ORANG-UTAN FEEDING BEHAVIOUR IN SABANGAU, CENTRAL KALIMANTAN

By

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To my friends, family and Sonya, for making it all worthwhile.

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"*It is not the critic who counts: not the one who points out how the strong man stumbles, or where the doer of deeds could have done better. The credit belongs to the man who is actually in the arena, whose face is marred with sweat and dust and blood, who strives valiantly, who errs and comes up short again and again, because there is no effort without error or shortcoming, but who knows the great enthusiasms, the great devotions, who spends himself in a worthy cause; who, at best, knows, in the end, the triumph of high achievement, and who, at the worst, if he fails, at least he fails while daring greatly, so that his place shall never be with those cold and timid souls who know neither victory nor defeat.*"

Theodore Roosevelt, Speech at the Sorbonne, Paris, 23rd April, 1910.

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PREFACE

The work described in this thesis was conducted from the Wildlife Research Group, in the Anatomy School, University of Cambridge, under the supervision of Dr David J. Chivers. This thesis is the result of my own research and includes nothing that is the outcome of work done in collaboration, except where specifically indicated in the text. No part of this thesis has been submitted to this or any other university for any degree or diploma. The text does not exceed 80,000 words (excluding references and appendices).

Mark E. Harrison

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SUMMARY

Detailed studies of energy/nutrient acquisition and food selection have been completed for both African apes and orang-utans in mast-fruiting dipterocarp forests, but, to date, no studies of this type have been completed on orang-utans in non-masting forests, which experience more muted fluctuations in fruit availability. Such studies may be instructive in understanding whether the observations on orang-utans in masting habitats are specific to orang-utans, or specific only to orang-utans in masting habitats. To investigate this, orang-utan diet composition, energy intake, food selection and behaviour were studied in relation to orang-utan fruit/flower availability, and chemical and non-chemical food properties, in the Sabangau peat-swamp forest, Central Kalimantan from July 2005-June 2007. All data were collected using standard methods, and comparisons made with published data on orang-utans in mast-fruiting habitats and on African apes.

Orang-utan fruit availability in Sabangau was lower and less variable than in the masting forests of Gunung Palung National Park, West Kalimantan. Daily energy intake was below requirements in most months, and similar to periods of very low food availability between mast-fruiting events in Gunung Palung. Mechanisms through which orang-utans may have survived this prolonged energetic shortfall are suggested. In addition, unlike in Gunung Palung, where energy intake and fruit availability are tightly linked in both sexes, the only age-sex class in which energy intake in Sabangau was related to fruit availability was flanged males. Although selection of preferred *vs.* fall-back food types in Sabangau appears to be governed at least partially by the expected rate of energy returns, fruit and flower selectivity rank appears better explained by food quality: the best multi-

variate model of adult female fruit selectivity rank contained only protein/fibre ratio, and bivariate correlations between fruit-pulp selectivity rank and protein/fibre ratio were also significant for flanged males. Furthermore, adult female and flanged male fruit selectivity rank was negatively affected by fibre, weight or energy intake in at least one bivariate analysis. This is suggested to represent selection against ingestion of large amounts of relatively indigestible fibre, and implies that maximising dietary quality, rather than energy intake, as has been suggested in masting forests in Borneo, may be the optimal feeding strategy for orang-utans in habitats where fruit quality is relatively poor and/or fruit availability is relatively consistent. Finally, compared to orang-utans in Bornean masting forests, Sabangau orang-utans exhibit a relative lack of modifications in non-feeding behaviours in response to reductions in preferred food availability.

These results suggest that, compared to masting forests in Borneo, lower mean quality and quantity of fruit, and lower variability in these parameters, in the Sabangau peat swamps leads to important differences in feeding behaviour between these habitat types. When compared to data on orang-utans in other sites and African great apes, these observations are compatible with a graded-response hypothesis, in which the less predictable the availability of high-energy fruit in a site: (1) the stronger the relationship between fruit availability, fruit consumption and energy intake, (2) the more food is selected based on energy content, and (3) the stronger the influence of fluctuations in fruit availability on behaviour and, ultimately, probably also female reproduction. The implications of these findings are discussed.

ABSTRAK

Penelitian tentang perolehan energi/nutrisi dan pemilihan pakan untuk kera Afrika dan orang-utan di hutan dipterocarp yang mengalamani *mast fruiting* sudah dilakukan. Tapi sampai sekarang belum ada penelitian tentang perilaku makan orang-utan di hutan yang tidak mengalami *mast fruiting* dan yang lebih tetap untuk ketersediaan buah. Penelitian seperti ini mungkin dapat membantu kita untuk mengerti apakah pengamatan pada orang-utan di hutan yang mengalami *mast fruiting* adalah secara khusus untuk orang-utan, atau khusus hanya pada orang-utan di hutan yang mengalami *mast fruiting.* Komposisi pakan, konsumsi energi, pemilihan pakan dan perilaku orang-utan telah diteliti dalam hubungan dengan ketersediaan buah/bunga yang dimakan orang-utan, dan kandungan kimia serta non-kimia di hutan gambut Sabangau, Kalimantan Tengah, dari bulan Juli 2005-Juni 2007. Semua data di koleksi dengan metode yang standar, dan observasinya dibandingkan dengan data orang-utan dari hutan yang mengalami *mast fruiting* dan kera Africa yang sudah dipublikasi.

Ketersediaan buah pakan orang-utan di Sabangau rendah dan kurang bervariasi dari pada hutan yang mengalamani *mast fruiting* di Taman Nasional Gunung Palung, Kalimantan Barat. Konsumsi energi kurang dari keperluannya dan serta mirip seperti pada waktu berkurangnya ketersediaan buah di Gunung Palung. Mekanisme dimana orang-utan mungkin akan bertahan hidup pada keadaan kekurangan energi adalah di sarankan. Di Gunung Palung ada hubungan yang erat di antara konsumsi energi dan ketersediaan buah, tapi di Sabangau hubungan ini hanya terlihat pada jantan dewasa yang berpipi besar. Sepertinya pemilihan jenis pakan di Sabangau diatur oleh rata-rata pengembalian energi yang diharapkan, tapi tingkat pilihan buah dan bunga dapat

dijelaskan dengan baik dari kualitas makanan. Untuk betina dewasa, model *multi-variate* adalah yang paling baik untuk prediksi tingkat pemilihan buah yang ditentukan oleh nilai rasio protein/serat, dan korelasi *bivariate* antara tingkat pemilihan daging buah dan nilai rasio protein/serat juga signifikan untuk jantan dewasa yang berpipi besar. Untuk betina dewasa dan jantan dewasa yang berpipi besar, tingkat pemilihan berhubangan negatif pada pemasukan serat, berat dan energi pakan dalam satu atau lebih analisa *bivariate*. Hal ini disarankan untuk melakukan seleksi terhadap pemasukan jumlah sedikit dari serat yang relatif tidak mudah di cerna. Hasil penelitian ini menunjukan bahwa peningkatan kualitas pakan dari konsumsi energi adalah strategi mencari makan yang terbaik untuk orang-utan di habitat yang kualitas buahnya rendah dan/atau punya ketersediaan buah yang lebih tetap. Akhirnya, jika dibandingkan dengan orang-utan di hutan *masting* di Borneo, perubahan perilaku yang tidak masuk perilaku makan karena kekurangan pakan yang lebih disukai kurang untuk orang-utan di Sabangau.

Hasil penelitian ini menyarankan bahwa, jika dibandingkan dengan hutan *mast-fruiting* di Borneo, kualitas dan ketersediaan buah yang kurang, serta kurang variasi untuk hal ini, di hutan gambut Sabangau membawa kepada perbedaan yang penting untuk perilaku makan orang-utan antara dua jenis habitat tersebut. Jika dibandingkan dengan data untuk kera besar di Asia dan Afrika di tempat lain, pengamatan ini adalah cocok dengan hypotesa *graded-response*, di mana jika kera kurang bisa diduga ketersediaan buah yang berisi banyak energi: (1) hubungan antara konsumsi energi, konsumsi buah dan ketersediaan buah lebih kuat, (2) lebih banyak buah yang dipilih berdasarkan kandungan energi, dan (3) pengaruh fluktuasi yang kuat dari ketersediaan buah pada perilaku dan akhirnya mungkin juga untuk reproduksi betina.

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ABBREVIATIONS USED

AF	=	adult (parous) female
AFR	=	age at first reproduction
AP	=	active period (duration of)
CIMTROP	=	Centre for the International Cooperation in Management of Tropical Peatlands
CP	=	crude protein
DBH	=	diameter at breast height (of trees)
DM	=	dry matter
DR	=	day range (distance in metres travelled in one full day)
ELG	=	eastern lowland gorilla
ENSO	=	El Niño Southern Oscillation
FBF	=	fall-back food
FLM	=	flanged male
IBI	=	inter-birth interval
kya	=	thousand years ago
LCF	=	low-canopy forest
LF	=	litter-fall
LIPI	=	*Lembaga Ilmu Pengetahuan Indonesia* (Indonesian Institute of Sciences)
LPF	=	low-pole forest
ME	=	metabolisable energy
ME_H	=	ME using high PFV for NDF (1.6 kcal/g)
ME_L	=	ME using low PFV for NDF (0.543 kcal/g)
ME_0	=	ME using zero PFV for NDF (0 kcal/g)
MG	=	mountain gorilla
MRT	=	mean retention time (of digesta in the gut)
MSF	=	mixed-swamp forest
Mya	=	million years ago
NDF	=	neutral-detergent fibre
NF	=	nulliparous (adolescent) female
NLPSF	=	Natural Laboratory of Peat-Swamp Forest (Sabangau)
OFT	=	optimal forging theory
OM	=	organic matter
OuTrop	=	Orang-utan Tropical Peatland Project
PE	=	part eaten
PFV	=	physiological fuel value
PNE	=	part not eaten
PS	=	party size
PSF	=	peat-swamp forest
QTE	=	quebracho tannin equivalent
SAMF	=	supra-annual mast fruiting
TEE	=	total (daily) energy expenditure
THV	=	terrestrial herbaceous vegetation
TNC	=	total non-structural carbohydrates
TPF	=	tall-pole forest
UFM	=	unflanged male
YM	=	Young's modulus
WLG	=	western lowland gorilla

1. INTRODUCTION

1.1 RESEARCH THEME AND AIMS

Acquiring sufficient food, and obtaining sufficient energy and nutrients from this food, is one of the most fundamental problems facing any primate, because (1) primate food is limited, both in quantity and quality (i.e., there are not permanent, inexhaustible supplies of super-nutritious foods, e.g., Fleagle, 1999; Hemingway and Bynum, 2005; Marshall and Wrangham, 2007), and (2) survival, growth and reproduction are compromised and, in extreme cases, impossible, when nutrient/energy balances become negative for prolonged periods (see review in Knott, 2001). Thus, in most environments, where food availability is permanently or temporarily limited, acquiring sufficient food is critical, and strong evolutionary pressures should exist towards adaptations that help ensure nutrient/energy requirements for survival, growth and reproduction are met. These pressures may manifest themselves in many ways, e.g., physiological, morphological, behavioural and life-history adaptations (e.g., Fleagle, 1999).

As a result, a thorough understanding of a species' feeding behaviour – what it eats, what it gets from its food, how it is affected by, and responds to, fluctuations in food availability, and why it eats what it does – is essential to understanding its socio-ecology, life history and evolution. Furthermore, as a result, in an age where primates are becoming increasingly threatened by anthropogenic disturbances, such an understanding is essential for informing conservation actions to ensure a species' long-term survival.

Orang-utans (*Pongo* spp.) are an ideal species in which to study such phenomena. Firstly, they are slow-moving and typically spend most of their time alone, and so it is possible to follow single individuals for prolonged periods and collect detailed data on feeding and other behaviours, which are less commonly affected by the actions of nearby conspecifics than in other species (Knott, 1999). Secondly, they are one of mankind's closest relatives (Glazko and Nei, 2003) and the earliest hominid was almost certainly a large frugivorous ape (Kay, 1977; Andrews and Martin, 1991; Pilbeam and Young, 2004), not overly dissimilar to the orang-utan (and present-day African apes). Thus, understanding such phenomena in orang-utans may provide a window of understanding into the pressures that shaped our own evolution.

Although the first studies on wild orang-utans were conducted over four decades ago (Schaller, 1961; Davenport, 1967), to date, detailed studies of orang-utan nutrient/energy intake in response to fluctuations in food availability and the food properties influencing selection have only been completed in mast-fruiting habitats (Leighton, 1993; Knott, 1998, 1999). These forests are characterised by huge peaks and troughs in fruit availability, of a degree not experienced by African apes (Knott, 2005; van Schaik and Pfannes, 2005; **Chapter 3**). As a result, it is difficult to assess whether the apparent lesser effect of fluctuations in food availability on energy intake in African apes (Conklin-Brittain *et al.*, 2006; Masi, 2007; Rothman *et al.*, 2008b), compared to orang-utans in masting habitats (Knott, 1998, 1999), and differences in food selection between African apes (e.g., Calvert, 1985; Rogers *et al.*, 1990; Remis, 2003; Hohmann *et al.*, 2006; Ganas *et al.*, 2008) and orang-utans in masting habitats (Leighton, 1993), are more likely the

result of true inter-specific differences, or merely differences in ecology between ape habitats.

Thus, the main aim in this study is to provide information on feeding behaviour from an orang-utan population in a non-masting habitat with more muted fluctuations in fruit availability, in order to bridge this gap in the literature, and to attempt to establish whether the patterns seen in Bornean orang-utans in masting forests (Leighton, 1993; Knott, 1998, 1999) are more likely specific to orang-utans, or to orang-utans in masting habitats. Thus, *the null hypothesis throughout the thesis is "observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats".* To do this, data were collected from orang-utans in the non-masting Sabangau peat-swamp forest, Central Kalimantan on (1) food availability, (2) dietary composition and food-energy intake, and the effects of fluctuations in food availability on these, (3) food-selection criteria, and (4) the effects of changes in dietary composition/ intake and food-availability fluctuations on non-feeding behaviours. Introductions to each of these subject areas are given in the relevant chapters.

1.2 THESIS OVERVIEW

This thesis is organised into seven chapters. In this first chapter, I provide a general introduction to the themes studied, and give a brief overview of the structure of the thesis, before giving a general introduction to orang-utan biology. In **Chapter 2**, I describe the study site, study design, sampling regime, orang-utan study population and other general methodological issues. In **Chapter 3**, I document fluctuations in orang-utan food

availability, and compare this to observations in other sites where orang-utans and African apes have been studied. In **Chapter 4**, I describe orang-utan diet composition and nutrient/energy intake, and assess these in relation to fluctuations in food availability and nutrient/energy requirements. I then compare these observations to those made in other studies on orang-utans and African apes. In **Chapter 5**, I assess food-selection criteria for all the major food types, and discuss this in light of ecological differences between Sabangau and other study sites. In **Chapter 6**, I describe orang-utan behaviour in Sabangau and the effects of fluctuations in food availability, diet composition and energy intake on this, before again drawing comparisons with observations in other orang-utan and African ape studies. In the final chapter (**Chapter 7**), I sum up my major findings and discuss their broader implications.

1.3 ORANG-UTAN BIOLOGY

1.3.1 TAXONOMY

Orang-utans are classified in the great-ape family (Hominidae), along with gorillas (*Gorilla* spp.), chimpanzees *(Pan troglodytes*), bonobos (*P. paniscus*) and humans (*Homo sapiens*). Traditionally, only one species of orang-utan was recognised, with the Bornean and Sumatran orang-utans being classed as sub-species. Today, following a number of genetic studies, the Sumatran (*P. abelii*) and Bornean (*P. pygmaeus*) orang-utans are generally recognised as separate species (Xu and Arnason, 1996; Zhi *et al.*, 1996; Groves, 2001; Goossens *et al.*, 2009). Estimates for the date of divergence of the two orang-utan species differ, but recent meta-analyses suggest a separation occurring ca. 5-2.7 Mya

(Steiper, 2006). Three sub-species of Bornean orang-utan are now generally recognised: *P. pygmaeus pygmaeus* from north-west Kalimantan to Sarawak, *P. p. wurmbii* in south-west and central Kalimantan, and *P. p. morio* from north-west Kalimantan to Sabah (Groves, 2001; Singleton *et al.*, 2004; Goossens *et al.*, 2009, but see also Muir *et al.*, 1998, 2000; Warren *et al.*, 2001; Brandon-Jones *et al.*, 2004).

The different (sub-) species will hybridise in captivity, but survival rates among Sumatra-Borneo hybrids are much lower, and captive Bornean orang-utans, many of which are probably hybrids of the different Bornean sub-species, are less fertile than captive Sumatran orang-utans (Cocks, 2007). Differences in jaw morphology (Taylor, 2006), brain size (Taylor and van Schaik, 2006), life history (Wich *et al.*, 2004b, 2009a) and various behavioural aspects, including diet, between (sub-) species are thought to reflect a gradient of reduced mean fruit availability and increased incidence of periods of extreme fruit scarcity from west to east (van Schaik *et al.*, 2009b).

1.3.2 POST-CRANIAL MORPHOLOGY

Orang-utans are the second largest ape, with Bornean flanged males (see below) weighing an average 86.3 kg (range 80-91 kg, Markham and Groves, 1990). Females typically weigh less than half this, averaging about 38.7 kg (33-45 kg, Markham and Groves, 1990). In captivity, flanged males average 124 kg (Leigh and Shea, 1995), but this is probably a consequence of obesity, brought about through over-feeding and under-activity (Harrison and Chivers, 2007).

Unique among the great apes, and unusual among primates, adult male orang-utans occur in two distinct morphs. Flanged males possess large cheek pads, a large throat sac, are twice the size of unflanged males and produce loud 'long calls' to advertise their presence (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978). Unflanged males are about the same size as females and lack the secondary sexual characteristics possessed by flanged males (Galdikas, 1985c; Kingsley, 1988). The two morphs are now thought to represent two alternative mating strategies (Galdikas, 1981, 1985a, c; Kingsley, 1988; Maggioncalda *et al.*, 1999, 2000, 2002, see below).

1.3.3 LOCOMOTION

Unlike gorillas and chimpanzees, orang-utans spend almost all of their time in the canopy and rarely descend to the ground, though flanged males do so more regularly than females (MacKinnon, 1974; Rodman and Mitani, 1987; pers. obs.) and this behaviour is commoner in Borneo, where large terrestrial predators, such as tigers, are absent (Delgado and van Schaik, 2000). Despite being the world's largest arboreal animal (Cant, 1987), the orang-utan's long arms, highly-flexible shoulder and hip joints, hand-like feet and high intelligence make them perfectly adapted to a life in the canopy (Fleagle, 1999; MacLatchy, 1996; Knott, 1999). These features enable orang-utans to contort their bodies into seemingly painful positions, allowing them to access hard-to-reach food items and travel safely through the canopy. In some senses, the orang-utan's large body size is advantageous for travelling through the canopy, with individuals using their body weight to bend and sway trees to bridge canopy gaps (MacKinnon, 1974; Thorpe *et al.*, 2007).

Movement through the trees is most frequently by 'quadrumanual scrambling', where all four limbs are used to clamber through the canopy (Knott, 1999). Different age-sex classes were observed to travel through the canopy in a broadly-similar manner in Ketambe, Sumatra, though adult females travelled more cautiously (i.e., avoided less stable supports) than other age-sex classes (Thorpe and Crompton, 2005). In Sabangau, as in other sites, orang-utans travel mostly by orthograde suspension, but incidence of tree-swaying and use of trunks as supports is higher, and use of lianas is lower (Manduell, 2008). Average travel speed, both in the trees and on the ground, is about 0.35 km/hr, roughly one-tenth the average speed of chimpanzees (Rodman, 1984; Rodman and Mitani, 1987). Orang-utan positional behaviour is highly complex, representing a large diversity of positional modes, and is largely similar to African apes (Thorpe and Crompton, 2006).

1.3.4 DIGESTION AND CRANIO-DENTITION

Orang-utans have adapted to their plant-based, highly-fibrous diet by evolving a long small intestine for absorption of digestive end-products and an enlarged, haustrated colon, in which microbial fermentation of structural polysaccharides occurs (Chivers and Hladik, 1980; Stevens and Humes, 1995). Similar digestive strategies are employed by other frugivores, including the other ape species (although there is some variation in gut measurements among apes, with the more folivorous gorillas having a higher coefficient of gut differentiation than the other ape species, Chivers and Hladik, 1980). Consistent with optimal digestion theory and the fact that microbial fermentation is a relatively slow process, voluminous colons, such as that possessed by the orang-utan, allow foods to be

retained for long periods, enabling more thorough digestion of poor-quality food items (Hume, 1989). Caton *et al.* (1999) found that captive orang-utan gut transit time was long, with mean retention time (MRT) of particle markers averaging 73.7 ± 15.5 h in one female and two flanged males. Thus, based on their gut anatomy, orang-utans should be expected to consume more nutritional/energy-rich/easily-digested foods, such as fruit, when available, but should also be capable of digesting large amounts of less nutritious/easily-digested foods, such as bark, when necessary. This is in agreement with field observations on feeding (MacKinnon, 1974; Rodman, 1977; Galdikas, 1988; Rodman, 1988; Leighton, 1993; Knott, 1998, 1999; Vogel *et al.*, 2008b; this study).

The cranio-dental adaptations of the orang-utan also indicate a diet in which hard, obdurate, fibrous foods feature strongly. Orang-utan molar enamel is the thickest of any extant primate and their surface is crenulated, reducing the risk of tooth shatter; adaptations towards feeding on hard objects, such as seeds and bark (Kay, 1981; Lucas and Luke, 1984; Martin, 1985; Rodman, 1988; Maas, 1991; Vogel *et al.*, 2008b). The anterior maxillary dental complex, which includes small lateral incisors, broad central incisors and relatively short canines, and wear patterns on the lateral maxillary incisors, is also indicative of bark stripping (Rodman, 1988). Orang-utans also have high molar shearing crests, high molar-surface slopes and steep molar-cusp slopes; adaptations enabling efficient breakdown of structural carbohydrates during mastication (i.e., leaf eating, Kay, 1977, 1981; Ungar, 2006). Observations on jaw morphology concur: the robust orang-utan mandible can resist large loads from masticatory and incisal forces (Taylor, 2006). Recently-collected data on the physical properties of wild orang-utans diets confirm these observations, and support the hypothesis that the routine consumption

of tough and obdurate food items favoured the evolution of thick molar enamel, steep molar-cusp slopes, and relatively great occlusal relief (Vogel *et al.*, 2008b).

1.3.5 LIFE-HISTORY PARAMETERS

Orang-utan life history is slow, with orang-utans having the highest inter-birth interval (IBI), age at first reproduction (AFR) and, probably, life span among the great apes (Wich *et al.*, 2004b, 2009a). Current best estimates of orang-utan life-history parameters are: IBI 8.2-9.3 yrs in Sumatra and 6.1-7.7 yrs in Borneo, AFR 15.2 yrs in Sumatra and 15.7 yrs in Borneo, and longevity 58 yrs for males and 53 yrs for females in Sumatra (Wich *et al.*, 2004b, 2009a).

1.3.6 RANGING AND DISPERSAL

Comparisons of orang-utan home range sizes across sites show that estimates from different sites differ widely, but in all studies male home ranges are larger then females' (Delgado and van Schaik, 2000; Singleton and van Schaik, 2001; Singleton *et al.*, 2009). The largest home ranges observed so far are in Suaq Balimbing, Sumatra, where female home ranges are ca. 850 ha, and males' > 2,500 ha (Singleton and van Schaik, 2001). In Sabangau, home-range sizes are estimated as: 211-285 ha for adult females, 236-436 ha for non-sexually active females, 326-504 ha for flanged males, and 251-550 ha for unflanged males (Morrogh-Bernard, submitted). Range overlap is also high: up to 9 flanged males, 15 unflanged males and 16 females were seen within a single 4-ha square in Suaq Balimbing; though this figure may be higher than at other sites, as orang-utan

density in Suaq is also the second highest on record (Singleton and van Schaik, 2001; estimated at 7.44 individuals/km^2, Husson *et al.*, 2009).

Rijksen and Meijard (1999) recognise three dispersal syndromes in orang-utans:

1. Residents: found for many years to be present in a particular area for most of each year.
2. Commuters: seen regularly for several weeks or months each year for many years.
3. Wanderers: seen very infrequently (or once) in a period of at least three years and might never return to the area.

In Suaq Balimbing, Singleton and van Schaik (2001) followed animals far outside of their main study area, in an attempt to verify these suggestions. They found no evidence for commuters, though some unflanged males may have been wanderers without a stable home range. Adult females, and probably also flanged males, appear to have stable home ranges in all sites studied to date, though flanged male home ranges are normally much larger than study areas and, hence, individual flanged males may only be seen occasionally in a study area (Singleton and van Schaik, 2001; Singleton *et al.*, 2009).

Females are thought to be the philopatric sex, and males the dispersing sex, in orang-utans (MacKinnon, 1974; Galdikas, 1985b; van Schaik and van Hooff, 1996; Singleton and van Schaik, 2001, 2002). Males are thought to disperse soon after leaving the protection of their mother, and are probably nomadic for a considerable time before establishing a home range (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978; Galdikas,

1985c; Mitani, 1989; Galdikas, 1995; Delgado and van Schaik, 2000). A recent study of relatedness in Bornean orang-utans in Kinabatangan (Goossens *et al.*, 2006) indicated philopatry in both sexes, but this observation may be due to habitat fragmentation around the study area, which may have blocked male dispersal. Similar studies in Sabangau (Morf, 2008; Morrogh-Bernard, submitted) are in agreement with earlier suggestions: females were more closely relate to one another than were males.

1.3.7 ACTIVITY PATTERNS

Orang-utans typically spend most of their time awake feeding, with the rest of their time divided between resting, travelling, socialising and nest building (e.g., Galdikas, 1988; Mitani, 1989; Knott, 1999; Morrogh-Bernard *et al.*, 2009). Knott (1999) and Rodman (1988) provide summaries of orang-utan activity budgets at a number of different sites. Combining these, orang-utans spend 43% of their time feeding, 41.5% resting, 13.5% travelling and 2% in other activities, such as nest-building, socialising and calling. Orang-utans in Sabangau conform to this pattern, but spend more time feeding (Morrogh-Bernard *et al.*, 2009; Morrogh-Bernard, submitted; **Chapter 6**). These percentages may vary greatly between individuals, age-sex classes, seasons and areas, depending on the individual's condition and reproductive status, food availability and human disturbance (Rodman, 1979; Galdikas, 1988; Mitani, 1989; Rao and van Schaik, 1997; Knott, 1999; Delgado and van Schaik, 2000; Morrogh-Bernard *et al.*, 2009; Morrogh-Bernard, submitted; **Chapter 6**).

1.3.8 SOCIAL ORGANISATION

Historically, orang-utans were regarded as essentially solitary, but it is now known that, although orang-utans are solitary for most of the time, a much more gregarious and complex social life exists than was initially realised (Galdikas, 1985b; van Schaik and van Hooff, 1996; van Schaik, 1999; Singleton and van Schaik, 2002). The benefits of socialising to orang-utans are most probably rare and social (rather than continuous benefits, such as increased discovery/exploitation/defence of food and decreased predation risk), e.g., access to mates, protection from coercion in females, and socialisation and social learning in young animals (van Schaik, 1999). Orang-utans in Suaq Balimbing have been shown to exhibit an individual-based fission-fusion social system similar to chimpanzees, with individuals spending a lot more time in association with others than would be expected by chance (van Schaik, 1999). Similar observations have been made by Mitani *et al.* (1991) in Kutai and Gunung Palung National Parks (referred to as "Kutai" and "Gunung Palung" hereafter), suggesting that this system is ubiquitous in orang-utans.

Sociality is thought to be energetically costly for orang-utans, as reports indicate that travel time and day range increases, and feeding and resting time decrease, when socialising (Galdikas, 1988; Mitani, 1989; van Schaik, 1999; Wich *et al.*, 2006a). The same costs are not reported in all studies, however, indicating that potential differences in costs incurred may exist between sites. This, and the fact that orang-utans suffer from relatively little predation threat, is probably the reason why orang-utans spend so little time in association with one another compared to the other ape species (van Schaik and

van Hooff, 1996). This is supported by the observation that, in Borneo, where fruit availability is lower than Sumatra (Marshall *et al.*, 2009a), mean party size is lower (van Schaik, 1999), and orang-utan sociality is influenced by fruit abundance (Knott, 1999; this is not observed in Sumatra, van Schaik, 1999; Wich *et al.*, 2006a).

Based on observations in Suaq Balimbing, Singleton and van Schaik (2002) suggest that clusters of reproductively-synchronised female orang-utans exist, and that the movements of females within these clusters are, to some degree, coordinated. They regard the female cluster as the basic social unit in orang-utans, and this is supported by data from multiple sites (Singleton *et al.*, 2009).

1.4 ORANG-UTAN EVOLUTION

1.4.1 ORANG-UTAN EVOLUTION AS INTERPRETED THROUGH THE FOSSIL RECORD AND MOLECULAR STUDIES

The divergence dates of the different primate lineages are now reasonably well established. To cite one recent example, Glazko and Nei (2003) estimated the dates of divergence from the human lineage to be 6 Mya (range 7-5 Mya) for chimpanzees, 7 Mya (8-6) for gorillas, 13 Mya (15-12) for orang-utans, 23 Mya (25-21) for gibbons (Hylobatidae) and 33 Mya (36-32) for Old World monkeys. However, the questions of how, where and by which route each species evolved remain highly controversial.

Until recently, it was generally assumed that the ape lineage evolved in Africa, and that the ancestors of the modern-day gibbons and orang-utans then migrated out of Africa into Eurasia over land bridges during the Miocene. It now seems likely, however, that much of the early evolution of the ape lineage occurred outside of Africa. In their 'in-and-out-of-Africa' model, Stewart and Disotell (1998) present strong evidence, based on molecular, fossil and biogeographic data, in favour of the hypothesis that the common ancestor of the hominoids left Africa about 20 Mya and then migrated back to Africa (minus the gibbon and orang-utan lineages that remained in Eurasia) about 10 Mya, although many do not accept this theory (e.g., Cote, 2004; Pilbeam and Young, 2004). The recent discovery of *Pierolapithecus catalaunicus* (Moyà-Solà *et al.*, 2004), a middle Miocene (13-12.5 Mya) ape, with basic, derived great ape features, found in Spain, adds support to the in-and-out-of-Africa hypothesis. Hence, it seems likely that the orang-utan's ancestor evolved around the Mediterranean and then dispersed east into Asia, possibly to avoid competition from other Eurasian ape species (of which there were many during the Miocene), or to occupy newly-available areas that were previously unsuitable, due to desert-like conditions, for example (Stewart and Disotell, 1998).

1.4.2 HYPOTHESES FOR THE EVOLUTION OF TRAITS POSSESSED BY THE MODERN-DAY ORANG-UTAN

Orang-utans possess a number of interesting characteristics: they have a semi-solitary individual-based fission-fusion social organisation (van Schaik, 1999), are almost exclusively arboreal (Rijksen, 1978; Delgado and van Schaik, 2000), show almost no territoriality (Singleton and van Schaik, 2001), are highly intelligent (e.g., Galdikas,

1982; van Schaik *et al.*, 1996; Russon 1998; van Schaik *et al.*, 2003a, b), show high degrees of sexual dimorphism in body size and secondary sexual characteristics (MacKinnon, 1971; Rijksen, 1978; Markham and Groves, 1990), have two different adult male morphs/reproductive strategies (Galdikas, 1985a, c; Utami *et al.*, 2002), and have the longest inter-birth interval and life history of all primates (Galdikas and Wood, 1990; Wich *et al.*, 2004b, 2009a). The reasons why some of the observed differences between orang-utans and other ape species occur are not immediately obvious and, hence, have been the subject of much speculation, a brief overview of which is given here.

Wrangham (1979) suggested that the large size of the orang-utan relative to other primates might be an adaptation to enable the monopoly of fruit sources, but this seems unlikely considering the low displacement levels of other species from food sources by orang-utans and the low level of aggression towards other species exhibited by the orang-utan (MacKinnon, 1977; pers. obs.). It is unlikely that large body size evolved in order to reduce predation risk, as the orang-utan's only real predators, tigers in Sumatra and clouded leopards, are easily avoided by remaining in the trees and building night nests away from major fruiting trees (van Schaik and van Hooff, 1996). A more likely explanation (Wheatley, 1982, 1987; Leighton, 1993; Knott, 1998) is that the orang-utan's large body size enables:

(a) increased digestive efficiency and, hence, consumption of lower-quality food sources, important in times of food shortage,

(b) greater absolute and relative fat storage, allowing orang-utans to convert excess calories consumed during periods of food abundance to fat, which can be drawn upon in periods of food shortage, and

(c) that as energy and protein requirements scale to ca. 0.762 body weight (Lloyd *et al.*, 1978; Robbins, 1983; Nagy, 1994), a larger animal can live for longer from its bodily reserves.

This explanation seems highly plausible, although it is difficult to know how to interpret evidence that the *Pongo* genus may have shrunk slightly since the Late Pleistocene (see Cameron, 2001 and references therein) in relation to this, especially if, as suggested by Harrison and Chivers (2007), orang-utan food availability has declined over the past 8 Myrs. An additional benefit of large size is that large, tough food items, which were previously inaccessible, become available, increasing the number of potential food items, some of which (e.g., *Durio, Neesia*) are highly nutritious (Knott, 1998, 1999). Observations on sympatric orang-utans and gibbons have confirmed that orang-utans are capable of taking large/hard food items that gibbons cannot process (MacKinnon, 1977; Cheyne and Harrison, unpublished data).

It has been suggested (Hamilton and Galdikas, 1994) that the large sexual dimorphism in body size seen in orang-utans is an adaptation allowing better partitioning of food resources between sexes, with the larger males being able to consume more fibre, due to a larger gut and longer food retention time. Alternatively, this trait could be due to adaptations developed by the orang-utan's ancestors for a group-living lifestyle, with a large dominant male controlling a harem of females in a manner similar to the gorilla (MacKinnon, 1971, 1972; Utami Atmoko and van Hoof, 2004; Harrison and Chivers, 2007). Galdikas (1978) proposes that the orang-utan's semi-solitary nature evolved primarily to avoid intra-specific food competition brought about by their large size and

high food requirements, a suggestion supported by numerous other studies (Sugardjito *et al.*, 1987; te Boekhorst *et al.*, 1990; Utami *et al.*, 1997; Harrison and Chivers, 2007; see also references in **Section 1.3.8**).

Due to the large size of orang-utan home ranges (Singleton and van Schaik, 2001; Singleton *et al.*, 2009), orang-utans are unable to defend exclusive territories, resulting in the high degree of range overlap observed (van Schaik and van Hooff, 1996; Singleton and van Schaik, 2001).

Knott (1998, 1999, 2001) showed that dramatic changes in food availability due to mast-fruiting events, and consequent changes in energy acquisition and energy balance over time, may have important effects on orang-utan hormonal functioning and inter-birth intervals. Wich *et al.* (2006a) reviewed data collected in Sumatra (Ketambe) and Borneo (Gunung Palung), and concluded that higher fruit availability in Sumatra during non-mast periods and differences in energy contents of fall-back foods (FBFs, i.e., figs in Sumatra, and leaves and bark in Borneo) may be the reason why Sumatran orang-utans show a lack of reproductive seasonality compared to orang-utans from masting habitats in Borneo. It is unclear whether this is the case in non-masting Bornean habitats.

For a long time, it was thought that the unflanged male orang-utan was sexually inactive (or at least virtually sexually inactive) and that these males were merely 'waiting in the wings', ready for a flanged male to die, be defeated, or move away, before they could complete their development and begin to challenge for dominance/mates (Rodman, 1973; Rijksen, 1978; Galdikas, 1981). This has been shown not to be the case, however: the

number of observed matings involving unflanged males is generally higher than those involving flanged males (MacKinnon, 1974; Mitani, 1985a; Knott, 1999, but see also Schurmann and van Hooff, 1986), and recent genetic studies have shown that unflanged males achieve paternity in both Sumatra (Utami *et al.*, 2002) and Borneo (Goossens *et al.*, 2006). It is now believed that two mating strategies exist – 'chase-and-rape' in unflanged males, and 'call-and-wait' in flanged males (Galdikas, 1981, 1985a, c; Rodman and Mitani, 1987; Utami *et al.*, 2002). Flanged males are thought to be the preferred mate choice (Galdikas, 1985c; Schurmann and van Hooff, 1986; Nadler, 1988; van Schaik and van Hooff, 1996), with females seeking them out when they are most fertile, by navigating to them and distinguishing rival flanged males via their long calls (Galdikas, 1981; Utami and Mitra Setia, 1995; Delgado and van Schaik, 2000; Fox, 2002; Utami *et al.*, 2002; Delgado, 2006). This explains why the mating attempts of unflanged males are generally forced and less successful than those of flanged males (MacKinnon, 1974; Galdikas, 1985a; Mitani, 1985a).

