue (Chapter 1). Although orang-utans have been found to cope with disturbance, different levels of disturbance identified in this study have been found to influence orang-utan behaviour (Chapter 6). Orang-utans were found to avoid certain habitat-quality classes in preference for others. The taller forest classes, regardless of canopy completeness were preferred over those with lower canopy, indicating that they did not preferentially choose areas with complete canopy. The taller habitat classes have large trees which fruit more often and have large crop sizes. Thus, this is more important than canopy completeness (suggested as important for maintaining unbroken travel routes). Nevertheless, orang-utans did prefer areas with complete canopy for resting and nesting in, suggesting that this habitat factor provides orang-utans with greater security.

Illegal logging has also resulted in a skewed sex ratio, a probable consequence of the 2001 population crash (Chapter 1). Orang-utans retreated to the edge of their ranges during the years of intense illegal logging, resulting in over-crowding in the depauperate low-pole forest. Because female orang-utans are reluctant to move out of their range completely and have high energetic requirements, whereas males have much larger ranges (Chapter 7) and are able to range further in search of food, it is assumed that more females than males died during the logging-induced population crash.

10.2.2 Recommendations

The need for patches of large trees to be left by logging concessions, as orang-utans need large fruiting trees to meet their feeding needs, has been highlighted. The most heavily disturbed classes were rarely visited and hardly fed in, hence there appears to be a threshold at which logging becomes incompatible with orang-utan survival. These findings are important for management plans for production forests, as this is where most orang-utan populations are found. Good logging practices for selective-logging companies will enable orang-utans to persist in these areas, if logging regulations can be adhered to. Thus the use of peat-swamp forest for selective-logging operations that are well managed with strict guidelines, are clearly much better for habitat and biodiversity conservation than conversion to agriculture. Additionally it should be stressed that peat greater than 2 m deep is unsuitable for agriculture, due to problems of water logging and the low nutrient value of unforested peat.

Sabangau

In this research I have highlighted the differences between peat-swamp forest and other habitat types, and consequent differences in orang-utan behaviour, providing a good example of how fruiting patterns and degree of homogeneity can influence behavioural ecology. I have also highlighted how different degrees of disturbance can influence behaviour and even survival; as responses to disturbance are scale dependent. If the Sabangau forest is left to regenerate, orang-utan densities will recover to pre-logging levels. The most important challenge for the Sabangau forest, if it is going to remain an important habitat for orang-utans, is to dam the illegal canals which were built to extract logs from the forest during the late 1990s and early 21st century (Chapters 1 and 2). These canals are draining the forest and making it susceptible to fire, which is the greatest long-term threat and is responsible for much previous damage in the area. This is the most important management action that must be undertaken if the Sabangau population of orang-utans is going to survive.

REFERENCES

Ahmad, A.H. (1994). The ecology of mousedeer (*Tragulus* species) in a Bornean rain forest, Sabah, Malaysia. MPhil thesis, University of Aberdeen.

Ahsan, M.F. (2001). Socio-ecology of the hoolock gibbon (*Hylobates hoolock*) in two forests of Bangladesh. In: The Apes: Challenges for the 21st Century. Conference Proceedings of the Brookfield Zoo. Chicago Zoological Society, Chicago, IL.

Aleixo, A. (1999). Effect of selective logging on a bird community in the Brazilian atlantic forest. *The Condor*, 101, 537-548.

Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A. and Lackman-Ancrenaz, I. (2004a). Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation*, 7, 375-385.

Ancrenaz, M., Calaque, R. and Lackman-Ancrenaz, I. (2004b). Orang-utan nesting behavior in disturbed forest of Sabah, Malaysia: Implications for nest census. *International Journal of Primatology*, 25, 983-1000.

Anderson, A. and Weir, B. (2007). A maximum likelihood method for the estimation of pairwise relatedness. *Genetics*, 176 (1), 421-440.

Anderson, J.A.R. (1963). The flora of peat swamp forests of Sarawak and Brunei including a catalogue of all recorded species of flowering plants, ferns and fern allies. *Gardeners Bulletin (Singapore)*, 29, 131-228.

Anderson, J.A.R. (1964). The structure and development of the peat swamps of Sarawak and Brunei. *Journal of Tropical Geography*, 18, 7 –16.

Anderson, J.A.R. (1983). The tropical peat-swamp forests of western Malesia. In: Gore, A.J.P. (ed.) Mires, swamp, bog, fen and moor. B. Regional studies. Elsevier, Amsterdam, 181-199.

Anderson, J.R. (1998). Sleep, sleeping sites and sleep-related activities: Awakening to their significance. *American Journal of Primatology*, 46, 63-75.

Ashton, P.S., Givnish, T.J. and Appanah, S. (1988). Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist,* 132, 44-66.

Asner, G.P., Keller, M. and Silva, N.M. (2004). Spatial and temporal dynamics of forest canopy gaps following selective logging in the east Amazon. *Global Change Biology*, 10 (5), 765-783.

Asyraf, M. and Mansor, M. (2002). The diversity and composition of weeds in disturbed and undisturbed peat swamp forest in Peninsula Malaysia. In: Rieley, J.O. and Page, S.E. (eds.) Peatlands for People: Natural Resource Functions and Sustainable

Management. Proceedings of the International Symposium on Tropical Peatland, 22-23 August 2001, Jakarta, Indonesia. BPPT and Indonesian Peat Association.

Augspurger, C.K. (1981). Reproductive synchrony of a tropical shrub: experimental study on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology*, 62 (31), 775-788.

Bean, A. (1999). Ecology and sex differences in great apes. In: Lee, P.C. (ed.) Comparative primate socioecology. Cambridge University Press, 339-362.

Bendix, J., Homeier, J., Cueva Ortiz, E., Emck, P., Breckle, S.-W., Richter, M. and Beck, E. (2006). Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *International Journal of Biometeorology*, 50, 370–384.

Boesch, C. and Boesch-Achermann, H. (2000). The chimpanzees of the Tai Forest: Behavioural ecology and evolution. Oxford University Press, Oxford, UK.

Bolmgren, K. (1998). The use of synchronization measures in studis of plant reproductive phenology. *Oikas*, 82 (2), 411-415.

Brady, K. (2005). Butterfly diversity in a selectively logged peat swamp forest in Central Kalimantan, Indonesia. BSc. Dissertation, University of Southampton, UK.

Brearley, F.Q., Proctor, J., Suriantata, Nagy, L., Dalrymple, G., and Voysey, B.C. (2007). Reproductive phenology over a ten-year period in a lowland evergreen rain forest of central Borneo. *Journal of Ecology*, 95, 828-839.

Brugiere, D., Gautier, J-P., Moungazi, A. and Gautier-Hion, A. (2002). Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *International Journal of Primatology*, 23 (5), 999-1025.

Buckland, H. (2005). The Oil for Ape Scandal: How palm-oil is threatening the orangutan. Friends of the Earth UK and the Ape Alliance. http://www.foe.co.uk/campaigns/corporates/news/orangutan_report.html.

Buckley, C., Nekaris, K.A.I. and Husson, S.J. (2006). Survey of *Hylobates agilis albibarbis* in a logged peat-swamp forest: Sabangau catchment, Central Kalimantan. *Primates*, 47(4), 327-335.

Buij, R., Wich, S.A., Lubis, A.H. and Sterck, E.H.M. (2002). Seasonal movements in the Sumatran orangutan (*Pongo pygmaeus abelii*) and consequences for conservation. *Biological Conservation,* 107, 83-87.

Buij, R., Singleton, I. Krakauer, E. and van Schaik, C.P. (2003). Rapid assessment of orang-utan density. *Biological Conservation*, 114, 103-113.

Caldecott, J. and Miles, L. (eds.) (2005). World atlas of great apes and their conservation. Prepared at the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA.

Cannon, C. and Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques: Selection of canopy elements for crossing gaps. *American Journal of Physical Anthropology*, 93, 505–524.

Cannon, C.H., Curran, L.M., Marshall, A.J. and Leighton, M. (2007a). Beyond mast-fruiting events: Community asynchrony and individual sterility dominate woody plant reproductive behavior across seven Bornean forest types. *Current Science*, 93, 1558-1566.

Cannon, C.H., Curran, L.M., Marshall, A.J. and Leighton, M. (2007b). Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park, Indonesia: suprannual synchrony, temporal productivity, and fruiting diversity. *Ecology Letters,* 10, 956-69.

Cannon, C.H., Peart, D.R., Leighton, M. and Kartawinata, K. (1994). The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. *Forest Ecology and Management*, 67, 49-68.

Cant. J.G.H. (1987). Effect of sexual dimorphism in body size on feeding postural behaviour of Sumatran orang-utans (*Pongo pygmaeus*). *American Journal of Physical Anthropology*, 74 (2), 143-148.

Cant. J.G.H. (1992). Positional behaviour and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. *American Journal of Physical Anthropology*, 88, 273-283.

Chapman, C.A. and Chapman, L.J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, 40, 215-231.

Chapman, C.A., Wrangham, R. and Chapman, L.J. (1994). Indices of habitat-wide fruit abundance in tropical forest. *Biotropica*, 26, 160–171.

Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P. and Struhsaker, T.T. (2000). Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology*, 14 (1), 207-217.

Chivers, D.J. (1974). The Siamang in Malaya: a field study of a primate in tropical rainforest. Karger, Basel.

Chivers, D.J. (1980). Malayan forest primates. Plenum Press, New York.

Cleary, D.F.R. (2003). An examination of scale of assessment, logging and ENSO-induced fires on butterfly diversity in Borneo. *Oecologia*, 135, 313-321.

Cleary, D.F.R., Boyle, T.J.B., Setyawati, T., Anggraeni, C.D., van Loon, E.E. and Menken, B.J. (2007). Bird species and traits associated with logged and unlogged forest in Borneo. *Ecological Applications*, 17 (4), 1184-1197.

Clutton-Brock, T.H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London B*, 236, 339-372.

Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Clutton-Brock, T.H. (ed.) Primate Ecology: Studies of Feeding and Ranging in Lemurs, Monkeys, and Apes. Academic Press, London, 539-556.

Commitante, R., Husson, S., Morrogh-Bernard, H. and Chivers, D.J. (2003). Where the wild things are not – the plight of the wild orangutan. *Biologist*, 50(2), 75-80.

Cowlishaw, G. and Dunbar, R. (2000). Primate conservation biology. University of Chicago Press.

Csillery, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B., Spong, G. and Pemberton, J.M. (2006). Performance of marker-based relatedness estimator in natural populations of outbred vertebrates. *Genetics*, 173, 2091-2101.

Curran, L.M. and Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, 70, 101-28.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E. and Haeruman, H. (1999). Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science,* 286, 2184-2188.

D'arcy, L.J. and Page, S.E. (2002). Assessment of the effect of the 1997/98 forest fires and anthropgenic deforestation on peat swamp forest in Central Kalimantan, Indonesia. In: Rieley, J.O. and Page, S.E. (eds.) Peatlands for People: Natural Resource Functions and Sustainable Management. Proceedings of the International Symposium on Tropical Peatland, 22-23 August 2001, Jakarta, Indonesia. BPPT and Indonesian Peat Association.

Dasilva, G.L. (1992). The western black-and-white colobus as a low-energy strategist: Activity budget, energy expenditure and energy intake. *Journal of Animal Ecology*, 61 (1), 79-91.

Davies, G. and Payne, J. (1982). A Faunal Survey of Sabah. WWF Malaysia, Kuala Lumpur.

Decker, B.S. (1994). Effects of habitat disturbance on the behavioural ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology*, 15 (5), 703-737.

Delgado, R.A., Lameira, A.R., Ross, M.D., Husson, S.J., Morrogh-Bernard, H.C. and Wich, S.A. (2009). Geographical variation in orang-utan long calls. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Delgado, R.A. Jr. and van Schaik, C.P. (2000). The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology,* 9, 201-218.

Di Bitetti, M.S (2001). Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *Journal of the Zoological Society of London*, 253, 33-45.

Djojosudharmo, S. and van Schaik, C.P. (1992). Why are orang utans so rare in the highlands?: Altitudinal changes in a Sumatran forest. *Tropical Biodiversity*, 1, 11-22.

Doran, D.M. (1997). The influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees: A comparison with previous work. *International Journal of Primatology*, 18, 183–206.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. and Shah, N. (2002a). Western lowland gorilla diet and resource availability: New evidence, cross site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology*, 58, 91-116.

Doran, D.M., Jungers, W., Sugiyama, Y., Fleagle, J.G. and Heesy, C.P. (2002b). Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioural diversity. In: Boesch, C., Hohmann, G. and Marchant, L.F. (eds). Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, UK, 14-34.

Doran-Sheehy, D.M., Greer, D., Mongo, P. and Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology*, 64, 207-222.

Dove, M.R. (1993). The response of dayaks and bearded pigs to mast-fruiting in Kalimantan: an analysis of nature-culture analogies. In Hladik, C.M., Hladik, A., Linares, O.K. and Pagezy, H. (eds.) Tropical forest people and food: biocultural interactions and applications to development. UNESCO, Paris and the Parthenon Publishing Group, Carnforth, UK.

Dragiewicz, M. (2006). Fish of the Sabangau and nearby rivers. Orangutan Tropical Peatland Project Report.

Dragiewicz, M. and Husson, S.J. (2007). Herpefauna of the Sabangau Forest. Available from www.orangutantrop.com/pdfs/Reptile_list.pdf.

Dragiewicz, M., Husson, S.J., Allinson, T. and Page, S.E. (2007). Avifauna of the Sabangau Peat-Swamp Forest. Available from www.orangutantrop.com/BirdList2007.pdf.

Dunbar, R.I.M. (2002). Modelling primate behavioural ecology. *International Journal of Primatology*, 23 (4), 785-819.

Excoffier, L., Laval, G and Schenider, S. (2005). ARLEQUIN vers. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, 1, 47-50.

Fairgrieve, C. and Muhumuza, G. (2003). Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *African Journal of Ecology*, 41, 141-149.

Felton, A.M., Engstrom, L., Felton, A. and Knott, C.D. (2003). Orangutan population density, forest structure, and fruit availability in hand-logged and unlogged peat-swamp forests in West Kalimantan, Indonesia. *Biological Conservation*, 114 (9), 91-101

Fleming, T.H., Breitwish, R. and Whitesides, G.H. (1987). Patterns of tropical frugivore diversity. *Annual Review of Ecology and Systematics*,18, 91-109.

Fox, E.A. (2002). Female tactics to reduce sexual harassment in the Sumatran orang-utan (*Pongo pygmaeus abelii*). *Behavioural Ecology and Sociobiology*, 52, 93-101.

Fox, E.A., van Schaik, C.P., Sitompul, A. and Wright, D.N. (2004). Intra and inter-population differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*, 125, 162–174.

Fredriksson, G., Wich, S.A. and Trisno (2006). Frugivory in sun bears (*Helarctos malayanus*) linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society*, 89, 489-508.

Furuichi, T, Hashimoto, C. and Tashiro, Y. (2001). Fruit avalibility and habitat use by Chimpanzees in the Lalinzu forest, Uganda: Examination of fallback foods. *International Journal of Primatology*, 22 (6), 929-945.

Galdikas, B.M.F. (1979). Orang-utan Adaptation at Tanjung Puting Reserve: Mating & Ecology. In: Hamburg, D.E. and McCown, E.R. (eds.) The Great Apes. Benjamin/Cumings, Menlo Park, CA, 194-233.

Galdikas, B.M.F. (1985a). Orang-utan sociality at Tanjung Puting. *American Journal of Primatology*, 9, 101-119.

Galdikas, B.M.F. (1985b). Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. *American Journal of Primatology*, 8, 87-99.

Galdikas, B.M.F. (1988). Orang-utan Diet, Range and Activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, 9 (1), 1-35.

Galdikas, B.M.F. (1995). Social and reproductive behaviour of wild adolescent female orangutans. In: Nadler, R.D., Galdikas, B.M.F., Sheeran, L.K. and Rosen, N. (eds.) The Neglected Ape. Plenum Press, New York, 163-182

Galdikas, B.M.F and Wood, J.W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology*, 83, 185-191.

Gandon, S. (1999). Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology*, **200**, 345-364.