Orang-utans have long been known to be highly intelligent, although the reason why orang-utans 'need' to be so intelligent, given their relatively dull, anti-social lifestyle has been the subject of some speculation. Due to the high energetic demands of having a large brain (Parker, 1990) it should be expected that, were high intelligence not needed, it would soon be lost. A commonly-held view is that selection pressures for the processing of technically-difficult foods and feeding-related arboreal travel were most important in the evolution of orang-utan intelligence (Chevalier-Skolnikoff *et al.*, 1982; Russon, 1998, 2002). Improving the efficiency of food searching, by producing a 'cognitive map' of the forest, has been suggested as an important selective pressure driving the evolution of

primate intelligence (Milton, 1981a; Ludvig *et al.*, 2003) and this suggestion has been given support by studies on captive (MacDonald and Agnes, 1999; Scheumann and Call, 2006) and wild (Vogel *et al.*, 2008a) orang-utans, and other primates (see Janson, 2000 for a review). Byrne and Whiten (1988, 1997), in their 'Machiavellian-intelligence' hypothesis, argue that the development of intelligence has been influenced more by social pressures – the need to keep track of social relationships and to keep one step ahead of conspecifics. All of these mechanisms have likely played a role in the development of primate/orang-utan intelligence, but, without a universal currency to measure their benefits, it is difficult to know which has had the greater influence.

Orang-utans are capable of socially-transmitted learning (Dunkel, 2006; Jaeggi *et al.*, 2007; Bastian *et al.*, 2008), and this skill has led to the development of cultural variations in behaviour, with certain behaviours present in one area and not in others (van Schaik and Knott, 2001; van Schaik *et al.*, 2003a, b, 2006, 2009a). This occurs as a new behaviour, once discovered, is transmitted horizontally (i.e., between unrelated individuals), and then primarily vertically (from mother to infant), through the population by social learning, until it reaches a dispersal barrier, such as a mountain range or large river. The result is that behaviour on one side of the dispersal barrier differs from that on the other; i.e., it is cultural. The ability to learn from others is thought to be beneficial, because it enables quicker adaptation to changing conditions than can be achieved through either individual learning or genetic adaptations (Boyd and Richerson, 1995; Lefebvre, 1995; Alvard, 2003).

Due to its rarity, the process of innovation and the spread of a new behaviour through a population cannot normally be observed, and so cultural explanations for geographical variations in behaviour can only be accepted if genetic and ecological variations can first be discounted. Hence, it is not surprising that many of the documented cultural variations in orang-utan (van Schaik *et al.*, 2003a, 2009a) and chimpanzee (Whiten *et al.*, 1999, 2001) behaviour are in 'non-essential' behaviours, such as grooming techniques and the construction of roofs over nests to protect the occupant from rain. It is much more difficult to chart cultural variations in feeding behaviour, which may be due to either knowing whether an item constitutes food or not, or differences in food-processing techniques, which may affect the profitability of a food item and, hence, its inclusion in the diet. Some differences, such as the use of tools to open fruits like *Neesia* (van Schaik and Knott, 2001), are obvious. Iin the majority of cases, however, the fact that inclusion of a food item in the diet depends on its profitability relative to other food items and on the availability of more profitable food items (Stephens and Krebs, 1986), means that comparable data on food availability and profitability must be collected from a number of different sites. For logistical reasons, this is difficult, but current inter-site collaborations (of which this study forms a part) using standardised methods should help to bridge this gap in our knowledge.

1.5 ORANG-UTAN CONSERVATION

The range and numbers of orang-utans has declined dramatically since the end of the Pleistocene era 12.5 kya (Rijksen and Meijard, 1999). During the Pleistocene, sea levels were much lower than today, allowing the orang-utan to spread and inhabit a vast area of

at least 1.5 Mkm^2, stretching from northern India, through southern China and Malaysia, down to Java in the south (Rijksen and Meijard, 1999), though gene flow between these populations may have been limited, due to the presence of large rivers on the Sunda shelf (Harrison *et al.*, 2006). In the early Pleistocene, the total population of orang-utans, excluding those in India and China, may have been two million or more (Rijksen and Meijaard, 1999). Today, the orang-utan is found only on the islands of Borneo and Sumatra, where around 54,000 and 6,500 animals survive, respectively (Singleton *et al.*, 2004; Wich *et al.*, 2008). The Bornean orang-utan is now listed as 'Endangered' by the IUCN (International Union for Conservation of Nature), and the Sumatran species as 'Critically Endangered'(IUCN, 2008). Both species are listed on CITES Appendix 1, where trade is only permitted under exceptional circumstances (CITES, 2008). A number of factors may have contributed to this historic decline, but human encroachment and hunting (Rijksen and Meijard, 1999), and the massive eruption of the Toba volcano ca. 74 kya (Muir *et al.*, 2000), after which a period of population recovery may have occurred (Steiper, 2006), are thought to be the most important.

These anthropogenic threats still exist today and, especially for Sumatran orang-utans, strong actions are required immediately if extinction is to be prevented (Nellemann *et al.*, 2007; Wich *et al.*, 2008; Marshall *et al.*, 2009b). Rijksen and Meijard (1999) estimate that, of the orang-utan population at the beginning of the twentieth century, in Borneo no more than 7%, and in Sumatra no more than 14%, survive today. The present decline is attributed mainly to habitat destruction, degradation and fragmentation, and hunting in some areas (Rijksen and Meijard, 1999; Singleton *et al.*, 2004; Marshall *et al.*, 2006;

Wich *et al.*, 2008; Marshall *et al.*, 2009b). The continuing rapid expansion of oil-palm plantations is a particularly severe threat (Fitzherbert *et al.*, 2008; Wich *et al.*, 2008).

Selective logging is highly damaging to orang-utan populations, especially when major fruit trees are removed (van Schaik *et al.*, 1995; Rao and van Schaik, 1997; Rijksen and Meijard, 1999; van Schaik *et al.*, 2001; Felton *et al.*, 2003; Morrogh-Bernard *et al.*, 2003; Husson *et al.*, in prep). Illegal logging is particularly damaging, as it does not operate under the same restrictions concerning the species and sizes of tree that can be harvested as concession logging (Rijksen and Meijard, 1999). Even when food trees are not removed, incidental damage to food trees close to target trees from the logging process can still cause drastic reductions in food availability (Johns, 1988). Illegal logging of protected areas is rampant in Borneo, with over 56% (29,000 km^2) of Kalimantan's protected forest being lost between 1985 and 2001 (Curran *et al.*, 2004) and nearly 30,000 km^2 of forest cover lost in Kalimantan following forest fires during the 1997-98 El Nińo-induced drought (Fuller *et al.*, 2004). Over two-thirds of this burning was in actual or proposed protected areas (Fuller *et al.*, 2004).

The Sabangau orang-utan population is now estimated at about 6,900 individuals (Singleton *et al.*, 2004; Wich *et al.*, 2008), making it the largest contiguous population in the world. Long-term population monitoring in Sabangau has demonstrated large shifts in orang-utan distribution in response to illegal logging and a sharp decline in numbers as a result of the 'compression effect', where animals retreat into less disturbed areas, exceed the carrying capacity of these areas and then die off (Husson *et al.*, in prep). Illegal logging, forest fires and peatland collapse (as a result of peat drainage caused by illegal

logging canals) are considered the main threats to the area's orang-utan population (Husson *et al.*, 2002; Morrogh-Bernard *et al.*, 2003; Husson *et al.*, in prep).

Orang-utan density in Sumatra is limited by food availability during periods of low abundance (Wich *et al.*, 2004a) and removal of food trees sustaining them during these periods is likely to have serious effects on their populations. Identifying these important food trees is vital, but the traditional method of estimating the importance of food items to a species (i.e., the proportion of time spent eating it) is not ideal, as energy contents of different orang-utan foods vary widely (Leighton, 1993; Knott, 1998, 1999; this study).

Long-term monitoring, particularly in protected areas, where considerable resources may be being spent on protection efforts, is essential in order to detect changes in the numbers, structure and health of orang-utan populations (Harrison *et al.*, 2007a), and the effectiveness of conservation efforts (Husson *et al.*, 2007). Unfortunately, long-term monitoring can also be expensive and funds are difficult to acquire. Hence, the development of easy, quick, cost-effective techniques for monitoring orang-utan population viability is of great importance.

As well as being of interest for anthropologists, the importance of culture in feeding behaviour is also important for orang-utan conservation. If socially-transmitted feeding skills are important for the maintenance of energy budgets in an area, then a decline in orang-utan density, or decreased gregariousness, due to anthropogenic disturbances may result in fewer opportunities for transmission of essential skills (van Schaik, 2002). Potentially, this could lead to these skills being lost from the population (Russon, 2002;

van Schaik, 2002). Whilst the conservation of distinct cultural repertoires in orang-utans should be considered worthwhile in its own right, as it is in humans, if the skill in question is particularly important in sustaining the orang-utan population during times of food stress, its loss due to anthropogenic disturbances could be disastrous for the population. Only by identifying the importance of culture in orang-utan feeding behaviour, can we hope to understand the consequences to a population of losing these skills.

1.6 PEAT SWAMP FORESTS

1.6.1 ECOLOGY OF PEAT SWAMP FORESTS

Peat-swamp forests (PSF) cover large areas of Kalimantan (68,000 km^2, Rieley *et al.*, 1996) but, compared to other forest types in the region, have been the subject of relatively few detailed investigations. Hence, there is still much to be learnt about PSF ecology. The establishment of the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP) by prominent peat-swamp researchers Suwido Limin and Jack Rieley is helping to address this imbalance, and a number of recent studies emanating from CIMTROP, and based mainly in Sabangau, have made important contributions to our understanding of tropical PSFs (Morley, 1981; Doody *et al.*, 1997; Page *et al.*, 1997; Shepherd *et al.*, 1997; Page *et al.*, 1999, 2002; Jauhiainen *et al.*, 2005; Jaya *et al.*, 2004; Limin *et al.*, 2004; Page *et al.*, 2004; Rieley *et al.*, 2004; Sulistiyanto, 2004; Sulistiyanto *et al.*, 2004).

The lowland PSFs of South-East Asia form extensive, gently-domed deposits, which can extend up to 200 km inland and reach thicknesses of up to 20 m (Anderson, 1983; Whitten *et al.*, 1987; Page *et al.*, 2004). PSF consists of a catena of forest types, replacing each other from the edge to the centre of the dome (Anderson, 1983; Brady, 1997; Stoneman, 1997; Page *et al.*, 1999). With the exception of peripheral, shallow peats subject to tidal or riverine inundations, the vast majority of nutrient influx to these forests comes from aerial precipitation (rain and, to a lesser extent, dust, Sulistiyanto, 2004). Smaller nutrient inputs come from nitrogen fixation (by micro-organisms, Jordan, 1985; Wild, 1989) and faunal migration (through animal faeces, Sturges *et al.*, 1974). These 'ombrotrophic' peatlands are acidic, nutrient-poor, subject to seasonal or permanent water-logging, and, although they support a lower diversity and density of flora and fauna than dryland rain forests, contain a large number of endemic species and are recognised as important reservoirs of biodiversity (Whitmore, 1984; Prentice and Parish, 1992; Page *et al.*, 1997; Shepherd *et al.*, 1997; Struebig *et al.*, 2006; Husson *et al.*, unpublished data). PSF also provides a home for five out of eight of the world's largest remaining orang-utan populations, comprising possibly a third or more of the total Bornean population (Meijarrd, 1997; Singleton *et al.*, 2004).

Tropical peatlands form in water-logged habitats over thousands of years (initiation of peat formation in Sabangau began around 26 kya, making it the oldest reported ombrotrophic peat formation in South-East Asia, Page *et al.*, 2004), where decomposition rates are exceeded by the addition of dead materials from the forest, leading to the accumulation of peat (Rieley *et al.*, 1992). As such, peat-forming wetlands act as important carbon sinks, with between one-fifth and one-third of global soil carbon locked

up in their soils (Gorham, 1991; Immirizi and Maltby, 1992). Despite occupying only 10% of the total global area of peatlands, tropical peatlands probably contain up to 20% (70 Pg, i.e., 7 x 10^{15} g) of global peat-soil carbon (Gorham, 1991; Immirizi and Maltby, 1992). As a result of the large amount of carbon stored in their soils, the stability of tropical peat swamps has major implications for global climate. Forest fires, brought about as a result of dry peat conditions, due to the synergistic affects of El Nińo-induced drought and peat drainage from illegal-logging canals, caused the release of huge amounts of carbon in 1997 (0.81-2.57 Gtons, i.e., 0.81-2.57 x 10^9 tons, equivalent to 13-40% of the total annual carbon emissions from fossil fuels), which contributed to the largest annual increase in global atmospheric CO_2 concentrations since records began in 1957 (Page *et al.*, 2002). Hence, the preservation of tropical peatlands is of immense importance, both locally and globally.

1.6.2 SUPRA-ANNUAL MAST FRUITING AND THE SIGNIFICANCE OF PEAT-SWAMP FOREST FOR THIS STUDY

As noted in **Section 1.1**, to date, detailed studies of orang-utan dietary intake and food selection have only been completed in mast-fruiting habitats (Leighton, 1993; Knott, 1998, 1999). These forests, which occur over much of lowland Borneo, are characterised by short periods of very high fruit availability, followed by long periods of very low availability (Knott, 2005; van Schaik and Pfannes, 2005; Cannon *et al.*, 2007a, b; see **Section 3.1**). This is thought to be primarily a strategy for trees to reduce losses due to seed predation, by fruiting when seed predators have been satiated and fruiting irregularly (Janzen, 1974; Kelly, 1994). These periods of very low fruit availability are not generally

experienced by African apes (Knott, 2005; van Schaik and Pfannes, 2005), thereby creating difficulties when attempting to compare observations on orang-utans in masting habitats to those on African apes. Due to a relative lack of mast-fruiting species, PSF does not experience these mast-fruiting events (van Schaik, 1996; Cannon *et al.*, 2007a, b). Thus, detailed studies on orang-utan feeding in PSF may help us to distinguish the relative importance of inter-specific variation and ecological differences in inducing the documented differences (see above and relevant chapters) in orang-utan and African ape feeding ecology.

1.7 SUMMARY

1. Obtaining sufficient energy and nutrients from food is critical for any primate, because (i) the quality and quantity of primate food is limited and (ii) survival, growth and reproduction are compromised when nutrient/energy balances become negative for prolonged periods. Thus, strong evolutionary pressures exist towards adaptations that help ensure requirements for survival, growth and reproduction are met, and a thorough understanding of a species' feeding behaviour is essential to understanding its socio-ecology, life history and evolution.
2. Detailed studies of feeding behaviour (energy/nutrient acquisition and food selection) have been conducted for both African apes and orang-utans in mast-fruiting habitats, but, to date, no studies on orang-utans have been completed in non-masting habitats, which have more muted fluctuations in fruit availability.
3. Thus, studies on orang-utans in non-masting habitats may be instructive in understanding whether various observations on orang-utans in masting habitats are specific to orang-utans, or specific to orang-utans in masting habitats.
4. In order to do this, data were collected from the non-masting Sabangau peat-swamp forest, Central Kalimantan on (i) food availability, (ii) dietary composition and food-energy intake, and the effects of fluctuations in food availability on this, (iii) food-selection criteria, and (iv) the effects of changes in diet composition/intake and food-availability fluctuations on behaviour.
5. A brief overview of the structure of the thesis is given, in addition to a background on orang-utan biology, evolution and conservation, and the ecology of peat-swamp forests.

2. METHODS

2.1 STUDY SITE

2.1.1 SITE DESCRIPTION

2.1.1.1 History

This research was conducted at the Natural Laboratory of Peat-Swamp Forest (NLPSF), in the Sabangau ecosystem, Central Kalimantan, Indonesia (21° 31' S and 113° 90' E, **Figure 2.1**). The site is directed by the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP). The NLSPF occupies an area of 500 km^2, representing a small fraction of the total 9,200 km^2 of forest in Sabangau (Morrogh-Bernard *et al.*, 2003). It is protected by governmental decree as a research area and development is not permitted. The work reported in this study was conducted in a 2 x 2 km^2 area of the NLPSF, in which a grid system has been constructed for primate research (see **Section 2.2.2** and **Figure 2.4**). In October 2004, a large part of the catchment (5,780 km^2), excluding the NLPSF, was designated a national park. The remainder of the catchment remains unprotected.

The last logging concession in the NLPSF finished in 1997, after which the area suffered from major fires in 1997-1998 and 2001-2002. Following the cessation of the logging concession, illegal logging became widespread, with chain saws being heard daily during

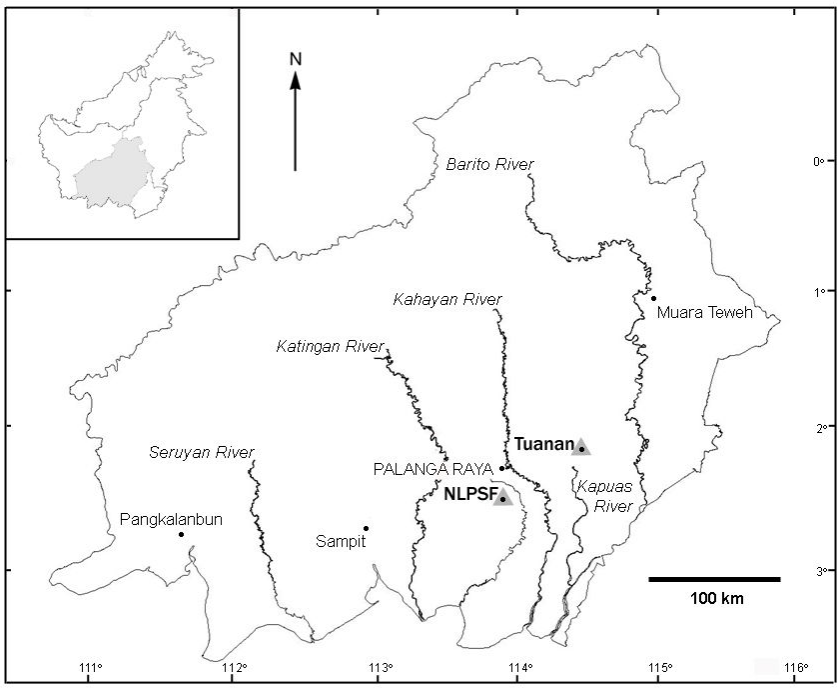


Figure 2.1 Map showing the location of the NLPSF and Sabangau Forest in Borneo. The entire Sabangau forest stretches from just south of Palangka Raya in the north to the coast in the south, and from the River Kahayan in the east to the River Katingan to the west. The location of the nearby Tuanan research site is also shown. Map adapted from Struebig *et al.* (2007).

the 2003 wet season (Husson and Morrogh-Bernard, 2002; Husson *et al.*, 2002; Husson *et al.*, in prep; pers. obs.). This led to the formation of the CIMTROP Patrol Team, who have been effective in helping to eliminate illegal logging in the NLPSF; there has been no further logging inside the NLPSF since 2003 (Husson *et al.*, 2007). Fires also burnt large areas of forest during the course of this study, in the dry season of 2006-2007 (one fire even came within 300 m of camp, pers. obs.). Although much of the rest of the Sabangau forest is protected as a national park, lack of resources for the local Forestry Department and the huge area of forest to be protected mean that illegal timber extraction probably occurs in many other areas of Sabangau. Drainage of the peat by illegal-logging

canals (dug to float out logs) has also led to a lowering of the water table, increasing the frequency and severity of fire and the risk of peat collapse, to the extent that peat collapse and fire are now considered the major threat to orang-utans in the area (Singleton *et al.*, 2004; Wich *et al.*, 2008; Husson *et al.*, in prep).

2.1.1.2 Climate

The climate in Sabangau is tropical, with high temperatures year-round (mean maximum 28.9^{o}C, mean minimum 22.0^{o}C) and high annual rainfall (2,912 mm/yr from 2003-2007, Husson and Harrison, unpublished data). Rain falls in every month, though there are distinct wet and dry seasons, typically lasting from October/November-May/June and June-September/October, respectively. Monthly rainfall during the course of this study is shown in **Figure 2.2**.

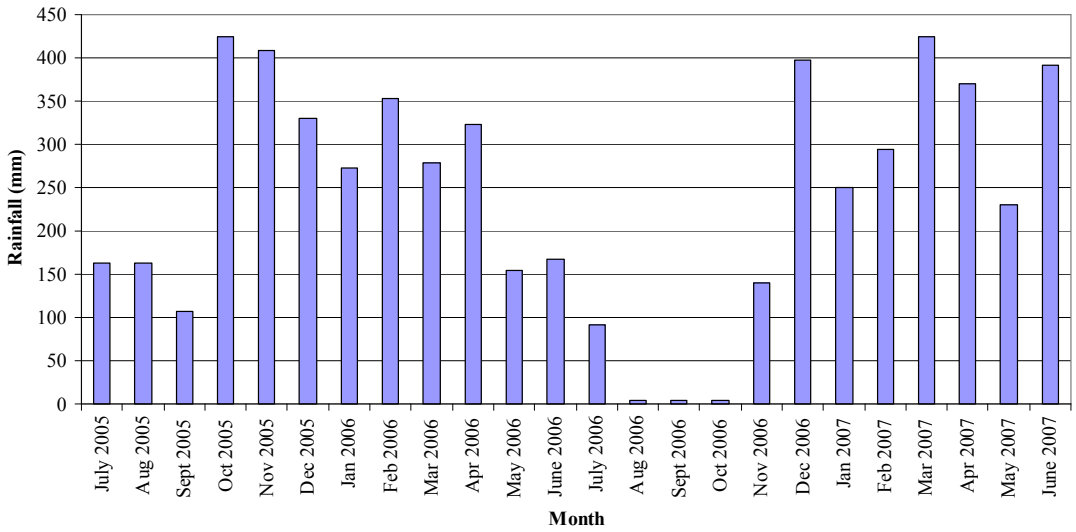


Figure 2.2 Monthly rainfall in NLPSF, July 2005-June 2007.

2.1.1.3 Habitats

The NLPSF is a fully-ombrogenous deep-peat-swamp forest (PSF); that is, the only nutrient input is through rainfall, though some riverine areas may receive nutrient influxes from wet season river flooding (Shepherd *et al.*, 1997). A brief overview of the ecology of PSFs is given in **Section 1.5**. The NLPSF is composed of four main habitat sub-types (see Shepherd *et al.*, 1997; Page *et al.*, 1999 for detailed habitat descriptions and **Figure 2.3** for the distribution of habitat sub-types around the NLPSF). The fifth habitat sub-type, riverine forest, is probably now extinct in Sabangau and has been replaced by low-growing sedge swamp (Page *et al.*, 1999). The distribution and main characteristics of these habitat sub-types are described briefly below (from Shepherd *et al.*, 1997; Page *et al.*, 1999, unless stated otherwise):

1. Mixed-Swamp Forest (MSF) – 0-4 km from the river. Peat depth is shallow and forest productivity is fairly high. During the wet season, and for much of the dry season, this area is water logged. This is considered good orang-utan habitat and supports intermediate orang-utan densities (Morrogh-Bernard *et al.*, 2003).
2. Low-Pole Forest (LPF) – found 6-11 km from the river (the forest is transitional from 4-6 km). This habitat sub-type is characterised by low productivity, small trees, thick undergrowth of *Pandanus* spp. and poor drainage, leading to almost year-round flooding (though recent drainage has led to this area becoming increasingly dry, pers. obs.). This sub-type covers a large area, but is considered to be sub-optimal orang-utan habitat unable to support a permanent orang-utan

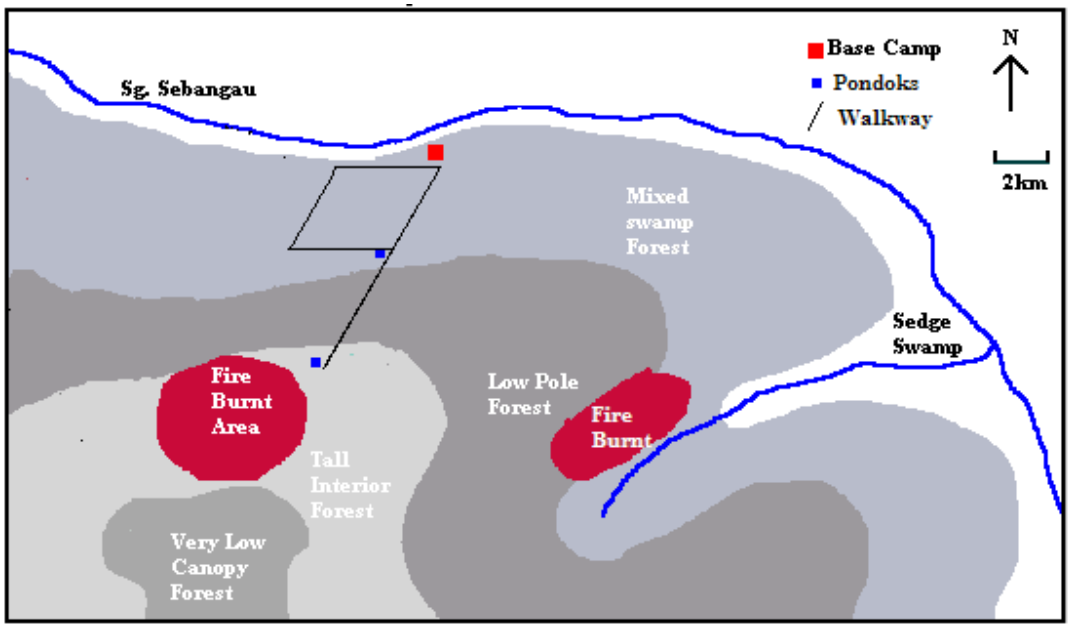


Figure 2.3 Distribution of habitat sub-types within the NLPSF. The walkway is along the old logging concession railway and the study grid within the rhombus. The railway is operational for about 800 m into the forest and a boardwalk extends up to about 1,600 m; after this, access to areas further in the forest is by a path along the broken railway line. The fire-burnt areas indicate those areas burnt during the El Nińo-induced drought of 1997 (map courtesy of OuTrop).

population (Morrogh-Bernard *et al.*, 2003), though it may act as an important over-flow/refuge area from illegal logging (Husson *et al.*, in prep).

3. Tall-Pole Forest (TPF) – found ≥ 12 km from the river, on the most elevated part of the peat dome, this habitat sub-type is characterised by tall trees, a less-dense undergrowth and high productivity. It is also the driest part of the forest, making it especially vulnerable to fire. This is considered prime orang-utan habitat and supports the highest orang-utan densities (Morrogh-Bernard *et al.*, 2003).
4. Low-Canopy Forest (LCF) – Extremely low, wet and open forest that occurs only in water-logged, inaccessible areas in the very centre of the dome. Orang-utans are not thought to use this habitat (Husson *et al.*, in prep).

2.1.2 PREVIOUS ECOLOGICAL RESEARCH AT THE SITE

Most research conducted in the NLPSF has focussed on the peat itself and/or issues relating to carbon emissions and climate change (e.g., Rieley *et al.*, 1992, 1996; Page *et al.*, 2002; Jauhiainen *et al.*, 2004; Jaya *et al.*, 2004; Limin *et al.*, 2004; Page *et al.*, 2004; Rieley *et al.*, 2004; Jauhiainen *et al.*, 2005; Limin *et al.*, 2007). The first ecological research conducted in the NLPSF concentrated on basic descriptions of the flora (Shepherd *et al.*, 1997; Page *et al.*, 1999) and fauna (Page *et al.*, 1997) of the area, and identified the NLPSF as being an important reservoir of both floral and faunal diversity. Prior to this, PSF was considered to support very little faunal diversity (Merton, 1962; Janzen, 1974). Ecological research in the NLPSF started in earnest after the cessation of the last logging concession, and particularly with the formation of the Orang-utan Tropical Peatland Project (OuTrop, directed by S. Husson, H. Morrogh-Bernard, L. D'Arcy and S. M. Cheyne) in 1999.

The first orang-utan studies in the area began in 1995 and were basic surveys to establish density and estimate population size of the catchment. These surveys, which continue to date, led to Sabangau being identified as home to the world's largest contiguous orang-utan population, which was estimated at ca. 6,900 individuals in 2004 (Morrogh-Bernard *et al.*, 2003; Singleton *et al.*, 2004; Wich *et al.*, 2008).

In 2003, an orang-utan behavioural ecology study began in Sabangau to collect baseline information on foods eaten, ranging, sociality, population composition and activity

patterns, and to assess the effects of logging and other anthropogenic disturbances on orang-utan behaviour (Morrogh-Bernard *et al.*, 2009; Morrogh-Bernard, submitted). The present study formed a continuation of this, in an attempt to gain further insights into the behaviour and future viability of this population. H. Morrogh-Bernard and I are collaborating on pooling together the data from our respective study periods (HMB: 2003-2005, MEH: 2005-2007) and summaries of the results from this collaboration are occasionally referred to in this thesis (e.g., Harrison *et al.*, in prep), when further insight can be gained from this larger dataset. This information cannot be included in my results sections, however, as it also forms part of another PhD thesis (Morrogh-Bernard, submitted). Following the cessation of my study, orang-utan research in Sabangau is being continued in the long term under the direction of H. Morrogh-Bernard.

A number of studies have also been/are being conducted in other areas of ecology and conservation by various CIMTROP and OuTrop personnel. These include studies on bat diversity (Struebig *et al.*, 2006) and hunting (Struebig *et al.*, 2007), forest regeneration (D'Arcy and Graham, 2007; Graham *et al.*, 2007; Page *et al.*, in press) and productivity (Sulistiyanto *et al.*, 2004; Harrison *et al.*, 2007b), biological monitoring of the success of conservation efforts (Harrison *et al.*, 2007a; Husson *et al.*, 2007), and an allied study on gibbon density and behavioural ecology (Cheyne, 2007; Cheyne *et al.*, 2007b; Cheyne, 2008). By ensuring that gibbon activity data were collected in an identical fashion to the orang-utan data in this study, we have created the opportunity for in-depth comparative studies of the feeding behaviour of the two species (Cheyne *et al.*, 2007a), which will form the basis of a number of planned publications.

2.2 STUDY DESIGN

2.2.1 FIELD TEAM

Orang-utans are notoriously difficult to locate and follow (e.g., Knott, 1999), and this is especially true in the Sabangau PSF, where the low orang-utan density (Morrogh-Bernard *et al.*, 2003), low visibility, and thick undergrowth of *Pandanus* spp. and vines amplify the problems experienced at other sites. In addition, for both data collection and safety reasons, a team of two individuals was required to follow each animal. As a result, it would have been physically impossible for me to collect anywhere near the required data for this project alone. Consequently, many assistants were needed to ensure that all the necessary orang-utan, food-property and forest-productivity data were collected each month. The number of people varied from 4-6 local Indonesian assistants collecting orang-utan behavioural data (shared between Cheyne's gibbon study and this study), 2 Indonesian post-graduate assistants from CIMTROP collecting productivity data, 0-1 post-graduate British assistants aiding supervision of local field assistants, and myself. In the beginning, the local assistants formerly employed by H. Morrogh-Bernard were used, but, as time went on and some assistants left the project, new ones were recruited to replace them. Some assistants remained working on the project for many years, throughout both Morrogh-Bernard's and my studies, and these were invaluable in assisting training new assistants and ensuring continuity on the project. I was present on 31% of orang-utan follows (a British post-graduate assistant was present on 50% of those follows where I was not present), processed/supervised the processing of ca. 90% of food

samples, joined productivity and litter-fall surveys at least once each month, and inputted virtually all data myself, which enabled me to check for any discrepancies in data collected by other observers.

All assistants received extensive training, both initially and throughout the course of the research, by both myself and H. Morrogh-Bernard. I was personally involved in the initial and subsequent training of each member of the team, during both the course of my research and while working as a field assistant/supervisor for H. Morrogh-Bernard in 2003-04. Initially, all assistants received extensive training on data-collection techniques, which involved "class-room" sessions, practice data collection at camp and simultaneous data collection in the field with myself and other experienced project personnel. Only when an individual's data matched my own did I deem that person's data as satisfactory and allow them to collect feeding/behavioural data. Periodic checks were made throughout the study to ensure that the quality of data collected by assistants did not slip. Indeed, many of the assistants became as good as, and in some cases possibly better than, myself at collecting the data. The only exception to this was for feeding rates, where some of the data collected by the local assistants appeared potentially unreliable when compared to my own. Hence, I restricted analysis of feeding rates to data collected by just myself and my British post-graduate assistants, whose data matched mine.

A number of measures were taken to assess and reduce inter-observer bias (c.f. Knott, 1999). Orang-utan followers were regularly rotated between individual orang-utans and age-sex classes, so that there was no systematic bias in who collected data on which

animals. I followed with each observer on a regular basis, to check their data against my own and iron out any potential data-collection issues. I also regularly paired the local assistants with my British post-graduate assistants as a further check. When I was not present on a follow, I discussed each follow at length with the observer/s and checked over all the data, in order to pick up any discrepancies, clarify any unusual observations and identify any missing data. In addition, periodical tests of quantifiable data (e.g., tree height and distances on the ground) and reinforcement training sessions were conducted on all staff.

For forest productivity data, the Indonesian post-graduate assistants who collected most of the data were very experienced (2-5 years experience of conducting monthly surveys) and incredibly good at spotting fruits/flowers/leaves in the trees. Occasionally, they were joined by members of the follow team, who received extensive training from the regular productivity assistants and myself, and also became competent at collecting these data.

2.2.2 SAMPLING REGIME

Data were collected between 1st July 2005 and 30th June 2007, representing two complete years. Due to the already-habituated and individually-identified orang-utan population, and the fact that my previous year following orang-utans in Sabangau in 2003-04 had enabled me to practice and refine my methods, no “learning” period was required (although staff did obviously require training in some aspects of data collection specific to my project) and I was able to start my data collection virtually straight away. The only

exception to this was that feeding-rate data and food samples were not collected for the first month, as I was focussing my efforts on staff training. It was possible to collect data for those food items eaten during this time in later months, however, and so this was not problematic.

As previously mentioned, orang-utans were very difficult to find and locate in the forest. Hence, it was not possible to adopt systematic criteria for following orang-utans and animals had to be followed at least partially opportunistically. In some months, no individuals of a particular age-sex class could be found and, hence, no data on that age-sex class were collected. In other months, many individuals of that age-sex class were present in the study area and followed. If a large volume of data already existed on an individual or age-sex class for that month (3-10 days), that individual was abandoned and other individuals/age-sex classes sought, in an attempt to acquire data for each age-sex class in each month.

Follows were conducted in a roughly 2 x 2 km (4 km^2) grid system (**Figure 2.4**). Despite the flat terrain, the forest's swampy nature, the tangled vegetation, and exposed tree roots and pneumatophores made travelling through the forest both very time consuming and tiring. Travel was particularly difficult in the wet season, when the water level was waist high in many places, and the area follows were conducted in had to be reduced to about 1.5 x 1.25 km (1.9 km^2). This is particularly relevant when one considers that, for an orang-utan far from camp in the wet season, a day's work could involve leaving camp at 0330 h (in order to ensure arrival at the nest before the orang-utan wakes up, typically at

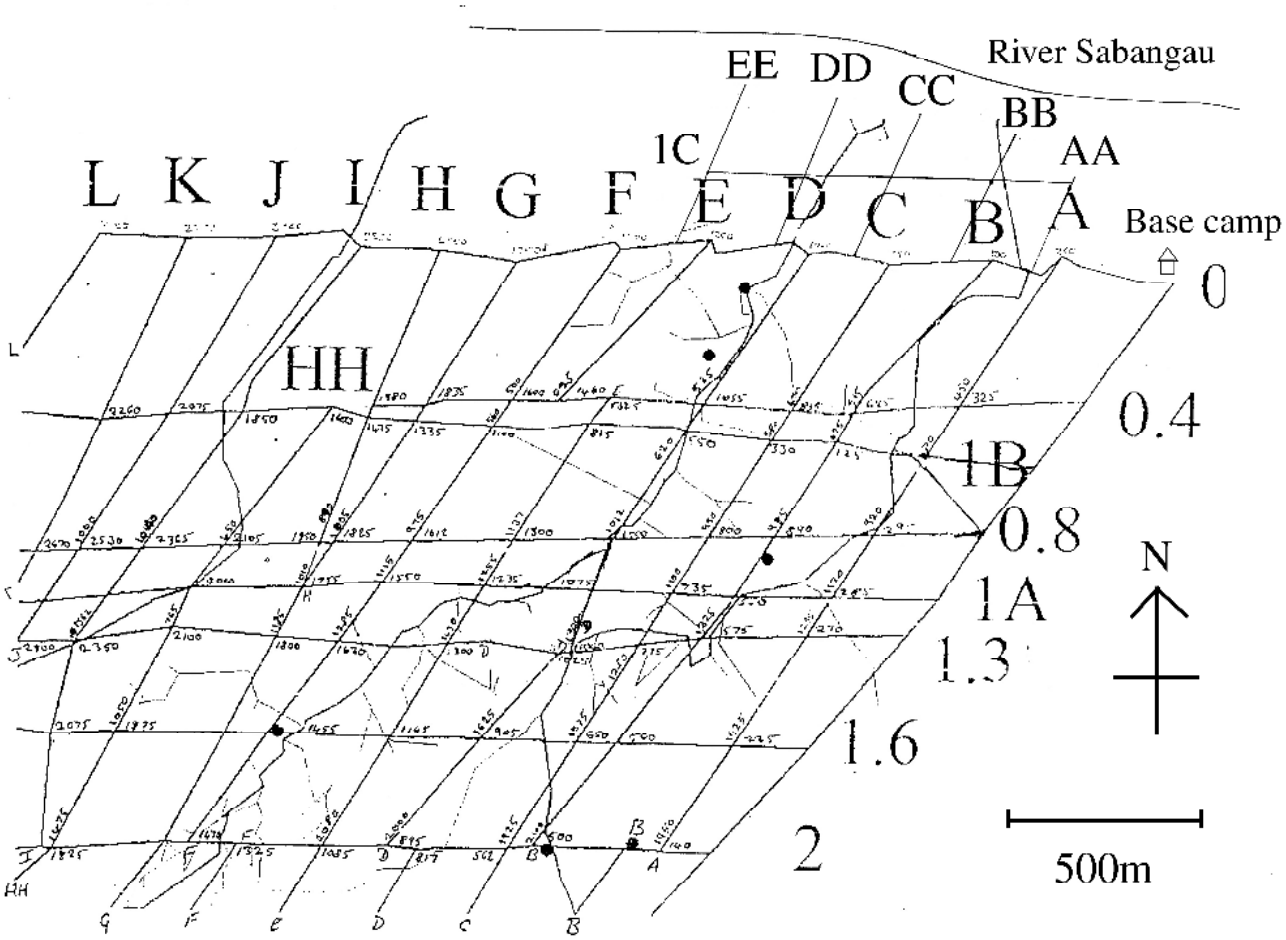


Figure 2.4 The grid system for orang-utan follows in the mixed-swamp forest, NLPSF, Sabangau. The lettered transects are 250 m apart along Transect 0, and the numbered transects are numbered according to their approximate distance in kilometres from Transect 0.