Ganzhorn, J.U. (2003). Habitat description and phenology. In: Setchell, J.M. and Curtis, D.J. (eds.) Field and Laboratory Methods in Primatology: A Practical Guide. Cambridge University Press, Cambridge, UK, 40-56.

Ganzhorn, J.U., Ganzhorn, A.W., Abraham, J.P., Andriamanario, A. and Ramananjatovo, A. (1990). The impact of selectice logging on forest structure and tenrec populations in western Madagascar. *Oecologia.* 84 (1), 126-133.

Gerloff, U., Hartung, B., Fruth, B., Hohmann, G. and Tautz, D. (1999). Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London B*, 266, 1189–1195.

Gibson, A. (2005). Orangutan nesting preference in a disturbed tropical deep-peat swamp forest, Central Kalimantan, Indonesia. MSc. Thesis, University of East Anglia.

Gillespie, T.R., Chapman, C.A. and Greiner, E.C. (2005). Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *Journal of Applied Ecology*, 42, 699-707.

Goldsmith, M.L. (2003). Comparative behavioral ecology of a lowland and highland gorilla population: Where do Bwindi gorillas fit? In: Taylor, A.B. and Goldsmith, M.L. (eds.) Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, UK, 358–384.

Goossens, B., Setchell, J.M., James, S.S., Funk, S.M., Chikhi, L., Abulani, A., Ancrenaz, M., Lackman-Ancrenaz, I. and Bruford, M.W. (2006a). Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*). *Molecular Ecology*. 15, 2577-2588.

Goossens, B., Chikhi, L., Ancrenaz, M., Lackman-Ancrenaz, I., Andau, P. and Bruford, M.W. (2006b). Genetic signature of anthropogenic population collapse in orang-utans. *Public Library of Science: Biology*, 4, 285-291.

Greenwood, P. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140-1162.

Groves, C.P. (1986). Systematics of the great apes. In: Swindler, D.R. and Erwin, J. (eds.) Comparative primate biology I. Systematics, evolution and anatomy. Alan R. Liss, New York, 187-217.

Groves, C.P. (1999). The taxonomy of orang-utans. In: Yeager, C. (ed.) Orang-utan Action Plan. Direktorat Jenderal Perlindungan dan Konservasi Alam, Jakarta, World

Wildlife Fund, Indonesia, and Center for Environmental Research and Conservation (CERC), Columbia University, New York, 27-30.

Gupta, A.K. and Chivers, D.J. (1999). Biomass and use of resources in south and south-east Asian primate communities. In: Fleagle, J.G., Janson, C. and Read, C.K. (eds.) Primate Communities. Cambridge University Press, Cambridge, 38–54.

Hanum, I.F and Lepun, P. (1999). Tree species composition of Kuala Langat North peat swamp forest, Selangor. Paper presented at the International Symposium on Tropical Peatlands - Safegarding a Global Natural Resource. August 1999, Universiti Sains Malaysia, Penang, August 1999.

Hardy, O.J. and Vekemans, X. (2002). SPAGeDi: a versatile computer programme to analyse spatial genetic structure at the individual or population level. *Molecular Ecology Notes*, 2, 618-620.

Harrison, M.E. (2009). Orang-utan feeding behaviour in Sabangau, Central Kalimantan. PhD Thesis, University of Cambridge, UK

Harrison, M.E and Chivers, D.J. (2007). The orang-utan mating system and the unflanged male: A product of increased food stress during the late Miocene and Pliocene? *Journal of Human Evolution*, 52, 275-293.

Harrison, M.E., Vogel, E.R., Morrogh-Bernard, H.C. and van Noordwijk, M.A. (2008). Methods for calculating activity budgets compared: A case study using orangutans. *American Journal of Primatology*, 70, 1-6.

Harrisson, B. (1969). The nesting behaviour of semi-wild juvenile orangutans. *Sarawak Museum Journal*, 17, 336–384.

Hayne, D.W. (1949). Calculation of size of home range. *Journal of Mammalogy*, 30, 1-18

Hearn, A.J. (2002). Bornean orang-utan (*Pongo pygmaeus*) habitat association in relation to forest structure and disturbance. MSc. Thesis, Department of Behavioural and Environmental Biology, Manchester Metropolitan University.

Heydon, M.J. and Bulloh, P. (1997). Mouse deer densities in a tropical rainforest: the impact of selective logging. *Journal of Applied Ecology*, 34, 484-496.

Homsy, J. (1999). Ape tourism and human diseases: How close should we get? A Critical Review of Rules and Regulations Governing Park Management and Tourism for the Wild Mountain Gorilla, *Gorilla gorilla beringei.* Consultancy for the International Gorilla Conservation Program. Nairobi. Available from: http://www.mountaingorillas.org/files/ourwork/Homsy_rev.pdf>.

van Hooff, J.A.R.A.M (1995). The orang-utan: A social outsider. A socio-ecological test case. In: Nadler, R.D., Galdikas, B.M.F., Sheeran, L.K. and Rosen, N. (eds.) The Neglected Ape. Plenum Press, New York, 153-162.

van Hooff, J.A.R.A.M. and van Schaik, C.P. (1994). Male bonds: Affilliative relationships among nonhuman primate males. *Behaviour*, 130, 309–337.

Hooijer, A., Silvius, M., Wosten, H. and Page, S.E. (2006). PEAT-CO_2: Assessment of CO2 emissions from drained peatlands in SE Asia. Delft Hydraulics report Q3943.

Horr, D.A. (1975). The Borneo orang-utan: population structure and dynamics in relationship to ecology and reproductive strategy. In: Rosenblum, L.A. (ed.) Primate Behaviour 4. New York, 307-323.

Husson, S.J. and Morrogh-Bernard, H.C. (2003). The Orang-utan population of the Sebangau River catchment. Orangutan Tropical Peatland Project Report.

Husson, S.J., Morrogh-Bernard, H., McLardy, C., Driscoll, R., Fear, N.F. and Page, S.E. (2002a). The effects of illegal logging on the population of orang-utan in the Sebangau tropical peat swamp forest, Central Kalimantan. In: Rieley, J.O. and Page, S.E. (eds.) Peatlands for People: Natural Resource Functions and Sustainable Management. Proceedings of the International Symposium on Tropical Peatland, 22-23 August 2001, Jakarta, Indonesia. BPPT and Indonesian Peat Association.

Husson, S.J., Baker, N. and Rieley, J.O. (2002b). The use of canals for illegal timber extraction in the Sebangau peat swamp forest ecosystem in Central Kalimantan, Indonesia. In: Rieley, J.O. and Page, S.E. (eds.) Peatlands for People: Natural Resource Functions and Sustainable Management. Proceedings of the International Symposium on Tropical Peatland, 22-23 August 2001, Jakarta, Indonesia. BPPT and Indonesian Peat Association.

Husson, S.J., Morrogh-Bernard, H.C., Dragiewicz, M., Struebig, M., Pearce, H. and Page, S.E. (2007). Mammal Fauna of the Sabangau Peat-swamp Forest. Available from www.orangutantrop.com/Mammallist2007.pdf

Husson, S.J., Morrogh-Bernard, H., Darcy, L., Cheyne, S., Harrison, M. and Dragiewicz, M. (2008). The importance of ecological monitoring for habitat management: A case study in the Sabangau forest, Central Kalimantan, Indonesia. In: Rieley, J.O. and Radjagukguk, B. (eds.) Carbon-climate-human interaction on tropical peatlands. Proceedings of the International Symposium and Workshop on Tropical Peatlands. Yogyakarta, 27-29 August 2007. Gadjah Mada University, Indonesia and University of Leicester, UK.

Husson, S.J., Wich., S.A., Marshall, A.J., Dennis, R.D., Ancrenaz, M., Brassey, R., Gumal, M., Hearn, A.J., Meijaard, E., Simorangkir, T. and Singleton, I. (2009). Orang-utan distribution, density, abundance and impacts of disturbance. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Husson, S.J., McLardy, C.S., Morrogh-Bernard, H.C., D'Arcy, L.J. and Limin, S.H. (in prep.) Changes in orangutan population density in the Sabangau forest between 1996 and 2007: evidence of logging-induced crowding and a sudden decline in population size.

Ibrahim, S. (1997). Diversity of tree species in peat swamp forest in Peninsular Malaysia. In : Rieley, J.O. and Page, S.E. (eds.) Biodiversity and Sustainability of Tropical Peatlands. Samara Publishing, Cardigan.

Isbell, L.A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143-155.

Jacobs, J. (1974). Quantitative measurements of food selection: a modification of the forage ratio and Ivlev's selectivity test. *Oecologia*, 14, 413-417.

Janzen, D.H. (1974). Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica*, 6, 69-103.

Johns, A. (1986). Effects of selective logging on the behavioural ecology of West Malaysian primates. *Ecology*, 67 (3), 684-694.

Johns, A.D. (1988). Effects of “selective” timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica*, 20(1), 31-37.

Johns, A.D. (1997). Timber Products and Biodiversity Conservation in Tropical Rain Forests. Cambridge University Press, Cambridge.

Johns, A.D. and Skorupa, J.P. (1987). Response of rainforest primates to habitat disturbance: A review. *International Journal of Primatology*, 8, 157-191.

Johns, J.S., Barreto, P. and Uhi, C. (1996). Logging damage during planned and unplanned logging in the eastern amazon. *Forest Ecology and Management*, 89, 59-77.

Johnson, A.E., Knott, C.D., Pamungkas, B., Pasaribu, M. and Marshall, A.J. (2005). A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. *Biological Conservation*, 121, 495-507.

Kalinowski, S.T., Taper, M.L. and Marshall, T.C. (2006). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16, 1099-1106.

Kano, T. and Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In: Susman, R.L. (ed.) The pygmy chimpanzee, evolutionary biology and behaviour. Plenum Press, New York, 233-274.

Kappeler, P.M. (1997). Intrasexual selection in *Mirza coquereli*: Evidence for scramble competition polygyny in a solitary primate. *Behavioral Ecology and Sociobiology*, 41, 115–128.

Kappeler, P.M and van Schaik, C.P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23 (4), 707-740.

Karasov, W.H. (1981). Daily energy expenditure and the cost of activity in a free living mammal. *Oecologia*, 51, 253- 259.

Kenyon, M.A. (2008). The ecology of the golden-cheeked gibbon (*Nomascus gabriellae*) in Cat Tien National Park, Vietnam. PhD Thesis, University of Cambridge, UK.

Knop, E., Ward, P.I. and Wich, S.A. (2004). A comparison of orang-utan density in a logged and unlogged forest on Sumatra. *Biological Conservation,* 120, 187-92.

Knott, C.D. (1998). Changes in orangutan diet, caloric intake and ketones in response to fluctuating fruit availability. *International Journal of Primatology*, 19, 1061-1079.

Knott, C.D. (1999a). Orang-utan behaviour and ecology. In: Dolhinow, P. and Fuentes, A. (eds.) The Nonhuman Primate. Mayfield Publishing Company, Mountain View, CA, 50-57.

Knott, C.D (1999b). Reproductive, physiological and behavioural responses of orang-utans in Borneo to fluctuations in food availability. PhD Thesis. Department of Anthropology, Harvard University, Cambridge, USA.

Knott, C.D. (2001). Female reproductive ecology of the apes: implications for human evolution. In: Ellison, P.T. (ed.) Reproductive Ecology and Human Evolution. Walter de Gruyter, New York, 429-463.

Knott, C.D. (2005). Energetic responses to food availability in the great apes: Implications for human evolution. In: Brockman, D. and van Schaik, C.P. (eds.) Primate seasonality: implications for human evolution. Cambridge University Press, Cambridge, UK, 351-378.

Knott, C.D., Beaudrot, L., Snaith, T., White, S., Tschauner, H and Planansky, G. (2008). Female-female competition in Bornean orang-utans. *International Journal of Primatology*, 29, 975-997.

von Koenigswald, G.H.R. (1982). Distribution and evolution of the orangutan, *Pongo pygmaeus.* In: de Boer, L.E.M. (ed.) The orang utan: its biology and conservation. Dr. W. Junk Publishers, The Hague.

Kondgen, S., Kuhl, H., N'Goran, P.K., Walsh, P.D., Schenk, S., Ernst, N., Biek, R., Formenty, P., Matz-Rensing, K., Schweiger, B., Junglen, S., Ellerbrok, H., Nitsche, A., Bries, T., Lipkin, W.I., Pauli, G., Boesch, C. and Leendertz, F.H. (2008). Pandemic human viruses cause decline of endangered great apes. *Current Biology*, 18, 260-264.

Lackman-Ancrenaz, I. and Ancrenaz, M. (2006). Eight years of orang-utan behaviour studies in Kinabatangan. KOCP Internal Publications, Kota Kinabalu, Sabah.

Laurent, D. (1986). Kalimantan Ramin and Agathis, where do you come from and how are you harvested? *Bois et Forets des Tropiques*, 211, 59-73.

Lehmann, J., Korstjens, A.H. and Dunbar, R.I.M. (2008). Time and distribution: a model of ape biogeography. *Ethology, Ecology and Evolution*, 20 (4).

Leighton, M. (1993). Modeling dietary selectivity by Bornean orang-utans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology*, 14 (2), 257-313.

Leighton, M. and Leighton, D.R. (1983). Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds.) Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publishers, Oxford, 181-196.

Li, C.C., Weeks, D.E. and Chakravarti, A. (1993). Similarity of DNA fingerprints due to chance and relatedness. *Human Heredity*, 43, 45-52.

Lodwick, J.L., Borries, C., Pusey, A.E., Goodall, J. and McGrew, W.C. (2004). From nest to nest - influence of ecology and reproduction on the active period of adult Gombe chimpanzees. *American Journal of Primatology*, 64, 249-260.

Lynch, M. and Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, 152, 1753-1766.

MacKinnon, J. (1971). The orang-utan in Sabah today. *Oryx,* 11 (2-3), 141-191.

MacKinnon, J. (1974). The behaviour and ecology of wild orang-utans. *Animal Behaviour*, 22, 3-74.

MacKinnon, J.R. (1977). A comparative ecology of Asian apes. *Primates*, 18, 747-772.

MacKinnon, J. (2007). Palm oil: The biofuel of the future driving an ecological disaster now. *The Guardian*, April 4th 2007.

Maggioncalda, A.N., Czekala, N.M. and Sapolsky, R.M. (2002). Male orang-utan subadulthood: A new twist on the relationship between chronic stress and developmental arrest. *American Journal of Physical Anthropology,* 118, 25-32.

Mansor, M., Mansor, A., Ahmad, A., Ali, A. and Ahmad, A.H. (2001). Fish and insect diversity in Malaysian peat swamp ecosystem. *International Journal for the Management of Tropical Peatlands*, 1, 27-29.

Maple, T. (1980). Orang-utan behaviour. van Nostrand Reinhold, New York.

Marr, C. (1996). Mega-project spells doom for Kalimantan peat forests. *Down to Earth Newsletter*, 29/30, August 1996

Marsh, C.W., Johns, A.D. and Ayres, J.M. (1987). Effects of habitat disturbance on rainforest primates. In: Marsh, C.W. and Mittermeier, R.A. (eds.) Monographs of Primatology, Vol 9. Primate Conservation in the Tropical Rain Forest. Alan R. Liss, New York, 83-108.

Marshall, A.J. and Wrangham, R.W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28, 1219-1235.

Marshall, A.J., Nardiyono, Engström, L.M., Pamungkas, B., Palapa, J., Meijaard, E. and Stanley, S. (2006). The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biological Conservation,* 129, 566-578.

Marshall, A.J., Lacy, R., Ancrenaz, M., Byers, O., Husson, S.J., Leighton, M., Meijaard, E., Rosen, N., Singleton, I., Stephens, S., Traylor-Holzer,K., Utami Atmoko., S.S., van Schaik, C.P. and Wich, S.A. (2009a). Orang-utan population biology, life history and conservation. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Marshall, A.J., Ancrenaz, M., Brearley, F.Q., Fredriksson, G.M., Ghaffar, N., Heydon, M., Husson, S.J., Leighton, M., McConkey, K.R., Morrogh-Bernard, H.C., Proctor, J., van Schaik, C.P., Yeager, C.P. and Wich, S.A. (2009b). The effects of forest phenology and floristics on populations of Bornean and Sumatran orang-utans. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Marshall, T.C., Slate, J. and Pemberton, J.M. (1998). Statistic confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, 7, 639-655.

Martin, P. and Bateson, P. (1986). Measuring Behaviour. Cambridge University Press, Cambridge, UK.

McConkey, K. (2005). Bornean orangutan. In: Caldecott, J. and Miles, L. (eds.) World atlas of great apes and their conservation. University of California Press, Berkeley, CA, 161-184.

McConkey, K.R., Ario, A., Aldy, F. and Chivers, D.J. (2003). Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan. *International Journal of Primatology*, 24 (1), 19-32.

McGrew, W.C. (1992). Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge, UK.

McGrew, W.C. (1998). Behavioral diversity in populations of free-ranging chimpanzees in Africa: Is it cultural? *Human Evolution*, 13, 209-220.

McNeilage, A. (2001). Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins, M.M., Sicotte, P., and Stewart, K.J. (eds.) Mountain Gorillas: Three Decades of Research at Karisoke, Cambridge University Press, Cambridge, UK, 265-292.

Meijaard, E., Sheil, D., Nasi, R. and Stanley, S.A. (2006). Wildlife conservation in Bornean timber concessions. *Ecology and Society*, 11(1), 47.

Meijaard, E. and Sheil, D. (2008). The presence and conservation of Borneo's mammals in lowland rainforest managed for timber: Observations, overview and opportunities. *Ecological Research*, 23, 21-34.

Meijaard, E., Sheil, D., Nasi, D.R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S. and O'Brien, T.G. (2005). Life After Logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo. Center for International Forestry Research, Jakarta, Indonesia.

Meijaard, E., Sheil, D., Marshall, A.J. and Nasi, R. (2008). Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica*, 40 (1), 76-85.

Milton, K. (1980). The foraging strategy of howler monkeys: A study in primate economics. Columbia University Press, New York.

Mitani, J.C. (1985). Mating behaviour of male orang-utans in the Kutai Reserve, Indonesia. *Animal Behaviour*, 33, 392-402.

Mitani, J.C. (1989). Orangutan activity budgets: monthly variations and the effects of body size, parturition, and sociality. *American Journal of Primatology*, 18, 87-100.

Mitani, J.C. and Rodman, P.S. (1979). Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioural Ecology and Sociobiology*, 5, 241-251.

Mitani, J.C., Grether, G.F, Rodman, P.S. and Priatna, D. (1991). Associations among wild orang-utans: sociality, passive aggregations or chance? *Animal Behaviour*, 42, 33-46.

Mitra Setia, T., Delgado, R.A., Utanmi Atnoko, S.S., Singleton, I. and van Schaik, C.P. (2009). Social organisation and male-female relationships. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Mongabay.com (2007). 2006 Indonesian forest fires worst since 1998. http://news.mongabay.com/2007/0301-nasa.html.

Morf, N. (2008). Sex-biased dispersal in Bornean orang-utans (*Pongo pygmaeus wurmbii*). MSc. thesis. University of Zurich.

Morrogh-Bernard, H.C. (2008). Fur-Rubbing as a Form of Self-Medication in *Pongo pygmaeus. International Journal of Primatology*, 29(4), 1059-1064.

Morrogh-Bernard, H.C. and Husson, S.J. (2002). Annual report on research undertaken in the greater Sebangau catchment, Central Kalimantan, Indonesia. Orang-utan Tropical Peatland Research Project.

Morrogh-Bernard. H., Husson, S. and McLardy, C. (2002). Orangutan data collection standardisation. LSB Leakey Foundation Orang-utan Culture Workshop, San Anselmo, CA.

Morrogh-Bernard, H., Husson, S.J., Page, S.E. and Rieley, J.O. (2003). Population status of the Bornean Orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. *Biological Conservation*, 110 (1), 141-151.

Morrogh-Bernard, H.C., Husson, S.J., Knott, C.D., Wich, S.A., van Schaik, C.P., van Noordwijk, M.A., Lackman-Ancrenaz, I., Marshall, A.J., Kanamori, T., Kuze, N. and bin Sakong, R. (2009). Orang-utan activity budgets and diet. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Moses, R.A. and Millar, J.S. (1994). Philopatry and mother–daughter associations in bushy-tailed woodrats: space use and reproductive success. *Behavioral Ecology and Sociobiology*, 35, 131-140.

Mossman, C.A. and Waser. P.M. (1999). Generic detection of sex-biased dispersal. *Molecular Ecology*, 8, 1063-1067.

Muir, C. (1998). Is there sufficient evidence to elevate the orang-utan of Bornean and Sumatra to separate species? *Journal of Molecular Evolution*, 46, 378-381.

Murray, C.M., Mane, S.V. and Pusey, A.E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): towards an ideal despotic distribution. *Animal Behaviour*, 74, 1795-1804.

Murray, C.M., Gilby, I.C., Mane, S.V. and Pusey, A.E. (2008). Adult male chimpanzees inherit maternal ranging patterns. *Current Biology*, 18, 20-24.

Nei, M. (1987). Molecular evolutionary genetics. Columbia University Press, New York.

Nellemann, C., Miles, L., Kaitendorn. B.P., Virtue, M. and Ahlenius, H. (2007). The last stand of the orang-utans - State of emergency: Illegal logging, fire, and oil palm in Indonesia's National Parks. UNEP Report, GRID-Arendal, Norway.

Nelson, J. (1995). Determinents of male spacing behaviour in microtines: an experimental manipulation of female spatial distribution and density. *Behavioural Ecology and Sociobiology*, 37, 217-223.

Nesbitt, M. (2001). Spatial distribution of fruit abundance and diversity and the possible link with orang-utan, P*ongo pygmaeus* distribution**.** BSc. Dissertation, University of Leeds, UK

Nijman, V. (2004). Effects of habitat disturbance and hunting on the density and the biomass of the endemic Hose's leaf monkey *Presbytis hosei* (Thomas, 1889) (Mammalia: Primates: Cercopithecidae) in Borneo. *Contribution to Zoology*, 73(4), 283-291.

Nishida, T., Takasaki, H. and Takahata, Y. (1990). Demography and reproductive profiles. In: Nishida, T. (ed.) The Chimpanzees of the Mahale Mountains. University Press of Tokyo, Tokyo, 63–97.

van Noordwijk, M.A. and van Schaik, C.P. (2005). Development of ecological competence in Sumatran orang-utans. *American Journal of Physical Anthropology*, 127, 79-94.

Page, S.E., Rieley, J.O., Doody, K., Hodgson, S., Husson, S., Jenkins, P., Morrogh-Bernard, H., Otway, S. and Wilshaw, S. (1997). Biodiversity of tropical peat swamp forest: a case study in Central Kalimantan. In: Rieley, J.O. and Page, S.E. (eds.) Biodiversity and Sustainability of Tropical Peatlands. Samara Publishing, Cardigan, UK, 231-242.

Page, S.E., Rieley, J.O., Shotyk, W. and Weiss, D. (1999). Interdependence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society of London B*, 354, 1885-1897.

Page, S.E., Rieley, J.O. and Wűst, R. (2006). Lowland tropical peatlands of Southeast Asia. In: Martini, I.P., Martínez Cortizas, A. and Chesworth, W. (eds.) *Peatlands: Evolution and Records of Environmental and Climate Changes,* Elsevier, Amsterdam/Oxford, 145–172.

Page, S.E., Siegert, F., Rieley, J.O., Boehm, H-D.V., Jaya, A. and Limin, S. (2002). The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, 420, 61-63.

Peres, C.A. (1994). Primate responses to phenological changes in an Amazonian terra firma forest. *Biotropica*, 26 (1), 98-112.

Perrin, N. and Mazalov, V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist*, 155, 116–127.

Plumptre, A.J and Johns, A.G. (2001). Changes in primate communities following logging disturbance. In: Fimbel, R.A., Grajal, A. and Robinson, J.G. (eds). The cutting edge: Conserving wildlife in tropical forests. Columbia University Press, New York.

Plumptre, A.J. and Reynolds, V. (1994). The effect of selective logging on primate populations in the Budongo forest, Uganda. *The Journal of Applied Ecology*, 331 (4), 631-641.

Poulin, B., Wright, S.J., Lefebvre, G. and Calderon, O. (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology*, 15, 213-227.

Powell, R.A. (2000). Animal home ranges and territories and home range estimators. In: Boitani, L. and Fuller, T.K (eds.) Research techniques in animal ecology. Controversies and consequences. Columbia University Press, New York.

Pusenius, J., Viitala, J., Marianberg, T. and Ritvanen, S. (1997). Matrilinear kin clusters and their effect on reproductive success in the field vole. *Behavioral Ecology*, 9, 85–92.

Pusey, A.E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution*, 2, 295-299.

Pusey, A.E. and Packer, C. (1987). Dispersal and philopatry. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Struhsaker, T.T. (eds.) Primate Societies. Chicago University Press, Chicago, 250-266.

Putz, F.E. (1979). Aseasonality in Malaysian tree phenology. *Malaysian Forester*, 42, 1-24.

Queller, D.C. and Goodnight, K.F. (1989). Estimating relatedness using genetic-markers. *Evolution*, 43, 258-275.

Rao, M. and van Schaik, C.P. (1997). The behavioural ecology of Sumatran orang-utans in logged and unlogged forest. *Tropical Biodiversity*, 4 (2), 173-185.

Rieley, J.O. (2001). Overview of tropical peatlands: location, extent, importance and impact. *International Journal of Tropical Peatlands*, 1, 1-7.

Rieley, J.O., Sieffermann, R.G. and Page, S.E. (1992). The origin, development, present status and importance of the lowland peat swamp forests of Borneo. *Suo*, 43, 241-244.

Rieley, J.O., Page, S.E., Limin, S.H. and Winarti, S. (1997). The peatland resources of Indonesia and the Kalimantan Peat Swamp Forest Research Project. In: Rieley, J.O. and Page, S.E. (eds.) Biodiversity and Sustainability of Tropical Peatlands. Samara Publishing, Cardigan, UK, 37-44

Rieley, J.O., Page, S.E. and Limin, S.H. (2005). Peatlands in southeast asia as habitat for orang-utans. In: Caldecott, J. and Miles, L. (eds.) World atlas of great apes and their conservation. Prepared at the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA.

Rijksen, H.D. (1978). A Field Study on Sumatran Orang Utans (*Pongo pygmaeus abelii* Lesson 1827). Ecology, Behaviour and Conservation. H. Veenan and Zonen, Wageningen.

Rijksen, H.D. and Meijaard, E. (1999). Our Vanishing Relative: The status of wild orang-utans at the close of the twentieth century. Kluwer Academic Publishers, Dordrecht.

Rijksen, H.D., Ramono, W., Sugardijito, J., Lelana, A., Leighton, M., Karesh, W., Shapiro, G., Seal. U.S., Traylor-Holzer, K. and Tilson, R. (1995). Estimates of orang-utan distribution and status in Borneo. In: Nadler, R.D., Galdikas, B.M.F., Sheeran, L.K. and Rosen, N. (eds.) The Neglected Ape. Plenum Press, New York, 117-122.

Robertson, J.M.Y. and van Schaik, C.P. (2001). Causal factors underlying the dramatic decline of the Sumatran orang-utan. *Oryx*, 35(1), 26-38.

Rode, K.D., Chapman, C.A., McDowell, L.R. and Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtailed monkeys (*Cercopithecus ascanius*). *Biotropica*, 38 (5), 625-634.

Rodman, P.S. (1973). Population composition and adaptive organisation among orang-utans of the Kutai Reserve. In: Crook, H.D. (ed.) Comparative ecology and behaviour of primates. Academic Press, London, 171–209.

Rodman, P.S. (1977). Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brock, T.H. (ed.) Primate ecology. Academic Press, London, 381-413.

Rodman, P.S. (1988). Diversity and consistency in ecology and behaviour. In: Orang-utan Biology. Schwartz, J. (ed.) Oxford University Press, New York, 31-51.

Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., Mcfarland, K., Nishihara, T., Remis, M. and Tutin, C.E.G. (2004). Western gorilla diet: A synthesis from six sites. *American Journal of Primatology*, 64, 173-192.

Rohlf, F.J. (1973). Algorithm 76: Hierarchical clustering using the minimum spanning tree. *Computer Journal*, 16, 93-95.

Russon, A.E., Erman, A. and Dennis, R. (2001). The population and distribution of orang-utans (*Pongo pygmaeus pygmaeus*) in and around the Danau Sentarum Wildlife Reserve, West Kalimantan, Indonesia. *Biological Conservation*, 97, 21-28.

Russon, A.E., Wich, S.A., Ancrenaz, M., Kanamari, T., Knott, C.D., Kuze, N., Morrogh-Bernard, H.C., Pratje, P., Ramlee, H., Rodman, P., Sawang, A., Sidiyasa, K., Singleton, I. and van Schaik, C.P. (2009). Geographic variation in orang-utan diets. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Sakai, S., Harrison, R.D., Momose. K., Kuraji, K., Nagamasu, H., Yasunari, T., Chong, L. and Nakashizuka, T. (2006). Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany*, 93, 1134-1139.

Sastrawan, R. (2006). Burning peatlands is threatening the orang-utans. Bornean Orangutan Survival Foundation, www.save the orangutan.co.uk.

van Schaik, C.P. (1986). Phenological changes in a Sumatran rainforest. *Journal of Tropical Ecology,* 2, 327-347.

van Schaik, C.P. (1996). Social evolution in primates: The role of ecological factors and male behaviour. *Proceedings of the British Academy*, 88, 9-31.

van Schaik, C.P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, 40, 69-86.

van Schaik, C.P. and van Hooff, J.A.R.A.M. (1996). Towards an understanding of the orang-utan's social system. In: McGrew, W.C., Marchant, L.F. and Nishida, T. (eds.) Great Ape Societies. Cambridge University Press, Cambridge, 3-15.

van Schaik, C.P. and Knott, C.D. (2001). Geographic variation in tool use on Neesia fruits in orangutans. *American Journal of Physical Anthropology*, 111, 331-342.

van Schaik, C.P and Pfannes, K.P. (2005). Tropical climate and phenology: A primate perspective. In: Brockman, D.K. and van Schaik, C.P. (eds.) Primate seasonality: implications for human evolution. Cambridge University Press, Cambridge, 23-54.

van Schaik, C.P., Terborgh, J.W. and Wright, S.J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*, 24, 353-377.

van Schaik, C.P., Azwar, M.S. and Priatna, D. (1995). Population estimates and habitat preferences of the orang-utan based on line transects of nests. In: Nadler, R.D., Galdikas, B.M.F., Sheeran, L.K. and Rosen, N. (eds.) The Neglected Ape. Plenum Press, New York and London, 129-147

van Schaik, C.P., Monk, K.A. and Yarrow Robertson, J.M. (2001). Dramatic decline in orang-utan numbers in the Leuser Ecosystem, Northern Sumatra. *Oryx*, 35(1), 14-25.

van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B.M.F., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S. and Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299, 102-105.

Schurmann, C.L. (1982). Courtship and mating behavior of wild orangutans in Sumatra. In: Chiarelli, A.B. and Corrucini, R.S. (eds.) Primate behavior and socio-biology. Springer Verlag, Berlin, 129–135.

Schurmann, C.L. and van Hooff, J.A.R.A.M. (1986). Reproductive strategies of the orang-utan: new data and a reconsideration of existing sociosexual models. *International Journal of Primatology*, 7, 265–287.

Seaman, D.E. and Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77 (7), 2075-2085.

Setiawan, E., Knott, C.D. and Budhi, S. (1996). Preliminary assessment of vigilance and predator avoidance behaviour of orang-utans in Gunung Palung National Park, West Kalimantan, Indonesia. *Tropical Biodiversity*, 3 (3), 268-279.

Shepherd, P.A., Rieley, J.O. and Page, S.E. (1997). The relationship between forest vegetation and peat characteristics in the upper Sebangau catchment, Central Kalimantan. In: Rieley, J.O. and Page, S.E. (eds.) Biodiversity and Sustainability of Tropical Peatlands. Samara Publishing, Cardigan, UK, 191-210.

Siegel, S. and Castellan, N.J. (1988). Nonparametric Statistics for the Behavioural Sciences. 2nd Ed. McGraw-Hill, New York.