0500 h) and not returning until 1900 h (after waiting for the orang-utan to settle into its night nest), thus placing a logistical limit on the distance that could be travelled from camp to follow animals.

Orang-utans were found by systematically searching the grid system along the transects, which were marked with distance tags at 12.5-m intervals to aid navigation. Observers searched alone with a two-way radio, and so were able to call over fellow observers when they contacted an orang-utan. The orang-utan would then be followed by two observers. In this way, more of the grid could be covered without compromising observer safety. Orang-utans were almost always heard (either through crashing through the canopy during travel, food dropping to the floor, kiss squeaking at the observer or flanged males long calling) before they were seen. Other researchers working on other projects would also frequently encounter orang-utans and alert us to their presence. The length of time taken to find an orang-utan varied greatly, from ten minutes to a week of daily searching by four observers with no success. This variability was due to movements of orang-utans into and out of the study area, the intensity of search effort, the observers searching and, to a large extent, the weather (rain and subsequent dripping makes hearing, and hence finding, orang-utans very difficult). Once found, an individual was followed to nest and cotton attached to the nearest transect, enabling observers to return easily to the nest the next day before dawn.

2.2.3 HABITUATION AND DATA EXCLUDED FROM THE ANALYSIS

Unhabituated orang-utans react to human presence by kiss squeaking (and, in the case of flanged males, long calling and even charging) extensively, running away, hiding, travelling at a greater height in the canopy, and resting more and feeding less than habituated animals (Setiawan *et al.*, 1996; Knott, 1999; pers. obs.). Thus, it is important that only data from habituated animals are used in analyses. Following earlier research in Sabangau (Morrogh-Bernard, submitted), the main criteria used for classifying an animal as "unhabituated" or, more accurately, "disturbed" was that it emitted ≥ 15 kiss squeaks/hour followed. In addition, data on days with abnormal amounts of resting/travelling/feeding, long distances travelled or high prevalence of hiding and/or threatening behaviours towards observers (e.g., snag crashing and charging) were also excluded, particularly if the individual in question was newly encountered or rarely followed.

Data from very short follows were also excluded from analyses, as possible bias in orang-utan feeding and other behaviours could occur in very short follows, especially if these are concentrated at particular times of day, potentially skewing the results (M. van Noordwijk, pers. comm.). For example, an orang-utan followed for only an hour could eat termites for all this time and, if this was the only follow on an age-sex class that month, this could give the false impression that all members of this age-sex class spent 100% of their waking hours eating termites that month! Most authors presenting data on

orang-utan diet have either stated that all partial follows were included or have not stated any criteria for minimum follow length and, hence, have presumably included data from all partial follows (e.g., Rodman, 1977; Galdikas, 1988; Ungar, 1995; Wich *et al.*, 2006b). However, some authors have applied different criteria to deal with this: Knott (1998, 1999) included all partial follows when reporting variables as percentages of feeding time etc., but restricted analyses to full-day (FD) follows only when calculating daily intakes, whereas Fox *et al.* (2004) included FD follows and all partial follows that fell within one standard deviation of mean active-period (AP, see **Section 6.2** for definition) duration. While three hours has been recommended as the minimum follow length for inclusion in analysis of activity profiles (Morrogh-Bernard *et al.*, 2002), this may not be appropriate for analysing dietary composition, due to differences in dietary composition throughout the day (Rodman, 1977). Excluding too much data by imposing too high a limit is clearly undesirable, however, as, not only may a shorter limit not actually introduce any bias to the data, but, when data sets are small, this can lead to no data being included for certain age-sex classes in certain months (as I experienced with my own data, and as has also been experienced by researchers in Sungai Lading, M. Bastian, pers. comm.). Thus, a compromise minimum follow limit for inclusion in analyses must be found.

In an attempt to find such a compromise, Harrison *et al.* (in press) analysed percentage time spent feeding by orang-utans on different food types (fruit, flowers, leaves etc.) for all age-sex classes combined in Sabangau and Tuanan, also in Central Kalimantan. Data were presented from both sites using a 3-h limit, 6-h limit, FD follows only, and FD follows plus partial follows within one standard deviation of full-day follow length (cf.

Fox *et al.*, 2004). For the Sabangau data set (i.e., the data set presented in this thesis), it was found that significant differences existed between the 3-h and 6-h limits, but not between either limit and full-day follows. In the larger Tuanan data set, where the possibility of Type II errors is reduced, when compared to higher follow limits, the number of differences found using a 3-h limit > 6-h > Fox *et al.*'s limit.

In terms of the number of follow hours included in my Sabangau data set, there is little difference between the 3-h (3,614 h) and 6-h limit (3,120 h), but follow hours are much reduced when using Fox *et al.*'s (2004) criteria (2,355 h) or full-day follows only (2,277 h). Thus, using a 6-h limit appears to be an adequate compromise between avoiding potential bias from short follows and excluding too much data from the data set, and this limit has therefore been applied on the data presented herein. It should be noted, however, that, broadly speaking, very similar means are obtained when using a shorter or longer follow limit (in 81% of cases where Harrison *et al.*, in press found significant differences between minimum follow limits, the difference between means was < 2% and, in 54% of cases, < 1%; calculated values for daily energy intake also did not differ between the 6-h limit and FD follows only, **Section 4.3.3**).

As a final criterion, only data on independent individuals (i.e., individuals whose mother has already had another baby or, in cases where this is the mother's last baby, that have reached eight years of age, Morrogh-Bernard *et al.*, 2002) were used in all analyses, as a dependent animal's behaviour is generally dictated by what its mother is doing. The resulting data set used for analysis after all these data were excluded comprised 3,120 follow hours.

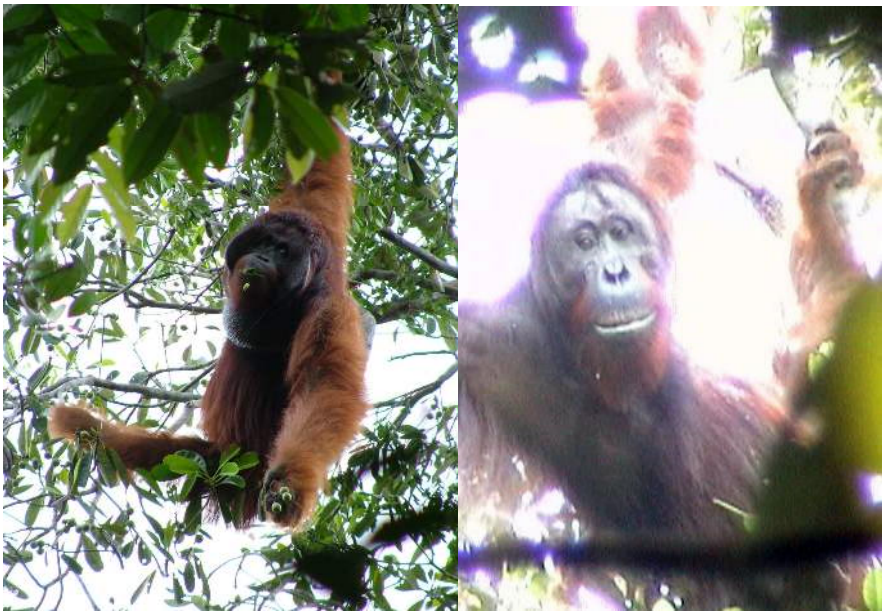
2.2.4 THE ORANG-UTAN STUDY POPULATION

Since orang-utan behavioural research began in Sabangau in 2003 until the cessation of this study in June 2007, we have named 27 independent individuals (Morrogh-Bernard and Harrison, unpublished data), though many of these only passed through the study area briefly and some rarely-encountered individuals may have been named twice. Data included in the analysis for this study comprised data from 24 individuals, five of which were of unknown identity (**Table 2.1**). Adult (parous) females (AF) are individuals of reproductive age and nulliparous females (NF) are those thought to have not yet reproduced. Flanged males (FLM) are those with fully-developed cheek pads and throat sac (**Figure 2.5.A**). Unflanged males (UFM) either did not possess or were in the process of developing these features **(Figure 2.5.B)**. The terms "adult/sub-adult" or "developed/undeveloped" have been avoided for males, as unflanged males are known to be both sexually mature and capable of fathering infants (Utami *et al.*, 2002; Goossens *et al.*, 2006).

Table 2.1 Orang-utans included in the data.

Adult females	Nulliparous females	Flanged males	Unflanged males
Cleopatra (5)	Ella (2)	Beethoven (9)	Archimedes (2)
Gracia (1)	Feb (16)	Drake (1)	Darwin (2)
Indah (18)	Indy (3)	Hengky (1)	Leonardo (1)
Viola (2)	Unknown (1)	Jupiter (6)	Mozart (5)
Unknown (1)		Mozart (6)	Romeo (4)
		Wallace (4)	Shogun (1)
		Unknown (3)	

Numbers in parentheses are the number of months for which data was acquired on that individual. Indy only became dependent from her mother, Indah, after Indah's newest baby was born in October 2005. Mozart developed from an unflanged to a flanged male during the course of the study, and was finally classified as a flanged male in March 2006.



A. B.

Figure 2.5 Flanged (A) and unflanged (B) male Bornean orang-utans. Note the flanged male's cheek pads, throat sac, large body size, and long hair at the base of the back. These features are absent in the unflanged male. Photographs by A. Gibson (A) and H. Morrogh-Bernard (B).

As can be seen, due to the varying presence of individuals in the study area, different individuals were sampled with different intensities, with some being sampled most months ("residents"), and some in only one month ("transients" or animals residing mostly outside the study area).

The number of individuals followed is shown in **Table 2.2** and the number of follows conducted on each age-sex class during each month of the study is shown in **Table 2.3**. The total number of follow days in the data set was 321, representing 3,120 h of observations. In only one month, August 2006, were there no data for any age-sex class. In this month, despite intensive search effort, only one follow < 6 h was accrued, due to a lack of orang-utans in the study area. While most data were acquired from FD follows, in

Table 2.2 Number of individuals from each age-sex class sampled by month. Across the whole study period, data were collected on 24 individuals (5 adult females, 4 nulliparous females, 9 flanged males and 6 unflanged males).

Year	Month	All combined	Adult females	Nulliparous females	Flanged males	Unflanged males
2005	July	4	2	1	1	0
2005	August	6	3	1	1	1
2005	September	7	2	1	3	1
2005	October	10	2	1	3	4
2005	November	4	1	1	1	1
2005	December	6	2	1	1	2
2006	January	6	1	2	2	1
2006	February	5	1	2	2	0
2006	March	4	1	1	2	0
2006	April	6	2	0	3	1
2006	May	2	1	1	0	0
2006	June	2	1	0	1	0
2006	July	1	1	0	0	0
2006	August	0	0	0	0	0
2006	September	2	1	0	0	1
2006	October	4	1	1	1	1
2006	November	2	1	0	1	0
2006	December	3	0	1	2	0
2007	January	3	0	1	1	1
2007	February	4	1	2	1	0
2007	March	4	0	2	2	0
2007	April	4	2	1	1	0
2007	May	3	1	1	1	0
2007	June	2	0	1	0	1

some months the only data for a particular age-sex class was from partial follows. Due to males' larger and less fixed home ranges (Singleton and van Schaik, 2001; Morrogh-Bernard, submitted), and hence their less reliable presence in the study area, fewer follows were obtained on males than on females, despite efforts undertaken to attempt to ensure even sample sizes for each age-sex class each month.

Table 2.3 Number of follows conducted on each age-sex class by month. The number of full-day follows are in parentheses.

Year	Month	All combined	Adult females	Nulliparous females	Flanged males	Unflanged males
2005	July	21 (18)	12 (11)	8 (6)	1 (1)	0 (0)
2005	August	23 (16)	17 (12)	2 (1)	3 (2)	1 (1)
2005	September	33 (26)	14 (14)	11 (10)	6 (2)	2 (0)
2005	October	31 (18)	11 (7)	5 (3)	6 (3)	9 (5)
2005	November	17 (12)	9 (9)	6 (2)	1 (1)	1 (0)
2005	December	10 (4)	2 (0)	3 (2)	3 (2)	2 (0)
2006	January	21 (14)	7 (5)	5 (2)	6 (4)	3 (3)
2006	February	15 (5)	1 (0)	7 (2)	7 (3)	0 (0)
2006	March	22 (15)	2 (2)	4 (2)	16 (11)	0 (0)
2006	April	10 (3)	3 (1)	0 (0)	6 (2)	1 (0)
2006	May	9 (7)	7 (6)	2 (1)	0 (0)	0 (0)
2006	June	10 (8)	8 (8)	0 (0)	2 (0)	0 (0)
2006	July	6 (4)	6 (4)	0 (0)	0 (0)	0 (0)
2006	August	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
2006	September	8 (5)	7 (5)	0 (0)	0 (0)	1 (0)
2006	October	10 (4)	1 (1)	2 (1)	4 (0)	3 (2)
2006	November	5 (2)	3 (2)	0 (0)	2 (0)	0 (0)
2006	December	5 (1)	0 (0)	3 (0)	2 (1)	0 (0)
2007	January	4 (1)	0 (0)	2 (0)	1 (1)	1 (0)
2007	February	10 (6)	3 (2)	6 (4)	1 (0)	0 (0)
2007	March	13 (9)	0 (0)	9 (8)	4 (1)	0 (0)
2007	April	16 (13)	5 (5)	9 (7)	2 (1)	0 (0)
2007	May	15 (15)	4 (4)	10 (10)	1 (1)	0 (0)
2007	June	7 (4)	0 (0)	6 (4)	0 (0)	1 (0)
	Total	**321 (210)**	**122 (98)**	**100 (65)**	**74 (36)**	**25 (11)**

2.2.5 "REAL" AND "TRY" FOODS, AND THE DISTICTION BETWEEN FOOD TYPES AND FOOD ITEMS

While the majority of foods eaten during the course of the study could accurately be referred to as "real" or "true" orang-utan foods, some foods were eaten only once and for one or two minutes. When many thousands of hours of data have been collected at a site (such as in Sabangau, where almost 10,000 h of observations have been collected), it is probably more likely that these foods represent "*try foods*" being taste-tested, rather than real orang-utan foods. Try foods present a problem when drawing up species lists of foods eaten and, importantly, when assessing food availability. Some try foods may occur in high numbers in the forest and/or bear fruits or flowers very regularly; thus, their inclusion as "real" foods would erroneously elevate estimates of orang-utan food availability, and, hence, potentially influence analyses assessing the effects of food availability on behaviour etc.

As a result, all try foods were excluded from analyses of food availability estimates, based on the entire Sabangau dataset from September 2003-June 2007, and Zweifel (2008) and Bastian *et al.*'s (in prep) recommendations that *real orang-utan foods* must have been eaten for ≥ 2 bouts and for ≥ 6 minutes total feeding time across the whole study period. Try foods were not excluded for analyses of percentage feeding on food types or intake rates, as, due to their very small contribution to overall feeding, their effect here will be negligible.

In this study, a *food item* was considered to be a specific part of a certain species (e.g., *Palaquium leiocarpum* fruit, *Dyera lowii* bark, etc.). In contrast, a *food type* refers to all food items of a given type, e.g., fruit, flowers, leaves, invertebrates, etc.

2.2.6 STATISTICAL ANALYSIS

Here, I give a brief description of the general 'rules' I applied when performing statistical analyses on orang-utan data. For details on statistical analyses of specific data sets, please see the relevant chapters.

Figures for average dietary composition and activity profiles are frequently given in studies on both orang-utans (e.g., Rodman, 1979; Galdikas, 1988; Mitani, 1989; Knott, 1998, 1999; Wich *et al.*, 2006b) and other primates (e.g., *Cercopithecus Sabaeus*: Harrison, 1983; *Papio* spp.: Hill and Dunbar, 2002; *Hylobates* spp.: McConkey *et al.*, 2003), but, in many cases, the exact methods used to calculate these figures are not given and no standard approach exists (Fox *et al.*, 2004). In orang-utan studies, data have been presented as overall percentages, with individuals weighted equally, or by using monthly means of individuals or individual follow days as independent data points (Rodman, 1979; Galdikas, 1988; Mitani, 1989; Knott, 1998, 1999; see discussions in Fox *et al.*, 2004 and Harrison *et al.*, in press).

In this study, potential seasonal fluctuations in diet/intake/activity in relation to food availability were of primary consideration. Thus, all statistics were based on a mean calculated for each age-sex class each month, with all age-sex classes and all months

represented equally in any combined analyses (c.f. Knott, 1998, 1999) to accommodate potential differences between age-sex classes and seasons, and to avoid pseudo-replication (where "independent" data points actually comprise > 1 data point on the same individual sampled repeatedly and, hence, are not truly independent). For example, if presenting average figures for flanged males for the whole study period, both November 2005 (1 follow day) and March 2006 (16 follow days) would contribute towards one-nineteenth of the mean. This is justified when one considers that, e.g., 91% of flanged male feeding time was spent eating fruit in November 2005 and only 77% in March 2006.

Even with this approach, however, the basic statistic – a mean calculated for each age-sex class each month – can still be calculated in numerous different ways and the exact method used is very rarely given, even though statistical differences can exist between values calculated using different methods (Harrison *et al.*, in press), and advantages and disadvantages exist for each method. In this study, this basic statistic was calculated using the "proportions" method (Harrison *et al.*, in press), as follows for, e.g., percentage time spent feeding on an item:

$$\text{Percentage time feeding}_i = \frac{\sum_{a=1}^{n}\left(t_{ia}/T_a\right)+\cdots+\left(t_{in}/T_n\right)}{n}$$

where t_{ia} = total time spent feeding on item i across all follows in a month by individuals a through to n; T = total time spent feeding on all food items across all follows in that month; and n = the number of individuals of that age-sex class followed in that month.

There are various problems associated with this approach, including that (a) sample size for statistical analysis is reduced (and, hence, the possibility of Type II errors increased), as many data points are compressed into one, and (b) weighting each individual (or month) equally over-represents individuals (or months) that were sampled infrequently (Knott, 1999). For example, an individual followed for 60 h in a month is likely to be more representative of "typical" orang-utan behaviour in that month than one followed for 6 h. This argument holds less well if inter-month or inter-individual differences (inter-individual differences in time feeding have been found between flanged males in Gunung Palung, Knott, 1999) are expected, however, in which case weighting individuals according to follow effort will also introduce bias, especially if sample sizes are similar.

Unfortunately, no perfect method for handling this type of data exists (Knott, 1999, pers. comm.; Fox *et al.*, 2004; Harrison *et al.*, in press) and, for the purposes of this study, in which understanding temporal variations in diet and behaviour in relation to food availability is the primary aim, I consider weighting each individual/age-sex class/month equally when computing means to be the optimal approach. This is because differences between individuals have been found in orang-utans (time feeding: Knott, 1999), whereas, to date, there is no evidence that increases in the number of follow days included in a sample produces similar differences. For example, differences between estimates of daily energy intake in Sabangau (see **Chapter 4**) do not differ between means derived from all FD follows in a month and only one (the second of each month, selected so that inclusion is systematic and to avoid any potential influence of new follow/observer-presence effect) FD follow from the same month (paired t-test, $t = 0.414$, $df = 38$, p = NS). Fortunately, however, the same general patterns typically emerge in

orang-utan studies, regardless of the method used (though more statistical differences are found when using individual follow days as independent data points, due to larger sample sizes, Knott, 1999; Fox *et al.*, 2004).

When performing multiple comparisons, a Bonferroni correction was applied following Hochberg (1988), in order to reduce the risk of Type I errors associated with multiple tests (i.e., to ensure the family-wise error rate ≤ 5%). Results of statistical tests that were significant prior to, but not after, correction for multiple comparisons are presented and interpreted as non-significant "trends". In all tables, uncorrected test results are in normal font and Bonferroni-corrected results are highlighted in bold. Corrections for multiple comparisons were not performed in exploratory analyses, in which the aim was to explore potential differences/relationships, rather than test specific hypotheses (Roback and Askins, 2004). All correlations are two-tailed unless otherwise stated, and *alpha* was set at 0.05 throughout.

2.3 SUMMARY

1. This study was conducted in the Natural Laboratory of Peat-Swamp Forest, part of the Sabangau ecosystem, Central Kalimantan, Indonesia. This is an area of deep peat-swamp forest, which has been the subject of orang-utan research since 1996.
2. It was instigated in July 2005 and data were collected for two years, until June 2007. This timeframe enabled seasonal variations in food availability and feeding behaviour to be captured. Rainfall was recorded daily, in order to aid interpretation of seasonal fluctuations in food availability.
3. In order to ensure that all the necessary orang-utan, food-property and forest-productivity data were collected each month, 6-9 assistants aided data collection. All assistants were given thorough training in data collection techniques, and were only permitted to begin collecting data when their data matched my own. In addition, regular checks were made to ensure continued reliability of data collected by assistants.
4. Orang-utans were found by systematically searching the study area, and were nearly always heard before they were seen. Once found, orang-utans were followed from nest to nest, or until they were lost or left the study area. Orang-utans were abandoned and other individuals followed when sufficient data were collected (usually after 3-10 days). As orang-utans were very difficult to find and locate in the forest, it was not possible to adopt systematic criteria for following animals and animals had to be followed at least partially opportunistically, though attempts were made to collect data on each age-sex class each month. In some months, however, no individuals of a particular age-sex class could be found and, hence, no data were collected. In other

months, many individuals of that age-sex class may have been present in the study area and followed.

5. Only data from habituated independent individuals were included in analyses. The primary criteria used to define habituation was that the animal emitted < 15 kiss squeaks/hour. Furthermore, short follows < 6-h long were also excluded, as short follows could potentially skew the data. After these data were excluded, the resulting data set used for analyses comprised 3,120 h observations over 321 days, with follows conducted on 24 individuals (5 parous/adult females, 4 nulliparous/adolescent females, 9 flanged males and 6 unflanged males). Due to varying presence in the study area, some individuals and age-sex classes were sampled more intensely than others.
6. For analyses of dietary composition and food availability, "try foods" were excluded from the data. These were defined as items eaten only once and for less than 6-min total feeding time since orang-utan research in Sabangau begun in 2003.
7. Methods used to calculate mean dietary composition and statistical considerations relevant throughout are detailed.

3. FOREST PRODUCTIVITY AND FOOD AVAILABILITY

3.1 INTRODUCTION

Despite having a relatively stable climate, it is now recognised that large temporal variations in fruit and flower availability in tropical rain forests exist (e.g., McClure, 1966; Medway, 1972; Janzen, 1974; Struhsaker, 1978; Gautier-Hion, 1980; Raemaekers *et al.*, 1980; van Schaik, 1986; van Schaik *et al.*, 1993; Cannon *et al.*, 2007a, b). Recognition of this, and consequent data on environmental food availability, collected independently from data on primate diet, has aided greatly in the interpretation of primate behaviour across many species, e.g., blue monkeys (*Cercopithecus mitis doggetti*, Kaplin *et al.*, 1998), macaques (*Macaca fuscata fuscata,* Takahashi, 2002), mangabeys (*Cercocebus albigena,* Olupot *et al.*, 1997), gorillas (Ganas *et al.*, 2004), chimpanzees (Newton-Fisher *et al.*, 2000; Hashimoto *et al.*, 2003), gibbons (McConkey *et al.*, 2003; Marshall and Leighton, 2006) and even entire primate communities (Tutin *et al.*, 1997; Brugiere *et al.*, 2002). Unsurprisingly, food-availability data have also been important in understanding orang-utan ranging, sociality, reproduction, activity profiles, diet composition and intake (te Boekhorst *et al.*, 1990; Knott, 1998, 1999; van Schaik, 1999; Singleton and van Schaik, 2001; Wich *et al.*, 2006a, b). Variations in food availability and habitat productivity are also thought to be important determinants of orang-utan

densities between sites (Rijksen and Meijard, 1999; Delgado and van Schaik, 2000; see also articles in Wich *et al.*, 2009b).

Much of Borneo is covered by lowland dipterocarp forests, which experience supra-annual mast-fruiting (SAMF) events, occurring at irregular intervals every 2-10 years. These SAMF events involve primarily dipterocarps, but also many other tree families (Ashton *et al.*, 1988; Appanah, 1993; Sakai *et al.*, 1999). During SAMF events, 55-60% of tree species may bear fruit, compared to only 20-25% in non-mast years (McClure, 1966; Medway, 1972). These masting events lead to huge peaks and troughs in fruit and flower availability in the forest, which has dramatic effects on many species, including orang-utans (see review in Harrison and Chivers, 2007). In contrast, peat-swamp forest (PSF) is non-masting and, as a result, fruit production in PSF is relatively consistent and lacks the dramatic peaks and troughs in fruit availability that occurs in dipterocarp forests (Cannon *et al.*, 2007b). Despite this, temporal variations in orang-utan fruit and flower availability in PSF do occur, as demonstrated by van Schaik (1999), Cannon *et al.* (2007b), Vogel *et al.* (2008b) and in this chapter. As rainfall is often considered a primary cause of variations in primate food availability (e.g., Hill and Dunbar, 2002), preliminary assessment of temporal variations in fruit and flower availability in relation to monthly rainfall are conducted. More detailed analysis of this topic (cf. Anderson *et al.*, 2005) will form the topic of future publications. This chapter is descriptive – the primary aim is to compare fruit availability between Sabangau, masting habitats in which orang-utan feeding ecology has been studied previously and African ape habitats, to aid interpretation of observed differences in feeding behaviour in **Chapters 4-6**.

3.2 METHODS

3.2.1 LITTER-FALL

In order to assess overall forest productivity, litter-fall (LF) was collected twice monthly and separated into its component parts (leaves, reproductive parts, branches ≤ 5 cm diameter, bark and miscellaneous debris), following Proctor (1983) and the recommendations of Morrogh-Bernard *et al.* (2002) for orang-utan studies. Sixteen 1-m^2 fixed systematically-positioned traps were used, giving a combined trap area similar to previous studies in Sabangau (Sulistiyanto, 2004; Sulistiyanto *et al.*, 2004). Eight traps were placed inside the productivity plots on both Transect 0.4 and 1.6, in order to facilitate direct comparisons with orang-utan fruit and flower availability data. Branches > 5 cm diameter were excluded. For the purpose of this study, analyses were restricted to total LF. Litter was oven dried at 40°C for two weeks and then weighed.

LF traps were erected specifically for this study. As the emphasis during the first few months of the study were on food sample collection and staff training, these traps were not erected until November 2005 and data were collected from December 2005-June 2007 (19 months). No attempt was made to assess fruit or flower availability through LF traps, as the spatial variation in these components tends to be so large as to make the values virtually meaningless (Proctor *et al.*, 1983a).

3.2.2 ORANG-UTAN FOOD AVAILABILITY

Orang-utan fruit and flower availability was assessed through productivity plots (total area 2.4 ha), within which all trees, figs and lianas above a set minimum diameter at breast height (DBH) were enumerated, measured and identified (by H. Morrogh-Bernard, S. Husson and E. Shinta prior to the onset of this study). Six plots were positioned at varying distances from the river (on Transects 0.4, 1A, 1.6, 2.25, 2.75 and 3.5, see **Figure 2.4**), in order to encompass any variation in fruit and flower availability resulting from increased distance from the river (c.f. Payne, 1979). The start distance of each plot along the transects was random.

Each plot was divided into two sub-plots: "sub-plot 0" (300 x 5 m, total 0.9 ha) to the north of the transect and including all trees ≥ 10 cm DBH, and all figs and lianas ≥ 3 cm DBH, and "sub-plot 1" (500 x 5 m, total 1.5 ha) to the south of the transect and including all trees ≥ 20 cm DBH, and all figs and lianas ≥ 3 cm DBH. This division was necessary as, for logistical reasons, it was desirable to sample one plot in one day. This would have been incredibly difficult if all trees ≥ 10 cm DBH were monitored in both sub-plots, as trees of this size are very numerous in the forest. Thus, sampling all trees 10-20 cm DBH in both plots would have required more observers or more time, which would have increased inter-observer bias in the data and the length of time between the first and last surveys in a month, respectively. Thus, in order to incorporate both sub-plots into analyses, the proportion of trees 10-20 cm DBH in sub-plot 1 was assumed to be the same as in sub-plot 0, and availability estimates adjusted accordingly. This is justifiable, as

transects were not cut according to any forest features and, hence, there is no reason to expect any systematic differences between the forest on different sides of the transect.

A 10-cm minimum DBH limit for "trees" (as opposed to smaller "poles" and "saplings") in sub-plot 0 was imposed as, with the exception of leaf-feeding trees, which are generally very small and occur at densities so high they would be incredibly difficult to monitor, very few orang-utan fruit/flower trees in Sabangau are < 10 cm DBH (12% of total records). A 20-cm minimum DBH limit for trees in sub-plot 1 was imposed as the large majority of orang-utan non-leaf food trees in Sabangau were > 20 cm DBH (66%). A 3-cm minimum DBH limit for lianas and figs was applied in order to avoid the inclusion of tiny lianas and vines from which orang-utans generally do not eat or only eat leaves, but it is worth noting that this may underestimate fruit availability from these sources, as some lianas/figs with small DBH may be quite large in the canopy.

All plots were monitored monthly (with start date typically around the 16th) using binoculars and the presence, number and percentage cover of fruits (ripe/unripe), flowers (open/bud) and new leaves were recorded for each stem, following Morrogh-Bernard (submitted). Some trees died during the course of the study, and these were removed from the data sheets. Some new trees were also added during the course of the study.

Most previous orang-utan studies have only included fruiting stems in their estimates of food availability (e.g., Knott, 1998, 1999; van Schaik, 1999; Buij *et al.*, 2002; Wich *et al.*, 2006b). In this study, I also included flowering stems for general analysis of food

availability, as, in Sabangau, 8% of foods eaten are flowers (17 items from 9 genera, many of which are eaten regularly), and flowers can constitute ≥ 60% of monthly diet, both in terms of time spent feeding and energy intake (**Section 4.3.1**).

Unlike many previous orang-utan (e.g., van Schaik, 1999; Wich *et al.*, 2006b) and African ape (e.g., gorillas: Doran *et al.*, 2002; Remis, 2003; chimpanzees: Wrangham *et al.*, 1998; both: Stanford and Nkurungi, 2003) researchers, who only included ripe fruit in their analysis, on the basis that ripe fruit is preferred, I also included unripe fruit in my estimates (unripe fruits have also been included in estimates by some African ape researchers, e.g., Chapman *et al.*, 1999; Newton-Fisher *et al.*, 2000). This is because, in Sabangau, (a) fruits are eaten at many stages of ripeness and distinguishing these in the field can be difficult, especially for fruits with which the observer is less familiar, and (b) of those fruit-feeding bouts for which data were reliably recorded, 23% were on unripe fruit. As described in **Section 2.2.5**, all "try" foods were excluded from analysis of food availability, and the resulting average number of "real" orang-utan fruit/flower trees monitored was 1,072 (SD ± 20, range 1,000-1,089). Note that the number of trees included in the sample each month differed, due to the removal of dead trees, addition of new trees, and occasional "lost" trees that could not be found in certain months. Thus, food availability was expressed as the *percentage of orang-utan fruit/flower stems monitored that month bearing fruit or flowers* (see **Table 3.1** for a summary of definitions). In line with this, if a tree contained both fruit and flowers, it was only counted once (i.e., a stem either had food or it did not).

Table 3.1 Summary of definitions used for assessment of food availability.

Term	Definition
All fruit	Includes all fruits, regardless of whether eaten by orang-utans or not. Most researchers have used only ripe fruits in these estimates (e.g., van Schaik, 1999; Wich *et al.*, 2006b), but, in this study, unripe fruits have also been included (see text).
Orang-utan fruit	Includes only "real"[1] orang-utan fruits; i.e., fruits that are actually eaten by orang-utans (e.g., Knott, 1998).
Orang-utan fruit/flower	Includes only "real"[1] orang-utan fruits and flowers; i.e., fruits and flowers that are actually eaten by orang-utans (used for the first time in this study).
Orang-utan food-energy	The energy of orang-utan fruits and flowers available (kcal/ha)

1. "Real" foods include only those eaten for ≥ 2 bouts and for ≥ 6 mins total feeding time, based on the entire Sabangau dataset (2003-2007, Morrogh-Bernard, submitted; this study, see **Section 2.2.5**).

In many studies, particularly on African apes, DBH is incorporated into measures of food availability, in reflection of the fact that, generally, the amount of fruit contained within a tree increases with increased DBH (e.g., Leighton and Leighton, 1982; Chapman *et al.*, 1992; Newton-Fisher *et al.*, 2000; Murray *et al.*, 2006). DBH has not been used to index food abundance in this study, however, as index methods are less useful for inter-site comparisons than the percentage of individuals bearing fruit (van Schaik and Pfannes, 2005). When using such an index, differences in typical DBHs of trees may confound comparisons between forests (data on average DBH of trees in forests is rarely given by primate researchers, but, for example, the average DBH of chimpanzee fruit trees in Kibale is 75.1 cm, compared to 52.9-59.9 for orang-utans in Ketambe, Wich *et al.*, 1999, and only 24.1 cm in Sabangau, this study), and this index is rarely used by orang-utan researchers. This variation may be due in part to differences in average tree heights between forests, and relationships between DBH and fruit abundance in tree crowns are likely to be inconsistent between sites, especially where species assemblages are very

different, thereby limiting the utility of this method for inter-species/inter-site comparisons (e.g., a 20 cm DBH canopy-height tree in Sabangau possibly contains more fruit than a 20 cm DBH tree in Ketambe or Kibale). This problem could be resolved in future by documenting food-weight/energy availability in different sites (Knott, 2005; van Schaik and Pfannes, 2005), as performed in this study (**Sections 3.2.3** and **3.3.3**).

When comparing periods of low-high orang-utan fruit/flower availability, the following categories were used (adapted from Morrogh-Bernard, submitted):

- < 4% - low
- 4-5.9% - medium-low
- 6-7.9% - medium-high
- ≥ 8% - high

Orang-utan fruit/flower availability during the course of this study was lower than during the previous two years (Morrogh-Bernard, submitted; this study), and there were no periods of "high" fruit/flower availability during this study. Thus, Morrogh-Bernard's "medium" category (from 4-7.9%) was split into "medium-low" and "medium-high" for the purposes of this study.

3.2.3 AVAILABILITY OF DRY WEIGHT AND ENERGY OF ORANG-UTAN FRUITS AND FLOWERS

It has been suggested that the energy of foods available/ha would be a useful "common currency" for comparing food availability between sites (Knott, 2005; Emery Thompson and Knott, 2008). Furthermore, if energy intake is limiting, it is reasonable to assume that this, in turn, is limited by food-energy availability in the environment. Thus, in this study, I also quantify the weight and energy of orang-utan fruits/flowers available in the environment. As bark and pith are continually available, leaves and invertebrates relatively continually available, and all are highly abundant in the environment, I limit this assessment to the *weight and energy of orang-utan fruits and flowers available* ("orang-utan food-weight" and "food-energy" availability, **Table 3.1**), which is more likely to influence orang-utan weight and energy intake and, hence, behaviour.

For each orang-utan fruit/flower tree recorded as bearing fruit and/or flowers in the monthly productivity surveys, crop size (i.e., the number of fruits and/or flowers) was also recorded on a semi-logarithmic scale (c.f. Morrogh-Bernard, submitted, **Table 3.2**). Crop size was recorded by counting the number of fruits/flowers in a small sub-sample of the crown and then estimating the number in the total tree crown by extrapolation. This method was used because (a) the data provided through this method were sufficient to enable the available weight and energy of orang-utan foods to be calculated, (b) this method had been in use in Sabangau since 2003, and all assistants were trained in its use, and (c) it is consistent with the methods established by Morrogh-Bernard for long-term

monitoring in Sabangau and those used by orang-utan researchers in mast-fruiting habitats (Leighton, 1993; Knott, 1998, 1999; to my knowledge, semi-logarithmic scales such as this have not been used by African ape researchers). The relative frequency with which different crop sizes were recorded was similar for both flowers and fruits, though the total number of records for fruit was higher, probably as a result of trees more frequently bearing fruit than flowers for more than one consecutive month (**Figure 3.1**).

Table 3.2 Fruit and flower availability categories used during productivity surveys and mid values used for calculations of weight and energy availability.