Siegert, F., Rucker, G., Hinrichs, A. and Hoffmann, A. (2001). Increased fire impacts in logged over forests during El Nino driven fires. *Nature*, 414, 437-440

Silverman, B.W. (1986). Density estimation for statistics and data analysis. Chapman and Hall, London.

Singleton, I. (2000). Ranging Behaviour and Seasonal Movements of Sumatran Orangutans (*Pongo pygmaeus abelii*) in Swamp Forests. PhD Thesis, Durrell Institute of Conservation and Ecology, University of Kent at Canterbury, UK.

Singleton, I. and van Schaik, C.P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, 22 (6), 877-911.

Singleton, I. and van Schaik, C.P. (2002). The social organisation of a population of Sumatran orang-utan. *Folia Primatologica*, 73, 1-20.

Singleton, I., Wich, S., Husson, S., Stephens, S., Utami Atmoko, S., Leighton, M., Rosen, N., Traylor-Holzer, K., Lacy, R. and Byers, O. (2004). Orangutan Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA.

Singleton, I., Knott, C.D., Morrogh-Bernard, H.C., Wich, S.A and van Schaik, C.P. (2009). Ranging behavior of orangutan females and social organization. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Spitzer, K., Jaros, J., Havelka, J. and Leps, J. (1997). Effects of small scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, 80, 9-15.

Stamps, J. (1995). Motor learning and the value of familiar space. *Animal Naturalist*, 146, 41-58.

Sterck, E.H.M. (1998). Female dispersal, social organisation, and infanticide in langurs: Are they linked to human disturbance? *American Journal of Primatology*, 44, 235-254.

Strier, K.B. (1987). Ranging behavior of woolly spider monkeys, or muriquis, *Brachyteles arachnoides*. *International Journal of Primatology*, 8, 575-591.

Strier, K.B. (2000). Primate Behavioural Ecology. Allyn and Bacon, Pearson Education Inc.

Sugardjito, J. (1983). Selecting nest sites of Sumatran orang-utans, *Pongo pygmaeus abelii*, in the Gunung Leuser National Park, Indonesia. *Primates*, 24 (4), 467-474.

Sugardjito, J. and van Schaik, C.P. (1991). Orang-utans: Current Population Status, Threats and Conservation Measures. In: Proceedings of the Great Ape Conference, December 15-22, 1991, Indonesia.

Sugardjito, J., te Boekhorst, I.J.A. and van Hooff, J.A.R.A.M. (1987). Ecological constraints on the grouping of wild orangutans in the Gunung Leuser National Park, Sumatra, Indonesia. *International Journal of Primatology*, 8(1), 17-41.

Sugiyama, Y. (1991). Habitat isolation and population structure of wild chimpanzees in and around Bossou, West Africa. In: Maruyama, N., Bobek, B., Ono, Y., Regelin, W., Bartos, L. and Ratcliffe P.R. (eds.) Wildlife Conservation: Present Trends and Perspectives for the 21st Century. Japan Wildlife Research Center, Tokyo, Japan, 32-35.

Sutherland, W.J. (1996). Ecological census methods. Cambridge University Press, Cambridge, UK.

Suzuki, A. (1991). Feeding adaptations of orang-utans after the forest fires in East Kalimantan. In: Proceedings of the Great Ape Conference, December 15-22, 1991, Indonesia.

Suzuki, A. (1992). The population of Orangutans and other non-human primates and the forest conditions after the 1982-83's fires and droughts in Kutai National Park, East Kalimantan, Indonesia. In: Ismail, G., Mohamed, M. and Omar, S. (eds). Forest biology and conservation in Borneo. Center for Borneo Studies, Kota Kinabalu, 190-205.

Taylor, A.B. (2006). Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of Pongo. *Journal of Human Evolution,* 50, 377-393.

Thompson, C.J.H. (2007). Gibbon locomotion in disturbed peat swamp forest, Sebangau, Central Kalimantan. MSc. Thesis, The Anatomy School, University of Cambridge.

Thorpe, W. H. (1963). Learning and instinct in animals. Methuen, London.

Thorpe, S.K.S. and Crompton, R.H. (2005). Locomotor ecology of wild orangutans (*Pongo pygmaeus abelli*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modelling. *American Journal of Physical Anthropology*, 127, 58-78.

Thorpe, S.K.S., Crompton, R.H. and Alexander, R.M. (2007). Orang-utans use compliant branches to lower the energetic cost of locomotion. *Biological Letters*, 3, 253-256.

Trent, S. (ed). (1998). The Politics of Extinction: The Orang-utan Crisis and the Destruction of Indonesia's Forests. Environmental Investigation Agency, Emmerson Press.

Trevor-Deutsch, B. and Hackett, D.F. (1980). An evaluation of several grid trapping methods by comparison with radio telemetry in a home range study of the Eastern chipmunk (*Tamias striatus L).* In: Amlaner, C.J and Macdonald, D.W. (eds.) A hand book on biotelemetry and radio tracking. Pergamon, Oxford, 375-386.

Tutin, C.E.G. (1996). Ranging and social structure of lowland gorillas in the Lope Reserve. Gabon. In: McGrew, W.C., Marchant, L.F. and Nishida, T. (eds.) Great Ape Societies. Cambridge University Press. Cambridge, 58-70.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A., McGrew, W.C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope´ Reserve, Gabon. *Philosophical Transactions of the Royal Society of London Series B*, 334, 179-186.

Uchida, A. (1998). Variation in tooth morphology of *Pongo pygmaeus*. *Journal of Human Evolution*, 34, 71-79.

Ungar, P.S. (1995). Fruit preference of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. *International Journal of Primatology*, 16 (2), 221-245.

Utami, S.S. and van Hooff, J.A.R.A.M. (1997). Meat-eating by adult female Sumatran orang-utans (*Pongo pygmaeus abelli*) *American Journal of Primatology*, 43, 159-165.

Utami, S.S. and Mitra Setia, T. (1995). Behavioral changes in wild male and female Sumatran orangutans (*Pongo pygmaeus*) during and following a resident male take-over. In: Nadler, R.D., Galdikas, B.M.F., Sheeran, L.K. and Rosen, N., (eds.) The Neglected Ape. Plenum Press, New York, 183-190.

Utami, S.S., Wich, S.A., Sterck, E.H.M. and van Hooff, J.A.R.A.M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology*, 18, 909-927.

Utami, S.S., Goossens, B., Bruford, M.W., De Ruiter, J.R. and van Hooff, J.A.R.A.M. (2002). Male bimaturism and reproductive success in Sumatran orangutans. *Behavioural Ecology*, 13(5), 643-652.

Utami Atmoko, S.S, Mitra Setia, T., Goossens, B., James, S.S., Knott, C.D., Morrogh-Bernard, H.C., van Schaik, C.P. and van Noordwijk, M.A. (2009). Orangutan mating behavior and strategies. In: Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Wang, J.L. (2002). An estimator for pairwise relatedness using molecular markers. *Genetics*, 160, 1203-1215.

Warren, R.D. and Crompton, R.H. (1998). Diet, body size and the energy costs of locomotion in salutatory primates. *Folia Primatologica*, 69(suppl 1), 86-100.

Warren, K.S., Verschoor, E.J., Langenhuijzen, S., Heriyanto Swan, R.A., Vigilant, L. and Heeney, J.L. (2001). Speciation and intrasubspecific variation of Bornean orangutans, *Pongo pygmaeus pygmaeus*. *Molecular Biology and Evolution*, 18, 472-480.

Watts, D. (1991). Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology*, 24, 211-225.

Weiss, D., Shotyk, W., Rieley, J., Page, S., Gloor, M., Reese, S. and Martinez-Cortizas, A. (2002). The geochemistry of major and selected trace elements in a forested peat bog, Kalimantan, SE Asia, and its implications for past atmospheric dust deposition. *Geochimica et Cosmochimica Acta*, 66, 2307-2323.

Wheatley, B.P. (1982). Energetics in foraging in *Macaca fascicularis* and *Pongo pygmaeus* and the selective advantage of large body size in the orangutan. *Primates*, 23 (3), 348-363.

Wich, S.A. and van Schaik, C.P. (2000). The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology*, 16, 563-577.

Wich, S.A., Sterck, E.H.M. and Utami, S.S. (1999). Are orang-utan females as solitary as chimpanzee females? *Folia Primatoligica*, 70, 23-29.

Wich, S.A., Fredriksson, G. and Sterck, E.H.M (2002). Measuring fruit patch size for three sympatric Indonesian primate species. *Primates*, 43(1), 19-27.

Wich, S.A., Utami-Atmoko, S.S., Mitra Setia, T., Rijksen, H.D., Schurmann, C., van Hooff, J.A.R.A.M. and van Schaik, C.P. (2004a). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution,* 47, 385-398.

Wich, S.A., Buij, R. and van Schaik, C.P. (2004b). Determinants of orangutan density in the dryland forests of the Leuser Ecosystem. *Primates*, 45, 177-182.

Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T., Djojosudharmo, S. and Geurts, M.L. (2006b). Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *International Journal of Primatology,* 27, 1535-50.

Wich, S.A., Geurts, M.L., Mitra Setia, T. and Utami Atmoko, S.S. (2006b). Influence of fruit availability on Sumatran orangutan sociality and reproduction. In: Hohmann, G., Robbins, M.M. and Boesch, C. (eds.) Feeding Ecology of the Apes and other Primates. Cambridge University Press, Cambridge, 337-358.

Wich, S.A., Utami Atmoko, S.S., Mitra Setia, T. and van Schaik, C.P. (eds.) (2009). Orangutans: Geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, UK.

Wich, S.A., Morrogh-Bernard, H.C., Husson, S.J., Geurts, M.L. and van Schaik, C.P. (in prep.). Diet differences between two Bornean orangutan (*Pongo pygmaeus wurmbii*) populations.

Williams, D.K. and Dunbar, R. (1999). Energetics, time budgets and group size. In: Lee, P.C. (ed.) Comparative primate socioecology. Cambridge University Press, Cambridge, UK.

Williams, J.M., Pusey, A.E., Carlis, J.V., Farm. B.P. and Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, 63, 357-360.

Williams, J.M., Oehlert, G.W., Carlis, J.V. and Pusey, A.E. (2004). Why do chimpanzees defend a group? *Animal Behaviour*, 68, 523-532.

Williamson, E.A. and Feistner, A.T.C. (2003). Habituating primates: Processes, techniques, variables and ethics. In: Setchell, J.M. and Curtis, D.J. (eds.) Field and laboratory methods in primates. Cambridge University Press, Cambridge, UK. 25-39.

Wilson, C.C. and Wilson, W.L. (1975). The influence of selective logging on primates and some other animals in East Kalimantan. *Folia Primatologica*, 23, 245-274.

Worton, B.J. (1989). The kernel method for estimating the utilisation distribution in home range studies. *Ecology*, 70, 164-168.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.

Wrangham, R.W, Conklin, N.L., Chapman, C.A. and Hunt, K.D. (1991). The significance of fibrous foods for Kibale forest chimpanzees. *Philosophical Transactions of the Royal Society of London*, 334, 171-178.

Xu, X.F. and Arnason, U. (1996). The mitochondrial DNA molecule of Sumatran orang-utan and a molecular proposal for two (Bornean and Sumatran) species of orang-utan. *Journal of Molecular Evolution*, 43, 431-437.

Yamagiwa, J. and Kahekwa, J. (2001). Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins, M.M., Sicotte, P. and Stewart, K.J. (eds.) Mountain Gorillas: Three Decades of Research at Karisoke. Cambridge University Press, Cambridge, UK, 90-122.

Yasuda, M., Matsumoto, J., Osada, N., Ichikawa, S., Kachi, N., Tani, M., Okuda, T., Furukawa, A., Nik A.R. and Manokaran, N. (1999). The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology*, 15, 437-449.

Yeager, C.P., Marshall, A.J., Stickler, C.M. and Chapman, C.A. (2003). Effect of fire on peat swamp and lowland dipterocarp forest in Kalimantan, Indonesia. *Tropical Biodiversity*, 8 (1), 121-138.

Zhang Yan-Wu, Ryder, O.A. and Zhang, Y. (2001). Genetic divergence of the orang-utan subspecies (*Pongo pygmaeus*). *Journal of Molecular Evolution*, 52, 516-526.

Appendix I. List of mammal species recorded in the Sabangau from 1993-2007 (Husson *et al.*, 2007).

English Name	**Latin Name**	**Habitat**	**IUCN**
South-east Asian white-toothed shrew	*Crocidura fuliginosa*	Camp	
Slender treeshrew	*Tupaia gracilis*	MLT	
Common treeshrew	*Tupaia glis*	MLT	
Painted treeshrew	*Tupaia picta*	MLT	
Ruddy treeshrew	*Tupaia splendidula*	MLT	
Lesser treeshrew	*Tupaia minor*	MLT	
Colugo	*Cynocephalus variegates*	M	
Large flying fox	*Pteropus vampyrus*	RM	
Tailless fruit bat	*Megarops ecaudatus*	M	
Lesser tube-nosed bat	*Murina suilla*	M	
Small woolly bat	*Kerivoula intermedia*	ML	NT
Least woolly bat	*Kerivoula minuta*	M	
Whitehead’s woolly bat	*Kerivoula whiteheadi*	M	
Clear-winged woolly bat	*Kerivoula pellucida*	M	
Hardwicke’s woolly bat	*Kerivoula hardwickii*	M	
Trefoil horseshoe bat	*Rhinolophus trifoliatus*	M	
Whiskered ? bat	*Myotis muricola*	M	
Slow loris	*Nycticebus coucang*	MT	
Western tarsier	*Tarsius bancanus*	M	
Red langur	*Presbytis rubicunda*	MT	
Silver langur	*Trachypithecus cristatus*	RM	
Proboscis monkey	*Nasalis larvatus*	RM	E
Long-tailed macaque	*Macaca fascicularis*	RM	NT
Pig-tailed macaque	*Macaca nemestrina*	MT	V
Bornean agile gibbon	*Hylobates albibarbis*	MLT	NT
Bornean orang-utan	*Pongo pygmaeus*	MLT	E
Pangolin	*Manis javanica*	M	
Giant squirrel	*Ratufa affinis*	MT	
Prevost's squirrel	*Callosciurus prevostii*	MT	
Horse-tailed squirrel	*Sundasciurus hippurus*	M	
Low's squirrel	*Sundasciurus lowii*	M	
Shrew-faced ground squirrel	*Rhinosciurus laticaudatus*	M	
Black-eared pygmy squirrel	*Nanosciurus melanotis*	MT	
Plain pygmy squirrel	*Exilisciurus exilis*	MT	
Plantain squirrel	*Callosciurus notatus*	MLT	
Black flying squirrel	*Aeromys tephromelas*	M	
Whiskered flying squirrel	*Petinomys genibarbis*	M	
Dark-tailed tree rat	*Niviventer cremoriventor*	M	
Grey tree rat	*Lenothrix canus*	M	
Muellers rat	*Sundamys muelleri*	MT	
Polynesian rat	*Rattus exulans*	ML	
Red spiny rat	*Maxomys rajah*	M	
Whiteheads rat	*Maxomys whiteheadi*	MLT	
Common porcupine	*Hystrix brachyura*	T	
Thick-spined porcupine	*Thecurus crassipinis*	T	
Sun-bear	*Helarctos malayanus*	MLT	DD
Yellow-throated marten	*Martes flagula*	M	

English Name	Latin Name	Habitat	IUCN
Malay weasel	*Mustela nudipes*	M	
Oriental small-clawed otter	*Abolnyx cinereus*	RM	NT
Hairy-nosed otter	*Lutra sumatrana*	R	
Common palm civet	*Paradoxurus hermaphroditus*	MT	
Malay civet	*Viverra tangalunga*	MT	
Small-toothed palm civet	*Arctogalidia trivirgata*	MT	
Banded Linsang	*Prionodon linsang*	ML	
Binturong	*Arctictis binturong*	MT	
Short-tailed mongoose	*Herpestes brachyurus*	(M)L	
Clouded leopard	*Neofelis nebulosa*	MT	V
Leopard cat	*Prionailurus bengalensis*	M	
Marbled cat	*Pardofelis marmorata*	M	V
Flat-headed cat	*Felis pleniceps*	M	
Bearded pig	*Sus barbatus*	RMLT	
Lesser mouse-deer	*Tragulus javanicus*	MT	
Greater mouse-deer	*Tragulus napu*	MT	
Borneo yellow muntjac	*Muntiacus atherodes*	T	
Sambar deer	*Cervus unicolor*	MT	

Key:

Habitats: R= River and Marsh habitat; M = Mixed Swamp Forest; L = Low Pole Forest; T = Tall Interior Forest; B = Burnt forest.

IUCN: CR = Critically endangered; E = Endangered; V = Vulnerable; NT = Near-threatened; DD = Data deficient

Appendix II. List of bird species recorded in the Sabangau from 1993-2007 (Dragiewicz *et al.*, 2007).

English name	**Latin Name**	**Habitat**	**IUCN**
Oriental darter	*Anhinga melanogaster*	R	
Great billed heron	*Ardea sumatrana*	R	
Purple heron	*Ardea purpurea*	R	
Striated heron	*Butorides striatus*	R	
Javan pond-heron	*Ardeola speciosa*	R	
Little egret	*Egretta garzetta*	R	
Cinnamon bittern	*Ixobrychus cinnamomeus*	R	
Storms stork	*Ciconia stormi*	RMT	E
Lesser adjutant stork	*Leptoptilos javanicus*	R	V
White-shouldered ibis	*Pseudibis davisoni*	R	CR
Lesser whistling duck	*Dendrocygna javanica*	R	
Osprey	*Pandion haliaetus*	M	
Brahminy kite	*Haliastur indus*	RM	
Wallaces hawk eagle	*Spizeatus nanus*	MLT	V
Black eagle	*Ictinaetus malayensis*	RML	
Jerdon's baza	*Aveiceda jerdoni*	M	NT
White-bellied fish eagle	*Haliaeetus leucogastur*	R	
Crested goshawk	*Accipter trivirgatus*	M	
Black-thighed falconet	*Microhierax fringillarius*	M	
Black partridge	*Melanoperdix nigra*	M	
Crestless fireback	*Lophura erythrophtalma*	MT	V
Great argus	*Argusianus argus*	M	NT
White breasted waterhen	*Amaurornis phoenicurus*	R	
Common sandpiper	*Tringa hypoleucos*	R	
Wood sandpiper	*Tringa glareola*	R	
Gull-billed tern	*Sternia nilotica*	R	
Thick-billed pigeon	*Treron curvirostra*	RMT	
Pink-necked green pigeon	*Treron vernans*	M	
Green imperial pigeon	*Ducula aenea*	MT	
Emerald dove	*Chalcophaps indica*	L	
Spotted dove	*Streptopelia chinensis*	R	
Blue-crowned hanging parrot	*Loriculus galgulus*	MLT	
Long-tailed parakeet	*Psittacula longicauda*	RMT	NT
Banded bay cuckoo	*Cacomantis sonnerati*	MT	
Plaintive cuckoo	*Cacomantis merulinus*	MTB	
Violet cuckoo	*Cacomantis xznthorhynchus*	M	
Drongo cuckoo	*Surniculus lugubris*	MT	
Chestnut-bellied malkoha	*Phaenicophaeus sumatranus*	MLT	NT
Chestnut-breasted malkoha	*Phaenicophaeus curvirostris*	MT	
Raffles malkoha	*Phaenicophaeus chlorophaea*	MT	
Greater common coucal	*Centropus sinensis*	M	
Lesser coucal	*Centropus bengalensis*	R	
Oriental bay owl	*Phodilus badius*	M	
Buffy fish-owl	*Ketupa ketupu*	M	
Brown hawk-owl	*Ninox scutulata*	MT	
Brown wood owl	*Strix leptogrammica*	MT	

English Name	Latin Name	Habitat	IUCN
Gould's frogmouth	*Batrachostomus stellatus*	L	
Savannah nightjar	*Caprimulgus affinis*	R	
Malaysian eared nightjar	*Eurostopodus temminckii*	M	
Bonaparte's nightjar	*Caprimulgus concretus*	LM	
Edible-nest Swiftlet	*Collocslisw fuciphaga*	R	
Glossy swiftlet	*Collacalia esculenta*	R	
Silver-rumped swift	*Raphidura leucopygialis*	RML	
Little swift	*Apus affinis*	RMLT	
Grey-rumped tree swift	*Hemiprocne longipennis*	MLT	
Red-naped trogon	*Harpactes kasumba*	MT	NT
Scarlet-rumped trogon	*Harpactes duvaucelii*	MT	NT
Diard's trogon	*Harpactes diardii*	MT	NT
Blue-eared kingfisher	*Alcedo coerulescens*	RMT	
Stork-billed kingfisher	*Pelargopsis capensis*	RML	
Black-backed kingfisher	*Ceyx erithacus*	RMT	
Rufous-backed kingfisher	*Ceyx rufidorsa*	MT	
Blue-throated bee-eater	*Merops viridis*	RMLT	
Dollarbird	*Eurystomus orientalis*	MT	
Wrinkled hornbill	*Aceros corrugatus*	MT	NT
Asian black hornbill	*Anthracoceros malayanus*	MT	NT
Oriental pied hornbill	*Anthracoceros albirostris*	M	
Rhinoceros hornbill	*Buceros rhinocerus*	MT	NT
Helemeted hornbill	*Buceros vigil*	T	NT
Blue-eared barbet	*Megalaima australis*	MLT	
Red-crowned barbet	*Megalaima rafflesi*	MLT	NT
Brown barbet	*Calorhamphus fliginosus*	MLT	
Rufous piculet	*Sasia abnormis*	MT	
Olive-backed woodpecker	*Dinopium raffesii*	ML	
Buff-rumped woodpecker	*Meiglyptes tristus*	MT	
Buff-necked woodpecker	*Meiglyptes tukki*	MLT	NT
White-bellied woodpecker	*Dryocopus javensis*	MT	
Grey-capped woodpecker	*Dendrocopus canicapillus*	MTB	
Sunda woodpecker	*Picoides moluccensis*	B	
Grey-and-buff woodpecker	*Hemicircus concretus*	MLT	
Maroon woodpecker	*Blythicipus rubiginosus*	M	
Crimson-winged woodpecker	*Picus pineus*	L	
Great slaty woodpecker	*Mulleripicus pulverulentis*	MLT	
Orange-backed woodpecker	*Reinwardtipicus validus*	MLT	
Black-and-red broadbill	*Cymbirhynchus macrorhynchus*	ML	
Banded broadbill	*Eurylaimus javanicus*	MLT	
Black-and-yellow broadbill	*Eurylaimus ochromalus*	MT	NT
Green broadbill	*Calyptomena vividis*	MT	NT
Garnet pitta	*Pitta granatina*	R	NT
Barn swallow	*Hirundo rustica*	RM	
Pacific swallow	*Hirundo tahitica*	RM	
Black-winged flycatcher shrike	*Henipus hirundinaceus*	MT	
Lesser cuckoo shrike	*Coracina fimbriata*	RML	

English Name	**Latin Name**	**Habitat**	**IUCN**
Bar-bellied cuckoo shrike	*Coracina striata*	M	
Fiery minivet	*Pericrocotus ignaeus*	MLT	NT
Scarlet minivet	*Pericrocotus flammeus*	MLT	
Green iora	*Aegithina viridissima*	MLT	NT
Common iora	*Aegithina tiphia*	MT	
Lesser green leafbird	*Chloropsis cyanopogon*	MLT	NT
Greater green leafbird	*Chloropsis sonnerati*	MLT	
Yellow-vented bulbul	*Pycnonotus goiavier*	RM	
Cream-vented bulbul	*Pycnonotus simplex*	RMLT	
Hook-billed bulbul	*Setornis criniger*	MLT	V
Greater racket-tailed drongo	*Dicrurus remifier*	RM	
Hair-crested drongo	*Dicrurus hottentottus*	R	
Dark-throated oriole	*Oriolus xanthonotus*	MT	
Asian fairy-bluebird	*Irena puella*	M	
Black Magpie	*Platysmurus leucopterus*	M	
Slender-billed crow	*Corvus enca*	MT	
Bornean bristlehead	*Pittyriasis gymnocephala*	MLT	NT
Velvet-fronted nuthatch	*Sitta frontalis*	MLT	
Black-capped babbler	*Pellorneum capistratum*	MLT	
White-chested babbler	*Trichastoma rostratum*	MLT	NT
Short-tailed babbler	*Malacocincla malaccense*	MLT	NT
Scaly-crowned babbler	*Malacocincla cinerum*	MT	
Rufous-crowned babbler	*Malacocincla magnum*	M	
Grey breasted babbler	*Malacocincla albogulare*	MT	
Chestnut-rumped babbler	*Stachyris maculata*	MT	NT
Black-throated babbler	*Stachyris nigricolis*	MLT	NT
Chestnut-winged babbler	*Stachyris erythroptera*	MLT	
Striped tit babbler	*Macronous ptilosus*	RMLTB	NT
Fluffy-backed tit babbler	*Macronous saularis*	MLT	
Magpie robin	*Copcychus saularis*	RMT	
White-rumped shama	*Copcychus malabaricus*	MLT	
Rufous-tailed shama	*Trichixos pyrrhopygus*	MLT	NT
Golden-bellied gerygone	*Gerygone sulphurea*	M	
Ashy tailorbird	*Orthotomos ruficeps*	MLT	
Rufous-tailed tailorbird	*Orthotomos sriceus*	MT	
Yellow-bellied prinia	*Prinia flaviventris*	RM	
Grey-chested jungle flycatcher	*Rhinomyias umbratilis*	MT	NT
Pied fantail	*Rhipidura javanica*	RMT	
Black naped monarch	*Hypothymis azurea*	MLT	
Rufous-winged philentoma	*Philentoma pyrhopterum*	MT	
Asian paradise flycatcher	*Terpsiphone paradis*	MT	
Mangrove whistler	*Pachycephala grisola*	MLT	
White-breasted wood swallow	*Artamus leucorhynchus*	RB	
Long-tailed shrike	*Lanius schach*	RB	
Hill mynah	*Gracula religiosa*	MT	
Plain-throated sunbird	*Anthreptes malacensis*	ML	
Ruby-cheeked sunbird	*Anthreptes singalensis*	MLT	
Purple-naped sunbird	*Hypogramma hypogrammicum*	RMT	
Copper-throated sunbird	*Nectarina calcostetha*	M	

English Name	Latin Name	Habitat	IUCN
Purple-throated sunbird	*Nectarina sperata*	MLT	
Olive-backed sunbird	*Nectarina jugularis*	RMT	
Crimson sunbird	*Aethopyga siparaja*	MB	
Little spiderhunter	*Arachnothera longirostra*	MT	
Spiderhunter sp.	*Arachnothera sp.*	MT	
Scarlet-breasted flowerpecker	*Prionochilus thoracicus*	MT	NT
Yellow-breasted flowerpecker	*Prionochilus maculatus*	MT	
Orange-bellied flowerpecker	*Dicaeum trigonostigma*	MLT	
Scarlet-backed flowerpecker	*Dicaeum cruentatum*	RML	
Crimson-breasted flowerpecker	*Prionchilus percussus*	MT	
Dusky munia	*Lonchura fuscans*	R	
Eurasian tree sparrow	*Passer montanus*	R	

Key:

Habitats: R= River and Marsh habitat; M = Mixed Swamp Forest; L = Low Pole Forest; T = Tall Interior Forest; B = Burnt forest.

IUCN: CR = Critically endangered; E = Endangered; V = Vulnerable; NT = Near-threatened; DD = Data deficient

Appendix III. List of reptile and amphibian species recorded in the Sabangau from 1993-2007 (Dragiewicz and Husson, 2007).

English name	Latin Name	Habitat
Snakes		
Red tailed pipe snake	*Cylindrophis rufus*	L
Reticulated python	*Python reticulatus*	M
Iridescent earth snake	*Xenopeltis unicolor*	M
Malayan brown snake	*Xenelaphis hexagonatus*	MT
Puff-faced water snake	*Homalopsis buccata*	L
Striped kukri snake	*Oligodon octolineatus*	M
Banded vine snake	*Ahaetulla fasciolata*	M
Green vine snake	*Ahaetulla prasina*	M
Painted mock viper	*Psammodynastes pictus*	M
Jasper cat snake	*Boiga jaspidea*	M
Paradise tree snake	*Chrysopelea paradis*	T
Elegant bronze-back	*Dendrelaphis formosus*	M
Striped bronze-back	*Dendrelaphis caudolineatus*	M
Painted bronze-back	*Dendrelaphis pictus*	ML
Grey-tailed racer	*Gonyosoma oxycephalum*	MT
Bornean black snake	*Stegnotus borneensis*	M
Speckle-bellied Keelback	*Rhabdophis chrysarga*	M
Yellow-headed Krait	*Bungarus flaviceps*	M
Blue coral snake	*Maticora bivirgata*	M
Sumatran cobra	*Naja sumatrana*	M
King Cobra	*Ophiophagus hannah*	M
Sumatran pit viper	*Trimeresurus sumatrana*	M
Waglers pit viper	*Tropiodolaemus wagleri*	M
Crocodilians		
Crocodile		R
False Gharial		R
Turtles		
Spiny turtle	*Heosemys spinosa*	M
Malayan box turtle	*Cuora amboinensis*	M
Asian Leaf Turtle	*Cyclemys dentata*	M
Lizards		
Agamid	*Bronchocela cristatella*	M
House Gecko	*Hemidactylus frenatus*	Camp
Gecko	*Cyrtodactylus pubisulcus*	M
Forest Gecko	*Gekko smithii*	MT
Flying lizard	*Draco quinquefasciatus*	MT
Monitor lizard	*Varanus salvator*	SML
Skink sp.	*Dasia/Lamprolepis group*	MLT
Banded tree skink	*Dasia vittatum*	ML
Skink sp.	*Lygosoma sp. (sens. lat.)*	MLT
Skink sp.	*Mabuya multifasciata/Rubis complex*	M
Skink sp.	*Sphenomorphus sp.*	M

English Name	**Latin Name**	**Habitat**
Frogs		
Collett's Tree Frog	*Polypedates colletti*	M
Four-lined Tree Frog	*Polypedates leucomystax*	M
Dark-eared Tree Frog	*Polypedates macrotis*	M

Key:

Habitats: R= River and Marsh habitat; M = Mixed Swamp Forest; L = Low Pole Forest; T = Tall Interior Forest; B = Burnt forest.

Appendix IV. Behaviour work sheets.

Sheet 1. Behaviour data sheet.

BDS		**Tanggal:**		**Obs:**			**Ou:**				**Weather:**
Time/ Jam	**Primary Activity**	**Secondary Activity**	**o**	**Distance traveled / Jarak Jalan**	**Height in tree / Ou ketinggian de pohon**	**Tree Ht / Tinggi pohon**	**Forest quality**	**Human Dist**	**KS**	**Party size**	**Notes / tanda**
4.45											
4.50											
4.55											
5.00											
5. 05											
5.10											
5.15											
5.20											
5.25											
5.30											
5.35											
5.40											
5.45											
5.50											
5.55											
6.00											
6.05											
6.10											
6.15											
6.20											
6.25											
6.30											
6.35											
6.40											
6.45											
6.50											
6.55											
7.00											
7.05											
7.10											
7.15											
7.20											
7.25											
7.30											
7.35											
7.40											
7.45											
7.50											
7.55											
8.00											
8.05											
8.10											
8.15											
8.20											
8.25											
8.30											
8.35											
8.40											
8.45											
8.50											
8.55											
9.00											
9.05											
9.10											
9.15											
9.20											
9.25											
9.30											
9.35											
9.40											

Sheet 2. Feeding data sheet.

FDS **Obs:** **Date:** **Focal:**

Loc/ *Locasi*	Time start/ *Jam Mulai*	Time stop/ *Jam Salasai*	GPS name/ *nama*	Pohon /Tree/ *no*	Nama Pohon / Species	spl/ conton	Dbh	Tree Ht/ *tinggi pohon*	part eaten	Crop size	Feeding technique/*Makan kamahiran*

Sheet 3. GPS ranging data sheet.