No. fruits/flowers			Mid value used for calculations
1	-	5	3
5	-	10	8
11	-	25	18
26	-	50	38
51	-	100	75
101	-	500	300
501	-	1,000	750
1,001	-	2,000	1,500
2,001	-	4,000	3,000
4,001	-	6,000	5,000
6,001	-	8,000	7,000
8,001	-	10,000	9,000
10,001	-	15,000	12,500
15,001	-	20,000	17,500
20,001	-	25,000	22,500
25,001	-	30,000	27,500
30,001	-	50,000	40,000
> 50,000			50,000

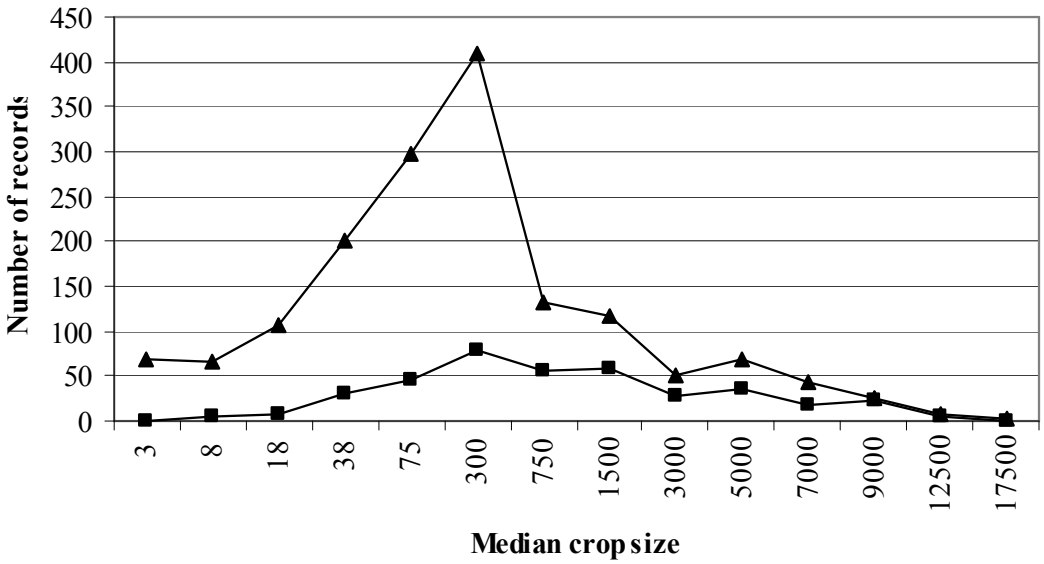


Figure 3.1 Total number of recordings of different crop-size values in productivity plots, July 2005-June 2007. Triangles = fruit; squares = flowers.

For each orang-utan fruit and flower species, dry weight and energy content/item was determined (for methods see **Sections 4.2.2-3**). The total weight and energy of fruits and flowers available in each individual fruiting/flowering tree was then calculated as follows: (mid value for fruit crop-size category x weight or energy/fruit) + (mid value for flower crop-size category x weight or energy/flower). The weight or energy of food in each individual fruiting/flowering tree from all real-food species in all six plots were then summed (with trees 10-20 cm DBH in sub-plot 1 extrapolated from sub-plot 0) to estimate the availability of dry weight/energy produced by *all* orang-utan fruit and flower trees within the plots (2.4 ha). Thus, patch density was accounted for in the calculations. This was then divided by 2.4, to yield the kg or kcal of orang-utan fruits and flowers available/ha (referred to as "food-weight" or "food-energy" availability, **Table 3.1**).

3.3 RESULTS

3.3.1 LITTER-FALL

In the 19 months from December 2005 - June 2007, total LF varied considerably between months, averaging 741 ± 433 kg/ha/month (range: 363-2,374 kg/ha/month). This variation was due chiefly to a very large peak towards the end of the 2006 dry season (**Figure 3.2**). A two-tailed Pearson's correlation between LF and rainfall revealed a negative trend (r = -0.448, n = 19, p = 0.055). The majority of the LF collected in traps (75.6%) was leaves. Continued data collection by one of my assistants after I left the field has allowed for a comparison of LF in the two years December 2005-November 2006 and December 2006-November 2007. LF was significantly higher in 2005-2006 (mean 850 ± 508 kg/ha/month) than 2006-2007 (518 ± 126 kg/ha/month) (Mann-Whitney, p = 0.003).

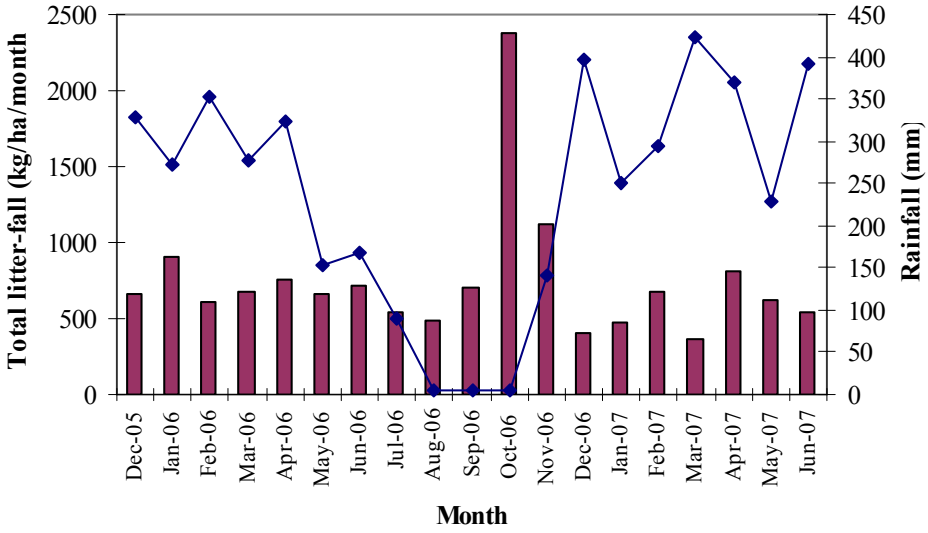


Figure 3.2 Monthly total litter-fall production in relation to rainfall.

3.3.2 ORANG-UTAN FOOD AVAILABILITY

To aid comparison with previous studies using just fruit-availability estimates and to incorporate flower availability into analyses, food-availability data were expressed in three ways: percentage of all trees > 10 cm DBH bearing fruit, percentage of real-fruit trees > 10 cm DBH bearing fruit, and percentage of real-food (fruit/flower) trees > 10 cm DBH bearing food (see **Table 3.1**). Average statistics for the 24-month study period are given in **Table 3.3**. The three measures were all very highly correlated ($r \geq 0.96$ and $p \leq 0.001$ in all cases, **Figure 3.3**). Thus, as I consider percentage orang-utan fruit/flower stems with food to be the most appropriate measure of food availability, due to the inclusion of flowers, the majority of the analyses presented herein are conducted using the orang-utan fruit/flower availability measure.

Table 3.3 Average statistics for percentage all fruit, orang-utan fruit and orang-utan fruit/flower availability in productivity plots from June 2005 – July 2007.

Measure (%)	Mean	SD	Min.	Max.
All fruit	**3.9**	1.2	1.6	5.8
Orang-utan fruit	**4.6**	1.3	2.2	7.1
Orang-utan fruit/flower	**4.9**	1.5	2.5	7.5

See **Table 3.1** for definitions of food availability measures.

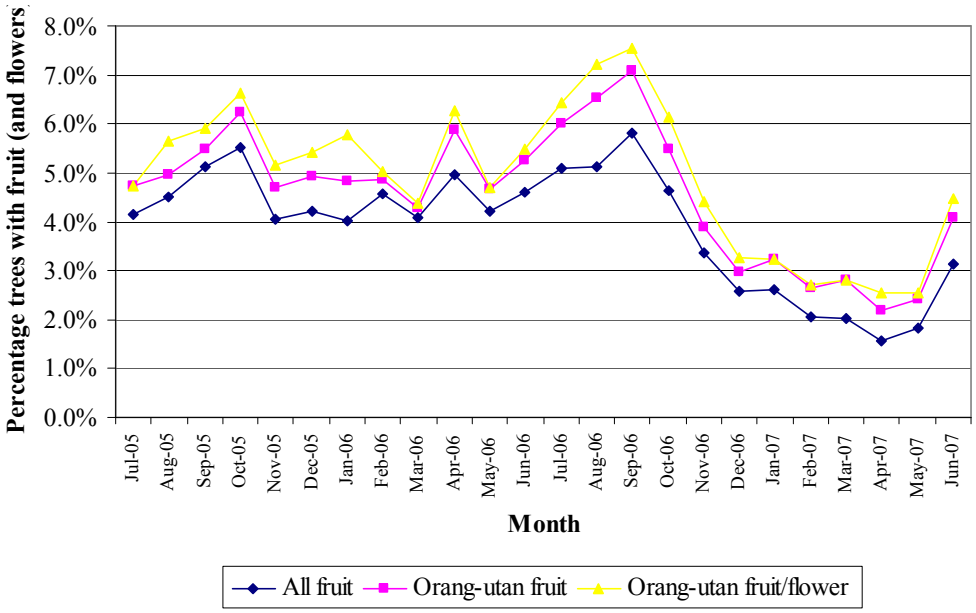


Figure 3.3 Percentage trees bearing "all fruit", "orang-utan fruit" and "orang-utan fruit/flowers" from July 2005 – June 2007. See **Table 3.1** for definitions of food availability measures.

As for LF, considerable variation in orang-utan fruit/flower availability exists between months (**Table 3.3, Figure 3.4**). When using the availability categories defined above, orang-utan fruit/flower availability was "low" for six months of the study, "medium-low" for 12 months and "medium-high" for six months (no months were "high", **Figure 3.4**). Surprisingly, all three food availability measures were negatively correlated with rainfall during the study period (all fruit: r = -0.482, p = 0.017; orang-utan fruit: r = -0.516, p = 0.010; orang-utan fruit/flower: r = -0.515, p = 0.010; n = 24 in all cases). This would appear to be due to a peak in fruit/flower availability from June-October 2006, when rainfall was virtually zero, and a period of low fruit/flower availability during the following wet season. Both all-fruit and orang-utan-fruit availability were positively correlated with the number of genera bearing fruit/month ($r \geq 0.488$, n = 24 and $p \leq 0.015$ in both cases), but the number of fruiting genera/month was not significantly

correlated with rainfall (r = -0.072, n = 24, p = NS). Similarly, the percentage of orang-utan flower stems bearing flowers was not significantly correlated with rainfall (r = -0.199, n = 24, p = NS). Neither all-fruit, orang-utan fruit or orang-utan fruit/flower availability were significantly correlated with total LF in one-tailed tests ($r \leq 0.250$, n = 24, p = NS in all cases).

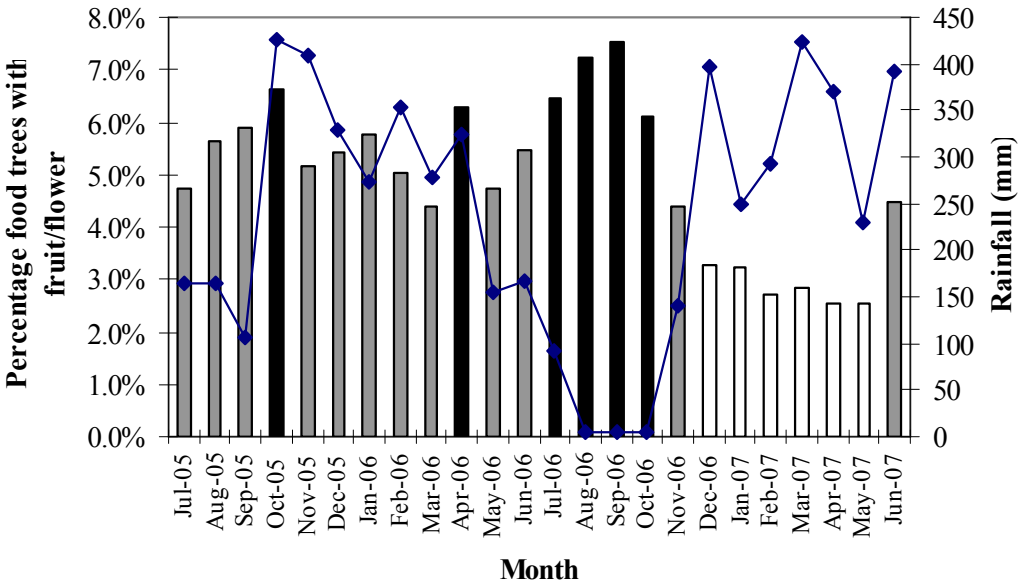


Figure 3.4 Monthly percentage of orang-utan fruit/flower stems with food in relation to rainfall. Black bars indicate months of "medium-high", grey bars "medium-low" and white bars "low" food availability (see text for definitions).

3.3.3 AVAILABILITY OF DRY WEIGHT AND ENERGY OF ORANG-UTAN FOODS

Average statistics for availability of weight and energy of orang-utan fruits/flowers are given in **Table 3.4**. Monthly variations in weight and energy of orang-utan fruit/flowers available in relation to rainfall are shown in **Figures 3.5** and **3.6**.

Table 3.4 Average statistics for dry weight and energy of orang-utan fruits/flowers available from July 2005 – June 2007.

Measure	Mean	SD	Min.	Max.
Weight (kg/ha)	**12.01**	6.77	2.38	30.14
Energy (kcal/ha)	**31,137**	16,681	5,941	73,452

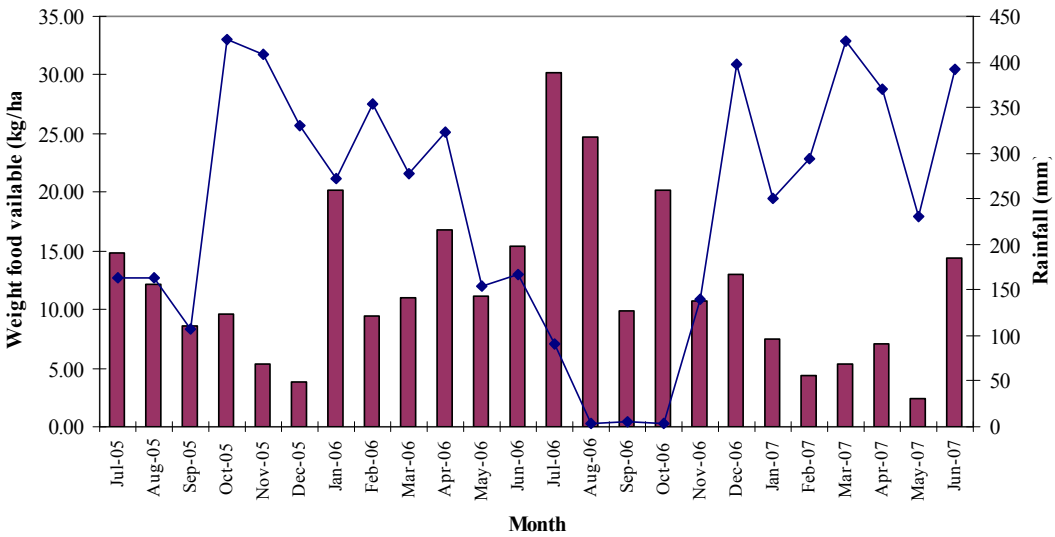


Figure 3.5 Monthly dry weight of orang-utan fruits/flowers available in relation to rainfall.

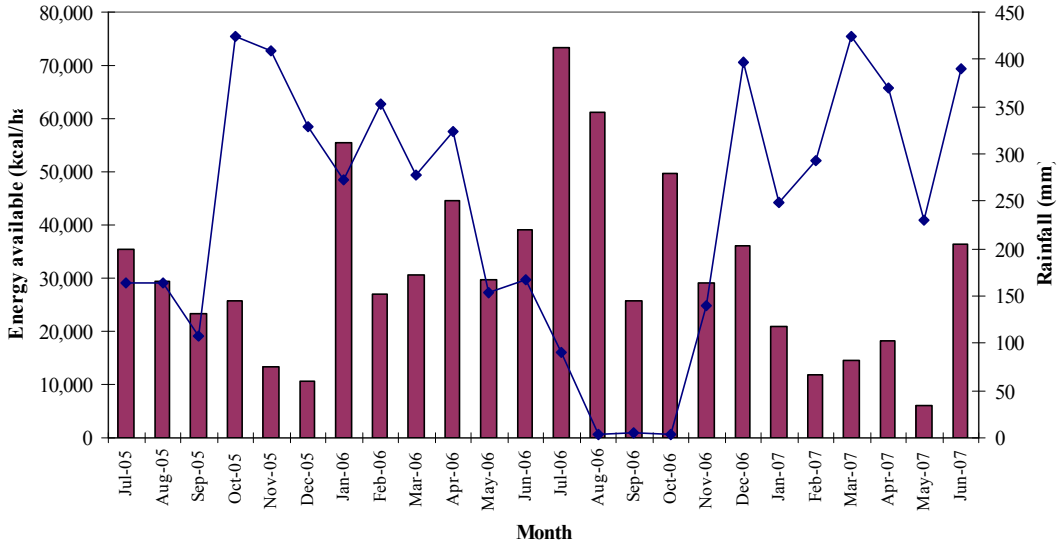


Figure 3.6 Monthly energy of orang-utan fruits/flowers available in relation to rainfall.

Both the weight and energy of orang-utan foods available were highly correlated with percentage orang-utan fruit/flower trees bearing food (r = 0.584 and 0.579, respectively, n = 24 and p = 0.003 in both cases), and with each other (r = 0.995, n = 24, p < 0.001). Similarly, orang-utan food-weight and food-energy availability were also negatively correlated with rainfall during the study period (r = -0.495 and -0.463, and p = 0.014 and 0.023, respectively; n = 24). Neither orang-utan food-weight or food-energy availability were significantly correlated with total LF in one-tailed tests ($r \leq 0.217$, n = 19, p = NS in both cases). The difference between minimum and maximum values was much greater for food-weight (the highest value was 13-times greater than the lowest) and food-energy (12-times), than orang-utan fruit/flower availability (3-times).

3.4 DISCUSSION

3.4.1 RELATIONSHIPS BETWEEN DIFFERENT METHODS OF ESTIMATING FOOD AVAILABILITY

The data collected in this chapter allow for comparisons between different methods of estimating food availability and, ultimately, for comparing observed orang-utan diet composition, intake and behaviour with variations in food availability. These methods differ in the effort involved to collect the data, from LF requiring least effort, through percentage orang-utan fruit/flower stems bearing food, and weight and energy of orang-utan fruits/flowers available. Unfortunately, the food-availability data that are easiest to collect are also likely to be the least informative in terms of interpreting variations in orang-utan diet, intake and behaviour. Thus, for future research, strong correlations between the different measures are desirable, as, for example, energy of fruits/flowers available could then be reliably estimated through relatively easy-to-collect LF or percentage-orang-utan-fruit/flower-stems-bearing-food data.

Unfortunately, for the 19 months from December 2005-June 2007, total LF production was not significantly correlated with any of the other measures of food availability (though relationships were all in the expected direction). As three quarters of the litter collected in traps was leaves, this is not surprising, as peaks in LF production should be expected to correspond to peaks in leaf replacement/replenishment (c.f. van Schaik, 1986), rather than peaks in fruit/flower availability. These LF data may still prove useful

for orang-utan studies in Sabangau, however, as they provide a measure of overall habitat productivity, which may be responsible for much of the variation in orang-utan densities between sites (Rijksen and Meijard, 1999; Delgado and van Schaik, 2000).

Part of the explanation may also be due to the unusual El Niño dry season of 2006 and associated smoke (see **Section 3.4.2**). LF and plot-productivity data collection have both continued after the cessation of fieldwork for this study, which should enable us to establish whether the lack of a relationship between LF and food availability was a consequence of the unusual 2006 El Niño dry season. The high correlations between the other three measures of food availability (percentage orang-utan fruit/flower stems bearing food, and weight and energy of orang-utan fruits/flowers available), however, indicate that percentage orang-utan fruit/flower stems bearing food can be used as a reliable indicator of the weight and energy of orang-utan fruits/flowers available in Sabangau, despite relatively higher levels of variation in the latter two measures.

Finally, it should be pointed out that, although the measures of food availability used here are relatively precise compared to some other studies, they are still imperfect (Knott, 2005). Plot size was necessarily limited and, hence, complete data on the full range of species eaten could not be collected. Detection of variations in the quality of fruits and flowers produced over time (see Chapman *et al.*, 2003) was also not possible in this study, and variations in food preference (**Chapter 5**) and home-range quality between individuals were also not considered. Thus, these estimates are, at best, approximations.

3.4.2 SEASONALITY OF ORANG-UTAN FOOD AVAILABILITY: RELATIONSHIPS TO RAINFALL

Surprisingly, both LF and all of the measures of food availability derived from the productivity plots were negatively correlated with total monthly rainfall. In a meta-analysis of forest productivity data compiled from 106 published studies, van Schaik and Pfannes (2005) showed that leaf flush and flower production in the tropics are typically highly seasonal, and occur generally at the start of the wet season. In contrast, fruiting peaks did not show a relationship with the start of the wet period, and were less constrained by climate than leaf flush/flowering peaks (though the authors do add that this includes all fruit, and that greater seasonality may occur for water-rich, pulpy primate fruits). The negative trend observed between total LF and rainfall is not surprising, and most probably reflects increased leaf shedding by trees in response to the very dry El Niño dry season in 2006.

The percentage of orang-utan flower stems bearing flowers was not significantly correlated with rainfall, in contrast to van Schaik and Pfannes' (2005) and Anderson *et al.*'s (2005) observations of trees flowering during wet periods and then fruiting during subsequent dry periods. Thus, while the results obtained in this study for LF and fruit availability are not surprising, they run contrary to the expectation that orang-utan flower availability should be positively associated with rainfall.

I suspect that at least part of the explanation for these observations may lie in the unusual El Niño dry season of 2006, in which rainfall was almost zero, and in which a peak in both LF and orang-utan fruit/flower availability occurred. From a climatic perspective, this dry season was unusual in its length and the amount of rain received (five consecutive months with < 150 mm rain/month, compared to a maximum three consecutive months with this little rainfall from 2003-present, excluding 2006) and, consequently, the amount of smoke in the atmosphere as a result of forest fires (Cheyne, 2007; Harrison *et al.*, 2007b). Harrison *et al.* (2007b) compare LF data collected during the dry, smoky 2005-2006 El Niño year included in this study to previous data collected in the NLPSF during the "normal" smoke-free year of 2000-2001. We found that, not only was total LF higher in 2005-2006, but also the height of the end of dry season peak in 2005-2006 was almost double that in 2000-2001. This indicates that either water stress during the prolonged, intense 2006 dry season and/or thick smoke clouds caused increased LF through leaves being shed in response to these stresses (Harrison *et al.*, 2007b). The observation made herein that LF was higher in the El Niño year of 2005-2006 than in 2006-2007 supports this contention. Thus, 2005-2006 may just have been an unusual year and further data collection is required to confirm the true relationship between LF and rainfall.

Similarly, the negative relationship shown here between the three measures of orang-utan food availability and rainfall should also be interpreted with caution. Long-term forest-productivity data in Gunung Palung indicate that fruit production in PSF was more consistent than in any other habitat type and that PSF does not participate in supra-annual

mast fruiting events (Cannon *et al.*, 2007b), which are typically associated with El Niño events in South-east Asian countries (see review in Harrison and Chivers, 2007). Although fruit production in PSF over 68 months did not show synchrony with mast-fruiting events in other habitat types in Gunung Palung, the largest peak did overlap with a period of mast fruiting in other habitat types (Cannon *et al.*, 2007b), indicating that PSF may not be entirely free of the influence of the El Niño Southern Oscillation (ENSO) and mast fruiting. Thus, the 2006 dry season peak in fruit/flower availability documented here could be related to the 2006 El Niño event. Analysis of data collected over a longer timeframe is therefore needed to confirm the relationships observed in this thesis (this will form the topic of future publications). As the number of fruiting genera did not correlate with rainfall, it would appear that the negative correlation found here was a result of a greater number of individuals of a genus fruiting during low-rainfall periods, rather than an increase in the number of genera fruiting (both are generally found in mast-fruiting events elsewhere in Borneo, Knott, 1999; Cannon *et al.*, 2007b).

3.4.3 COMPARISON OF FOOD AVAILABILITY ESTIMATES IN SABANGAU WITH OTHER STUDIES

3.4.3.1 Comparison with Other Orang-Utan Sites

Recently, detailed inter-site comparisons have indicated that orang-utan fruit availability in Sumatra is higher than in Borneo (Marshall *et al.*, 2009a), and that these differences in fruit availability may underpin differences between the morphology, sociality and life

history of Sumatran and Bornean orang-utans (see articles in Wich *et al.*, 2009b, in particular van Schaik *et al.*, 2009b). While data from Sabangau were included in these broad comparisons, specific comparisons of orang-utan fruit availability in Sabangau with other sites, and with African apes, have not been made. Different researchers have used different methods of estimating food availability; the terms used below match those in **Table 3.1**.

Gunung Palung, West Kalimantan

Orang-utan fruit availability in Gunung Palung between January 1994 and December 1996 was estimated by monitoring selected orang-utan food trees along transects (Knott 1998, 1999). Thus, while these data broadly represent orang-utan fruit availability, there was some bias in the species included and the effect of variations in density of fruiting stems between Gunung Palung and other sites cannot be assessed. Based on Knott's data, which included both ripe and unripe fruit, lowest monthly orang-utan fruit availability was 3%, compared to 24% during a mast-fruiting period (range = 21%). This is much greater than the range of 4.9% documented for orang-utan fruit availability in Sabangau. Furthermore, in Gunung Palung, orang-utan fruit availability during a 12-month "extended period of low fruit availability" between masts was 3-9% (Knott, 1999). Thus, fruit availability in Sabangau during this study was entirely within the range of this "low fruit" period in Gunung Palung. Similarly, the percentage of fruiting genera/month in Gunung Palung (14-64%, calculated from data in Knott, 1999) is more variable than in Sabangau (15-50% for all fruits). Recently, data on orang-utan fruit-energy availability have also been presented for Gunung Palung (Emery Thompson and Knott, 2008),

allowing for less biased comparison. Based on Figure 4a in Emery Thompson and Knott (2008), monthly fruit-energy availability in Gunung Palung varies from ca. < 5,000-165,000 kcal/ha, and is ≥ 50,000 kcal/ha for ca. 40% of months. In contrast, in Sabangau, orang-utan food-energy availability (i.e., including both fruit and flowers) ranged from 5,941-73,452 kcal/ha (mean 31,137), and exceeded 50,000 kcal/ha in only 3/24 (12.5%) of months. This comparison illustrates the large differences in the cycles of forest productivity between the (mostly) masting habitats included in Knott's study and the non-masting PSF studied here. As will be seen, these differences lead to large differences between the sites in orang-utan food and energy intake, and in the relationships between intake, behaviour and food availability.

Tuanan, Central Kalimantan

Data on ripe all-fruit availability in the Tuanan PSF from productivity plots between July 2003 and April 2006 are given by Vogel *et al.* (2008b). Based on their Figure 3, the percentage of stems bearing ripe fruit varied between ca. 0.6-14%. All-fruit (including unripe) availability in this study was 2.5-7.5%, indicating that fruit availability in Tuanan is generally higher than Sabangau. Although Tuanan and Sabangau are very similar in terms of orang-utan food species present (Wich et al., in prep), the peat in Tuanan is shallower and the research area is partly alluvial (Wich *et al.*, 2009b), which should be expected to lead to higher fruit production in Tuanan.

Ketambe, Sumatra

Wich *et al.* (2006b) collected 215 months' data on all-fruit availability in Ketambe from a mixture of trails and plots. Statistics on percentage fruit availability are not given, but high habitat productivity and a high density of relatively non-seasonally-fruiting strangler figs in the area means that there are always a few large fruit trees available. This leads Wich *et al.* (2006b) to conclude that fruit availability in Ketambe is probably higher and less variable than in Gunung Palung. This is supported by Marshall *et al.* (2009a), who found that, in terms of percentage of all-fruit stems bearing fruit, Ketambe was the most productive of the three Sumatran and nine Bornean sites analysed (including Sabangau). Thus, fruit availability in Sabangau is clearly much less than Ketambe.

Suaq Balimbing, Sumatra

In PSF in Suaq Balimbing, percentage ripe all-fruit availability from productivity plots varied from ca. 0.7-13.5% (Fox *et al.*, 2004). Of the 43 months included in Fox *et al.*'s study, > 6.7% of trees were fruiting in 12 months (28%), compared to only 1/24 (4%) of months in this study. Thus, fruit availability in Suaq is clearly substantially greater than in Sabangau, especially as the Sabangau data also include unripe fruits. Suaq is an undeniably more productive than Sabangau: it supports an exceptionally high orang-utan density (7.44 km^2, Husson *et al.*, 2009) and level of gregariousness, which led van Schaik (1999) to conclude that Suaq has "unusual habitat productivity and relatively constant production" and, consequently, represents an optimum habitat for orang-utans.

3.4.3.2 Comparison with African Apes

Based on analysis of 106 published studies, van Schaik and Pfannes (2005) conclude that the predominant pattern in Africa is of relatively consistently high fruit production, with occasional bust years, in comparison to generally relatively low fruit production with occasional boom years associated with community-level mast fruiting in South-east Asia. Numerous other lines of evidence point towards the same conclusion: differences in socio-ecology (relatively cohesive social groups in African apes compared to semi-solitary in orang-utans), dentition (i.e., thick molar enamel in orang-utans for feeding on hard items and bark, one of the least nutritious foods available to apes, and which is thought to reflect adaptation towards more seasonal conditions, de Bonis and Koufos, 1993; Andrews, 1996) and linear enamel hypoplasia (an indicator of physiological stress, which is more commonly seen in orang-utans than African apes, Skinner and Hopwood, 2004; Hannibal and Guatelli-Steinberg, 2005) all suggest that orang-utans experience greater food stress than African apes (reviewed in Harrison and Chivers, 2007). This suggestion is supported by comparison of studies on African apes using similar fruit-abundance indices to this study or that provide figures from which such an index can be calculated (**Table 3.5**).

Table 3.5 Comparison of estimates of fruit availability in African ape research sites using methods comparable to those in this study.

Species	Site	Measure	Mean (%)	Range (%)	Study duration	Reference
MG	Bwindi (Ruhija)	All ripe fruit	-	23-57	1 yr[1]	Stanford and Nkurunungi (2003)
MG	Bwindi (Ruhija) Bwindi (Buhoma)	Important gorilla fruits	39.9 ± 2.6 38.8 ± 5.4	35.8-44.2 33.3-52.2	1 yr[2]	Nkurunungi *et al.* (2004)
WLG	Bai Hoku	All ripe fruit	-	4-72 (35-72 in good years)	10 yr	Remis (2003)
WLG	Modika	Important ripe gorilla fruits	9	2-21	3 yr	Doran *et al.* (2002)
Chimpanzee	Bossou	Main chimpanzee fruits	-	7-19	13 mo	Figure 2 in Yamakoshi (1998)
Chimpanzee	Bwindi (Ruhija)	All ripe fruit	-	23-57	1 yr	Stanford and Nkurunungi (2003)
Chimpanzee	Fongoli	Chimpanzee fruit	-	2-41[3]	22 mo	Pruetz (2006)
Chimpanzee	Kanyawara	All ripe fruit	3.5	0.3-8.2	1 yr	Wrangham *et al.* (1998)
Chimpanzee	Rubondo Island	All fruit	-	15-32	11 mo	Figure 1 in Moscovice *et al.* (2007)

Abbreviations: MG = mountain gorilla (*Gorilla beringei*), WLG = western lowland gorilla (*Gorilla gorilla gorilla*).
Study sites: Bwindi = Bwindi Impenetrable National Park, Uganda; Bai Hoku = Bai Hoku, Dzanga-Ndoki National Park, Central African Republic; Modika = Modika, Dzanga-Ndoki National Park, Democratic Republic of Congo; Bossou = Bossou, Republic of Guinea; Fongoli = Fongoli, Senegal; Kanyawara = Kanyawara, Kibale National Park, Uganda; Runondo Island = Rubondo Island, Tanzania.

Terms used are analogous to those in **Table 3.1** and all measures indicate the percentage of individuals bearing fruit in a month. Where "ripe" is not specified, figures include both ripe and unripe fruits. All sites included only stems ≥ 10 cm DBH in their analyses (with the exception of Yamakoshi, 1998, who did not state a minimum DBH limit).

1. Data collected from 1999-2000.
2. Data collected from 2001-2002.
3. Availability was ≥ 10% in 17/22 months and ≥ 20% in 10/22 months.

Measures of fruit availability described in other African ape studies (many of which index fruit availability by DBH/basal area, e.g., Chapman *et al.*, 1995; Newton-Fisher *et al.*, 2000; Basabose, 2002, 2004; Yamagiwa *et al.*, 2005; Anderson *et al.*, 2006; Murray *et al.*, 2006 or some arbitrary point scale, e.g., Tutin *et al.*, 1991, 1997, have assessed fruit availability via fallen fruit, e.g., Nishihara, 1995; Furuichi *et al.*, 2001; Hashimoto *et al.*, 2001. or have used comparable methods, but not provided the necessary figures for comparison, e.g., Tweheyo and Babweteera, 2007) are not comparable to those given by orang-utan researchers. Bonobo fruit availability has not been recorded using comparable methods, but available data indicate bonobos experience shorter periods of low food availability than chimpanzees (Malenky, 1990; White, 1996; Hohmann *et al.*, 2006).

As can be seen, with the exception of Kanyawara, where fruit availability was slightly lower and more variable than Sabangau during Wrangham *et al.*'s (1998) and Conklin-Brittain *et al.*'s (2006) studies, all of these sites appear to have higher levels of fruit availability than Sabangau. Although not amenable to direct comparison, evidence suggests that fruit availability at many other African sites is also fairly high (e.g., Budongo, Newton-Fisher *et al.*, 2000). Due to differences in study lengths, methods and ape density/biomass between sites, which have not been accounted for here, inter-site comparisons such as I have attempted here should be treated with caution. Nevertheless,

it can be said with reasonable confidence that orang-utan fruit availability in Sabangau is low in comparison to other orang-utan sites studied, even within Borneo. Variations in orang-utan fruit (and flower) availability in Sabangau between months, however, appears lower than in many other orang-utan study sites, particularly those that experience huge fluctuations in fruit/flower availability due to mast-fruiting events. With the exception of chimpanzees in Kanyawara, which appear to experience similar levels of fruit availability to Sabangau orang-utans (at least during the timeframe of Conklin-Brittain *et al.*'s, 2006 and Wrangham *et al.*'s, 1998 studies), African apes appear to experience generally higher levels of fruit availability than orang-utans. Based on this preliminary comparison, studies of orang-utans in Sabangau may be particularly informative in interpreting the differences between energy intake in orang-utans in Gunung Palung and chimpanzees in Kanyawara reported in Conklin-Brittain *et al.* (2006), because, during the periods for which published data are available, variability in ape fruits in Sabangau < Kanyawara < Gunung Palung, thus providing data from orang-utan sites with both higher and lower variability in fruit availability than the more intermediate chimpanzee site.

As suggested by Knott (2005), the calculations of orang-utan food-energy available/ha presented here will hopefully facilitate future comparisons of food availability between sites, as many of the data required for estimating environmental energy availability are now becoming available at a number of sites. Ideally, future comparisons should also consider variations in ape biomass between sites, so that food availability can be expressed in terms of the number of fruiting (/flowering) stems/ha/kg ape or ape fruit (/flower)-energy available/ha/kg ape.

3.5 SUMMARY

1. Peat-swamp forests (PSF) are temporally relatively consistent in terms of fruit production and do not participate in the supra-annual mast-fruiting events that characterise lowland dipterocarp forests in Borneo. Temporal variations in fruit availability in PSF do exist, however, and this could potentially influence orang-utan diet, intake and behaviour. Furthermore, differences in habitat productivity and fruit availability are thought to be important causes of differences in orang-utan density, diet composition, intake, sociality and activity profiles between sites.
2. Temporal variations in habitat productivity and orang-utan fruit and flower availability in Sabangau were monitored through litter-fall (LF) traps and forest productivity plots, respectively. LF was collected from 16 x 1 m^2 traps twice-monthly and oven dried. Total dry weight of litter was calculated each month from December 2005-June 2007. Orang-utan fruit/flower availability from July 2005-June 2007 was documented in 6 x 0.4 ha plots (total 2.4 ha), in which all trees ≥ 10 cm DBH, and all figs and lianas ≥ 3 cm DBH were identified, tagged and monitored for fruit and flower production.
3. Both LF and orang-utan fruit/flower availability varied between months, with total LF ranging from 363-2374 kg/ha/month, and percentage orang-utan fruit/flower stems bearing food ranging from 2.5-7.5%.
4. The weight and energy of orang-utan fruits/flowers available/ha were also calculated using crop-size estimates from productivity surveys and food nutrient-content data. These ranged from 2.38-30.14 kg/ha and 5,941-73,452 kcal/ha, respectively, and

provide a useful measure of fruit/flower availability for assessing temporal changes in orang-utan food-energy intake, and for comparing food availability between ape study sites.

5. All measurements of food availability derived from plots were negatively correlated with rainfall during the study period. Although PSF is not a masting habitat, it is suggested that this may be the result of the 2006-2007 El Niño event, which caused very low rainfall and coincided with a peak in fruit/flower availability (though it is impossible to say whether this peak was also caused by the El Niño event, as in masting habitats).
6. Comparisons with other orang-utan study sites indicate that fruit availability in Sabangau is relatively low, and that variations in fruit availability are much lower than in the masting habitats of Gunung Palung, West Kalimantan, in which orang-utan energetics have been studied previously. As will be seen in subsequent chapters, these differences in fruit availability are associated with considerable differences in dietary intake and behaviour between the two sites.
7. Similarly, in most sites, African apes appear to enjoy relatively high levels of fruit availability compared to orang-utans. Fruit availability for chimpanzees in Kanyawara, where chimpanzee energetics has been studied previously, appears slightly higher and more variable than orang-utan fruit availability in Sabangau, but lower and less variable than orang-utan fruit availability in Gunung Palung. Thus, three-way comparisons between these sites should be particularly informative in interpreting inter-specific differences in the effects of fluctuations in food availability on energy intake.