GPS SHEET **NAME:** **Date:**

Focal:

Time/Jam	GPS co-ordinate
4.30	
5.00	
5.30	
6.00	
6.30	
7.00	
7.30	
8.00	
8.30	
9.00	
9.30	
10.00	
10.30	
11.00	
11.30	
12.00	
12.30	
13.00	
13.30	
14.00	
14.30	
15.00	
15.30	
16.00	
16.30	
17.00	
17.30	
18.00	
18.30	
19.00	

Time	GPS co-ordinate	Pohon makanan / feeding tree number	Species

Nesting/ Sarang			GPS	Time
Serang siang	/ Day nest			
Serang Malam	/ Night nest			

Sheet 4. Nesting and calls data sheet.

Nesting and interesting data - data sheet

Focal orangutan / Orangutan yang dimengikuti: **Tanggal / Date:**

OBSERVER:

SARANG / NESTS									
Macam sarang **DN** (Sarang siang) **/** **NN** (Sarang malam)	**Tinggi pohon / tree ht:**	**Tinggi sarang / nest ht:**	**(sarang baru), rebuilt nest (sarang tua dimemperbaiki**	**GPS:**	**Posisi (A, B, C1, C2, C3, ….., D**	**Ukuran sarang / nest size**	**Start / Jam mulai**	**End / jam selesai**	**Species Pohon**

Suara Panjang (LC)								
LC dari OU Lain					**LC dari OU Fokal**			
Jam mulai	**Jam selesai**	**Jarak (m)**	**dari arah (U,S,T,B.)**	**Reaksi OU fokal ke LC**	**Jam mulai**	**Jam selesai**	**ke arah (U,S,T,B.)**	**Aktivatas OU Fokal sebulum, sambil dan sesudah buat LC**

Any interesting behaviour:

Time	**Aktivitas khusus**

Ya = Jam, *tidak* = X, *tidak tahu* = ?

Jam	**bantal**	**selimut**	**selimut di kepala**	**alas**	**jarak antara sarang party**	*Suara.* Jam mulai	Jam selesai	**Berapa**	**Sambil bikin: ?**
Jam DN/NN									Sambil bikin: Bantal, selimut, alas
Jam DN/NN									Sambil bikin: Bantal, selimut, alas
Jam DN/NN									Sambil bikin: Bantal, selimut, alas
Jam DN/NN									Sambil bikin: Bantal, selimut, alas
Jam DN/NN									Sambil bikin: Bantal, selimut, alas

Sheet 5. Social data sheet.

Perilaku-Perilaku Sosial / Social data sheet

Party size > 1 OU (< 50m), Individu lain dalam jarak pandang kurang dari 50m

Jam Datang	Berapa OU	ID - OU lain	Aktifitas focal	Aktifitas OU lain

Sheet 6. Abbreviations used for taking behavioural data.

Aktifitas Utama: *1=makan, 2 = membuat sarang, 3 = Bermain sendiri, 4 = Perilaku-perilaku sosial, 5 = Perjalan, 6 = Agresif to orang, 7 = Penyuaraan, 8 = Beristirahat,*

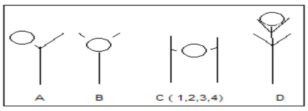
1. FEEDING ((*Aktifitas utama*))/ Makan	**F**
FOOD SEARCH (*Aktifitas utama*) / Berbagi makam	**FS**
TOOL PREPERATION (*Aktifitas utama*) /Mempersiapkan alat	**TP**
CO -FEEDING ((*Aktifitas utama*)) / Makan bersama	**CF**

Fruit : (*Sub-aktifitas*)	
Fruit ripe / buah masak	fr
fruit unripe / buah muda	fum
Pulp / daging buah	/ p
Seeds/ biji	/ s
Skin / kulit buah	/ sk
whole fruit / saluruh buah	/ wh
Leaves / daun-daunan	l
Shoots / daun - daun muda	ls
Epiphytes / Tanaman tanaman epifit	e
rotan	r
pandan,	pp
liana	li
pith	pi
Flowers / bunga	fl
Flower bud / kuncup bunga	flb
roots /akar-akaran	rt
Bark / kulit pohon	b

Invertebrates / Hewan tak bertulang punggung (e.g.semut / rayap)	iv
Honey / madu	h
Fungi / jamur	fg
Meat (vertebrates) / daging - bertulang	m
Soil / tanah	sl
Rotten wood (describe) / kayu gabuk	rw
Water /air	w

5. TRAVELLING (*Aktifitas utama*) / Melakukan perjalanan	**T**
Treesway / membengkokan pohon untuk menggapai pohon lain	tt
Clambering / berjalan di antara pohon	cla
Climbing / memanjat	cl
tangan	br
kaki	qw

2. NEST BUILDING /Membuat sarang (*Aktifitas utama*)	**N**
Day nest / sarang siang	dn
Night nest / sarang malam	nn
New Nest / sarang baru	nen
Rebuilt nest / memperbarui sarang lama	rb
Reused nest / menggunakan sarang lama	ru
A- Branch / Cabang-cabang	A
B-Trunk / Batang Pohon	B
C-Tyed trees / Pohon yang terikat/bertautan/	C
D-top of tree / Atas pohon	D



3. AUTOPLAY (*Aktifitas utama*)/ bermain sendiri	**AP**

4. SOCIAL BEHAVIOURS (*Aktifitas utama*) / Perilaku-perilaku sosial	**S**
Mating / kawin	ma
Long-calls / suara panjang	lc
Social play / bermain bersama	p
Aggressive kiss squeak / agresif KS	aks
Non-aggressive chase / jantan tidak agresif mengikuti betina	nach
Aggressive chase / mengusir orangutan lain	ach
Aggressive snage crashing / mematahkan pohon gabuk	asc
Aggressive branch breaking / mematahkan cabang pohon	abb
Aggressive contact / menyentuh dengan agresif	act
Non-aggressive contact / Kontak tidak agresif	nac
Submissive / Perilaku mengalah	sb
Allogroom / Perawatan / pengasuhan	alg
Food share / makanan bagian ke OU lain	fsh
Begging / Meminta minta makanan dari OU lain	b
Giving Birth / Melahirkan	**GB**

6. Aggresion to Observer / agresif ke peneliti **Aggresion to other people/ agresif ke orang lain**	**ATO** **AOP**
Kiss squeak toword observer / bersuara ke peneliti	skto
Threatening observer / mengancam peneliti	thto

7. VOCALISATION / penyuaraan	
Long call /suara panjang	lc
Kiss squeak	ks
Rumble / bibir bergetar	ru
Cry / squeak / menangis	cy

8. RESTING (Aktifitas utama) / Beristirahat	**R**
Sitting / Duduk	s
Standing / berdiri	st
Lying Down / rebahan	ld
Hanging / Bergelayut / bergelantung	h
Quadrupedal / berdiri diam dengan tangan dan kaki	q

Substrate Types / tempat istirahat :	
Tree / pohon	tr
Ground / Tanah / dasar	gr
Day Nest / sarang siang	dn
Night Nest / sarang malam	nn

A. Human Disturbance / keributan disebabkan manusia	
No human presence / tidak ada orang	0
Human presence - can see or hear / dangar atau lihat orang lain	1
Activily logging etc.. / aktifitas penebangan	2

C. Buah / bunga di delam pohon:

1 = 1-25%
2 = 26-50%
3 = 51-75%
4 = 76 - 100%

B. Forest Quality / kondisi hutan	
21 - 35m - Complet forest / hutan bagus. 75 - 100 %	1
21 - 35 m - Un-complet forest 50 -75% / kurang sempurna. 50 -75 %	2a
21 - 35m - Un-complet forest 25 - 50% / kurang bagus. 25 / 50 %	2b
16 - 20m complete canopy forest / Hutan 15-20m - hutan bagus >50%	3
16 - 20m in-complete canopy forest / Hutan 15-20m - hutan kurang bagus < 50%	3/2b
10 - 15m - Secondary / hutan muda	3a
2 - 10m - Secondary / hutan muda	3b
Clearing / terang / terbuka	4
Forest edge / sisi (tepi) hutan	5

Sheet 7. Identification data sheet.

ORANG-UTAN IDENTIFICATION SHEET

Ou-Code: **Relatives:**
Age class:
Sex: **Infant, Juvenile, Adulesent female, Adult female, Unflanged male, flanged male**
Size:
Key Features:

Colour of face:
Face shape:
Facial marks:
Eyes:
Eares:
Forehead:
Throat sac:
Cheeks:

Hair of top of head:
Hear on side of head:
Hear on back of head:
Hair on neck:
Hair on chin:

Over all body colour:
Over all body shape:
Bald patches:
Back:
Chest:
Shoulders:
Arms:
Legs:
Belly:
Hands / fingers:
Feet / toes:
Rear:
Genitals:

Vocalisations:
Companions:

Trail seen on:
Firest recorded by: **Date:**
Comments:

Appendix V. Density of trees species in the vegetation plots.

Family	Genus	Species	Density / ha	N	Logged
Anacardiaceae	Bouea	oppositofolia	1.11	1	x
Anacardiaceae	Campnosperma	coriaceum	53.33	48	
Anacardiaceae	Campnosperma	squamatum	12.22	11	
Anisophyllaceae	Combretocarpus	rotundatus	14.44	13	
Annonaceae	Cyathocalyx	biovulatus	15.56	14	
Annonaceae	Mezzetia	leptopoda	57.78	52	x
Annonaceae	Mezzetia	umbellata	5.56	5	x
Annonaceae	Polyalthia	glauca	4.44	4	
Annonaceae	Polyalthia	hypoleuca	3.33	3	
Annonaceae	Xylopia	cf. malayana	5.56	5	
Annonaceae	Xylopia	coriifolia	10.00	9	
Annonaceae	Xylopia	fusca	44.44	40	x
Apocynaceae	Dyera	lowii	27.78	25	
Aquifoliaceae	Ilex	hypoglauca	26.67	24	
Burseraceae	Canarium	sp. 1	13.33	12	
Burseraceae	Santiria	cf. griffithi	6.67	6	
Burseraceae	Santiria	cf. laevigata	4.44	4	
Burseraceae	Santiria	sp. 1	3.33	3	
Burseraceae	Santiria	sp. 2	1.11	1	
Burseraceae	Santiria	sp. 3	2.22	2	
Celesteraceae	Lophopetalum	sp. 1	1.11	1	
Clusiaceae	Calophyllum	hosei	116.67	105	x
Clusiaceae	Calophyllum	sclerophyllum	13.33	12	x
Clusiaceae	Calophyllum	soulattri	34.44	31	x
Clusiaceae	Calophyllum	sp. 2	1.11	1	x
Clusiaceae	Calophyllum	sp. 3	12.22	11	x
Clusiaceae	Garcinia	bancana	24.44	22	
Clusiaceae	Garcinia	sp. 1	16.67	15	
Clusiaceae	Garcinia	sp. 2	3.33	3	
Clusiaceae	Garcinia	sp. 3	3.33	3	
Clusiaceae	Garcinia	sp. 8 hombroniana	2.22	2	
Clusiaceae	Mesua	sp. 1	52.22	47	
Crypteroniaceae	Dactylocladus	stenostachys	17.78	16	
Dipterocarpaceae	Cotylelobium	cf. lanceolatum	7.78	7	x
Dipterocarpaceae	Dipterocarpus	borneensis	7.78	7	x
Dipterocarpaceae	Shorea	teysmanniana	141.11	127	x
Dipterocarpaceae	Shorea	uliginosa	2.22	2	x
Dipterocarpaceae	Vatica	mangachopai	2.22	2	x
Ebenaceae	Diospyros	bantamensis	51.11	46	x
Ebenaceae	Diospyros	cf. evena	7.78	7	x
Ebenaceae	Diospyros	confertiflora	7.78	7	
Ebenaceae	Diospyros	lanceifolia	1.11	1	
Ebenaceae	Diospyros	siamang	8.89	8	x
Ebenaceae	Diospyros	sp. 7	1.11	1	
Elaeocarpaceae	Elaeocarpus	cf. griffithi	2.22	2	
Elaeocarpaceae	Elaeocarpus	marginatus	1.11	1	
Elaeocarpaceae	Elaeocarpus	mastersii	17.78	16	
Euphorbiaceae	Baccaurea	bracteata	16.67	15	
Euphorbiaceae	Baccaurea	stipulata	2.22	2	
Euphorbiaceae	Blumeodendron	tokbrai	77.78	70	
Euphorbiaceae	Cephalomappa	sp. 1	6.67	6	

Family	Genus	Species	Density / ha	N	Logged
Euphorbiaceae	Macaranga	sp. 1	1.11	1	
Euphorbiaceae	Neoscortechinia	kingii	62.22	56	
Euphorbiaceae	Pimelodendron	griffithi	1.11	1	
Euphorbiaceae	sp. 4		1.11	1	
Fabaceae	Adenanthera	pavonina	1.11	1	
Fabaceae	Koompassia	malaccensis	7.78	7	x
Fagaceae	Castanopsis	foxworthyii	4.44	4	
Fagaceae	Lithocarpus	rassa	1.11	1	
Fagaceae	Lithocarpus	sp. 1 cf. dasystachys	35.56	32	
Fagaceae	Lithocarpus	sp. 3	10.00	9	
Fagaceae	Lithocarpus	sp. 4	1.11	1	
Fagaceae	Lithocarpus	sp. 7	3.33	3	
Fagaceae	Lithocarpus	sp. 8	3.33	3	
Fagaceae	Lithocarpus	sp. 9	1.11	1	
Hypericaceae	Cratoxylon	arborescens	15.56	14	
Hypericaceae	Cratoxylon	glaucum	35.56	32	
Icacinaceae	Platea	excelsa	8.89	8	
Icacinaceae	Platea	sp. 2	4.44	4	
Icacinaceae	Stemonurus	cf. scorpiodes	48.89	44	
Lauraceae	Alseodaphne	coriacea	1.11	1	
Lauraceae	Litsea	cf. elliptica	20.00	18	
Lauraceae	Litsea	cf. rufo-fusca	10.00	9	
Lauraceae	Litsea	sp. 1 cf. resinosa	36.67	33	
Lauraceae	Nothaphoebe	sp. 1	1.11	1	
Lauraceae	Phoebe	cf. grandis	11.11	10	
Linaceae	Ctenolophon	parvifolius	3.33	3	
Magnoliaceae	Magnolia	bintuluensis	17.78	16	
Melastomataceae	Memecylon	sp. 1	4.44	4	
Melastomataceae	Memecylon	sp. 3	1.11	1	
Melastomataceae	Pternandra	cf. coerulescens	3.33	3	
Meliaceae	Aglaia	rubiginosa	11.11	10	
Meliaceae	Sandoricum	beccanarium	52.22	47	
Moraceae	Ficus	cf. spathulifolia	1.11	1	
Moraceae	Parartocarpus	venenosus	2.22	2	
Myristicaceae	Gymnacranthera	cf. farquhariania	35.56	32	
Myristicaceae	Horsfieldia	crassifolia	113.33	102	
Myristicaceae	Knema	intermedia	15.56	14	
Myristicaceae	Myristica	lowiana	6.67	6	
Myrsinaceae	cf. Rapanea	borneensis	3.33	3	
Myrtaceae	Eugenia	cf. spicata	11.11	10	
Myrtaceae	Syzygium	garcinifolia	21.11	19	
Myrtaceae	Syzygium	havilandii	56.67	51	x
Myrtaceae	Syzygium	sp. 10	1.11	1	x
Myrtaceae	Syzygium	sp. 11	1.11	1	x
Myrtaceae	Syzygium	sp. 12	1.11	1	x
Myrtaceae	Syzygium	sp. 2	38.89	35	x
Myrtaceae	Syzygium	sp. 3 cf. nigricans	51.11	46	x
Myrtaceae	Syzygium	sp. 5	15.56	14	x
Myrtaceae	Syzygium	campanulatum	3.33	3	x
Myrtaceae	Syzygium	sp. 7	18.89	17	x
Myrtaceae	Syzygium	sp. 8	2.22	2	x
Myrtaceae	Syzygium	sp. 9 cf. lineatum	1.11	1	x
Myrtaceae	Tristaniopsis	sp. 2	7.78	7	

Family	Genus	Species	Density / ha	N	Logged
Myrtaceae	Tristaniopsis	sp. 3 cf. merguensis	8.89	8	
Myrtaceae	Tristaniopsis	sp. 4	12.22	11	
Pittosporaceae	Pittosporum	sp. 1	8.89	8	x
Rhizophoraceae	Gynotroches	sp. 1	4.44	4	
Rubiaceae	Canthium	dydimum	2.22	2	
Rubiaceae	Gardenia	tubifera	1.11	1	
Rutaceae	Tetractomia	tetrandra	46.67	42	
Sapindaceae	cf. Cubilia	cubili	1.11	1	
Sapindaceae	Nephellium	lappaceum	12.22	11	
Sapindaceae	Nephellium	maingayi	6.67	6	
Sapindaceae	Nephellium	sp. 1	1.11	1	
Sapindaceae	Xerospermum	laevigatum	8.89	8	
Sapotaceae	Isonandra	lanceolata	4.44	4	x
Sapotaceae	Madhuca	mottleyana	12.22	11	x
Sapotaceae	Palaquium	cochlearifolium	13.33	12	x
Sapotaceae	Palaquium	leiocarpum	267.78	241	x
Sapotaceae	Palaquium	pseudorostratum	27.78	25	x
Sapotaceae	Palaquium	ridleyii	16.67	15	x
Sapotaceae	Palaquium	sp. 1	2.22	2	x
Simaroubaceae	Quassia	borneensis	1.11	1	
Sterculiaceae	Sterculia	rhoidifolia	1.11	1	
Sterculiaceae	Sterculia	sp. 1	1.11	1	
Tetrameristaceae	Tetramerista	glabra	18.89	17	
Theaceae	Ternstroemia	hosei	5.56	5	
Theaceae	Ternstroemia	magnifica	10.00	9	
Thymelaeaceae	Gonystylus	bancanus	34.44	31	
Tiliaceae	Microcos	sp. 1	4.44	4	

All trees > 6 cm dbh used from 0.9ha plots. Highlighted species are species which are in the top 20 orang-utans food list; x=species that have been logged.

Appendix VI. Monthly fruiting patterns for figs and lianas.

Months	Number of figs checked	%	Number of lianas checked	%
Oct	3	0	24	8.3
Nov	4	0	25	12.0
Dec	4	0	22	13.6
Jan	9	22.2	33	6.1
Feb	9	11.1	35	5.7
Mar	9	22.2	33	9.1
Apr	9	22.2	35	5.7
May	9	11.1	36	2.8
Jun	9	33.3	36	2.8
Jul	10	20.0	35	2.9
Aug	10	10.0	37	0.0
Sep	10	40.0	37	5.4
Oct	10	30.0	37	2.7
Nov	9	11.1	37	5.4
Dec	8	12.5	37	5.4
Jan	8	25.0	37	10.8
Feb	8	25.0	36	8.3
Mar	8	25.0	37	0.0
Apr	8	25.0	36	0.0
May	8	12.5	36	2.8
Jun	8	25.0	37	0
Jul	8	12.5	37	0
Aug	8	0	37	0

APPENDIX VII. Food Species list for Sabangau 2003-2005.

Family	**Genus**	**Species**	**Local Name**	**Type**	**Fr**	**Fl**	**L**	**B**	**Pi**	**Rt**
Anacardiaceae	*Buchanania*	*cf. arborescens*	Kenyem Burung	Tree	X					
Anacardiaceae	*Campnosperma*	*coriaceum*	Terontang	Tree	X		X			
Anacardiaceae	*Campnosperma*	*squamatum*	Nyating	Tree	X					
Anisophyllaceae	*Combretocarpus*	*rotundatus*	Tumih	Tree	X					
Annonaceae	*Artobotrys*	*cf. roseus*	Kalalawit Hitam	Liana	X	X				
Annonaceae	*Artobotrys*	*suaveolins*	Bajakah Balayan	Liana	X		X			
Annonaceae	*Cyathocalyx*	*biovulatus*	Kerandau	Tree	X		X			
Annonaceae	*Fissistigma*	sp. *1*		Liana			X			
Annonaceae	*Mezzetia*	*leptopoda / parviflora*	Keripak	Tree	X		X			
Annonaceae	*Mezzetia*	*umbellata*	Kambalitan Hitam	Tree	X					
Annonaceae	*Polyalthia*	*glauca*	Kayu Bulan	Tree	X					
Annonaceae	*Polyalthia*	*hypoleuca*	Rewoi	Tree	X	X				
Annonaceae	*Xylopia*	*cf. malayana*	Tagula	Tree	X			X		
Annonaceae	*Xylopia*	*coriifolia*	Nonang	Tree	X					
Annonaceae	*Xylopia*	*fusca*	Rahanjang	Tree	X	X	X			
Apocynaceae	*Alyxia*	sp. 1	Kelanis	Liana			X		X	
Apocynaceae	*Dyera*	*lowii*	Jelutong	Tree	X	X	X	X	X	
Apocynaceae	*Willughbeia*	sp. *1*	Bajakah Dango	Liana	X	X	X	X		
Aquifoliaceae	*Ilex*	*hypoglauca*	Sumpung	Tree	X			X		
Araceae	*Raphidophora*	sp. *1*		Liana			X			
Araliaceae	*Schleffera*	sp. *1*	Sapahurung	Liana					X	
Araliaceae	*Schleffera*	sp. 2		Tree					X	
Arecaceae (*Palmae*)	*Calamus*	sp. *1*	Uey Liling	Climber	X				X	
Asclepiadaraceae	*Astrostemma*	*spartioides*	Anggrek Rangau	Epiphyte			X			
Asclepiadaraceae	*Dischidia*	*cf. latifolia*		Epiphyte			X			
Asclepiadaraceae	*Dischidia*	sp. *1*		Epiphyte			X			
Asclepiadaraceae	*Dischidia*	sp. 2	Bajakah Tapuser	Epiphyte			X			
Asclepiadaraceae	*Hoya*	sp. *1*		Epiphyte			X			
Burseraceae	*Santiria*	*cf. griffithi*	Teras Bamban	Tree			X			
Burseraceae	*Santiria*	sp. *1*	Gerrongang Putih	Tree			?			
Chrysobalanaceae	*Licania*	*splendens*	Bintan	Tree	X		X			
Clusiaceae (*Guttiferae*)	*Calophyllum*	*cf. fragrans*	Kapurnaga Kalakei	Tree	?					
Clusiaceae (*Guttiferae*)	*Calophyllum*	*cf. lanigerum*	Mahadingan	Tree	X					
Clusiaceae (*Guttiferae*)	*Calophyllum*	*hosei*	Jinjit	Tree	X		X			
Clusiaceae (*Guttiferae*)	*Calophyllum*	*sclerophyllum*	Kapurnaga	Tree	X	X	X			

Family	**Genus**	**Species**	**Local Name**	**Type**	**Fr**	**Fl**	**L**	**B**	**Pi**	**Rt**
Clusiaceae (*Guttiferae*)	*Calophyllum*	*soulattri*	Takal	Tree	X					
Clusiaceae (*Guttiferae*)	*Calophyllum*	sp. *1*	Mahadingan	Tree	X					
Clusiaceae (*Guttiferae*)	*Calophyllum*	sp. *2*	Kapurnaga Kalakei	Tree	?					
Clusiaceae (*Guttiferae*)	*Calophyllum*	sp. *3*	Kapurnaga Kalakei	Tree	?					
Clusiaceae (*Guttiferae*)	*Calophyllum*	sp. *4*	Kapurnaga Kalakei	Tree	?					
Clusiaceae (*Guttiferae*)	*Garcinia*	*bancana*	Manggis	Tree	X		X			
Clusiaceae (*Guttiferae*)	*Garcinia*	*cf. parvifolia*	Gandis	Tree	X					
Clusiaceae (*Guttiferae*)	*Garcinia*	sp. *10*		Tree	X					
Clusiaceae (*Guttiferae*)	*Garcinia*	sp. *11*	Mahalilis	Tree	X					
Clusiaceae (*Guttiferae*)	*Garcinia*	sp. *3*	Gantalan	Tree	X					
Clusiaceae (*Guttiferae*)	*Garcinia*	sp. *5*	Manggis	Tree	X					
Clusiaceae (*Guttiferae*)	*Mesua*	sp. *1*	Tabaras	Tree	X					
Crypteroniaceae	*Dactylocladus*	*stenostachys*	Mertibu	Tree	X	X				
Dipterocarpaceae	*Shorea*	*teysmanniana*	Meranti Sumut	Tree	X		X	X		
Ebenaceae	*Diospyros*	*bantamensis*	Aring Pahe	Tree	X	X	X	X		
Ebenaceae	*Diospyros*	*cf. evena*	Gulung Haduk	Tree	X		X			
Ebenaceae	*Diospyros*	*confertiflora*	Arang	Tree	X		X			
Ebenaceae	*Diospyros*	*lanceifolia*	Arang	Tree	?					
Ebenaceae	*Diospyros*	*siamang*	Ehang	Tree	X		X			
Elaeocarpaceae	*Elaeocarpus*	*acmocarpus*	Patanak	Tree			X			
Elaeocarpaceae	*Elaeocarpus*	*cf. griffithi*	Rarumpuit	Tree			X			
Elaeocarpaceae	*Elaeocarpus*	*mastersii*	Mangkinang	Tree	X	X	X			
Euphorbiaceae	*Antidesma*	*coriaceum*	Dawat	Tree	X					
Euphorbiaceae	*Antidesma*	*phanerophleum*	Tanundang	Tree	X					
Euphorbiaceae	*Blumeodendron*	*elateriospermum / tokbrai*	Kenari	Tree	X		X			
Euphorbiaceae	*Neoscortechinia*	*kingii*	Pupu Palanduk	Tree	X	X	X			
Euphorbiaceae	sp. *2*	sp. *2*		Liana			X			
Fabaceae (*Leguminosae*)	*Adenanthera*	*pavonina*	Tapanggang	Tree	X					
Fabaceae (*Leguminosae*)	*Dalbergia*	sp. *1*		Liana			X		X	
Fabaceae (*Leguminosae*)	*Dialium*	*patens*	Kala Pimping Napu	Tree		X	X			

Family	**Genus**	**Species**	**Local Name**	**Type**	**Fr**	**Fl**	**L**	**B**	**Pi**	**Rt**
Fabaceae (*Leguminosae*)	*Koompassia*	*malaccensis*	Bungaris	Tree				X		Fabaceae (*Leguminosae*)
Fabaceae (*Leguminosae*)	*Leucomphalos*	*callicarpus*	Akar Kamunda	Liana			X		X	Fabaceae (*Leguminosae*)
Fabaceae (*Leguminosae*)	*Ormosia*	sp. *1*		Tree			X			
Fagaceae	*Castanopsis*	*foxworthyii / jaherii*	Takurak	Tree	X		X			
Fagaceae	*Lithocarpus*	*cf. dasystachys*	Pampaning Bitik	Tree	X		X	X		
Fagaceae	*Lithocarpus*	*conocarpus*	Pampaning Bayang	Tree	X					
Fagaceae	*Lithocarpus*	sp. *1*	Pampaning Suling	Tree	X					
Gesneraceae	sp. *1*	sp. *1*		Liana			X			
Gnetaceae	*Gnetum*	sp. *1*	Bajakah Luaa	Liana	X	X	X			
Gnetaceae	*Gnetum*	sp. *2*		Liana	X					
Hypericaceae	*Cratoxylon*	*glaucum*	Geronggang	Tree			X			
Icacinaceae	*Stemonorus*	*cf. scorpiodes*	Tabaras	Tree	X		X			
Lauraceae	*Litsea*	*cf. elliptica*	Medang (Species Medang)	Tree	X					
Lauraceae	*Litsea*	*cf. resinosa*	Medang	Tree	X		X			
Lauraceae	*Litsea*	*cf. rufo-fusca*	Tampang	Tree	X					
Lauraceae	*Phoebe*	*cf. grandis*	Tabitik	Tree			X			
Linaceae	*Ctenolophon*	*parvifolius*	Kayu Cahang	Tree	X	X	X			
Loganiaceae	*Fragraea*	sp. *1*	Kalamuhe	Liana			X			
Loranthaceae	*Dendrophtoe*	*incurvata*		Epiphyte	X					
Loranthaceae	*Lepidaria*	sp. *1*	Mentawa	Epiphyte		X				
Magnoliaceae	*Magnolia*	*bintulensis*	Asam Asam	Tree	X	X	X	X		
Melastomataceae	*Memecylon*	sp. *3*	Tabati Himba	Tree	X					
Melastomataceae	*Pternandra*	*cf. coerulescens / galeata*	Kemuning yg bergaris tiga	Tree			X			
Meliaceae	*Aglaia*	sp. 1	Bangkuang Napu	Tree	X					
Meliaceae	*Sandoricum*	*beccanarium*	Papong	Tree	X		X			
Menispermaceae	*Fibraurea*	*tinctoria*	Kalamuhe	Liana	X		X			
Moraceae	*Ficus*	*cf. spathulifolia*	Lunuk Punai	Fig	X					
Moraceae	*Ficus*	*cf. stupenda*	Lunuk Tingang	Fig	X					
Moraceae	*Ficus*	sp. *1*	Lunuk Bunyer	Fig	X					
Moraceae	*Ficus*	sp. *2*	Lunuk Buhis	Fig	X					
Moraceae	*Ficus*	sp. *3*	Lunuk Sambon	Fig	X					
Moraceae	*Ficus*	sp. *4*	Lunuk	Fig	X					
Moraceae	*Ficus*	sp. *5*	Lunuk	Fig	X	X	X	X		
Moraceae	*Parartocarpus*	*venenosus*	Tapakan	Tree	X	X				

Family	**Genus**	**Species**	**Local Name**	**Type**	**Fr**	**Fl**	**L**	**B**	**Pi**	**Rt**
Myristicaceae	*Gymnacranthera*	*farquhariania*	Mendarahan daun kecil	Tree				X		
Myristicaceae	*Horsfieldia*	*crassifolia*	Mendarahan daun besar	Tree	X	X	X	X		
Myristicaceae	*Myristica*	*lowiana*	Mahadarah Hitam	Tree				X		
Myrsinaceae	*Ardisia*	*cf. sanguinolenta*	Kalanduyung himba	Tree	X					
Myrsinaceae	*Ardisia*	sp. *2*	Kamba Sulan	Tree				X		
Myrsinaceae	*cf. Rapanea*	*borneensis*	Mertibu	Tree	X					
Myrtaceae	*Syzygium*	*cf. E.spicata*	Kayu Lalas Daun Kecil	Tree	X					
Myrtaceae	*Syzygium*	*cf. garcinifolia*	Jambu Burung	Tree	X		X			
Myrtaceae	*Syzygium*	*cf. valevenosum*	Kayu Lalas Daun Besar	Tree	X		X			
Myrtaceae	*Syzygium*	*havilandii*	Tatumbu	Tree	X					
Myrtaceae	*Syzygium*	sp. *2*	Tampohot Himba	Tree	X					
Myrtaceae	*Syzygium*	sp. *3*	Milas	Tree	X		X			
Myrtaceae	*Syzygium*	sp. *4*	Hampuak Galaget	Tree	X					
Myrtaceae	*Syzygium*	sp.*1*	Kemuning Putih	Tree	X		X			
Myrtaceae	*Tristaniopsis*	*cf. merguensis*	Blawan Putih	Tree	X					
Ochnaceae	sp. *1*	sp. *1*		Tree			X			
Oleaceae	*Chionanthus*	sp. *1*		Tree			X			
Orchidaceae	*Eria*	sp. *1*	Anggrek Bawang	Epiphyte			X			
Pandanaceae	*Freycinetia*	sp. *1*	Akar Gerising	Climber					X	X
Pandanaceae	*Freycinetia*	sp. *2*	Katipei Pari	Climber			X			
Pandanaceae	*Pandanus*	sp. *1*	Sambalaun	Shrub	X	X			X	
Pandanaceae	*Pandanus*	sp. *2*	Rasau	Shrub		X				
Pittosporaceae	*Pittosporum*	sp. *1*	Prupuk Tulang	Tree			X	X		
Polygalaceae	*Xanthophyllum*	*cf. ellipticum*	Pohon Kemuning	Tree			X	X		
Rhamnaceae	*Zyzyphus*	*angustifolius*	Karinat	Liana	X					
Rubiaceae	*Canthium*	*dydimum*	Kopi Kopi	Tree	X					
Rubiaceae	*Ixora*	*havilandii*	Keranji	Tree	X		X			
Rubiaceae	sp. *1*	sp. *1*		Liana			X			
Rubiaceae	*Uncaria*	sp. *1*	Kalalawit Bahandang	Liana			X			
Rutaceae	*Tetractomia*	*tetrandra*	Rambangun	Tree			X	X		
Sapindaceae	*Nephellium*	*lappaceum*	Manamun	Tree	X		X			
Sapindaceae	*Nephellium*	*maingayi*	Kelumun Buhis	Tree	X		X			
Sapindaceae	*Xerospermum*	*laevigatum / noronhianum*	Kelumun Bakei	Tree	X		X			
Sapotaceae	*Isonandra*	*lanceolata*	Nyatoh Palanduk	Tree	X	X				
Sapotaceae	*Isonandra*	sp. *1*	Nyatoh Palanduk	Tree	X	X				
Sapotaceae	*Madhuca*	*mottleyana*	Katiau	Tree	X	X	X	X		