4. DIETARY COMPOSITION

4.1 INTRODUCTION

There are four main aims in this chapter: (1) to provide a general description of orang-utan diet composition, nutrient and energy intake in Sabangau, (2) to establish whether there is any effect of age-sex class and fluctuations in fruit/flower availability on the above, (3) to assess the nutritional adequacy of the orang-utans' diet, and (4) to compare these observations with those from other orang-utan and great ape studies, in an attempt to identify any underlying patterns among apes.

Orang-utan diet is diverse; in a recent compilation of data from 15 research sites, Russon *et al.* (2009) identified 1,693 orang-utan food species. In Tanjung Putting alone, for example, Galdikas (1988) recorded 317 (with a further 20 unidentified) food items eaten in a four-year period. Due to the long-term fruiting cycles of many tree species, even towards the end of her study, Galdikas was still observing new food items being eaten every month, leading her to conclude that the orang-utans there may eat > 400 food items. Numerous authors (e.g., Rodman, 1977; Galdikas, 1988; Leighton, 1993; Knott, 1998) have shown that orang-utans are preferential frugivores, but also consume many other foods, including flowers, leaves, bark, invertebrates and, occasionally, meat (Utami and van Hooff, 1997).

Flanged male orang-utans are almost twice the size of females (Markham and Groves, 1990) and females also incur the reproductive costs of pregnancy and lactation. Thus, differences in diet and food/energy intake might be expected between sexes. Differences in time allocations for feeding between flanged males and adult females have been reported (Rodman, 1977, 1979; Galdikas and Teleki, 1981; Fox *et al.*, 2004; van Schaik *et al.*, 2009c) and researchers have hypothesised both that flanged male dietary quality is lower (Rodman, 1977, 1979; Hamilton and Galdikas, 1994) and higher (Wheatley, 1987) than adult females. These hypotheses were tested by Knott (1999), who found that neither the nutrient content of the diet (a low-quality diet would be high in fibre and low in protein, lipid and carbohydrates) or energy intake differed between flanged males and adult females in Gunung Palung across the entire study period. Knott did find, however, that flanged male energy intake and dietary quality was higher in some months and, hence, further investigation is warranted to confirm these observations.

Of the various potential responses to food scarcity seen in primates (van Schaik *et al.*, 1993; Hemingway and Bynum, 2005), only dietary shifting, seasonal movements, and changes in sociality/gregariousness and behaviour are typically available to orang-utans (Leighton and Leighton, 1983; te Boekhorst *et al.*, 1990; Knott, 1998, 1999; Singleton and van Schaik, 2001; Fox *et al.*, 2004). In contrast to other primate species, in which seasonal movements typically correspond to periods of food shortage, seasonal movements in orang-utans typically coincide with periods of food abundance (Leighton and Leighton, 1983; te Boekhorst *et al.*, 1990; Singleton and van Schaik, 2001). Due to the homogenous nature of the forest in the study area (**Chapter 2**), however, seasonal

movements are likely to be relatively ineffective in Sabangau, compared to more heterogenous habitats. Changes in sociality and behavioural profiles in response to fluctuations in fruit and flower availability are discussed in **Chapter 6**.

In common with many other species of primate (e.g., chimpanzees and cercopithecine monkeys: Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998; gibbons: McConkey *et al.*, 2003; tamarins *Saguinus* sp., capuchins *Cebus apella* and grey woolly monkeys *Lagothrix lagotricha cana*: Peres, 1994; lemurs: Petter, 1978), orang-utan dietary composition varies greatly, depending on the availability of different food types (Sugardjito *et al.*, 1987; Leighton, 1993; Knott, 1998, 1999). In Kutai, Leighton (1993) found that, when fruiting-tree density exceeded 4/ha, fruit composed over 85% of the diet. During a mast-fruiting event in Gunung Palung, orang-utans ate only fruit, whereas, when fruit availability was very low, fruit constituted just 21% of feeding time (Knott, 1998). This led to dramatic changes in the nutrient composition of the diet and energy intake between mast and non-mast periods (Knott, 1998, 1999). This dietary shift is less dramatic in Sumatra, probably because higher overall fruit availability means that Sumatran orang-utans are (1) able to consume more fruit during periods of low fruit availability and, hence, rely less on fall-back foods (FBFs), such as leaves and bark, and (2) have access to higher-quality FBFs (i.e., figs) than their Bornean counter-parts (Delgado and van Schaik, 2000; Wich *et al.*, 2006b). As the magnitude of fluctuations in fruit/flower availability in Sabangau is relatively low compared to Gunung Palung (**Chapter 3**), it might be expected that, in Sabangau, fluctuations in fruit/flower

availability have less or no effect on the nutrient composition of the diet and energy intake compared to orang-utans in Gunung Palung.

Published data on the nutritional content of the diet and energy intake for orang-utans are currently available only from Gunung Palung (Knott, 1998, 1999). Thus, by providing these data from a second site, which is non-masting and differs greatly from Gunung Palung in terms of orang-utan fruit/flower availability, it has been possible for me to investigate whether (a) differences in the nutritional composition of the diet and energy intake exist between masting and non-masting sites within the same sub-species, and (b) how these differences are related to differences in fruit/flower availability. Nutritional data from one other site in Borneo (Tuanan) and two sites in Sumatra (Ketambe and Suaq Balimbing) are currently being collected in a project coordinated by E. R. Vogel; thus, future analyses will enable us to identify whether the observations made herein are likely to apply to orang-utans as a whole. Furthermore, comparisons with African apes will help inform us of the generality of the observed patterns in orang-utans in Sabangau and Gunung Palung.

Thus, in keeping with the aims in this chapter and the over-riding null hypothesis expounded in **Section 1.1** that observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats (Leighton, 1993; Knott, 1998, 1999), the following null hypotheses are tested in this chapter:

$H_0 4.1$: Orang-utan diet composition, and nutrient and energy intake in Sabangau are comparable to orang-utans in masting habitats.

$H_0$4.2: Dietary quality does not differ between age-sex classes.

$H_0$4.3: Orang-utan diet composition and energy intake is strongly related to orang-utan fruit/flower availability in all age-sex classes.

$H_0$4.4: Daily energy and nutrient intake is adequate/above requirements during times of food plenty, but below requirements during periods of fruit/flower scarcity.

4.2 METHODS

The majority of the methods in this section follow those of Knott (1998, 1999) and Conklin-Brittain *et al.* (2006). This is for three main reasons: (1) these methods have been tried and tested on wild orang-utans, (2) there is often no other way to collect the data, and (3) to facilitate later inter-site comparisons with both Knott and other orang-utan researchers working at other sites and also using these methods.

4.2.1 DIETARY COMPOSITION

Similar to previous researchers (Knott, 1998, 1999; Morrogh-Bernard, submitted), while following orang-utans, data were collected on: (a) the start and end time of feeding bouts, from which bout length was calculated; (b) species eaten; (c) food type eaten, classified as: bark, flowers, fruit, invertebrates, leaves, pith and "other"; (d) part eaten, flowers: open flower, flower bud; fruits: pulp, seed, skin, combinations of these, and whole fruit; (e) DBH; and (f) crop size (see **Section 3.2.3**) of feeding trees. Similar methods have also been used in studies on African apes in which energy intake has been estimated (Conklin-

Brittain *et al.*, 2006; Masi, 2007; Rothman *et al.*, 2008b), though these studies all used instantaneous scan sampling (Altmann, 1974) as their main data collection method and, hence, start and end times of feeding bouts would not have been recorded. While this method does allow for estimation of energy intake, continuous data collection from full-day focal animal follows on one individual (as performed by Knott and in this study) are preferable, as (a) nutrient regulation appears to take place over the course of one day, (b) what an individual eats in the morning may affect what it eats in the afternoon, and (c) the relative contribution of nutrients may be under/over-estimated when only a small portion of daily feeding bouts are represented (Felton *et al.*, 2009).

Plant species were generally identified to species or genus level. This was made possible due to plant-species lists, collections and descriptions developed by H. Morrogh-Bernard and S. Husson in collaboration with E. Shinta from the CIMTROP (Centre for the International Cooperation in Management of Tropical Peatlands) herbarium, my own knowledge developed while assisting the above researchers in developing these, and the advice of my local field assistants, many of whom have many years' experience of working in the forest and have developed an in-depth knowledge of local tree species. DBH was measured at 1.3 m above the ground or, in the case of buttressed/stilted trees, 1.3 m above the top of tree buttresses/stilts. Where this was not possible, DBH was measured as high above the roots as possible. All fruit, flower and bark feeding trees were enumerated, in order to record revisit rates, provide a check on identifications as the study progressed, and to enable us to return to the tree to collect samples of foods for laboratory/field-kit analysis and/or to confirm identifications.

Data on feeding rates (number of items ingested/minute) were also recorded, in most cases using methods identical to Knott (1998, 1999; similar methods were also used in the African ape studies in which energy intake has been estimated, Conklin-Brittain *et al.*, 2006; Masi, 2007; Rothman *et al.*, 2008b). A stopwatch was used to record the data in one of two ways. In the first, a countdown timer was used to record the number of items ingested in one minute for items eaten quickly. In the second, used for items eaten more slowly, a stopwatch was used to record the number of items eaten in one distinct "picking bout" (i.e., from the start of one bout of picking to the start of the next, thus ensuring that searching and processing time were also incorporated). Feeding rate was then expressed as the number of items eaten/minute. Due to orang-utans not being visible while feeding for much of the time, it was rarely possible to record data at precise intervals (cf. Knott, 1998, 1999) and, hence, data were generally recorded opportunistically whenever the animal was visible, with at least three minutes left between counts. Feeding rates were collected throughout feeding bouts, to account for any variations in feeding rate during the bout (Knott, 1998, 1999).

For most food types, it was possible to collect feeding rate data in the manner described above, but, for bark, a different method had to be employed. Orang-utans only eat the thin phloem and cambium layers of bark; in the majority of cases, this is swallowed, but in some cases the fibres are merely chewed and spat out in a wad (Galdikas, 1988, Knott, 1998, 1999, Morrogh-Bernard, submitted; pers. obs.). Following Knott (1998, 1999), all bark remains discarded during a bark-feeding bout were collected from below the feeding tree and brought back to camp. When all pieces could not be collected, the percentage

collected was estimated. Once at camp, the area of each individual piece of bark was measured and the percentage of phloem/cambium scraped off by the orang-utan estimated by comparison with uneaten pieces, enabling the total area of bark consumed to be calculated. This was then divided by the length of the feeding bout to provide a measure of the surface area of bark eaten/minute. I also attempted to estimate visually bark consumption by estimating the surface area of the tree that had been stripped of bark (Knott, 1998, 1999), but, upon analysis, it was discovered that this method produced faster feeding rates than the above method, which I consider to be more reliable, and so data collected in this way were excluded from the analysis.

Invertebrates are generally eaten in one of two ways. Termites in rotten wood and ants in nests are eaten by breaking the wood/nest apart with the hands/mouth and then sucking up the insects, whereas ants/termites marching in columns/swarming on trees are eaten by using either the lips or the hand to pick off the insects and bring them to the mouth. Feeding rate was measured by recording the number of 'sucks' or 'picks' each minute and the amount of insects ingested each suck/pick. As more than one invertebrate is typically ingested/pick (Knott, 1998, 1999; pers. obs.), this must be accounted for when attempting to estimate the weight/energy of food ingested. Knott (1998, 1999) estimated from discarded feeding remains that a maximum of 10 termites could be consumed each mouthful from rotten wood. From my own observations of discarded feeding remains and orang-utans feeding on invertebrates in the field, this figure seemed rather high for Sabangau, and, hence, I used a figure of 3/mouthful for termites from rotten wood and 5/mouthful for ants from nests/branches (precise estimation of this parameter is

impossible). This difference between Knott's and my estimates probably made negligible difference to daily intake-rate calculations because, as noted by Knott (1998, 1999), due to the minute size of these animals (0.0001 g dry weight), even a doubling of the number ingested each mouthful would have a negligible effect on intake rates.

4.2.2 NUTRITIONAL ANALYSIS OF FOODS

4.2.2.1 Food Sample Processing Prior to Nutritional Analysis

Samples of foods eaten were collected either during focal-animal follows, or later by searching for samples in the forest and, where necessary, climbing trees. In all cases, care was taken to obtain samples of a similar size and maturation stage to those eaten by the orang-utans. Due to the high sample weight required for nutritional analysis in the LIPI lab (25 g dry weight), samples of most items (64%) consisted of at least some samples that were collected by tree climbing, as insufficient quantities could be collected from beneath feeding trees. This method could be considered superior in a way to collection from beneath feeding trees, as food dropped while feeding is, obviously, food that has not been eaten, whereas foods collected from in the trees could potentially be eaten. Thus, foods that have dropped/fallen/been discarded may be more likely to represent foods selected against than those collected from climbing trees.

All samples were then brought back to camp for processing, either later that day or, when this was not possible, early the next day. I either personally conducted or oversaw nearly

all sample processing and, hence, was able to identify whether each sample collected was of the appropriate size/stage and ensure that it was processed correctly. On occasions when I was unable to do this, one of my British post-graduate assistants and/or S. M. Cheyne, who was also collecting samples for gibbon foods, were able to perform/oversee this for me. At least five, and normally more, separate sample collections were generally performed for each food item, as (a) this provides a more accurate mean, which incorporates more of the between-sample variation within food items (variations in nutritional content of food items between trees of the same species have been recorded, making the sampling of multiple individuals important, Chapman *et al.*, 2003), and (b) it was not normally possible to collect sufficient dry weight of samples for analysis in fewer collections. While temporal variation in nutritional composition within a food type has also been reported, this is less than the variation between individuals of the same species (Chapman *et al.*, 2003). Thus, where possible, samples were collected from trees in which animals actually fed.

All samples were processed in the same fashion as they were processed by the orang-utan (so, e.g., if the orang-utans ate the seed along with the aril, then both seed and aril were included in the sample, but if the seed was eaten and the aril discarded, then the seed and aril were separated when processing samples). For comparative purposes, samples of parts not eaten were also collected. Each sample was given a unique lettered code and the number of food items in the sample was recorded. Once separated into parts eaten and not eaten, the samples were then weighed wet using an electronic balance accurate to 0.01 g. Samples were then dried (either in brown paper envelopes left open to allow moisture to

escape, or in plastic trays for moister samples) in a kerosene oven averaging 40-50°C. Care was taken not to exceed this temperature, in order to prevent the formation of Maillard product, which reduces the extractability of nutrients and elevates apparent fibre levels (Conklin-Brittain, pers. comm.). The oven was well ventilated, to ensure samples were dried as quickly as possible, and prevent fermentation and moulding during drying, which can alter the chemical composition of the sample (Harborne, 1984). Samples were stirred and checked regularly, and mouldy samples were discarded and recollected. In some cases, the recollected samples also became mouldy and I had no choice but to use these samples for analysis, in preference to having no sample at all for that food item (mouldy samples represented only 3.7% of the total samples collected). Similar problems have also been experienced by other ape researchers (Conklin-Brittain *et al.*, 2006).

Once in the oven, samples were weighed daily, until a constant weight was obtained, at which point the samples were removed from the oven and the "field-dry" weight (Conklin-Brittain *et al.*, 2006) recorded. From this, field-dry weight/individual item was calculated. Samples were then stored in two labelled grip-lock bags with silica gel, which were then placed inside a near-air-tight plastic box, also with plenty of silica gel, in order to prevent moisture re-absorption.

4.2.2.2 Laboratory Analysis of Nutrient Contents

All samples were analysed at the Laboratorium Pengujian Nutrisi, LIPI-Bogor, Indonesia under the guidance of Dr Wartika R. Farida, and (with minor exceptions) following the

methods of Knott (1998, 1999) and Conklin-Brittain *et al.* (2006). The exact methods used in this laboratory are described in detail by the Indonesian National Standardisation Institute (BSN, 1992). This laboratory and these methods are also being used by a number of orang-utan researchers working at other sites, thus facilitating inter-site comparisons (Vogel, pers. comm.). The methods used in this study, along with the differences between the methods of previous researchers, and the potential implications of these, are presented in **Table 4.1**. As can be seen, the methods used give results broadly comparable to Knott (1998, 1999) and Conklin-Brittain *et al.* (2006), and far greater sources of error are likely to reside in the field observations than in minor method differences in the laboratory (Conklin-Brittain, pers. comm.).

Ash (i.e., inorganic nutrients) provides no energy. Thus, while many authors have expressed nutrient contents as percentage *dry matter* (DM, e.g., Popovich *et al.*, 1997; Rothman *et al.*, 2006, 2007), if the ash values in various foods vary by > 5% (as they do in this study, see **Appendix I**), this is undesirable, as the amount of ash in DM is too variable and potentially confounding. In order to eliminate this potentially confounding variable and to ensure consistency with previous orang-utan studies, all values given in this study are expressed as percentage *organic matter* (OM, i.e., excluding ash), with OM calculated as: (1 - ash) x DM (Knott, 1998, 1999; Conklin-Brittain *et al.* 2006).

Table 4.1 Laboratory analysis methods used in this study and by previous researchers (Knott, 1998, 1999; Conklin-Brittain *et al.*, 2006), and implications of any differences.

Fraction	Method used in this study	Methods used by previous researchers	Implications of method differences
Dry Matter (DM)	Sub-sample dried in oven at 105°C for 3 h and weighed cold.	Sub-sample dried at 100°C for 8h and weighed hot.	Negligible (Conklin-Brittain, pers. comm.).
Ash	Sub-sample dried in oven at 550°C until completely turned to ash and weighed cold.	Sub-sample dried at 520°C for 8h and hot-weighed at 100°C.	Negligible (Conklin-Brittain, pers. comm.).
Lipids	Sub-sample dried in an oven at 80°C for 1 h. Lipids are then extracted using Soxhlet apparatus with a hexane solvent for 6 h. The hexane is then distilled off and the extract dried in an oven at 105°C. Drying is repeated until constant weight is obtained, then the sample is weighed cold and lipid content calculated. This is the only method for lipid extraction employed at the LIPI-Bogor laboratory.	1. Petroleum ether used instead of hexane for lipid extraction. 2. Lipid extracted at room temperature over four days, without the use of Soxhlet apparatus.	1. Hexane and petroleum ether were found to be equivalent at extracting lipids from meats with lipid contents as low as 0.32% (Dionex, 2004), i.e. at values similar to those obtained during the present study. Thus, the use of hexane here is unlikely to have influenced the results obtained. 2. Extraction at room temperature removes less of the indigestible wax and latex than extraction at higher temperatures, giving a more nutritionally-available estimate of lipid content (Conklin-Brittain *et al.*, 2006). Thus, the method used here may over-estimate the digestible fat content in samples with high amounts of wax/latex. In addition, these latexes will be measured in the NDF fraction and, hence, will erroneously elevate NDF content and lower TNC content (Conklin-Brittain, pers. comm.). This is less of a problem when extracting lipids at room temperature (Conklin-Brittain, pers. comm.).

Fraction	Method used in this study	Methods used by previous researchers	Implications of method differences
Crude Protein (CP)	The Kjeldahl procedure for total nitrogen was used, with the value being multiplied by 6.25 (Pierce and Haenish, 1947). The digestion mix contained SeO_2, K_2SO_4 and $CuSO_4$. The distillate was collected in 2% boric acid and titrated with 0.01 N HCl.	1. Digestion mix contained Na_2SO_4 and $CuSO_4$. 2. Distillate collected in 4% boric acid and titrated with 0.1 N HCl.	1. Negligible (Conklin-Brittain, pers. comm.). 2. Negligible (Conklin-Brittain, pers. comm.).
Neutral Detergent Fibre (NDF)	The Neutral Detergent System of fibre analysis developed by Goering and van Soest (1970) and modified by Robertson and van Soest (1980) was used to determine neutral detergent fibre (NDF), i.e., the insoluble fibre of the plant cell wall.	Same	N/A
Total Non-Structural Carbohydrate (TNC)	Calculated by difference: TNC = 100 – (NDF + CP + lipid + ash) for expressing as percentage DM or 100 - (NDF + CP + lipid) for expressing as percentage organic matter (OM – see below).	Same	N/A

Some potential sources of error exist in the nutritional analysis (Conklin-Brittain *et al.*, 2006; Conklin-Brittain, pers. comm.), and these are discussed briefly here. *Total non-structural carbohydrate* (TNC) is the most problematic, because, as a calculated number, it contains all the errors in the analyses of the other fractions. In high-fat samples (i.e., above about 10%), not all of the lipid will be removed during the *neutral detergent fibre* (NDF) extraction process, and hence the apparent fibre level will be elevated and the lipid counted twice: once in the fibre and once in the lipid fraction. Fortunately, few primate foods, including those analysed in this study, contain > 10% fat, and so this source of error should be small. Lipid content can also be contaminated by latex and cutin (waxy polymers typically found on plant cuticles covering surfaces exposed to the air), which are indigestible, but are related to lipid and will also be extracted by the solvent, especially when high temperatures are used for extraction. This is unlikely to be problematic in most cases, but the apparently high levels of lipid in certain species of Apocynaceae and Clusiaceae (e.g., *Dyera lowii, Willughbeia* and *Garcinia*) could be partly a result of this. Some protein can also be bound by fibre and not dissolved by the fibre extraction process and, hence, can be counted twice, but this is generally only small (1-3% of DM, though values of ca. 15% have been reported for gorilla foods in Bwindi Impenetrable National Park, Uganda, Rothman *et al.*, 2008a).

Orang-utans frequently fed on insects and, although these could generally be classified into broad categories ("termite", "ant", "bee/wasp"), many species were doubtless consumed. Unfortunately, identification to species level, and collection of samples for nutritional analysis, were beyond the scope of this study. As a result, sample collection

efforts were concentrated towards other food types, and published data on invertebrate (termite) nutrient composition were used (Oyarzun *et al.*, 1996). Field dry weights were obtained for caterpillars eaten, which are much larger than ants/termites, and the nutrient contents/item adjusted accordingly.

4.2.3 CALCULATING INTAKE AND NUTRITIONAL COMPOSITION OF DIET

In order to calculate energy intake from nutritional data, I followed standard practice (NRC, 2003) and assigned the following *physiological fuel values* (PFV) to the different fractions: lipid 9 kcal/g (37 kJ/g), protein 4 kcal/g (17 kJ/g) and TNC 4 kcal/g (16 kJ/g).

Assigning a PFV to fibre is more complicated, as (a) fibre digestion requires fermentation by gut bacteria, which extract some of the energy for their own needs and (b) the lignin portion of the NDF fraction is indigestible (see Conklin-Brittain *et al.*, 2006 for a full discussion). Since NDF is mostly composed of hemicellulose and cellulose, which are carbohydrates, the PFV for TNC could theoretically be applied, but gut microbes typically take 1 kcal/g for their own needs, leaving only 3 kcal/g for the consumer (Conklin and Wrangham, 1994; van Soest, 1994). By analysing the fibre contents of foods consumed and faeces, Milton and Demment (1988) calculated the fibre digestion coefficient for chimpanzees fed biscuits containing 34% NDF to be 0.543 (i.e., 54.3% of the fibre was digested). Digestion studies on orang-utans have yielded similar results (Schmidt *et al.*, 2005). In this study, three orang-utans were fed on five diets containing a mean of 44.4% (range 27.3-63.7%) NDF. Mean fibre digestibility was 59.4% (range

45.0-74.5%, Schmidt *et al.*, 2005). Considering the higher fibre content of the orang-utans' diet in Schmidt *et al.*'s (2005) study, compared to the chimpanzees studied by Milton and Demment (1988), this suggests that orang-utans are more efficient at digesting fibre than chimpanzees. Conveniently, wild orang-utan diets typically contain a similar amount of NDF to those diets fed to captive chimpanzees and orang-utans in the studies referenced above (Knott, 1999; this study), and so these coefficients can probably be applied to wild orang-utans with relatively little error.

Conklin-Brittain *et al.* (2006), citing their own unpublished data, argue that orang-utan diets contain a higher proportion of indigestible lignin than chimpanzees', and, hence, argue that the coefficient determined for chimpanzees by Milton and Demnent (1988) is likely too high for orang-utans. Conklin-Brittain *et al.* (2006) therefore prefer a lower fibre digestion coefficient of 0.181 for orang-utans, giving a PFV for NDF of 0.543 kcal/g (this is the figure used by Knott, 1998, 1999). Considering the relatively high fibre digestion coefficient determined for orang-utans by Schmidt *et al.* (2005), it is possible that a digestion coefficient of 0.181 for wild orang-utans is too low. Although the NDF content of the orang-utans' diet in Schmidt *et al.*'s study was similar to wild diets, lignin contents were low and, hence, the coefficient obtained by Schmidt *et al.* (mean 59.4%) is likely also too high for wild orang-utans. Bearing this in mind, the lower fibre digestion coefficient obtained for chimpanzees by Milton and Demnent (1988, 54.3%) is used for the majority of analyses in this study.

Thus, the PFV for NDF is 3 x 0.543 = 1.6 kcal/g. The use of this coefficient is supported by calculations of fibre digestibility in gorillas. In wild mountain gorillas, NDF digestibility during periods of high (> 90%) folivory was ca. 25% (Rothman *et al.*, 2008b). Unfortunately, the NDF digestion coefficients calculated by Rothman *et al.* during periods of high (> 40%) frugivory are not useful for this study, as, although the diet would have been fairly similar to that typical of wild orang-utans, this coefficient was calculated considering seeds, which are largely indigestible, as part of fruit intake (Rothman, pers. comm.). As orang-utans generally avoid eating seeds or eat unripe seeds that are more easily digestible, the low figures calculated for gorillas during periods of high frugivory (ca. 10% NDF digestibility) are probably unsuitable for orang-utans. Similarly, in a study of captive gorillas, Remis (2002) found NDF digestibility to be 57.5% (mean of 2000 and 2001) on a diet containing ca. 30% NDF (DM), similar to the values reported by Schmidt *et al.* (2005) for captive orang-utans and Milton and Demment (1988) for captive chimpanzees. This information all supports the contention that a NDF digestion coefficient of 0.181 for wild orang-utans may be too low. While an intermediate value, as suggested by Conklin-Brittain *et al.* (2006), may eventually be proven to be most accurate, this has not been used herein as (i) the value chosen will be subjective, whichever value is used, (ii) estimates for energy intake using an intermediate value will merely lie in between the estimates produced using high and low values, and (iii) data on energy intake produced using an intermediate value will not be directly comparable with any previously published estimates for orang-utans (a main aim in this study). This latter point is particularly important; estimates of energy intake will only ever be rough approximations and so figures presented should always be interpreted with

caution. Assuming data are collected and analysed in a similar fashion, however, great insights can be gleaned from comparing such estimates between sites. Thus, while I have presented data on energy intake using the lower NDF digestion coefficient of 0.181 used by for orang-utans in Gunung Palung (Knott, 1998, 1999) and a value of zero *metabolisable energy* (ME) from fibre for comparative purposes, for the majority of my analyses, I only present results using this higher NDF digestion coefficient/PFV.

The ME content of foods was then calculated as:

ME_H kcal/100 g OM = (4 x % TNC) + (4 x % CP) + (9 x % lipid) + (1.6 x % NDF)

The same (corrected) formula was used when calculating energy contents with low (ME_L) and zero (ME_0) ME from NDF. From this and the field-dried weights obtained above, the energy content of each individual food item could be calculated (Knott, 1998, 1999; Conklin-Brittain *et al.*, 2006). This value was then multiplied by the feeding rate for that item to calculate energy intake/minute, and then by feeding bout length to calculate energy intake over the course of a feeding bout. Daily energy intake was then calculated as the sum of all individual feeding bouts that day.

Due to restricted visibility, there were many feeding bouts for which it was not possible to obtain feeding rates (2,264 feeding rates were obtained during 710 feeding bouts, representing 11% of the total observed feeding bouts included in the data set; see **Section 2.2**). When there were no data for a particular bout, I used a mean value calculated for

that individual feeding on the same food item on the same day (cf. Knott, 1998, 1999). I used mean feeding rates for an individual/age-sex class across the whole study period when only one feeding rate was recorded on an item for any particular bout/day, however, as I do not regard one feeding rate as being an accurate representation of true feeding rate in all cases. Similarly, there were some (generally minor) food items eaten for which there were no nutritional data. In these circumstances, it was impossible to calculate energy intake on that item directly and intake rates had to be inserted. In instances where the identity of the food was known, intake-rate data from a closely-related, similar species were used. When there were no data from closely-related species available, or when the identity of the food was unknown, I used mean intake rates taken across that food type (e.g., mean intake rate for fruit pulp, leaf shoots, etc.). In both of these instances, means were taken across all age-sex classes, as no significant differences in feeding rates were found between age-sex classes (see above). This same method for inserting unknown nutritional values was also used by Knott (1998, 1999) (Knott, pers. comm.).

In order to incorporate partial follows into the dataset, for each individual each month, I calculated mean energy intake/minute followed, and mean active period (AP, see **Section 6.2.1**) duration. Periods of time when the orang-utan was "lost" (i.e., not visible/audible by the observer and, hence, activity unknown) were accounted for by subtracting "lost" minutes from total minutes followed. Where there were no full-day follows for that individual in that month, I used the mean AP for that age-sex class that month and, when this was not available, I used the mean AP for all age-sex classes combined for that

month. Only when none of these were available, did I use means for that age-sex class over all months. From this, mean energy intake/day was calculated, and this was the basic statistic (**Section 2.2.6**) used in analyses. The full procedure for calculating energy intake is outlined in the flow chart in **Figure 4.1.**

Reference to energy intake data for the period September 2003-June 2005 (i.e., the two years prior to the onset of this study) is also made on occasion. These estimates were derived from data on dietary composition and AP collected by Morrogh-Bernard (submitted) using methods identical to those described above, combined with data on food-energy contents and feeding rates collected in this study. Calculations of daily energy intake were performed as described above, thereby creating four years of continuous data on energy intake. These data cannot be included in the results section of this study, as they also form part of another PhD thesis (Morrogh-Bernard, submitted), but the data are being written up for publication in the very near future (Harrison *et al.*, in prep) and, hence, have been referred to in the discussion where pertinent.

4.2.4 ESTIMATING METABOLIC REQUIREMENTS

Total energy expenditure (TEE) in adult mammals includes the energy required for basic bodily functions (basal metabolic rate), thermoregulation, food digestion and typical daily activities (obtaining food, travelling, etc.) (NRC, 2003; NAS, 2005). This is often termed "maintenance energy requirements" or "daily energy expenditure (DEE)". If energy intake = TEE, then the animal has met its energy requirements, is in neutral energy

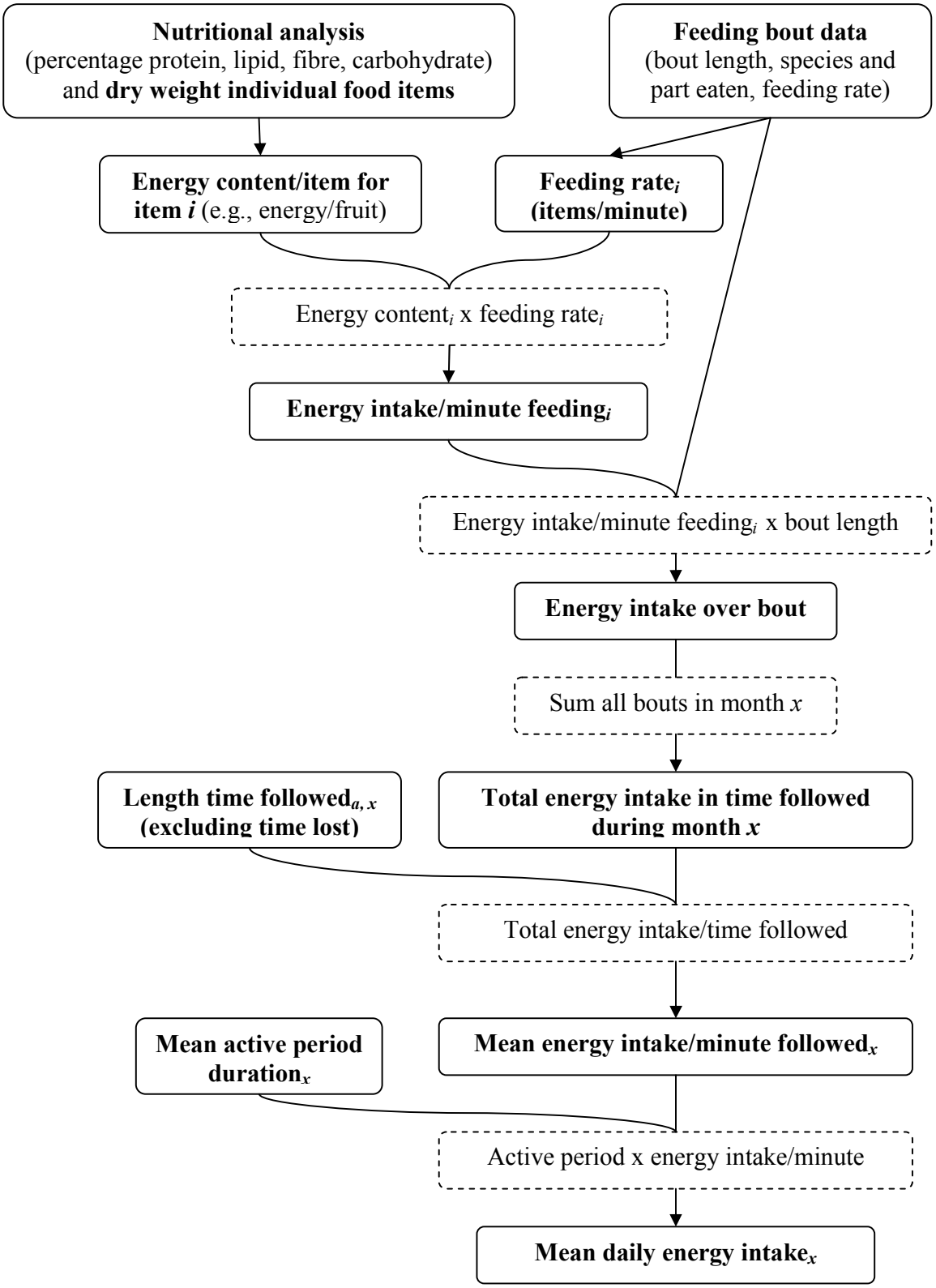


Figure 4.1 Flow chart showing steps involved in calculating mean daily energy intake for an individual orang-utan in a month. Dashed boxes indicate computational steps.

balance and will maintain a constant body mass. If energy intake < TEE, the animal enters negative energy balance, and caloric deficits are recouped by burning the body's energy stores (initially glycogen in the liver, then fat stores), resulting in weight loss. During periods of starvation/severe negative energy balance, the metabolism of bodily fat reserves results in the production of ketones in urine (Robinson, 1980; Knott, 1998). Ketones can be detected easily in wild primates by use of "urinalysis" strips (Knott, 1998, 1999; Wich *et al.*, 2006b). If energy intake > TEE, the animal enters positive energy balance, and the animal will begin to build up energy stores in the body and gain weight (in cases of prolonged high energy intake, this leads to obesity). Changes in energy budget are best established by assessment of changes in body weight, which is generally not feasible for wild primates. Thus, alternative methods – comparing estimates of energy intake and energy expenditure, and measurement of urinary metabolites (ketones and, more recently, C-peptides) – are used (e.g., Knott, 1998; Conklin-Brittain *et al.*, 2006; Sherry and Ellison, 2007; Rothman *et al.*, 2008b; Deschner *et al.*, 2008; Emery Thompson and Knott, 2008; Masi, 2007). Unfortunately, analysis of C-peptides was not possible in this study, due to a lack of facilities in Indonesia and restrictions on exporting samples from Indonesia. Hence, energy balance was estimated through comparison of energy intake and expenditure, and analysis of urinary ketones (cf. Knott, 1998, 1999).

Various formulas exist for calculating TEE in human and non-human primates based on either total body mass (e.g., Key and Ross, 1999; NRC, 2003; Shetty, 2005) or fat-free mass (e.g., Cunningham, 1991), with many also accounting for the metabolic costs of pregnancy and lactation in females, and the effects of physical activity levels. As the fat-

free mass of wild orang-utans is unknown, I will concentrate on methods involving total body mass (estimated at 38.7 kg and 86.3 kg for adult females and flanged males, respectively, Markham and Groves, 1990). While most of these methods yield broadly similar results for an animal of given weight, some are more conservative than others. A number of authors have also attempted to estimate TEE in wild orang-utans (Rodman, 1979; Wheatley, 1982; Leonard and Robertson, 1997; Knott, 1999). The most refined of these estimates are provided by Knott (1999), who quantified TEE in Gunung Palung in each study animal for each day of activity, and also incorporated the costs of reproduction for females. This was performed separately for both the mast and non-mast periods of Knott's study, and the computed estimates compare favourably to those derived from human energy requirements (ADA, 1992) of 40 kcal/kg body mass/day, and the orang-utan body masses given above (Knott, 1999). Estimated energy expenditure for adult female and flanged male orang-utans using these different methods is given in **Table 4.2**.

It was not possible to estimate TEE directly in this study, due to the difficulty of following orang-utans closely in disturbed peat-swamp forest, as a result of large amounts of *Pandan*, vines and fallen trees, in addition to wet conditions underfoot, which precluded the collection of detailed continuous activity data, as collected by Knott (1999). Thus, the figures calculated from published studies in **Table 4.2** were used as a basis for comparison with observed energy intake in Sabangau. Requirements for other nutrients were based on dietary reference intakes for humans (NAS, 2005), and comparisons made *sensu* Rothman *et al.* (2008b).

Table 4.2 Estimated total energy expenditure (kcal/day) for adult female (38.7 kg) and flanged male (86.3 kg) orang-utans using different methods.

Method based on	TEE formula	Estimate	ADF (exc. reproduction)	ADF (inc. reproduction)	FLM	Reference
Energy expenditure of normal, active adult humans.	40 x BM	-	1,550	2,325[a]	3,450	ADA (1992)
Literature review of energy expenditure of free-living adult humans, to compute the extreme limits of energy expenditure.	BMR x 1.21	Minimum possible[b]	1,074	1,611[a]	1,960	Shetty (2005), based on basal metabolic rates from the formula in McNab (1988)
	BMR x 4.5	Maximum possible[c]	3,994	5,991[a]	7,288	
	BMR x 1.6	Typical sedentary	1,420	2,130[a]	2,591	
	BMR x 1.35	Maintain BW[d]	1,198	1,797[a]	2,186	
Energy requirements for maintenance of body weight in adult placental mammals (including humans).	98 x $BM^{0.75}$	Mildly active	1,521	2,280[a]	2,775	Scott (1986)
	140 x $BM^{0.75}$	Moderately active	2,172	3,258[a]	3,964	
	210 x $BM^{0.75}$	Very active	3,258	4,888[a]	5,964	
Clinical practitioners' formula for calculating BMR for adult humans, adjusted by 30-40%[e] to represent typical (sedentary-moderate) activity of most free-living animals.	1.35 x 24 x BW	-	1,254	1,881[a]	2,796	Williams (1997), NRC (2003)

Method based on	TEE formula	Estimate	ADF (exc. reproduction)	ADF (inc. reproduction)	FLM	Reference
Analysis of activity data from literature on 19 species of wild primate; TEE calculated via factorial approach[f].	logTEE = 0.75 x logBM + 1.97	-	1,448	2,013[g]	2,642	Key and Ross (1999)
Detailed activity budgets from wild orang-utans, incorporating activity and reproductive costs; TEE calculated via factorial approach.	-	High fruit	1,900	-	3,400	Knott (1999)
	-	Low fruit	1,800	-	3,100	
	-	Mid point	1,850	2,300	3,250	

Abbreviations: ADF = adult females; BM = body mass (kg); BMR = basal metabolic rate; DLW = doubly-labelled water; FLM = flanged males; TEE = total energy expenditure (kcal/day).

a. Formula not given in reference cited; calculated as female costs excluding reproduction x 1.5 (NRC, 2003).
b. Expenditure for non-ambulatory, chair-bound subjects with no exercise.
c. Expenditure observed in *Tour de France* cyclists and polar explorers.
d. Suggested as the lowest physical activity level compatible with long-term weight maintenance in non-completely chair/bed-bound people.
e. Mid value (35%) taken for computations in this table.
f. Also used by Pontzer and Wrangham (2004) for calculating TEE in wild chimpanzees (these figures were later compared to estimated energy intake by Conklin-Brittain *et al.*, 2006).
g. Equal to TEE for adult females (excluding reproduction) x 1.39.

Analysis of ketones in urine was performed using Multistix 10 SG urinalysis sticks for human clinical analysis, following Knott (1998). Ketone levels in urine were measured semi-quantitatively on a scale from one to four (1 = negative, 2 = trace, 3 = positive, 4 = double positive). In addition to ketones, a variety of other useful health indicators can also be detected in urine (including leucocytes, blood and specific gravity; these results are not presented herein).

Energy and nutrient intake were then compared to the estimated requirements detailed above, both overall and during periods of low-high food availability (i.e., the food availability categories defined in **Section 3.2.2**), in order to test the hypothesis that energy and nutrient intake was sufficient during times of food plenty and inadequate during times of shortage ($H_0 4.4$). Similarly, the production of urinary ketones was also compared between periods of low-high food availability.

4.2.5 DATA EXPRESSION AND STATISTICAL ANALYSIS

Following Knott (1998, 1999), feeding data in this chapter are expressed in three ways: as total and/or percent time feeding, total and/or percent of grams consumed, and total and/or percent of kilocalories consumed. The former provides the most accurate representation of foraging effort, the second, the amount of food consumed, and the latter, the actual calorific contributions to the diet (the most physiologically-relevant measure) (Knott, 1999). Computational methods followed those described in **Section 2.2.6**.

Three different tests were used to test $H_0 4.2$ and $H_0 4.3$; these all incorporated age-sex class as a factor and orang-utan fruit/flower availability as a covariate, enabling the effect of age-sex class and food availability to be assessed simultaneously, and permitting data from all months and all age-sex classes to be included (paired tests would otherwise be needed to assess differences between age-sex classes, while excluding the potentially confounding influence of differences in fruit/flower availability between months; this would reduce sample size, as data were not obtained on all age-sex classes in all months). For normally distributed independent variables, general linear models (GLM, ANCOVA) were used. For non-normally distributed independent variables, generalized linear models or binomial logistic regression was used. The former was used when a large range of values existed for the independent variable (i.e., for percentage time spent feeding on, and energy derived from, fruit), and the latter when the range of values was small (i.e., for percentage time spent feeding on, and energy derived from, bark, flowers, invertebrates and leaves).

As fruit consumption was highly skewed to the right (i.e., positive values were more likely), a gamma distribution with a power (-1) link function (McCullagh and Nelder, 1989) was used for generalized linear models. In binomial regression analyses, the food type was either categorised as eaten/not eaten in a month (bark, flowers, invertebrates) or as forming < 10% > of the total diet in that month (leaves; this was necessary as leaves were eaten in most months; a value of 10% was chosen as this is close to the mean percentage of leaves in the diet, **Tables 4.4** and **4.9**). These initial analyses were focussed on the most important food types in the diet and, hence, did not include pith and “other”.

Further statistical tests (standard parametric/non-parametric correlations and tests for differences between categories, depending on whether the data satisfied normality assumptions) were then performed when the results of these tests were significant.

4.3 RESULTS

In this section, I first provide a general description of average orang-utan dietary composition in Sabangau (**Section 4.3.1**), after which I analyse the two potential sources of variation in dietary composition: differences between age-sex classes and responses to fluctuations in fruit/flower availability (**Section 4.3.2**). Finally, energy and nutrient intake is compared to estimated requirements (**Section 4.3.3**).

4.3.1 DIETARY COMPOSITION

4.3.1.1 Time Spent Feeding

Mean total minutes feeding/day and percentage of minutes followed spent feeding for all age-sex classes combined are given in **Table 4.3** (means for individual age-sex classes are shown later, in **Figure 4.3**). Mean percentage time feeding each day is similar to that in Sabangau from 2003-2005 (57.7-63.8%), but higher than in other sites, where mean percentage time spent feeding is ≤ 60% (Fox *et al.*, 2004; Morrogh-Bernard *et al.*, 2009)**.** While both the minimum total and percentage time spent feeding occurred in the same month (July 2006), maximum total and percentage time spent feeding did not. The two

variables were highly correlated (r = 0.956, n = 23, p < 0.001), but were not correlated with AP duration (total time feeding: r = 0.331, n = 23, p = NS; percentage time feeding: r = 0.0, n = 23, p = NS), indicating a temporal influence on time feeding, but not time spent awake.

Table 4.3 Total minutes feeding/day and percentage of minutes followed spent feeding from July 2005 – June 2007 (all age-sex classes combined). n = 23 months.

	Mean	**SD**	**Min.**	**Max.**
Time feeding/day (mins)	**419**	70	214	518
% time feeding	**63.6**	10.2	35.4	78.4

4.3.1.2 Percentage Time Spent Feeding on Major Food Types

The mean percentage of total feeding time spent feeding on major food types for all age-sex classes combined is given in **Table 4.4**. As in all other orang-utan populations studied (e.g., Morrogh-Bernard *et al.*, 2009), fruit constitutes the majority of the diet in Sabangau, with leaves, flowers, invertebrates, bark, pith and "other" food items constituting the remainder of the diet.

Table 4.4 Mean percentage total feeding time spent feeding on major food types from July 2005 – June 2007 (all age-sex classes combined). *n* = 23 months.

Food type	Mean	SD	Min.	Max.	CV
Bark	**3.9**	6.7	0	25.0	1.7
Flowers	**8.2**	16.8	0	60.0	2.0
Fruit	**68.5**	26.8	10.0	91.0	0.4
Invertebrates	**7.7**	6.4	0	22.0	0.8
Leaves	**9.9**	11.7	1.0	42.0	1.2
Pith	**1.7**	2.2	0	9.0	1.3
Other	**0.2**	0.2	0	1.0	1.0

4.3.1.3 Weight of Food Ingested

Average statistics for field dry weight intake/day over the study period are given in **Table 4.5.** Based on these data, nulliparous females would appear to ingest the least food, and flanged males the most, in line with expectations based on differences in body size.

Table 4.5 Mean dry weight consumption (g/day) from July 2005 – June 2007 by age-sex class.

Age-sex class	Mean	*n*	SD	Min.	Max.
All	**491**	23	164	255	854
Nulliparous females	**373**	18	125	207	658
Adult females	**516**	19	168	255	950
Flanged males	**628**	19	235	305	1,154
Unflanged males	**520**	11	251	200	986

n = number of months included in data set.

4.3.1.4 Nutrient Composition and Energy Content of Foods Eaten

Nutritional analysis was conducted on 183 samples, 93 of which were "real" orang-utan foods (see **Section 2.2.5** for definition). Complete nutritional data on these samples is provided in **Appendix I.** The energy contents of the five most-eaten foods in Sabangau (all age-sex classes combined) are given in **Table 4.6.**

Table 4.6 Energy content of the five most-eaten foods in Sabangau, July 2005-June 2007 (all age-sex classes combined).

Food	ME_H (kcal/100g)	ME_L (kcal/100g)
Mezzetia leptopoda fruit	435.8	394.4
Diospyros bantamensis fruit	234.0	157.3
Palaquim ridleyii/xanthochymum fruit	285.5	227.2
Termites	349.0	315.3
Unknown leaves	304.7	256.8
MEAN	321.9	270.2

Abbreviations: ME = metabolisable energy; "ME_H" = physiological fuel value of 1.6 kcal/g used for fibre; "ME_L" = physiological fuel value of 0.543 kcal/g used for fibre.

4.3.1.5 Energy Intake

Mean ME intake/day across the study period using different PFVs for NDF is given in **Table 4.7.** As discussed in **Section 4.2.3**, I have used the high PFV for NDF for the majority of my analyses, and the remainder of the analyses presented in this thesis are based on this high PFV for NDF (results of statistical tests using the lower NDF PFV were generally virtually identical, i.e., what was significant with one was significant with the other). Regardless of the PFV used for NDF, these data bear strong correspondence to

those on dry weight intake: nulliparous females ingest the least energy on average, and flanged males the most.

Table 4.7 Mean metabolisable energy intake (kcal/day) using different physiological fuel values for fibre[1] from July 2005 – June 2007 by age-sex class.

NDF PFV	Age-sex class	Mean	SD	Min.	Max
ME_H	All	**1,247**	381	709	2,187
	Nulliparous female	**1,035**	336	583	1,787
	Adult female	**1,335**	475	589	2,274
	Flanged male	**1,421**	533	658	2,357
	Unflanged male	**1,331**	660	611	2,646
ME_L	All	**963**	285	554	1,698
	Nulliparous female	**802**	263	430	1,421
	Adult female	**1,033**	373	425	1,694
	Flanged male	**1,076**	377	501	1,672
	Unflanged male	**985**	475	508	1,889
ME_0	All	**822**	249	471	1,454
	Nulliparous female	**686**	236	354	1,237
	Adult female	**883**	334	343	1,589
	Flanged male	**904**	311	422	1,438
	Unflanged male	**811**	389	414	1,511

Abbreviations: ME = metabolisable energy; NDF = neutral detergent fibre; PFV = physiological fuel value.

1. Fibre PFVs used: "ME_H" = 1.6 kcal/g, "ME_L" = 0.543 kcal/g, "ME_0" = 0 kcal/g.

4.3.1.6 Nutritional Composition of the Diet

The mean percent of total dry weight and energy consumed provided by the different nutritional fractions for all age-sex classes combined are shown in **Table 4.8.** Among fractions, differences between the percentage of total weight and energy intake provided were significant for lipids (paired t-test, t = 12.933, df = 22, $p < 0.001$, weight < energy) and TNC (t = -3.221, df = 22, p = 0.004, weight > energy).

Table 4.8 Mean percentage dry weight and energy provided by different nutritional fractions in the diet, July 2005-June 2007 (all age-sex classes combined). *n* = 23 months.

Percentage	Fraction	Mean	SD	Min.	Max.
Dry weight	Protein	**12.6**	5.5	7.0	32.5
	Lipids	**4.9**	2.0	2.4	11.3
	TNC	**50.9**	11.3	26.1	71.3
	NDF	**31.7**	9.5	16.6	52.0
Energy	Protein	**15.0**	4.0	8.4	23.5
	Lipids	**13.0**	4.8	7.3	26.2
	TNC	**38.1**	9.8	18.6	59.2
	NDF	**34.0**	7.7	13.0	50.2

Abbreviations: NDF = neutral detergent fibre; TNC = total non-structural carbohydrate.

4.3.1.7 Percentage Energy Obtained from Major Food Types

The percentage of total energy provided by different food types for all age-sex classes combined over the study period is shown in **Table 4.9.** When percentage time spent feeding on major food types was compared to the percentage energy derived from these food types, significant differences were found for fruit (Wilcoxon signed-rank, $p < 0.001$, % energy > % time), bark ($p = 0.001$, % energy < % time) and invertebrates ($p < 0.001$, % energy < % time) ($n = 23$ in all cases). Differences for the remaining food types were not significant.

Table 4.9 Percentage energy obtained from different food types from July 2005 – June 2007 (all age-sex classes combined). *n* = 23 months.

Food type	Mean	SD	Min.	Max.
Bark	**2.3**	4.6	0	16.6
Flowers	**7.8**	16.1	0	60.8
Fruit	**77.1**	24.8	20.0	98.4
Invertebrates	**1.6**	3.6	0	17.9
Leaves	**9.7**	13.0	0.7	47.5
Pith	**1.4**	3.1	0	13.4
Other	**0.1**	0.4	0	1.6

4.3.2 THE INFLUENCE OF AGE-SEX CLASS AND FLUCTUATIONS IN FOOD AVAILABILITY ON DIET

In all of the average statistics for all age-sex classes combined given above, it is evident that there is much variation in the data. There are two obvious potential explanations, which are not mutually exclusive: differences between age-sex classes and differences between months. The influence of these two factors was examined through general linear models (ANCOVA), generalized linear models and binomial logistic regression. The results of these tests are given in **Table 4.10**, monthly energy intake for each age-sex class is shown graphically in **Figure 4.2** and monthly dietary composition for each age-sex class in **Figure 4.3**. Terms used for food availability follow the definitions in **Table 3.1**.

Table 4.10 Results of tests for effects of age-sex class and fluctuations in orang-utan fruit/flower availability on diet composition and daily intake values: (a) General linear models (ANCOVA). Dependent variables are in *italics*.

	df	*F*	*p*
Minutes feeding/day			
Age-sex class	3, 62	0.638	NS
Orang-utan fruit/flower availability	1, 62	0.256	NS
Percentage time awake spent feeding			
Age-sex class	3, 62	1.129	NS
Orang-utan fruit/flower availability	1, 62	0.137	NS
Daily energy intake			
Age-sex class	3, 62	1,894	NS
Orang-utan fruit/flower availability	1, 62	4.437	0.039
Percentage energy from lipid			
Age-sex class	3, 62	0.183	NS
Orang-utan fruit/flower availability	1, 62	0.541	NS
Percentage energy from NDF			
Age-sex class	3, 62	0.410	NS
Orang-utan fruit/flower availability	1, 62	4.346	0.041
Percentage energy from protein			
Age-sex class	3, 62	0.226	NS
Orang-utan fruit/flower availability	1, 62	10.776	0.002
Percentage energy from TNC			
Age-sex class	3, 62	0.204	NS
Orang-utan fruit/flower availability	1, 62	0.378	NS

(b) Generalized linear models

	df	*Wald* χ^2	*p*
Percentage time feeding fruit			
Age-sex class	3, 62	0.417	NS
Orang-utan fruit/flower availability	1, 62	7.331	0.007
Percentage energy from fruit			
Age-sex class	3, 62	0.759	NS
Orang-utan fruit/flower availability	1, 62	5.235	0.022

(c) Binomial logistic regression

	df	*Wald*	*p*
Percentage time feeding leaves[1]			
Age-sex class	3, 62	0.331	NS
Orang-utan fruit/flower availability	1, 62	14.914	< 0.001
Percentage energy from leaves[1]			
Age-sex class	3, 62	1.618	NS
Orang-utan fruit/flower availability	1, 62	13.534	< 0.001
Percentage bark[2]			
Age-sex class	3, 62	2.248	NS
Orang-utan fruit/flower availability	1, 62	6.239	0.012
Percentage flowers[2]			
Age-sex class	3, 62	6.628	NS
Orang-utan fruit/flower availability	1, 62	8.552	0.003
Percentage invertebrates[2]			
Age-sex class	3, 62	4.120	NS
Orang-utan fruit/flower availability	1, 62	0.017	NS

Abbreviations: NDF = neutral detergent fibre, TNC = total non-structural carbohydrate, NS = not significant.

1. Categories represent < 10% > of time spent feeding/energy obtained from the food type in a month.
2. Categories represent whether the food type was eaten in a month (Y/N). Statistical significance levels were virtually identical for both percentage time and energy and, hence, are referred to as "percentage [food type]" in the table.

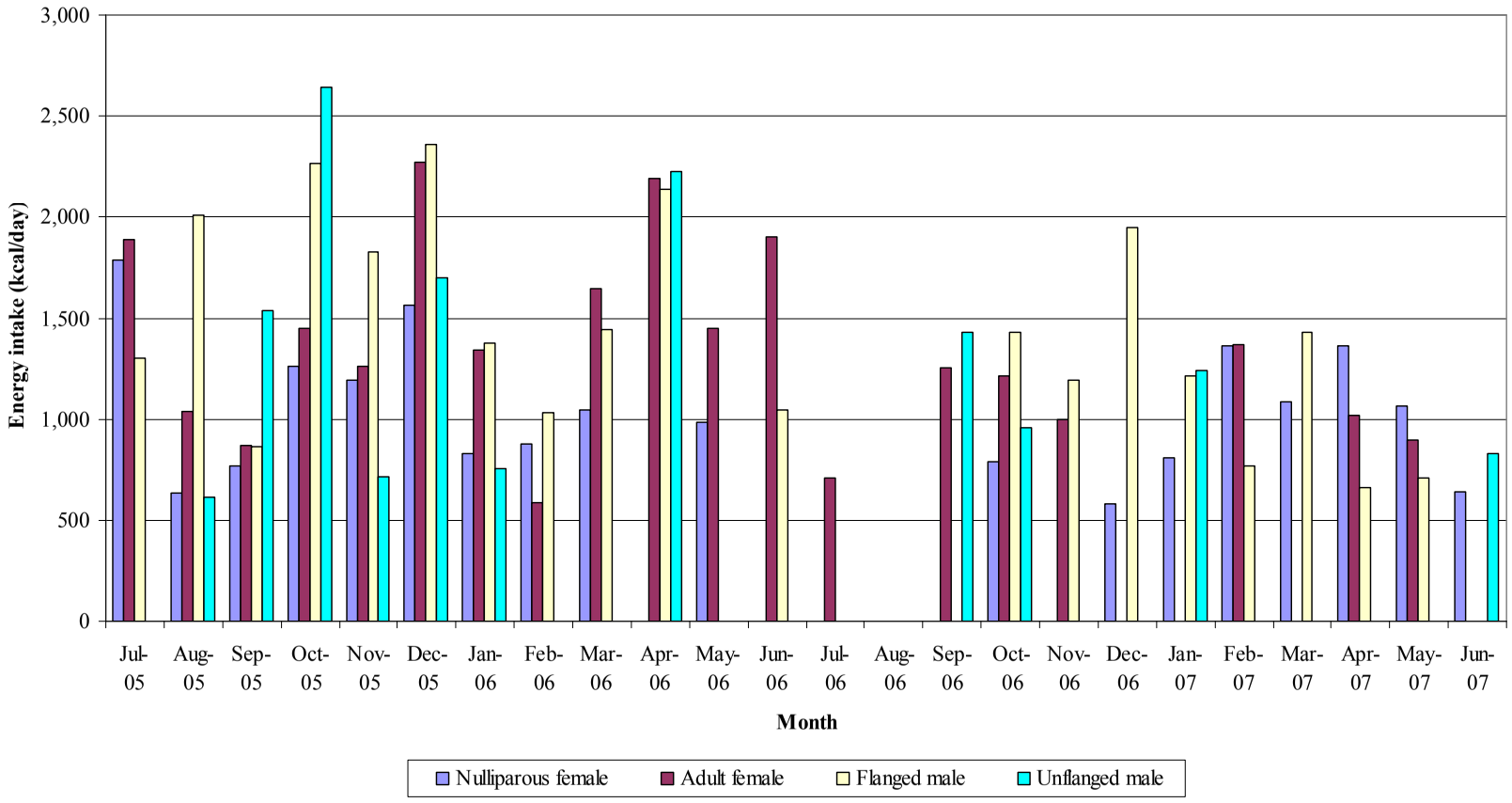


Figure 4.2 Daily energy intake (kcal) by age-sex class (July 2005-June 2007). Values using the high NDF digestion coefficient.

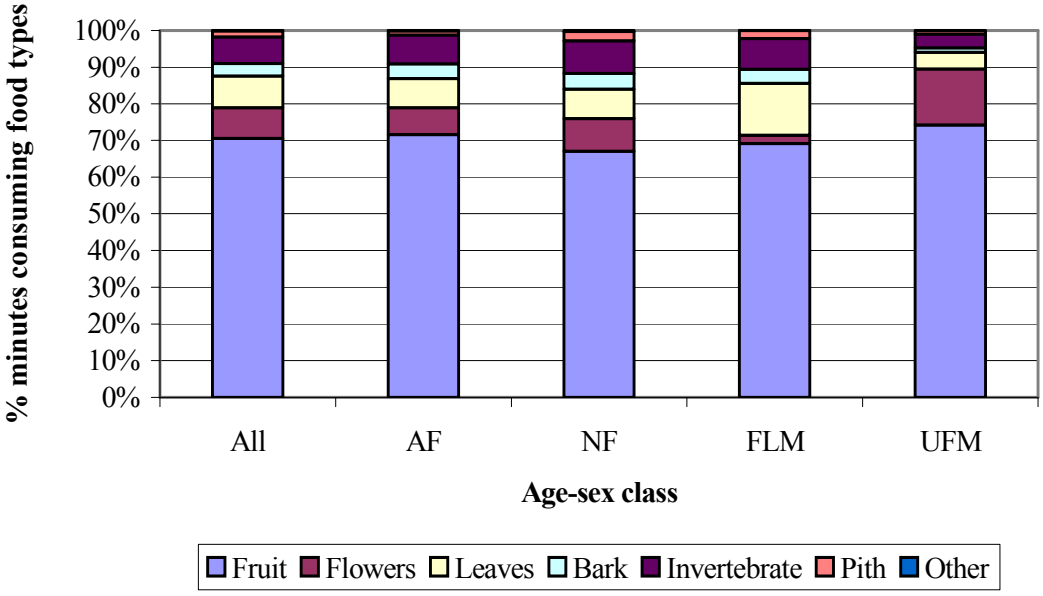


Figure 4.3 Mean percentage time spent feeding on major food types by age-sex class (July 2005-June 2007). All = all age-sex classes combined; AF = adult females; NF = nulliparous females; FLM = flanged males; UFM = unflanged males.

There was no significant effect of age-sex class on any of the dietary variables, but orang-utan fruit/flower availability had a significant effect on dietary composition (percentage time spent feeding on, and percentage energy derived from, bark, flowers, fruit and leaves) and daily energy intake; effects on total time spent feeding and percentage time spent feeding were not significant (**Table 4.10**). As a further test of age-sex class differences, I also tested for differences and correlations between percentage time spent feeding on the four most-common food items for adult females and flanged males (**Table 4.11**). Differences were not significant and correlations were highly significant. Thus, we can accept the null hypothesis that dietary quality does not differ between age-sex classes ($H_0 4.2$).

Table 4.11 Results of tests for correlations and differences between percentage time spent feeding on top-four most important foods for adult females and flanged males. *n* = 16 months.

Item	Mean % time (SD): ADF	Mean % time (SD): FLM	Wilcoxon rank (*p*)	r_s
Mezzetia leptopoda/parviflora (seed)	13.3 (20.4)	18.2 (25.1)	NS	0.738**
Diospyros bantamensis (pulp)	11.6 (22.3)	2.8 (4.7)	NS	0.679**
Palaquim ridleyii/xanthochymum (skin/pulp)	6.5 (12.6)	10.9 (20.8)	NS	0.929***
Termites	5.6 (8.1)	8.9 (9.6)	NS	0.621*

* = $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant.

Though these tests illustrate that diet composition and energy intake are related to orang-utan fruit/flower availability, further tests are required on these variables, to judge whether the hypothesis that these effects occur in both adult females and flanged males, as in Gunung Palung ($H_0 4.3$), can be accepted. In the remainder of this section, analyses are therefore performed on each age-sex class separately. In addition, tests are also performed for all age-sex classes lumped together. In these cases, all the monthly means for all age-sex classes are included (i.e., if data exist for all four ages-sex classes in a month, this month is represented four times in the analysis, etc.), as sample size and, consequently, statistical power are much greater than for individual age-sex classes. This is referred to as "all classes" and is distinct from the term "all age-sex classes combined", used when data from all-age sex classes combined are expressed graphically, which refers to a mean for each month derived from the monthly values for each age-sex class (so each month was represented only once in the analysis, as described in **Section 2.2.6**).

Where corrections were performed for multiple comparisons (Hochberg, 1988), these are performed with *alpha* set at 0.05 for each separate measure of food availability.

4.3.2.1 Influence of Food Availability on Percentage Time Spent Feeding on Major Food Types

Monthly variations in the percentage of feeding time spent feeding on major food types for all age-sex classes combined are shown in **Figure 4.4.** Fruit constituted the majority of the diet in most months, but the proportion of fruit and other food types in the diet varied considerably between months. The results of correlations between percentage dietary composition and orang-utan fruit, fruit/flower and food-energy availability for each age-sex class and "all classes" are given in **Table 4.12.** Orang-utan fruit availability was included in the analysis in order to facilitate comparisons with previous researchers who have used this measure (Leighton, 1993; Knott, 1998, 1999; Fox *et al.*, 2004; Conklin-Brittain *et al.*, 2006; Wich *et al.*, 2006b). As feeding data were not normally distributed, Spearman's correlations were used.

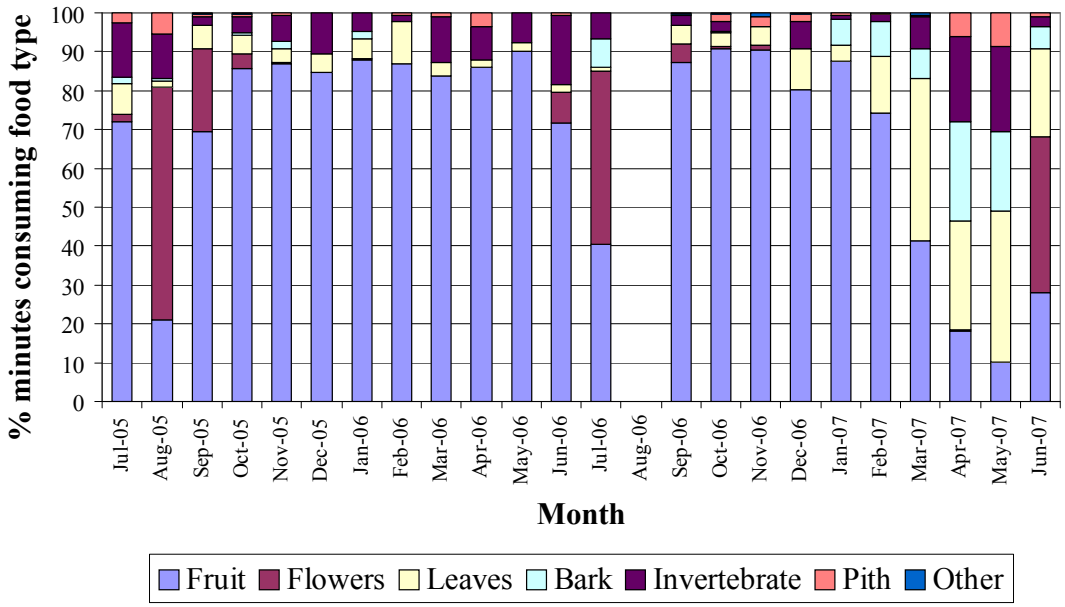


Figure 4.4 Monthly variations in percentage time spent feeding on major food types, July 2005-June 2007 (all age-sex classes combined).

I also tested for differences in percentage dietary composition between periods of "low", "medium-low" and "medium-high" fruit/flower availability (**Table 4.13**, see **Section 3.2.2** for category definitions). Non-parametric Kruskal-Wallis tests were used to test for differences between fruit/flower availability categories and, when significant differences were found, Dunn's non-parametric multiple comparisons tests (Dunn, 1964) were performed, in order to see which categories differed from which others.

Table 4.12 Spearman's correlations between percentage time spent feeding on major food types and orang-utan fruit/flower, orang-utan fruit and orang-utan food-energy availability. Values are correlation coefficients. Unless indicated otherwise, correlations were insignificant for all measures of food availability.

		Food type consumed						
Age-sex class	***n***	**Other**	**Bark**	**Flowers**	**Fruits**	**Invertebrates**	**Leaves**	**Pith**
All classes	70	NS	En: -0.285 * **Fo: -0.406** ** **Fr: -0.431** ***	Fo: 0.333 ** Fr: 0.320 **	Fo: 0.333 ** Fr: 0.301 *	NS	En: -0.291 * **Fo: -0.442** *** **Fr: -0.455** ***	NS
Adult females	19	NS	NS	NS	NS	NS	En: -0.637 ** **Fo: -0.693** *** Fr: -0.712 ***	NS
Nulliparous females	18	NS	En: -0.565 * Fo: -0.669 ** Fr: -0.660 **	Fo: 0.633 ** Fr: 0.604 **	NS	NS	Fo: -0.480 * Fr: -0.527 *	NS
Flanged males	20	NS	NS	Fo: 0.562 ** Fr: 0.568 **	NS	NS	En: -0.544 *	NS
Unflanged males	11	NS	NS	NS	Fo: 0.682 * Fr: 0.665 *	NS	NS	NS

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant. *n* = number of months included in analysis; Fo = orang-utan fruit/flower availability, Fr = orang-utan fruit availability, En = orang-utan food-energy availability (see **Table 3.1** for definitions). Boldface indicates *p*-values that remained significant post-Bonferroni correction.

Table 4.13 Results of tests for differences in percentage time spent feeding on major food types between fruit/flower availability categories. Values are: *p*-values for Kruskal-Wallis; listed below are categories that differed significantly in Dunn's multiple comparisons tests (α = 0.05).

Age-sex class	Other	Bark	Flowers	Fruit	Inverts	Leaves	Pith
All classes	NS	**< 0.001** **L > ML** **L > MH**	0.013 ML > L	**0.006** **ML > L** **MH > L**	NS	**< 0.001** **L > ML** **L > MH**	NS
Adult females	NS	0.011 L > ML	NS	0.048 MH > L	NS	0.007 L > MH	NS
Nulliparous females	NS	0.044	NS	NS	NS	NS	NS
Flanged males	NS	NS	NS	NS	NS	NS	NS
Unflanged males	NS	NS	NS	NS	NS	NS	NS

Abbreviations: L = "low", ML = "medium-low", MH = "medium-high" fruit/flower availability, NS = not significant. See text for details and **Section 3.2.2** for definitions. Boldface indicates results that remained significant post-Bonferroni correction (corrections performed with *alpha* = 0.05 all tests within each age-sex class).

Based on the results from **Tables 4.12** and **4.13**, time spent feeding on leaves and bark is negatively related to fruit/flower availability, and time spent feeding on fruit is positively related to fruit/flower availability (with a similar trend for flowers), for the population as a whole ("all classes"). The only significant result for the tests on individual age-sex classes was a negative relationship between time spent feeding on leaves and orang-utan fruit/flower availability for adult females. Trends across the age-sex classes were frequently in agreement with these observations, however, indicating that these relationships may become significant with increased sample size. Differences in the trends observed between age-sex classes also indicates that different age-sex classes may

respond differently to fluctuations in fruit/flower availability (with females falling back more on bark than males when fruit/flower availability is low), but, again, further observations are needed to confirm this suggestion. Conversely, it can be said with confidence that time spent feeding on invertebrates, pith and "other" foods are not related to orang-utan fruit/flower availability. The lack of apparent influence of fruit/flower availability on the consumption of pith and "other" foods is not surprising, as these form only a very small portion of the diet in all months for any age-sex class.

In order to test whether increases in the consumption of one food type were related to decreases in the consumption of any others, I performed Spearman's correlations between all the different food types. The results of these for the population as a whole ("all classes") are shown in **Table 4.14**. Pith and "other" were excluded, due to their very small overall contribution to the diet. These results indicate that increased fruit consumption is related to decreased bark, leaf, invertebrate and flower consumption, and increased leaf consumption is related to increased bark consumption.

Table 4.14 Matrix of Spearman's rank correlations for relationships between percentage time spent feeding on major food types (all classes). *n* = 67 months. Values are correlation coefficients.

	Flowers	**Fruit**	**Inverts**	**Leaves**
Bark	NS	**-0.339 ****	NS	**0.346 ****
Flowers	X	**-0.367 ****	NS	NS
Fruit		X	**-0.585 *****	**-0.396 *****
Inverts			X	NS

* $p < 0.05$; ** $p < 0.01$; NS = not significant. Boldface indicates *p*-values significant post-Bonferroni correction.

4.3.2.2 Influence of Food Availability on Energy Intake

Monthly variations in daily energy intake in relation to orang-utan fruit/flower availability for all age-sex classes combined are shown in **Figure 4.5**, and the results of correlations between daily and hourly energy intake, and orang-utan fruit/flower, orang-utan fruit and orang-utan food-energy availability in **Tables 4.15-16.** Correlations were one-tailed, as, based on Knott's (1998, 1999) findings, a positive relationship between fruit/flower availability and energy intake was expected. Based on these correlations, orang-utan fruit availability is positively related to daily energy intake for the population as a whole and for flanged males, and orang-utan fruit/flower availability is positively related to daily energy intake for flanged males (with a positive trend for the population as a whole). Daily energy intake is not related to food-energy availability in any age-sex class. Similar patterns are observed when hourly energy intake is considered: correlations are significant for flanged males and positive trends exist for the population as a whole.

No significant correlations were found between energy intake and AP duration, minutes spent feeding/day or percentage time spent feeding for any age-sex class (p = NS in all cases). Although all trends were in the expected direction, differences between periods of low, medium-low and medium-high orang-utan fruit/flower availability were not significant for any age-sex class (Kruskal-Wallis, p = NS in all cases), possibly due to the small sample sizes involved. In order to increase sample size and improve statistical power, I also analysed the data using full-day follows within each fruit/flower-availability category as independent data points (cf. Knott, 1999). The same results were produced:

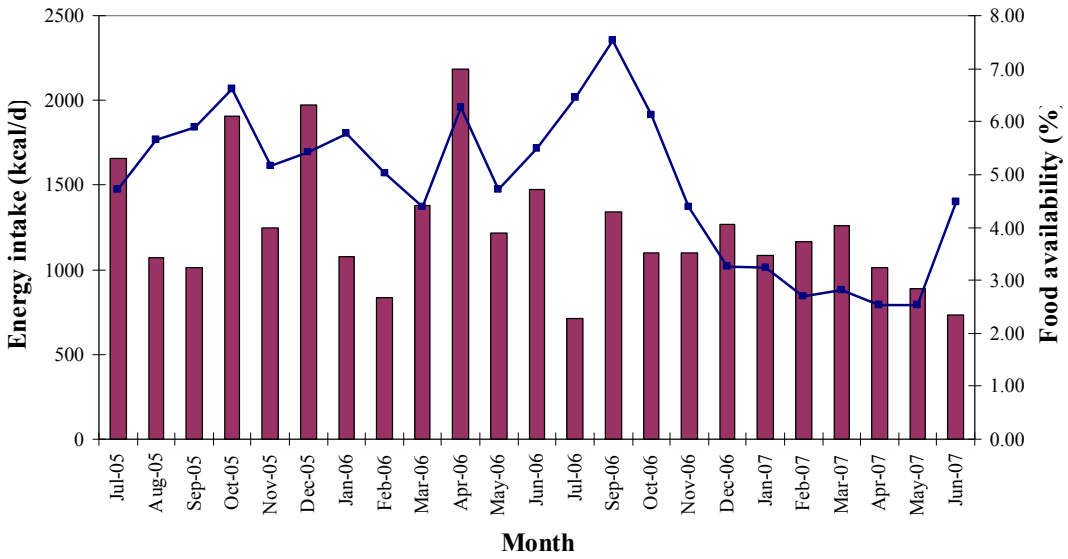


Figure 4.5 Monthly variations in daily energy intake (bars) in relation to orang-utan fruit/flower availability (line) for all age-sex classes combined, July 2005-June 2007.