Family	**Genus**	**Species**	**Local Name**	**Type**	**Fr**	**Fl**	**L**	**B**	**Pi**	**Rt**
Sapotaceae	*Palaquium*	*cf. xanthochymum*	Nyatoh Burung	Tree	X	X	X	X		
Sapotaceae	*Palaquium*	*cochlearifolium*	Nyatoh Gagas	Tree	X	X				
Sapotaceae	*Palaquium*	*leiocarpum*	Hangkang	Tree	X	X				
Sapotaceae	*Palaquium*	*pseudorostratum*	Nyatoh Bawoi	Tree	X	X		X		
Sapotaceae	*Palaquium*	*ridleyii*	Nyatoh Burung	Tree	X	X				
Sapotaceae	*Palaquium*	*sp. 1*	Nyatoh Burung	Tree	X					
Sapotaceae	*Palaquium*	*sp. 2*	Nyatoh Burung	Tree	X	X		X		
Simaroubaceae	*Quassia*	*borneensis*	Kayu Takang	Tree			X	X		
Smilacaceae	*Smilax*	*sp. 1*	Bajakah Tolosong	Liana	X					
Sterculiaceae	*Sterculia*	*rhoiidifolia*	Loting	Tree	X		X		X	
Tetrameristaceae	*Tetramerista*	*glabra*	Ponak	Tree	X	X	X	X		
Theaceae	*Ternstroemia*	*magnifica*	Tabunter	Tree	X	X				
Tiliaceae	*Microcos (Grewia)*	*sp. 1*	Brania himba	Tree	X		X			
Unknown	*Liana sp. 7*			Liana	X					
Unknown	*Liana sp. 8*			Liana	X					
Verbenaceae	*Clerodendron*	*sp. 1*	Sopang	Tree			X			
Vitaceae	*Ampelocissus*	*rubiginosa*	Bajakah Panamar Pari	Liana			X			
Vitaceae	*Ampelocissus*	*sp. 1*	Bajakah Oyang	Liana	X					
Zingiberaceae	*Zingiber*	*sp. 1*	Suli Tulang	Shrub					X	

Fr: fruit; Fl; flowers; L: leaves; B: bark; Pi: pith; Rt: roots.

APPENDIX VIII. *Pandanus* bush

APPENDIX IX. *Mezzetia leptopoda* fruit.

Mezzetia leptopoda seeds. The seed is cracked open and the seed pulp scraped out.

Seed pulp scraped out with teeth.

APPENDIX X. Mean active period length in minutes for each individual.

Orangutan	**Age/sex class**	**N**	**Mean**	***sd***
Shima	Adolescent female	15	646.0	*60.0*
Chopin	Adolescent female	1	700.0	.
Feb	Adolescent female	43	688.4	*43.5*
Viola	Nulliparous female	14	657.7	*52.4*
Indah	Sexually-active female	81	666.9	*59.5*
Cleopatra	Sexually-active female	28	685.5	*41.1*
Beethoven	Flanged male	26	687.0	*48.5*
Jupiter	Flanged male	10	633.6	*45.6*
Wallace	Flanged male	11	663.5	*49.1*
Fenser	Flanged male	2	703.0	*7.1*
Franky	Flanged male	3	661.0	*142.1*
Hengky	Flanged male	41	649.0	*74.1*
Einstein	Adolescent male	8	**721.6**	***52.5***
Kay	Unflanged male	2	703.5	*46.0*
Mozart	Unflanged male	3	707.3	*54.3*
Romeo	Unflanged male	4	678.3	*53.0*
Shogun	Unflanged male	2	699.0	*43.8*

Habituated data, using full nest to nest follows only. N is number of follows. The figure in bold is the individual with the longest active period and the figure underlined is the individual with the shortest active period.

Appendix XI. Individual means and standard deviations for primary activities, presented as minutes in a 12 hour day.

Primary Activity Name	**Age/sex Class**	**Feeding**			**Travelling**			**Resting**			**Social**			**Nesting**			**Other**		
		Mean	**N**	***sd***	**Mean**	**N**	***sd***	**Mean**	**N**	***sd***	**Mean**	**N**	***sd***	**Mean**	**N**	***sd***	**Mean**	**N**	***sd***
Chopin *	NSAF	596.7	1	.	86.1	1	.	31.5	1	.	0	1	.	5.7	1	.	0	1	.
Ella	NSAF	464.6	15	*58.8*	133.3	15	*42.2*	114.2	15	*60.7*	0.3	15	*1.3*	6.6	15	*5.9*	1.1	15	*3.0*
Feb	NSAF	439.7	43	*67.1*	128.2	43	*34.6*	120.8	43	*62.1*	12.0	43	*28.3*	15.6	43	*11.3*	3.7	43	*10.0*
Shima	NSAF	469.0	15	*49.4*	85.5	15	*22.8*	158.4	15	*53.3*	0.7	15	*1.8*	5.7	15	*2.4*	0.7	15	*2.6*
Viola[1]	NSAF	348.9	14	*83.5*	111.3	14	*36.1*	244.1	14	*87.6*	0.7	14	*1.8*	11.4	14	*3.5*	3.6	14	*9.5*
Cleo	SAF	481.2	28	*67.4*	89.3	28	*33.5*	127.1	28	*57.7*	5.3	28	*15.7*	13.8	28	*8.1*	3.3	28	*7.4*
Indah	SAF	428.5	81	*103.1*	101.2	81	*38.3*	152.4	81	*75.9*	27.8	81	*110.6*	9.3	81	*4.3*	1.9	81	*5.2*
B'hoven	FM	495.7	26	*52.7*	106.5	26	*32.0*	102.7	26	*49.7*	6.2	26	*11.0*	8.9	26	*4.7*	0.0	26	*0.0*
Fencer *	FM	568.4	2	*63.4*	67.3	2	*52.9*	69.4	2	*3.5*	7.5	2	*3.5*	7.5	2	*3.5*	0.0	2	*0.0*
Franky	FM	404.5	3	*126.3*	106.2	3	*59.2*	197.1	3	*186.3*	6.8	3	*7.6*	5.4	3	*5.5*	0.0	3	*0.0*
Hengky	FM	418.2	41	*130.1*	73.9	41	*46.8*	204.6	41	*127.1*	11.1	41	*9.5*	11.6	41	*5.9*	0.6	41	*2.4*
Jupiter	FM	422.0	10	*82.3*	65.8	10	*22.8*	219.2	10	*79.7*	1.5	10	*3.5*	10.4	10	*7.4*	1.1	10	*2.3*
Wallace	FM	475.7	11	*85.6*	91.9	11	*32.9*	137.0	11	*75.3*	0.5	11	*1.5*	13.5	11	*4.1*	1.5	11	*3.4*
Darwin	UFM	383.2	2	*106.8*	105.9	2	*28.6*	140.0	2	*14.6*	78.2	2	*89.2*	7.6	2	*3.6*	5.0	2	*0*
Mozart	UFM	454.5	3	*95.8*	133.4	3	*19.0*	120.1	3	*116.1*	0	3	*0.0*	12.0	3	*8.2*	0	3	*0*
Romeo	UFM	336.3	4	*167.5*	77.8	4	*36.5*	264.9	4	*130.3*	28.0	4	*38.7*	13.0	4	*5.9*	0	4	*0*
Shogun *	UFM	421.8	2	*26.2*	101.7	2	*0.6*	171.1	2	*18.2*	0	2	*0*	15.2	2	*7.1*	10.2	2	*14.4*
Einstein[2]	UFM	386.0	8	*69.6*	151.1	8	*41.4*	150.7	8	*66.0*	13.9	8	*11.9*	10.8	8	*6.9*	7.5	8	*19.3*
Total		**439.5**	**309**	***96.2***	**101.6**	**309**	***41.5***	**153.0**	**309**	***88.6***	**12.9**	**309**	***59.3***	**10.9**	**309**	***7.0***	**2.0**	**309**	***6.6***

Habituated data on full follows only (values for each individual are means of full-day follows on those individuals). N: is number of follows; NSAF: non-sexually-active female; SAF: sexually-active female; FM: Flanged male; UFM: unflanged male *individuals which have been excluded for further analysis due to number of hours followed not meeting the 50 hour criteria. Viola is a NLF (nulliparous female) but has been included with the NSAF; Einstein is a NSAM (non-sexually-active male) but has been included as an UFM.

APPENDIX XII. Predicted Classifications from Multinomial Logistic Regression.

Observed	**Predicted**							
	TCA	**TCB**	**TIC**	**MC**	**MIC**	**LMS**	**S**	**Percent Correct**
TCA	12	6	0	1	0	0	0	63.2
TCB	2	47	3	4	3	2	0	77.0
TIC	0	5	17	1	4	0	0	63.0
MC	1	8	2	18	0	1	0	60.0
MIC	0	3	2	2	10	2	0	52.6
LMS	0	1	0	1	1	15	2	75.0
S	0	0	0	0	0	1	12	92.3
Overall Percentage	7.9	37.0	12.7	14.3	9.5	11.1	7.4	69.3

Appendix XIII. Likelihood ratio test between habitat variables.

Effect	**-2 Log Likelihood of Reduced Model**	**Chi-Square**	**df**	**Sig.**
Intercept	330.387(a)	.000	0	.
TREE_FAL	356.586(b)	26.199	6	.000
COVER_20	368.861(b)	38.474	6	.000
COVER_10	338.115(b)	7.728	6	.259
DENS_20	341.283(b)	10.896	6	.092
DENS_10	345.095(b)	14.708	6	.023
AVE_DBH	350.328(b)	19.941	6	.003
AVE_HT	359.518(b)	29.131	6	.000
SAPLINGS	352.566(b)	22.180	6	.001
STUMP	357.397	27.010	24	.304

The chi-square statistic is the difference in -2 log-likelihoods between the final model and a reduced model. The reduced model is formed by omitting an effect from the final model. The null hypothesis is that all parameters of that effect are 0.

Appendix XIV. Pairwise relatedness (r) values based on the Wang estimator (2002).

ALL LOCI	Feb	Einstein	Cleo	Indah	Potret	Viola	B,hoven	Hengky	Archi	Drake	Romeo	Kay	Zeus	Indy	Mozart	Fencer
Feb		0.290	0.499	0.075	-0.094	0.207	-0.165	0.121	0.526	-0.117	-0.194	-0.109	0.039	0.319	0.053	0.031
Einstein	0.290		0.141	-0.032	0.014	0.072	-0.279	-0.235	0.139	-0.095	-0.176	0.068	0.094	0.088	-0.113	0.097
Cleo	0.499	0.141		0.324	0.157	0.327	-0.061	-0.003	0.813	-0.241	0.012	-0.155	0.143	0.408	-0.111	0.135
Indah	0.075	-0.032	0.324		-0.001	0.064	-0.001	-0.067	0.472	-0.150	-0.127	-0.439	0.262	0.396	0.075	0.155
Potret	-0.094	0.014	0.157	-0.001		-0.085	-0.210	-0.173	-0.163	-0.058	-0.192	-0.084	-0.165	0.090	-0.120	0.267
Viola	0.207	0.072	0.327	0.064	-0.085		-0.032	-0.134	0.267	0.098	-0.253	-0.165	-0.008	-0.191	-0.041	0.062
B,hoven	-0.165	-0.279	-0.061	-0.001	-0.210	-0.032		-0.265	-0.177	-0.056	-0.134	-0.237	-0.154	-0.002	-0.262	-0.190
Hengky	0.121	-0.235	-0.003	-0.067	-0.173	-0.134	-0.265		-0.100	-0.172	-0.235	-0.137	0.087	0.115	-0.053	-0.044
Archi	0.526	0.139	0.813	0.472	-0.163	0.267	-0.177	-0.100		-0.222	-0.221	-0.309	0.237	0.331	-0.118	-0.029
Drake	-0.117	-0.095	-0.241	-0.150	-0.058	0.098	-0.056	-0.172	-0.222		-0.299	-0.228	-0.104	-0.363	-0.125	0.274
Romeo	-0.194	-0.176	0.012	-0.127	-0.192	-0.253	-0.134	-0.235	-0.221	-0.299		0.017	0.054	0.162	0.059	0.131
Kay	-0.109	0.068	-0.155	-0.439	-0.084	-0.165	-0.237	-0.137	-0.309	-0.228	0.017		-0.337	-0.085	-0.199	-0.104
Zeus	0.039	0.094	0.143	0.262	-0.165	-0.008	-0.154	0.087	0.237	-0.104	0.054	-0.337		0.212	-0.069	0.160
Indy	0.319	0.088	0.408	0.396	0.090	-0.191	-0.002	0.115	0.331	-0.363	0.162	-0.085	0.212		0.176	0.286
Mozart	0.053	-0.113	-0.111	0.075	-0.120	-0.041	-0.262	-0.053	-0.118	-0.125	0.059	-0.199	-0.069	0.176		0.200
Fencer	0.031	0.097	0.135	0.155	0.267	0.062	-0.190	-0.044	-0.029	0.274	0.131	-0.104	0.160	0.286	0.200	

The estimates are calibrated to a population mean. Animals with a negative value share fewer alleles that are identical by descent than expected given the distribution of alleles within the population. Trying to identify between first cousins is very difficult as the error rate is just too high (Csillery *et al.,* 2006).

Appendix XV. Social encounters and percentage of time an individual spent with any other age-sex class (using focal data only).

Orang-utan	Mean party size	% of time alone	% of time in a party	% with adult females	% with Viola	% with adolescent females	% with flanged males	% with unflanged males	% with adolescent males	% with unknown
Indah	1.1	91.7	8.3	0.1	0.7	0.4	0.3	7.7	0	0.3
Cleopatra	1.5	66.4	33.6	0.3	0	30.7	2.9	4.4	2.6	0.2
Viola	1.5	56.5	43.5	2.7	0	1.8	29.6	10.2	0	0
Feb	1.3	82.5	17.5	12.4	0	0	1.0	7.4	3.5	0.4
Shima	1	97.3	2.7	1.4	0	0	0	0.8	0	0.5
Hengky	1	96.0	4.0	1.4	0	2.5	0.3	0	0	0.8
Beethoven	1.1	90.6	9.4	1.0	7.0	0.6	0.2	0	0	0.7
Wallace	1	97.1	2.9	1.8	0	0.4	0.1	0	0	0.6
Franky	1	98.6	1.4	0	0	1.1	0.2	0	0	0.1
Jupiter	1	99.4	0.6	0.4	0	0.2	0	0	0	0
Kay	1.3	74.2	25.8	9.1	0	14.7	0.4	6.0	0	1.3
Romeo	1.3	73.0	27.0	21.5	0	0.7	0.3	14.4	0	0.9
Mozart	1.1	85.0	15.0	9.1	0	5.5	0.4	0	0	0
Einstein	1.5	57.9	42.1	1.3	0	30.5	1.3	10.8	0	0.5

Only those 15 individuals that had more than 50 hours of focal observation are included. Percentage of time with other age-sex classes does not add up to 100% of the time in a party, because party sizes of more than one were combined.

APPENDIX XVI Unflanged male Romeo force mating the female Cleo (2007). Chivers is 4 years old.