Table 4.15 One-tailed Pearson's correlations between daily energy intake and orang-utan fruit/flower, orang-utan fruit and orang-utan food-energy availability. *n* = number of months included in analysis. Values are correlation coefficients.

Age-Sex Class	*n*	Orang-utan fruit/flower availability	Orang-utan fruit availability	Orang-utan food-energy availability
All combined	67	0.272 *	**0.307 ****	NS
Adult females	19	NS	NS	NS
Nulliparous females	18	NS	NS	NS
Flanged males	20	**0.537 ****	**0.524 ***	NS
Unflanged males	11	NS	NS	NS

* $p < 0.05$; ** $p < 0.01$; NS = not significant. Boldface indicates correlations that remained significant post-Bonferroni correction.

Table 4.16 One-tailed Pearson's correlations between hourly energy intake and orang-utan fruit/flower, orang-utan fruit and orang-utan food-energy availability. *n* = number of months included in analysis. Values are correlation coefficients.

Age-Sex Class	*n*	Orang-utan fruit/flower availability	Orang-utan fruit availability	Orang-utan food-energy availability
All combined	67	0.230 *	0.265 *	NS
Adult females	19	NS	NS	NS
Nulliparous females	18	NS	NS	NS
Flanged males	20	**0.544 ****	**0.527 ****	NS
Unflanged males	11	NS	NS	NS

* $p < 0.05$; ** $p < 0.01$; NS = not significant. Boldface indicates correlations that remained significant post-Bonferroni correction.

differences between orang-utan fruit/flower-availability categories were not significant for any age-sex class (ANOVA, AF: $F_{2, 95} = 1.450$, p = NS; NF: $F_{2, 62} = 1.514$, p = NS; FLM: $F_{2, 32} = 2.121$, p = NS; UFM: $F_{1, 9} = 1.049$, p = NS).

4.3.2.3 Influence of Food Availability on Nutritional Composition of the Diet

The percentage of total energy intake obtained through the different food fractions was generally not significantly correlated with orang-utan fruit/flower availability (**Table 4.17**). The only exception was that the population as a whole ("all classes") and flanged males obtained more energy through protein as orang-utan fruit/flower availability decreased. This may be explained by increased consumption of leaves, which are high in protein (mean 13.7% OM, compared to 8.1% for all other food types combined, see **Table 5.5**), during periods of low fruit/flower availability (**Tables 4.12-13** and **4.18-19**).

Table 4.17 Pearson's correlations between percentage energy obtained from different fractions and orang-utan fruit/flower availability by age-sex class. *n* = number of months included in analysis. Values are correlation coefficients.

Age-Sex Class	*n*	Protein	Lipid	NDF	TNC
All classes	67	**-0.414** ***	NS	0.270 *	NS
Adult females	19	NS	NS	NS	NS
Nulliparous females	18	NS	NS	0.529 *	NS
Flanged males	20	**-0.763** ***	NS	NS	NS
Unflanged males	11	NS	NS	NS	NS

$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant. Boldface indicates significant correlations post-Bonferroni correction.
Abbreviations: NDF = neutral detergent fibre; TNC = total non-structural carbohydrate.

4.3.2.4 Influence of Food Availability on Percentage Energy Obtained from Major Food Types

Monthly variations in the percentage of total energy obtained through different major food types for all age-sex classes combined are shown in **Figure 4.6**. Correlations with fruit/flower availability (**Table 4.18**) are very similar to those when diet composition was measured on a percentage time spent feeding basis (**Table 4.12**): percentage energy obtained through leaves was negatively correlated with orang-utan fruit and fruit/flower availability for the population as a whole ("all classes") and with food-energy availability for adult females, and percentage energy obtained through bark was negatively correlated with orang-utan fruit and fruit/flower availability for the population as a whole. Trends also existed for percentage energy obtained through leaves and bark (negative), and fruit and flowers (positive) and the different measures of food availability in some analyses. Further investigation is required to determine whether these trends become significant

with increased sample size. Of all the measures of food availability, food-energy availability appears to have the least effect on percentage energy obtained through food types (producing only one significant result and four trends, compared to two significant results and eight trends for both orang-utan fruit and fruit/flower availability).

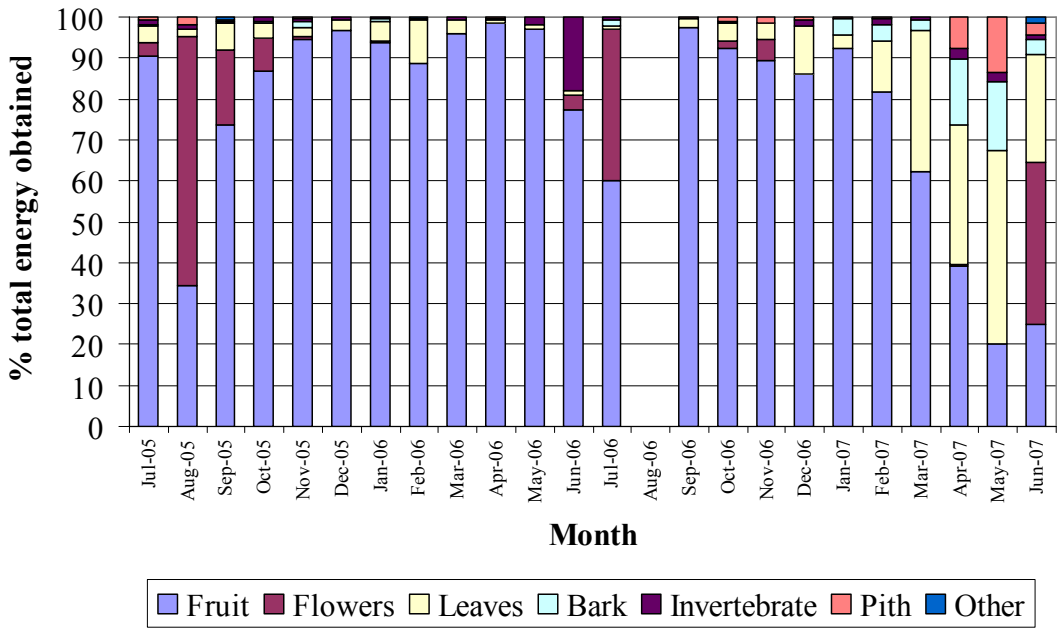


Figure 4.6 Monthly variations in percentage total energy obtained through major food types for all age-sex classes combined, July 2005-June 2007.

Table 4.18 Spearman's correlations between percentage total energy obtained through major food types and orang-utan fruit/flower, orang-utan fruit and orang-utan food-energy availability. *n* = number of months included in analysis. Values are correlation coefficients. Unless indicated otherwise, correlations were insignificant for all measures of food availability.

Age-Sex Class	*n*	Other	Bark	Flowers	Fruits	Invertebrates	Leaves	Pith
All classes	67	NS	En: -0.303 * **Fo: -0.414** *** **Fr: -0.443** ***	En: 0.244 * Fo: 0.319 ** Fr: 0.301 *	Fo: 0.341 ** Fr: 0. 326 **	NS	En: -0.259 * **Fo: -0.449** *** **Fr: -0.475** ***	NS
Adult females	19	NS	NS	NS	NS	NS	**En: -0.725** *** Fo: -0.608 ** Fr: -0.633 **	NS
Nulliparous females	18	NS	En: -0.474 * Fo: -0.642 ** Fr: -0.634 **	Fo: 0.656 ** Fr: 0.614 **	NS	NS	Fr: -0.475 *	NS
Flanged males	20	NS	NS	Fo: 0.442 *	Fo: 0.554 * Fr: 0.449 *	NS	Fo: -0.515 * Fr: -0.483 *	NS
Unflanged males	11	NS	NS	NS	NS	NS	NS	NS

$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant. Boldface indicates significant correlations post-Bonferroni correction.
Abbreviations: Fo = real-food availability, Fr = real-fruit availability, En = energy availability.
Trends were also found for: all combined and fruit (FR, $r_s = 0.346$, $p = 0.053$), adult females and flowers (Fo, $r_s = 0.384$, $p = 0.052$, Fr, $r_s = 0.383$, $p = 0.053$), and nulliparous females and leaves (Fo, $r_s = -0.397$, $p = 0.052$).

I also compared the percentage energy obtained through food types between different orang-utan fruit/flower availability categories for each age-sex class. The results of these analyses are shown in **Table 4.19.** For the population as a whole ("all classes"), percentage energy derived from bark and leaves increased, and percentage energy derived from fruit decreased, as fruit/flower availability decreased. Trends also existed for flowers, and for the above food types in other age-sex classes, indicating that these may become significant with increased sample size. Taken together, the results in this section indicate that increased orang-utan fruit/flower availability leads to decreased percentage energy obtained through leaves and bark, and increased percentage energy obtained through fruit (with a similar trend for flowers) for the population as a whole, and decreased percentage energy obtained through leaves for adult females. Similar trends also existed for the individual age-sex classes; thus, as it is quite possible that these trends would become significant with increased sample size, it would therefore be imprudent to conclude that any differences exist between age-sex classes in this regard.

To test whether increases in the energy obtained through food types were related to decreases in the energy obtained through others, I performed correlations between all the food types (**Table 4.20**, pith and "other" excluded). These results mirror those in **Table 4.14** for percentage time spent feeding on food types: percentage energy obtained through fruit was negatively correlated with all that from other food types (apart from "other"), which would be expected were fruit the preferred food type. Energy obtained through leaves and bark was also positively correlated, which would be expected for non-preferred foods eaten when fruit is scarce.

Table 4.19 Results of tests for differences in percentage energy obtained from major food types between fruit/flower availability categories. Values are: *p*-values for Kruskal-Wallis; listed below are categories that differed significantly in Dunn's multiple comparisons tests (α = 0.05).

Age-sex class	Other	Bark	Flowers	Fruit	Inverts	Leaves	Pith
All classes	NS	**< 0.001** **L > ML** **L > MH**	0.019	**0.002** **ML > L** **MH > L**	NS	**< 0.001** **L > ML** **L > MH**	NS
Adult females	NS	0.011	NS	NS	NS	0.010	NS
Nulliparous females	NS	NS	NS	NS	NS	NS	NS
Flanged males	NS	NS	NS	NS	NS	NS	NS
Unflanged males	NS	NS	NS	NS	NS	NS	NS

Abbreviations: L = "low", ML = "medium-low", MH = "medium-high" fruit/flower availability, NS = not significant. See text for details and **Section 3.2.2** for definitions. Boldface indicates results that remained significant post-Bonferroni correction (corrections performed with *alpha* = 0.05 all tests within each age-sex class).

Table 4.20 Matrix of Spearman's rank correlations for relationships between percentage total energy derived from major food types (all classes). *n* = 67 months included in analysis. Values are correlation coefficients.

	Flowers	Fruit	Inverts	Leaves
Bark	NS	**-0.381 ****	0.295 *	**0.351 ****
Flowers	X	**-0.436 *****	NS	NS
Fruit		X	**-0.344 ****	**-0.536 *****
Inverts			X	NS

* = $p < 0.05$; NS = not significant. Boldface indicates correlations that remained significant post-Bonferroni correction.

4.3.3 ENERGY AND NUTRIENT INTAKE IN RELATION TO ESTIMATED REQUIREMENTS

When compared with the estimates of TEE calculated for wild orang-utans in Gunung Palung (Knott, 1999), orang-utan energy intake in Sabangau is clearly low, even under the 'best-case scenario' of a high PFV for NDF (**Figure 4.7**). Mean energy intake for adult females (1,335 kcal/d) and flanged males (1,421 kcal/d) over the study period were both below Knott's TEE estimates (ADF: 1,850 kcal/d; FLM: 3,250 kcal/d). This is especially true for flanged males, for which energy intake < TEE in all months of this study. Adult females fell short in most months, but were able to consume energy in excess of requirements in 3/19 (16%) of months, based on a requirement of 1,850 kcal/day (excluding reproduction). Although maximum energy intake was close to estimated TEE (including reproduction) in Gunung Palung, it was never exceeded. When using the low NDF PFV, both adult female and flanged male energy intake < estimated TEE in all months. Tests for differences in energy intake (using the high NDF PFV) between food-availability categories were also not significant for any age-sex class (**Section 4.3.2.2**). Thus, based on this comparison, we must reject $H_0 4.4$ (that intake is adequate during periods of high food availability, and inadequate when food availability is low) for energy intake.

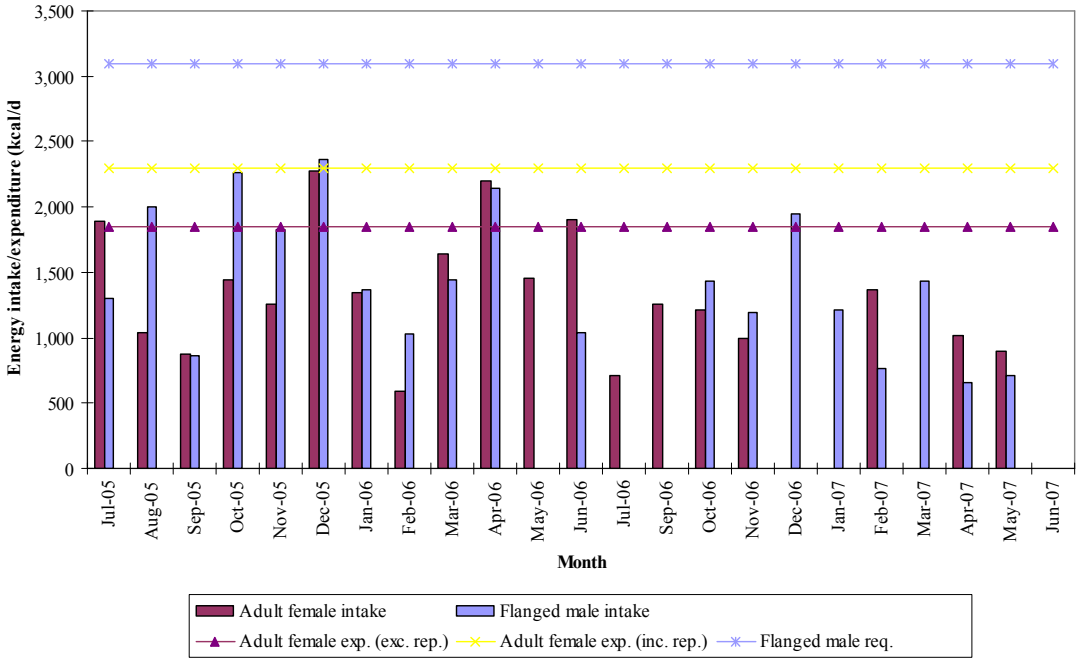


Figure 4.7 Monthly adult female and flanged male energy intake compared to estimated energy expenditure values from Knott (1999). Energy intake calculated using a high NDF digestion coefficient (**Section 4.2.3**). Energy expenditure values calculated by Knott (1999) for orang-utans in Gunung Palung (see text), and include estimates for adult females both including and excluding the costs of reproduction.

Analysis of ketones in urine provides equivocal support for the energy-intake data. A total of 74 urine samples were collected during the study period, but 21 of these were excluded based on very low specific gravity, which indicates likely contamination with rainwater (all these samples were negative for ketones). Based on the remaining 53 urine samples collected, ketones were present in 19% of samples, and were detected in 7/20 (35%) months for which there were data. For adult females alone (n = 26 samples), ketones were present in 19% of samples, and were detected in 4/11 (36%) of months. For flanged males alone (n = 9 samples), ketones were present in 33% of samples, and were detected in 1/7 (14%) of months. Spearman's correlations between percentage samples

with ketones, energy intake and real-food availability were not significant, and there was no difference in ketone presence between periods of low-high orang-utan fruit/flower availability (Kruskal-Wallis, p = NS) for the population as a whole and adult females. Due to the small sample size for flanged males (1-2 samples/month and only 9 months), correlations and tests for differences between periods of fruit/flower availability were not attempted. Thus, ketone production and, hence, fat metabolism and negative energy balance, occurred regularly in Sabangau orang-utans during this study, indicating a constant struggle to meet metabolic requirements.

Orang-utan energy intake in Sabanagau does not appear to be constrained by a limit to the amount of fibre that can be ingested, as has been suggested for orang-utans in Gunung Palung during inter-mast periods (Knott, 1999). Maximum fibre intake for orang-utans in Sabangau was 330 g/d (for flanged males in April 2006), compared to a maximum of ca. 800 g/d in Gunung Palung (Knott, 1999).

Orang-utans in Sabangau would appear to be meeting macro-nutrient requirements. Comparisons with human requirements, adjusted for differences in body mass (see above) concur: in Sabangau, adult female and flanged male orang-utans consume, on average, 4.1 and 2.7 g protein/kg body mass$^{0.762}$, respectively, compared to very active human requirements of 2.8 and 1.8 g protein/kg body mass$^{0.762}$ (NAS, 2005) in reproductively-active females and adult males, respectively. Requirements for total lipids, fibre and TNC in humans are not known, due to a lack of sufficient evidence on the prevention of chronic diseases in generally healthy individuals (NAS, 2005).

Recommended crude fibre intake in adult male and female humans is 1.5 and 13 g/kg body mass$^{0.762}$, respectively (NAS, 2005). This is far exceeded by both flanged males and adult females in Sabangau, which consume 77.6 and 49.1 g NDF/kg body mass$^{0.762}$, respectively. Differences in the daily dry weight of macro-nutrients ingested between food-availability categories were not significant for either adult females (ANOVA: $F_{2, 16}$ = 0.004 to 1.006, p = NS in all cases) or flanged males ($F_{2, 16}$ = 0.039 to 3.440, p = NS in all cases). Thus, orang-utans appear to be satisfying protein and fibre requirements in all months, and hypothesis $H_0 4.4$ must be rejected for these nutrients.

Analysis of Potentially Confounding Issues in the Calculation of Energy Intake

The comparison of energy intake to TEE presented above is striking, and may induce doubt as to whether the results above could be a mere consequence of the methods used and/or the imperfect data set obtained (see **Chapter 2**). As noted in **Section 4.2.2.2**, the largest potential source of error in estimated intakes resides in the field estimates obtained. Among these field estimates, the largest source of potential error probably resides in the estimation of feeding rates. This error was reduced as much as possible by only using data collected by myself and by the British post-graduate assistants whose data matched my own (**Section 2.2.1**). Nevertheless, some error may still exist in this estimate, though there is no reason to believe that this error would lead to under-estimation of energy intake, as opposed to over-estimation. The error involved in other field estimates (length of feeding bouts, species identifications, active period durations, etc.) is likely low, as these data were relatively simple to collect. Again, any errors are as likely to lead to over-estimation of intake as they are to under-estimation.

The use of a 6-h minimum follow limit (**Section 2.2.3**) could also be a potential source of error, if this leads to under or over estimation in comparison to estimates from full-day follows. Thus, I also computed mean daily energy intake using full-day follows only and compared this to the above values calculated using the 6-h minimum follow limit (monthly values for all age-sex classes were included to increase sample size). The difference was not significant ($mean_{FD} \pm SD = 1{,}242 \pm 405$ kcal/d; $mean_{6h} = 1{,}279 \pm 465$; paired t-test: $t = -1.468$, $df = 74$, p = NS) and values calculated using the different methods were very highly correlated ($r = 0.884$, $n = 75$, $p < 0.001$).

The above analyses also give no indication of the intra-age-sex-class, inter-individual variation in energy intake, which could potentially eclipse inter-age-sex-class variability. Unfortunately, low sample size for most individuals precluded formal statistical tests between individuals within age-sex classes. The largest sample size for comparison was between the two adult females, Indah and Cleopatra, who were followed in five of the same months. Mean values for these individuals over these five months (Indah ± SD: 1,242 ± 305 kcal/d; Cleopatra: 1,497 ± 868) did not differ greatly from, and lay either side of, the mean for all adult females in these five months (1,328 ± 570). Thus, while it is impossible to completely discount intra-class, inter-individual differences in energy intake as a confounding factor in the above analysis, it seems that any effect of this nature is likely to be relatively minor.

4.4 DISCUSSION

4.4.1 VARIATIONS IN DIETARY COMPOSITION AND ENERGY INTAKE

Based on the results of this study, variations in orang-utan dietary composition and energy intake exist as a result of fluctuations in fruit/flower availability, but not due to differences between age-sex classes. A similar lack of differences in the nutritional content of the diet and energy intake between flanged males and adult females in Gunung Palung was also observed by Knott (1999), when comparing data across the whole study period. This supports further the hypotheses that dietary quality does not differ between sexes (*$H_0$4.2*) and indicates that alternative hypotheses (Rodman, 1977, 1979; Wheatley, 1987; Hamilton and Galdikas, 1994) can be rejected. As noted by van Schaik *et al.* (2009c), age-sex class differences in diet may be so small because tooth morphology, rather than body size, determines food choice.

Importantly, dietary composition and weight/energy intake varied substantially between months for all age-sex classes, with energy intake in the lowest month being 3-4-times lower than the highest month, and SDs being ≥ half of the mean (**Table 4.7**). These variations in energy intake and variations in fruit/flower availability (**Chapter 3**) are much less than those reported for Gunung Palung (Knott, 1998, 1999). Hence, it might be expected that the documented effects of fruit availability on energy intake, behaviour and reproduction in Gunung Palung (Knott, 1998, 1999, 2001) would be less, or even non-existent, in Sabangau.

Orang-utan diet composition and energy intake in Sabangau *does* vary in relation to fruit/flower availability, however, and, furthermore, differences in the response of different age-sex classes to fluctuations in fruit/flower availability were also evident. For the population as a whole, daily and hourly energy intake increases with increased fruit/flower availability, as in Gunung Palung (Knott, 1998, 1999). This is explained by decreased percentage energy derived from bark and leaves, and increased energy derived from fruit (with a similar trend for flowers), as fruit/flower availability increases.

When different age-sex classes were considered separately, however, the only significant correlation between daily and hourly energy intake and fruit/flower availability was for flanged males. This is in contrast to observations in Gunung Palung, where energy intake and fruit availability were positively correlated in both flanged males and adult females (Knott, 1998, 1999). This leads to the rejection of $H_0 4.3$ and supports an alternative hypothesis, whereby orang-utan energy intake in non-masting forests is related to fruit/flower availability only in flanged males. Based on the results herein, it is not possible to formulate a definite explanation as to why this should be the case. If borne out by further investigation, however, trends in the data may provide some explanation. These trends indicate that, in males, percentage energy derived from fruit is positively related to fruit/flower availability. Similar trends did not exist for females, indicating that males may be less able than females to obtain sufficient energy through fruit during periods of shortage, leading to decreased energy intake for males during fruit-poor periods. As it is based merely on trends, however, this suggestion remains tentative.

An alternative explanation is that the energetic and social needs of the two sexes differ, not only on a general level, but also temporally (cf. van Schaik *et al.*, 2009c). Adult females with babies/infants are faced with a constant need to maintain high levels of energy intake: failure to do this, and consequent prolonged negative energy balance, could result in temporary cessation of ovarian cycling, and, when pregnant/lactating, aborted pregnancies, an inability to lactate, or, at the very least, reduced baby/infant growth due to reduced energy supply through the mother (cf. Wasser and Barash, 1983; Knott, 1999, 2001, see also Ellison, 1990; Ellison *et al.*, 1993; Ellison, 2003; Emery Thompson, 2005; Emery Thompson and Wrangham, 2008). This risk will increase the longer energy intake remains low, providing a very strong pressure on females to continually maintain energy-intake rate above critical levels. Thus, as long as fruit/flower availability does not become too low, a lack of relationship between fruit/flower availability and energy intake in females in Sabangau is not surprising. Conversely, males have less need to maintain consistently high levels of energy intake: provided periods of negative energy balance are not too long, shortfalls in one period can be recouped in the next period of high fruit/flower availability, when high-quality food is easier to find. Furthermore, the larger size of males means that they should be able to survive longer on their fat reserves than females (cf. Wheatley, 1982, 1987).

Thus, maintaining their position in the social hierarchy and competing for access to females may be more pressing demands for males, as a male may not be able to regain his position in the dominance hierarchy once displaced and missing an opportunity to mate with a cycling female could mean that opportunity is lost for another 7-9 years. This is

supported by observations in Suaq Balimbing of male-biased sex ratios at birth giving way to heavily female-biased sex ratios in adults, suggesting a net loss of males from the population as they mature (Singleton and van Schaik, 2002). While the possibility of differential dispersal from the study area could not be excluded in this study, observations of deaths resulting from fights between flanged males (Knott, 1999; van Schaik, 2004) and higher levels of leucocytes in male urine compared to females (Knott, 1999), suggest that differential mortality is a likely cause of this observation. Sexual selection by females for dominant males (Galdikas, 1981; Delgado and van Schaik, 2000; Utami *et al.*, 2002) and long-term "relationships" between individuals may also contribute towards this, with females selecting for males who can maintain dominance for long periods in spite of the energetic sacrifices this might entail (see also Knott, 1999). If males are sacrificing feeding in order to maintain their social status and avoid missing out on mating opportunities, with the hope of replenishing their reserves at a later date when fruit/flower availability is high and energy can be obtained quickly and easily, then a strong relationship between energy intake and fruit/flower availability should be expected.

Surprisingly, for all age-sex classes, the number of orang-utan fruit/flower stems bearing food appears to have a greater effect on dietary composition and energy intake than food-energy availability, indicating that the former may be the most relevant measure of fruit/flower availability for orang-utans. For example, when looking at percentage time spent feeding on food types (**Table 4.12**) and percentage energy derived from different food types (**Table 4.18**) together, food-energy availability produces one, orang-utan

fruit/flower availability five and orang-utan fruit availability four significant correlations. This indicates that the number/density of fruit/flower patches in the forest may be more important for orang-utans than patch size or total food-energy availability.

4.4.2 COMPARISONS WITH OTHER ORANG-UTAN STUDIES

Orang-utan dietary composition between sites has recently been compared by Morrogh-Bernard *et al.* (2009). Adding my figures to this data set, it appears that, in comparison to those mast-fruiting sites with irregular fruit supply (i.e., Kutai, Kinabatangan, Gunung Palung and Ulu Segama), mean percentage feeding time spent feeding on fruit in Sabangau is similar to or greater than in mast-fruiting forests, but, with the exception of Ulu Segama (which is the same as Sabangau), the minimum percentage time spent feeding on fruit is lower in Sabangau than in any of these sites. Flower consumption in Sabangau is notably higher than in any other site in which flowers have been recognised as a distinct food type (and is most probably much higher than in sites where flowers have not been recognised as a distinct food type, as presumably this lack of recognition is due to very low consumption levels). Mean percentage time spent feeding on bark is similar to or less than mast-fruiting sites, but the maximum percentage time spent feeding on bark is lower in Sabangau. For leaves, the mean for Sabangau is less than all mast-fruiting sites, and maximums in Sabangau are either similar to or lower than in mast-fruiting sites.

Published data to compare the nutritional content of the diet and energy intake between sites are only available from Gunung Palung (Knott, 1998, 1999). Comparisons of percentage total energy obtained through different food fractions in Gunung Palung (protein: ca. 7-26%, lipids: ca. 10-46%, NDF: ca. 3-21%, TNC: ca. 28-81%, based on Figure 4.16B in Knott, 1999) with those in **Table 4.8** indicate similar energy derived from protein between the two sites, but greater percentage energy derived from fibre, and lower percentage energy from energy-rich carbohydrates and lipids, in Sabangau. Correspondingly, weight and energy intake in Sabangau is similar to low-fruit periods, and much lower than fruit-rich periods, in Gunung Palung (see **Table 4.23** below). These comparisons indicate $H_0 4.1$ (orang-utan diet composition, nutrient and energy intake in Sabangau are comparable to orang-utans in masting habitats) cannot be accepted.

In Sabangau, as in other sites studied, orang-utan dietary composition varied in response to fluctuations in fruit/flower availability, though differences in mean dietary composition and energy intake between age-sex classes were not found. It has been recognised previously that age-sex class differences and responses to fruit/flower-availability fluctuations are not always consistent between sites (e.g., Rodman, 1988), and this is now bolstered with the availability of data on food nutrient/energy contents and nutrient/energy intake at more than one site. Thus, some of the observations made during this study are supported by other studies, whereas some are not. A summary of age-sex class differences in feeding behaviour between sites is given in **Table 4.21** and of responses to fluctuations in fruit/flower availability in **Table 4.22**. These data indicate that consistent differences between age-sex classes do not exist across sites. In addition,

Table 4.21 Comparison of age-sex class differences in feeding behaviour between sites.

Variable	Sabangau[1]	Gunung Palung	Kutai[2]	Tanjung Puting	Suaq Balimbing[3]
Time feeding/day	NS	NS (across all months)	Rodman - FLM >> AF Mitani – AF vs. UFM NS, AF > FLM (in three months)	Similar (FLM and AF)	AF > FLM and UFM
Percentage time spent feeding on food types	NS	NS (across all months[4])	Bark: FLM > AF Fruit: AF > FLM Invertebrates: AF > FLM	Bark: AF > FLM Invertebrates: FLM > AF Leaves: AF > FLM	Invertebrates: AF > UFM > FLM Fruit: FLM > UFM
Energy intake/d	NS	NS (across all months[5])	NA	NA	NA
Percentage energy derived from food fractions	NS	NS (across all months[6])	NA	NA	NA
Feeding rates	NS	NA	NA	NA	NA
Bout length	AF, FLM and UFM > NF[7]	NA	FLM > AF	NA	FLM > AF > UFM[8]

Abbreviations: AF = adult female; FLM = flanged male; NF = nulliparous female; NA = not applicable (data not available from that site); NS = not significant; UFM = unflanged male.

1. Paired analyses, pre-Bonferroni correction (as corrections of this nature have not been applied by most other authors, and many Type II errors probably exist even in the uncorrected test results, due to small sample size).
2. Both studies based on two-months' data for inter-sex comparisons; thus, results may not be very representative.
3. Comparison of simultaneous days yielded more significant differences than comparisons of overall means, as conducted in the other studies listed in this table. Sample size of simultaneous follows was too low to allow such analyses for Sabangau.
4. No differences found across all months, but some differences were found within months during the low-fruit period. Based on both partial and full-day follows, in two months, flanged male fruit-eating > females, and in two months adult female flower- and bark-eating < flanged male.

5. Flanged males > adult females in most months, but differences not significant. Some significant differences were found within months during the low-fruit period, when flanged male energy intake > adult female.
6. No differences found across all months, but some differences were found within months during the low-fruit period. Based on both partial and full-day follows, in two months, flanged male fruit-eating > females, and in one month adult female bark-, leaf- and flower-eating > flanged male.
7. For top-two food items in diet (*Mezzetia leptopoda/parvifolia* and *Diospyros bantamensis*). Kruskal-Wallis tests were performed, followed by Dunn's non-parametric multiple comparisons tests ($\alpha = 0.05$). Differences between nulliparous females and unflanged males were only significant for *M. leptopoda/parvifolia*.
8. For top food item in diet (*Tetramerista glabra*).

References: Sabangau, this study; Gunung Palung, Knott (1998, 1999); Kutai, Rodman (1977, 1979), Mitani (1989); Tanjung Puting, Galdikas and Teleki (1981); Suaq Balimbing, Fox *et al.* (2004), van Schaik *et al.* (2009c).

Table 4.22 Summary of responses to fluctuations in fruit/flower availability at different sites. +/-ve indicates the direction of significant correlations.

Variable	Sabangau	Gunung Palung	Kutai[1]	Ulu Segama[2]	Tanjung Putting	Suaq Balimbing	Ketambe
Time feeding/day	NS	FLM: high fruit > low fruit availability	Unclear[3]	High fruit > low fruit availability	N/A	NS	N/A
Percentage time spent feeding on food types	Bark: -ve Fruit: +ve Leaves: -ve	Bark and leaves: -ve Fruit: +ve	Fruit: +ve Bark, figs, leaves: -ve	Fruit: +ve Bark, leaves and vegetation: -ve	Flowers and fruit: +ve Other items: -ve	Fruit: high fruit > low fruit Vegetation[4]: low > high fruit	NS
Energy intake/day	+ve (FLM) NS (AF, NF, UFM)	+ve (AF r^2 > FLM)	N/A	N/A	N/A	N/A	No effect (inferred)[5]
Percentage energy derived from food types	Bark: -ve Fruit: +ve Leaves: -ve	Bark: -ve Fruit: +ve Inverts: -ve Leaves: -ve Pith: -ve	N/A	N/A	N/A	N/A	N/A
Percentage energy derived from food fractions	Protein: -ve	TNC: +ve Fibre: -ve Protein: -ve	N/A	N/A	N/A	N/A	N/A

Abbreviations: AF = adult female; NF = nulliparous female; FLM = flanged male; ; TNC = total non-structural carbohydrates; UFM = unflanged male.

1. Based on independent observations, not focal-animal follows.

2. Fruit availability not measured directly; “fruit” and “non-fruit” seasons compared, but not defined.
3. Percentage time spent feeding increased during *Durio* fruiting episode, but in other periods, feeding time increased as animals ate large amounts of bark and leaves.
4. Includes leaves, stems, shoots, epiphyte bulbs, thin vines, etc. Flowers were not distinguished as a separate category.
5. No traces of ketones (produced during periods of severe negative energy balance when fat reserves are metabolized, see below) found in 234 urine samples collected over 4 years during periods of varying fruit availability.

References: Sabangau, this study; Gunung Palung, Knott (1998, 1999); Kutai, Mitani (1989), Leighton (1993); Ulu Segama, MacKinnon (1974); Tanjung Putting, Galdikas (1988); Suaq Balimbing, Fox *et al.* (2004); Ketambe, Wich *et al.* (2006b).

consistent results cannot even be guaranteed in studies in the same site conducted at different times, as illustrated by the Kutai example.

Responses to fluctuations in fruit/flower availability, however, appear much more consistent between sites. When time spent feeding is affected by fruit/flower availability, the relationship is generally positive. In all sites other than Ketambe, which benefits from unusually high fig density/availability, the relative contribution of different food types to the diet varies according to fruit/flower availability, with fruit eaten preferentially when available, and bark and leaves (and at some sites invertebrates and pith) rising in importance when fruit is scarce. This leads to varying effects on energy intake, which correspond to differences in fruit/flower availability between the sites (**Chapter 3**). Fruit availability fluctuates widely in Gunung Palung, producing very large fluctuations in energy intake, and a strong relationship between energy intake and fruit availability. In Sabangau, fruit availability is lower and less widely fluctuating, leading to lower fluctuations in energy intake, and a weaker effect of fruit availability on energy intake (with no effect at all for females). In Ketambe, fruit availability is relatively high and constant and, hence, ketones have never been detected in urine (Wich *et al.*, 2006b). Despite the observations made herein that female energy intake is not related to food availability in Sabangau, these observations across sites are in general agreement with the hypothesis that fruit (/flower) availability is the primary factor limiting energy intake in orang-utans (though it should be remembered that all of these measures are imperfect, **Sections 3.4.1 and 4.2.3**).

4.4.3 ENERGY INTAKE AND METABOLIC REQUIREMENTS

The results of comparisons of energy intake and estimated TEE, in addition to data on ketones in urine, make it clear that the period included in this study represents a period of energetic shortfall for orang-utans in Sabangau. This builds on Knott's (1998, 1999) findings of orang-utans in Gunung Palung surviving a period of seven months of negative energy balance, and paints a grim picture for the health and survival of orang-utans in Sabangau. Estimates of TEE by different authorities do vary, however, and Knott's (1999) figures are higher than the majority of the TEE estimates for adult female and flanged male orang-utans calculated in **Table 4.2**. For example, using the formulas from Key and Ross (1999), from which estimated figures for TEE in chimpanzees in Kibale have been derived (Pontzer and Wrangham, 2004), and from Shetty (2005) for "typical sedentary" humans (activity levels in wild primates are often considered to be sedentary-moderate, NRC, 2003), wild orang-utan TEE is 1,420-1,448 (ca. 400 kcal/d lower than Knott's figures) for adult females and 2,591-2,642 kcal/d (ca. 600-650 kcal/d lower than Knott's figures) for flanged males. Compared to these figures, mean adult female energy intake in Sabangau is quite close to non-reproductive requirements, though mean flanged male energy intake is still markedly lower.

Responses to energy shortfalls are best understood in humans, in which, while mortality risk is clearly associated with malnutrition (e.g., Nieburg *et al.*, 1992; Young and Jaspars, 1995), many populations in developing countries have been observed to survive and reproduce successfully with average energy intakes below current recommendations

(Durnin *et al.*, 1973; Schofield and Lambert, 1975; Durnin, 1979; Edmundson, 1980; Waterlow, 1986; WFP, 2007). In India, for example, 31.2% of women suffer from chronic energy deficiency (Bharatu *et al.*, 2007), yet the country's population grew from 863 million in 1990-1992 to 1,050 million in 2001-2003 (WFP, 2007). In regions of India experiencing severe drought, reports have also indicated that 47% of the population may consume < 500 kcal/d and the entire population < 1,800 kcal/d, with "no reports of death through starvation" (Swaminathan *et al.*, 1967), though it is possible that deaths may have occurred and not been reported. The primary adaptation to energy shortfalls is to metabolise fat reserves, thereby reducing the effective shortfall and leading to decreased body weight and, consequently, energy requirements (Abbott *et al.*, 1988; Shetty, 1993; Leibel *et al.*, 1995; Kurpad *et al.*, 2005; NAS, 2005). In one incredible example, an obese man weighing 207 kg fasted for a 382 days under medical supervision (though water and vitamin pills were consumed, Stewart and Fleming, 1973). During this time, he lost 0.32 kg/d and, at the end of the fast, his weight had reduced to 82 kg. Although some medical effects were experienced during the fast, the patient suffered no long-term ill effects.

Wheatley (1982) estimates that the fat storage capacity of orang-utans is ca. 16%. Thus, based on a body mass of 86.3 kg (Markham and Groves, 1990), flanged males probably possess around 17.3 kg fat. If we assume the amount of energy stored in these fat reserves to be 87% (Newsholme and Start, 1973) and the energy yield/g fat to be 9 kcal/g (NRC, 2003), then the amount of energy stored in this fat is ca. 135,146 kcal; enough to last for 41 or 51 days without food, based on the TEE estimates of Knott (1999) and Key and Ross (1999), respectively. If flanged males possess 17 kg fat, then the minimum body

weight attainable after all fat is metabolised is ca. 70 kg. Based on Key and Ross' (1999) formula, this would reduce flanged male TEE to 2,259 kcal/d (exceeded in 2/19 months).

Furthermore, TEE in humans can be substantially reduced by decreased "spontaneous non-exercise activity" (i.e., fidgeting, which can raise energy expenditure compared to lying down by 54%, compared to a raise of only 4% from sitting without fidgeting, Levine *et al.*, 2000, and may increase daily energy expenditure by up to 12%, Garrow and Webster, 1984), and increased ergonomic efficiency (reductions in energy expended during sitting and standing by African and Asian subjects of 10-17% have been reported, see review in Shetty, 1993). Similar reductions in TEE have also been seen in primates subjected to long-term dietary restriction (Blanc *et al.*, 2003). Presumably, therefore, such adaptations in orang-utans could feasibly lower TEE by at least 10%. Based on Key and Ross' (1999) formulas, this would lower TEE to 1,303 kcal/d for a 38.7-kg adult female (excluding reproductive costs), and 2,378 kcal/d for a 86.3-kg flanged male. Including likely reductions in body mass through fat metabolism during periods of severe food shortage (ADF: 30 kg; FLM: 70 kg), a 10% decrease of this nature would result in a TEE of 1,077 kcal/d for adult females and 2,033 kcal/d for flanged males. With this minimum level of expenditure, energy intake would exceed requirements in 12/19 (63%) of months for adult females and 3/19 (16%) of months for flanged males (**Figure 4.8**).

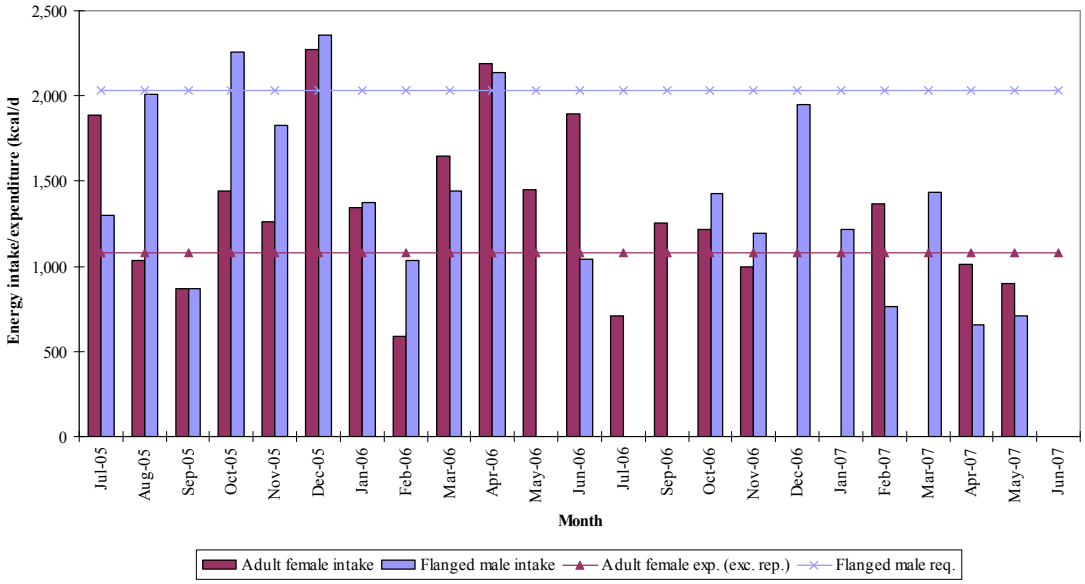


Figure 4.8 Monthly adult female and flanged male energy intake compared to minimum estimated energy expenditure. Energy intake calculated using a high NDF digestion coefficient (**Section 4.2.3**). Energy expenditure values represent minimum expenditures after weight loss through starvation, decreased energy expenditure through spontaneous non-exercise activity and increased ergonomic efficiency (see text for details).

In addition, there is reason to believe that the low energy intake levels seen in this study are a consequence of low overall fruit/flower availability during the study period. Orang-utan energy intake, weight intake, energy contents of most important foods and fruit availability in Sabangau during this study are all similar to Gunung Palung during periods of low fruit availability in between masts (Knott, 1998, 1999; Conklin-Brittain *et al.*, 2006), though Sabangau values are generally slightly higher (**Table 4.23**). The observation of lower energy intake in Sabangau than Gunung Palung is also supported by the proportion of fruit, which provides the highest energy returns, in the diet at the two sites. Although, on average, the figures are similar, the minimum contribution of fruit in the diet in Sabangau was lower than Gunung Palung (10 vs. 31% on a time spent feeding

Table 4.23 Comparison of energy and weight intake, food-energy contents and fruit availability between Sabangau and Gunung Palung National Park.

Variable	Sabangau	Gunung Palung (low fruit)	Gunung Palung (mast/high fruit)
Energy intake (kcal/day)[1]	1,378	1,252	6,151
Dry weight intake (g/day)[1]	572	468	2,262
Energy content top-five foods (kcal/100 g)[2]	270	245	328
Orang-utan fruit availability[3]	2.2-7.1	3-9	≤ 24

1. Values for adult females and flanged males combined. Energy intake data for Gunung Palung from Conklin-Brittain *et al.* (2006) using a high physiological fuel value (PFV) for fibre; dry weight intake data from Knott (1999).
2. Gunung Palung data (Knott, 1998, 1999) are only given using a low PFV for fibre; thus, Sabangau data are also given using a low fibre PFV. *Neesia* is excluded from the Gunung Palung data for this comparison.
3. Equivalent to the percentage of orang-utan fruit trees bearing fruit (**Table 3.1**).

and 20 vs. 41% on an energy-provided basis). Additionally, fruit comprised < 50% of the diet on a time spent feeding and energy provided basis on only 1/14 (7%) months in Gunung Palung (Knott, 1999), compared to 6/23 (26%) and 4/23 (17%) months, respectively, in Sabangau. Finally, the percentage of urine samples that tested positive for ketones in Sabangau during this study (19%) is higher than that generally recorded in Gunung Palung (6% from 1994-2003, Knott, pers. comm.), providing convincing evidence that this was a low-intake period. Analysis of urinary ketones in Sabangau from 2003-2005 (Morrogh-Bernard, submitted) also shows regular metabolism of fat reserves: ketones were detected in 9/12 months (the higher prevalence in this period than during the period included in my study is probably largely due to a greater number of samples collected each month by Morrogh-Bernard). The only period when ketones have

consistently been absent from orang-utan urine in Sabangau was during/just after the period of highest fruit/flower availability recorded to date (Morrogh-Bernard, submitted).

The contention that the low energy intake rates observed in this study are a consequence of low food availability during the study period is supported by the inclusion of daily energy intake data for Sabangau orang-utans during the period September 2003-June 2005 (Harrison *et al.*, in prep; Morrogh-Bernard, submitted). Mean energy intake using the high NDF PFV increased to 1,401 kcal/day for adult females and 1,811 kcal/d for flanged males during the four years from September 2003-June 2007, with maximum energy intake increasing to 10,781 kcal/day. Energy requirements were also met in many more months (36% for adult females, excluding reproduction, and 13% for flanged males, based on Knott's estimates of low-fruit TEE). Anecdotal observations support this: while flanged male condition appeared to become increasingly poor throughout the period included in this study (pers. obs.), observations made between the cessation of this study and the time of writing indicate that flanged male orang-utans are now gaining weight and improving in condition (B. Buckley, pers. comm.; pers. obs.).

Paradoxically, despite the obvious energetic difficulties faced, orang-utans in Sabangau appear to be comfortably meeting both protein and fibre requirements. Presumably, both these observations are a result of the relatively low carbohydrate content, and relatively high protein and fibre contents (particularly of fall-back foods), of orang-utan foods in Sabangau. Finally, these analyses support the use of the higher PFV for NDF (**Section**

4.2.3) as, without this extra energy derived from fibre, it is difficult to envisage orang-utans surviving this period of shortage.

4.4.4 COMPARISONS WITH OTHER GREAT APE STUDIES

The most comprehensive data on nutritional content of chimpanzee diet, and the only data on energy intake, exist for the Kanyawara (Conklin-Brittain *et al.*, 1998, 2006) and Ngogo (Potts, 2008) sites, Kibale National Park, Uganda. For gorillas, data on nutritional content of the diet exist for *G. gorilla gorilla* in Bai Hoku, Dzanga-Ndoki National Park, Central African Republic (Popovich *et al.*, 1997; Remis *et al.*, 2001), Lopé, Gabon (Rogers *et al.*, 1990) and Campo, Cameroon (Calvert, 1985), and for *G. beringei* in Karisoke**,** Rwanda (Waterman *et al.*, 1983; Rothman *et al.*, 2007) and Bwindi Impenetrable National Park, Uganda (Rothman *et al.*, 2006; Rothman *et al.*, 2008b). Data on energy intake are available only from Bai Hoku (Masi, 2007) and Bwindi (Rothman *et al.*, 2008b). Nutrient content data of bonobo foods has been collected in Lamoko (Malenky, 1990; Malenky and Wrangham, 1994) and Salonga National Park, Democratic Republic of Congo (Hohmann *et al.*, 2006), but, to date, no published data on energy intake are available. The first data on gibbon (*H. agilis*) nutritional and energy intake were collected in Sabangau simultaneously to the data collected in this study (Cheyne and Harrison, unpublished). These data have not been fully analysed yet, but will form the topic of planned future publications. Key observations for the different populations studied are given in **Table 4.24** (not all gorilla studies listed above provided summary data, and these have not been included in this comparison). The concentrations of

Table 4.24 Comparison of nutritional content of diet, energy intake and responses to fluctuations in fruit/flower availability in apes. See text for references.

Variable	Orang-utans (Sabangau)[1]	Orang-utans (Gunung Palung)[2]	Chimpanzees (Kanyawara /Ngogo)[3]	Bonobos (Salonga)[4]	Gorillas (Bwindi)	Gorillas (Bai Hoku)[5]
Mean energy intake (kcal/day)	1,421 (flanged males) 1,335 (adult females)	3,535 (mean) 1,252 (low fruit) 6,151 (high fruit)	2,340	NA	9,211 (silverbacks) 8,186 (adult females)	10,853 (silverbacks) 23,510 (adult females)
Energy intake influenced by fruit/flower availability[6]?	No (females) Yes (males, +ve)	Yes (females and males, +ve)	Variable	NA	No seasonal variation detected (food availability not measured)	No
% protein in foods	10.1 (OM) 7.6 (DM)	NA	NA	8.3 (DM)	2-28 (DM)	12.68 (DM)
% TNC in foods	33.4 (OM) 42.97 (DM)	NA	NA	NA	<1-50 (water-soluble carbohydrates, DM)	NA
% lipid in foods	3.3 (OM) 2.7 (DM)	NA	NA	6.6 (DM)	N/A	NA
% NDF in foods	53.3 (OM) 42.92 (DM)	NA	NA	26.8 (DM)	21-88 (DM)	61.63 (DM)
% ME from protein	15	ca. 8-26 (ME_L)	9.5 (% field-dry weight)	NA	NA	24 (food composition)
% ME from TNC	38	ca. 28-80 (ME_L)	53.7[7] (% field-dry weight)	NA	NA	16 (food composition)
% ME from lipid	13	ca. 11-46 (ME_L)	2.5 (% field-dry weight)	NA	NA	3 (food composition)

Variable	Orang-utans (Sabangau)[1]	Orang-utans (Gunung Palung)[2]	Chimpanzees (Kanyawara /Ngogo)[3]	Bonobos (Salonga)[4]	Gorillas (Bwindi)	Gorillas (Bai Hoku)[5]
% ME from NDF	34	ca. 2-22 (ME_L) 36.9 (ME_H)	24 (% ME_H) 33.6 (% field-dry weight)	NA	NA	57 (food composition)
Fruit availability[8]	2.2-7.1% (OU) 1.6-5.8% (all)	3-24% (OU)	0.3-8.2% (C)	Low, with low variability	23-57% (G)	4-72% (all)

Abbreviations: all = all fruit; C = chimpanzee fruit; DM = dry matter; NA = data not available; NDF = neutral detergent fibre; OM = organic matter; OU = orang-utan fruit; PFV = physiological fuel value; TNC = total non-structural carbohydrates.

1. Using the high PFV for NDF (ME_H, see **Section 4.2.3**). Percentage nutrient contents in foods is best presented as percentage OM (as this excludes ash, see **Section 4.2.2**), but values have also been expressed as percentage DM, in order to compare with gorilla studies that where data have been expressed data in this way.
2. Energy intake values quoted use the high PFV for NDF (ME_H), given by Conklin-Brittain *et al.* (2006). Percentage ME provided by different food fractions uses the low PFV for NDF (ME_L) given in Knott (1999), with the exception of NDF, for which figures using the high NDF PFV are from Conklin-Brittain *et al.* (2006).
3. Using the high PFV for NDF (ME_H).
4. For fruits only. Sample size of foods included in Hohmann *et al.* (2006, n = 47 fruit species) was larger than in Malenky (1990) and Malenky and Wrangham (1994, n = 19 fruit species); thus, the former data were used for comparison.
5. Data on percentage metabolisable energy provided by different food fractions is from analysis of 31 commonly-consumed foods and does not take into account the proportion of these foods in the diet (Popovich *et al.*, 1997). Figures for daily energy intake are likely over-estimates, for a number of reasons (Masi, 2007).
6. All measures of fruit/flower availability in Sabangau; orang-utan fruit availability in Gunung Palung (see **Table 3.1** for definitions).
7. Including both TNC and water-soluble carbohydrate, which was not recorded in this study and, hence, would have been included in the TNC fraction.
8. Percentage stems with fruit (see **Section 3.4.3** for details and **Table 3.1** for definitions). Sabangau, Bai Hoku and Salonga include both ripe and unripe fruits; Gunung Palung, Kanyawara and Bwindi include only ripe fruits.

different food fractions in mountain gorilla diets in Karisoke, Parc National des Volcans, Rwanda were very similar to those in Bwindi, despite the lower levels of frugivory and greater reliance on herbaceous vegetation by gorillas in Karisoke (Rothman *et al.*, 2007). Unfortunately, separate data for males and females are not given in all studies, and so male-male and female-female comparisons are not possible at this stage. As fruit availability for orang-utans in Sabangau and chimpanzees in Kanyawara is quite similar (**Section 3.4.3**), similar effects of fruit availability on ape diet and behaviour at these two sites might be expected.

This preliminary comparison indicates that, as a whole, gorilla energy intake > orang-utans > chimpanzees, as expected from size differences between the species. Orang-utan energy intake in Sabangau during this study was lower than chimpanzees in Kanyawara, but, when using data from September 2003-2007 (Harrison *et al.*, in prep; Morrogh-Bernard, submitted), this difference becomes much smaller (ca. 500 kcal/day) and, when using data from September 2003-June 2005 alone, Sabangau orang-utan energy intake is almost identical to chimpanzees (using the high NDF PFV). Although data are not directly comparable, they indicate that percentage ME obtained through carbohydrates and lipids for orang-utans > gorillas, and percentage ME obtained through protein and and fibre for orang-utans < gorillas, in line with observations of greater folivory and lower overall dietary quality for gorillas than orang-utans (e.g., Knott, 2005). Chimpanzee diet in Kanyawara and bonobo diet in Salonga appear to be of higher quality (lower fibre and higher carbohydrate) than both orang-utans and gorillas.

Changes in dietary composition in chimpanzees and gorillas in response to variations in fruit availability are well documented, with increased fruit consumption when available, and increased consumption of other foods when fruit is scarce (e.g., Remis, 1997b; Tutin *et al.*, 1997; Conklin-Brittain *et al.*, 1998; Remis *et al.*, 2001; Basabose, 2002; Yamagiwa *et al.*, 2005), though chimpanzee fruit consumption is not always positively correlated with fruit availability, indicating that chimpanzees continue to seek fruits even when they are scarce (Kuroda *et al.*, 1996; Yamagiwa *et al.*, 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006b). As for orang-utans in Ketambe (which varies relatively little in terms of fruit availability, due to very high fig densities) and adult female orang-utans in Sabangau, this would appear to enable these apes to maintain relatively constant levels of energy intake in the face of fluctuations in fruit availability.

While chimpanzees have been reported to lose weight during periods of fruit scarcity (Uehara and Nishida, 1987), provisioning may have affected these populations and ketones have never been detected in urine (Kelly *et al.*, 2004; Knott, 2005). In Kanyawara, chimpanzee daily energy intake was not correlated with fruit availability in 1992-1993 (Conklin-Brittain *et al.*, 2006), but foraging efficiency (i.e., net energy return *per* feeding/travelling bout, Potts, 2008) was correlated with basal fruiting area in 2006, when fluctuations in fruit availability were greater (K. Potts, pers. comm.). Similarly, foraging efficiency and fruit availability were not significantly correlated in Ngogo (K. Potts, pers. comm.), where mean fruit availability is higher, and variability in fruit availability much less, than Kanywara (Potts, 2008).

Thus, the situation in chimpanzees appears broadly comparable to that in orang-utans, in that the larger the fluctuations in fruit availability, the greater the effect of these fluctuations on energy intake. Lower fluctuations in the availability of bonobo foods compared to chimpanzees, and a lack of differences in diet composition between months (Malenky *et al.*, 1994; Malenky and Wrangham, 1994; White, 1998) suggest that bonobo energy intake is also likely to be influenced little, if at all, by fluctuations in fruit availability. To date, the only documented effect of fruit availability on energy intake in female apes is for orang-utans in Gunung Palung, where fruit availability fluctuates widely, as a result of mast-fruiting events. Effects on males have been observed in orang-utans in both Gunung Palung and Sabangau. Thus, a lack of influence of fruit availability on energy intake may be the norm for all apes, and especially for females, with the exception of orang-utans in mast-fruiting habitats. Effects in males in habitats with lower fluctuations in fruit availability may be expected if, as suggested herein, males are sacrificing energy acquisition for social/reproductive considerations, with the aim of recouping energy reserves when food availability is high. This suggestion is in agreement with Knott's (2005) hypothesis that apes should attempt to maximise energy intake in habitats with unpredictable future fruit/flower availability and, hence, potential to readily meet energy requirements, but not in habitats where future fruit/flower availability is more predictable (where maximisation may not be necessary).

4.5 SUMMARY

1. Data on orang-utan dietary composition, feeding rates and the nutrient composition of foods eaten in Sabangau were collected over a two-year period using standard methods, enabling the nutrient content of the diet and energy intake to be calculated.
2. This is the first time that these data have been collected for orang-utans in a non-masting habitat, and important differences in diet composition and energy intake are evident between Sabangau and the masting forests of Gunung Palung, which can be related to differences in fruit availability between the two sites.
3. Similar to other populations studied, including those in masting habitats, fruit made up the majority of the diet (69%), followed by leaves (10%), flowers (8%), invertebrates (8%), bark (4%), pith (2%) and "other" foods (< 1%), on a percentage-time-spent-feeding basis (the same order was found on a percentage-energy-provided basis, but invertebrates and bark were reversed).
4. Carbohydrates and fibre were the most important energy sources (providing 38 and 34% of total metabolisable energy, respectively), but substantial amounts of energy were also provided by proteins (15%) and lipids (13%). Orang-utans would appear to be meeting requirements for all macro-nutrients for which requirements/ recommendations have been determined.
5. Orang-utan energy intake in Sabangau was low for all age-sex classes, and especially for flanged males, both in comparison to theoretical requirements and estimated expenditure levels. Daily energy intake was similar to Gunung Palung during periods of low fruit availability in between masts. This is explained by similarly low levels of

fruit availability and energy content of most important food items between Sabangau and fruit-poor inter-mast periods in Gunung Palung.

6. Ketones were also detected regularly in urine, indicating regular periods of starvation. Orang-utans are suggested to have coped with this low level of energy intake by metabolising fat reserves, and reducing energy expenditure through decreased body weight and "non-exercise activity", and increased ergonomic efficiency. The low energy-intake rates documented are thought to be due primarily to unusually low fruit/flower availability during the study period.
7. When controlled for fluctuations in food availability, differences in overall dietary composition and energy intake between age-sex classes were not significant.
8. As expected, energy intake was positively related to fruit/flower availability for the population as a whole and for flanged males, but not for females or unflanged males. This is suggested to be a result of differences in relative energetic and social demands between the sexes.
9. Comparisons with other orang-utan populations studied reveal that, with the exception of sites with consistently very high fruit availability, fruit (and sometimes flowers) is preferentially consumed when available, and bark and leaves (and sometimes invertebrates and pith) rise in importance when fruit is scarce. Available data support the hypothesis that the magnitude of fruit availability fluctuations determines the relationship between fruit availability and energy intake, and that effects on females are seen only in habitats with very large fluctuations in fruit availability, whereas effects may be seen on males in habitats where food availability fluctuates less widely.

10. This hypothesis appears to hold true for apes as a whole: significant relationships between fruit availability and have energy intake have yet to be observed in African apes, which benefit from more consistent levels of fruit availability (Chapter 3). In turn, this supports the hypothesis that apes should attempt to maximise energy intake in habitats with unpredictable future fruit/flower availability, but not in habitats where future fruit/flower availability is more predictable.

5. FOOD SELECTION

5.1 INTRODUCTION

A large number of researchers have studied food selection in primates, including orang-utans (e.g., Milton, 1979; McKey *et al.*, 1981; Waterman *et al.*, 1983; Milton, 1984; Calvert, 1985; Gautier-Hion *et al.*, 1985; Marks *et al.*, 1988; Leighton, 1993; Hamilton and Galdikas, 1994; Conklin-Brittain *et al.*, 1998; Reynolds *et al.*, 1998; Plumptre, 1995; Wrangham *et al.*, 1998; Dominy *et al.*, 2001; McConkey *et al.*, 2002, 2003; Chapman *et al.*, 2004; Hohmann *et al.*, 2006). Many of these have compared various food properties between food types, or items that are eaten against those that are avoided (e.g., Milton, 1979; Waterman, 1983; Hamilton and Galdikas, 1994; Reynolds *et al.*, 1998). While these approaches have merit, in order to understand more fully the factors influencing primate food selection, they should be accompanied by detailed analysis of the factors influencing the relative preference of food items consumed, i.e., what makes some food items highly preferred and others less so? Comparatively few authors have attempted such analyses in wild primates, but important insights have been obtained by those that have (*Cebus apella*: Janson *et al.*, 1986; *Lagothrix lagothricha lugens*: Stevenson, 2004; gibbons: McConkey *et al.*, 2002; mountain gorillas: Plumptre, 1995; Ganas *et al.*, 2008; western gorillas: Calvert, 1985; orang-utans: Leighton, 1993).

Discussion of the distinctions between preferred *vs*. fall-back foods (FBF) and the influence of these on primate behaviour and evolution have, rightly, been prominent in the primate literature. FBFs are generally regarded as being foods of poorer nutritional

quality and high abundance that are eaten when preferred foods are unavailable, and their consumption is thought to have important influences on primate biology (see review in Marshall and Wrangham, 2007). Marshall and Wrangham operationally define FBFs as "*foods whose use is negatively correlated with the availability of preferred foods*" and preferred foods as "*foods that are selected disproportionately often relative to their abundance within the population's habitat"*. In light of this, it is necessary to highlight the distinction between importance and preference of foods; while the former is simply a measure of consumption, the latter is a measure of consumption in relation to availability. Thus, high importance in the diet is not necessarily indicative of high preference, and a FBF can also be a staple/important food, if preferred foods are unavailable most of the time (Marshall and Wrangham, 2007).

FBFs are generally widely available, but difficult to process, and, hence, offer relatively low energetic returns (Marshall and Wrangham, 2007; Vogel *et al.*, 2008b). Preferred foods are typically nutrient/energy rich and, hence, are less abundant in the environment (as they are expensive for plants to produce), but are easy to process and offer high energetic returns (Marshall and Wrangham, 2007). Based on this, Marshall and Wrangham suggest that the evolutionary importance of FBFs applies more to processing adaptations, whereas the evolutionary importance of preferred foods applies more to harvesting adaptations, and that reliance on preferred *vs.* FBFs has differing effects on primate socio-ecology. Furthermore, as has been demonstrated for preferred food types (e.g., Leighton, 1993; McConkey *et al.*, 2002), it is plausible that some FBFs may be more/less preferred than others, and the factors that determine this may, or may not, be

the same as for preferred foods. Thus, differences in food-selection criteria may exist between preferred and FBFs, and identifying these differences is important for understanding primate socio-ecology. Despite this, to date, detailed analyses of traits influencing primate food selection have generally been restricted to preferred foods (i.e., fruit, Janson *et al.*, 1986; Leighton, 1993; McConkey *et al.*, 2002; Stevenson, 2004; but see Ganas *et al.*, 2008).

It is necessary to reiterate here the distinction between food *types* (i.e., fruit, flowers, leaves, etc.) and food *items* (e.g., the flower of *Madhuca mottleyana*, the bark of *Dyera lowii*, etc., see **Section 2.2.5**). According to the definitions above, it is possible that preferred/FBFs may exist at both the level of food type and food item. Thus, for example, when compared to other food types, fruit may be the preferred food, but, among fruits, some may be highly preferred, and some may be eaten only when other more-preferred fruits are unavailable and, hence, constitute FBFs. This is thought to be the case for figs in Sumatran orang-utans (Wich *et al.*, 2006b), gibbons (Marshall, 2004; Marshall and Leighton, 2006) and chimpanzees (Wrangham *et al.*, 1991, 1993; Malenky *et al.*, 1994; Wrangham *et al.*, 1996; Tweheyo and Lye, 2003), and for some non-fig fruits in chimpanzees (Furuichi *et al.*, 2001) and gorillas (Doran *et al.*, 2002). Such between-item within-type distinctions may, or may not, be due to the same properties that govern distinctions between preferred/FBF types.

Researchers have long considered fruit to be the preferred food type for orang-utans, with leaves and bark constituting the major FBFs when fruit are not available (MacKinnon,

1974; Rodman, 1977; Galdikas, 1988; Rodman, 1988; Leighton, 1993; Knott, 1998, 2005; Vogel *et al.*, 2008b). By analysing the nutrient contents of orang-utan foods in Gunung Palung, Knott (1998, 1999) found that fruit has the highest energy content, whereas leaves and bark are low in energy, explaining the orang-utans' strong preference for fruit.

Leighton (1993) analysed fruit selectivity in Kutai in relation to a number of different chemical and non-chemical variables, and found that orang-utans selected food patches providing large crops of food. Among figs, where morphological differences between species are minimal, Leighton's analysis revealed that crop size, pulp dry weight/fruit and percentage carbohydrate (a correlate of energy content) positively influenced selection, and that selection was depressed by high phenolic contents. These results led Leighton to conclude that "orang-utan foraging decisions are strongly influenced by the meal size expected from a feeding visit (i.e., by patch size), that tannins and other toxins deter feeding, and that energy content, rather than the protein content, of foods is important in diet selection" (p 257).

In conjunction with Knott's (1998, 1999) observations that orang-utans in Gunung Palung were in positive energy balance during times of plentiful fruit supply and in negative energy balance when fruit was very scarce, this implies that orang-utans employ a strategy of maximising energy intake to build up fat reserves in times of plenty by consuming large quantities of high-energy fruit, in order to see them through the lean periods that will inevitably follow (Wheatley, 1982, 1987; Leighton, 1993; Knott, 1998,

1999). Thus, orang-utans appear to be attempting to maximise their rate of energy intake, whilst operating under the constraint imposed by an inability to tolerate large quantities of toxins (Leighton, 1993). As shown in **Chapters 3** and **4**, however, large differences in orang-utan fruit availability, diet composition and, importantly, energy intake exist between sites. Thus, differences in food-selection criteria between sites may also exist, particularly between masting sites, where fruit availability and energy intake fluctuate widely and are strongly related (i.e., the sites included in Leighton and Knott's studies), and non-masting sites, such as Sabangau (where energy intake is influenced less by food availability, **Chapter 4**).

To date, the only assessment of orang-utan food selection for non-fruit items is that of Hamilton and Galdikas (1994), who compared a variety of chemical properties between eaten and uneaten foods (defined as foods that were present in the same tree as eaten foods, but were not eaten) in Tanjung Puting National Park, Central Kalimantan. Statistical analyses were only possible for leaves, and these revealed that the protein content of leaves eaten was greater than those not eaten, and that a trend existed towards a higher protein/fibre ratio in eaten items (though this was not statistically significant). Hamilton and Galdikas also note that, due to the large amounts consumed, fruit may provide a substantial amount of dietary protein, that protein and tannins may have been important in the avoidance of two fruit species, and that fibre did not appear important in fruit selection. Although preliminary, these findings do suggest that differences in food-selection criteria may exist between food types and, potentially, study sites.

Thus, there are four aims in this chapter: (1) to attempt to identify preferred/FBF *types* and whether preferred/FBF *items* can be identified within these food types (e.g., do fall-back fruits exist?), (2) to assess differences between non- and real foods within food types, (3) to assess differences between preferred foods/FBFs, and (4) to assess the factors governing food-item preference rankings within food types, in order to identify differences in selection criteria between preferred/FBFs. In light of this, and the over-arching null hypothesis expounded in **Section 1.1** (i.e., that observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats, Leighton, 1993; Knott, 1998, 1999), the following null hypotheses were tested in this chapter:

$H_0 5.1$: Fruit is the preferred food, and bark, leaves, pith and invertebrates FBFs, for orang-utans in Sabangau.

$H_0 5.2$: Figs serve as fall-back fruits for orang-utans in Sabangau. Leighton (1993) showed that fig consumption was not related to fig availability in Kutai, but the necessary correlations to establish whether figs were true FBFs (i.e., fig consumption vs. preferred food (i.e., non-fig fruit) availability) were not performed. Studies on Sumatran orang-utans, Bornean agile gibbons and African apes suggest that figs frequently function as FBFs for apes (see above).

$H_0 5.3$: Orang-utan food selection follows the predictions of optimal foraging theory (Stephens and Krebs, 1986), i.e., food selection is geared towards maximising the rate of energy intake. Specifically (a) energy intake rate is greater in real foods than in non-foods, (b) energy intake rate is greater in preferred foods than

FBFs, and (c) food preference ranks within specific food types are determined primarily by the expected rate of energetic returns from the food item.

5.2 METHODS

Methods for collection of data on the availability of orang-utan foods in the forest and dietary composition are described in **Sections 3.2** (see definitions in **Table 3.1**) and **4.2**, respectively (see also **Sections 2.2.5-6**). Methods for calculating food-item preference/ selectivity and multi-variate techniques for analysing selection criteria were similar to those used by previous researchers (Leighton, 1993; McConkey *et al.*, 2002; Stevenson, 2004; Ganas *et al.*, 2008), with some modifications. In order to assess preference of individual food items within food types, selectivity was calculated by comparing the relative abundance and consumption of food items using a selectivity index.

5.2.1 IDENTIFYING PREFERRED AND FALL-BACK FOODS

In this study, I follow the definitions of preferred and FBFs offered by Marshall and Wrangham (2007), in which preferred foods are "selected disproportionately often relative to their abundance within the population's habitat" and FBFs are "foods whose use is negatively correlated with the availability of preferred foods". Implicit within these definitions, establishing preferred foods is a necessary pre-requisite for establishing FBFs. Positive correlations between a food type/item's consumption and its availability do not in themselves prove preference, as correlations may not be found because the food

type is eaten in high proportion despite its low availability, or because availability of the food is unpredictable and, hence, untrackable, or ubiquitous and, hence, does not require tracking (Hemingway and Bynum, 2005). Furthermore, such a relationship is also compatible with neutral selection, i.e., where consumption is directly related to availability.

Thus, classification of a food type as preferred was based on comparison of monthly percentage time spent feeding on a food type (relative consumption) against the monthly percentage of total available food stems composed of that food type (relative availability) of each food type. The food type was classified as preferred if relative consumption was significantly greater than relative availability. FBF types were then identified through significant negative correlations between their relative consumption and the relative availability of the preferred foods identified through the above tests. The same principle applied when considering the question of whether figs are fall-back fruits for orang-utans in Sabangau ($H_0 5.2$).

5.2.2 CALCULATING FOOD ITEM SELECTIVITY RANKS

5.2.2.1 Sample Composition and Calculation of Relative Consumption and Availability

In order to encompass temporal variations in the availability, consumption and, hence, preference of food items consumed during the study period, food selectivity ranks were

calculated monthly throughout the study period, using monthly figures of the relative availability and consumption of individual food items. Relative consumption of a food item was calculated simply as the minutes spent feeding on food item *i* in a month / total minutes spent feeding on *all* food items in that month. The ratio of minutes spent feeding on food item *i* / total minutes spent feeding on all food items *of that food type* was not used, as this could create bias towards less-preferred items that were eaten in large quantities during periods where more-preferred food types were unavailable. For example, consider a case where there was only one less-preferred fruit *a* available in a month, and total fruit consumption was low, e.g., 10% of the total diet. Fruit *a* would comprise only 10% of the diet overall, but would comprise 100% of time spent feeding on fruit. Hence, selectivity for that month would be low (as is true for this item) if using time spent feeding on all food items as the denominator, but would be very (erroneously) high if using time spent feeding on just fruit as the denominator.

This method differs from Leighton (1993) and McConkey *et al.* (2002), who used the number of "independent" observations of feeding on item *i* / the total number of feeding observations as their measure of relative consumption. Statistically, Leighton's and McConkey *et al.*'s method is certainly superior, as each observation is independent of the last, but there are three reasons why I considered percentage time feeding to be preferable for this study. Firstly, Leighton's data were collected during vertebrate censuses and, hence, were truly independent, but my data were collected from protracted focal-animal follows of the same individual, and, as a result, can never attain full independence. Secondly, Leighton's and McConkey *et al.*'s measure may be liable to bias towards

species containing relatively little food/patch, as animals will be able to spend less time feeding in these trees and, hence, will have to visit more trees of this species to fulfill their dietary requirements than for tree species with larger amounts of food available/patch. Finally, as discussed in **Chapter 4** and by Knott (1999), percentage feeding time is the most accurate reflection of foraging effort, which is what must ultimately be assessed. The number of feeding observations is a poor indicator of this, as, e.g., a snack-feeding bout of one-minute will be scored the same as a major four-hour feeding bout. Thus, I consider percentage time spent feeding to be the best indicator of foraging effort. It is worth noting, however, that, due to the focal-animal data-collection techniques employed in this study, the data are liable to suffer from pseudo-replication, as feeding bouts observed on the same individual on the same day are treated as independent, which they are not (Marshall and Wrangham, 2007).

Relative abundance was calculated separately for fruit pulp, fruit (all parts), fruit and flowers combined (as the analyses in **Section 5.3.1** support classifying both as preferred food types), bark and leaf species. The low number of flower species included in the sample prohibited analysis of flowers as a separate category. For fruit, flowers and bark, only trees ≥ 10 cm DBH and figs/lianas ≥ 3 cm DBH were included in the analysis. For leaves, however, trees 6-10 cm DBH were also included, as 20% of leaf-feeding bouts where DBH was recorded were in trees of this size (30% of bouts were in trees < 6 cm DBH, but trees this small could not be included in the productivity plots for logistical reasons, i.e., the large numbers of these trees). For fruit and flowers, relative abundance = the number of stems *i* with fruit or flower / total number of stems of all real-fruit/flower

species with fruit or flowers in the plots (data for productivity sub-plot 1 were extrapolated from sub-plot 0, in order to increase sample size of fruiting/flowering trees, see **Section 3.2.2**). Trees with both fruit and flowers were counted twice, as these represented different food items in the analysis. Unripe and ripe fruits were combined, as were open and closed flowers, because the ability of observers to distinguish these during productivity surveys was limited (**Section 3.2.2**).

For bark, relative abundance = the number of stems *i* / total number of stems of all real-bark species in the plots (data from sub-plot 0 only, as sufficient numbers of stems existed that there was no need to introduce the potential error associated with extrapolations from sub-plot 1). Leaf abundance was assessed through both the number of stems with new leaves (as, in common with other sites, e.g., Tanjung Puting, Galdikas, 1988, most leaf-feeding bouts were on new leaves) and total stem density (i.e., including mature leaves, which are also eaten in many tree species; sub-plot 0 only). This latter method may be more reliable as, not only are mature and half-mature leaves often eaten, but distinguishing leaf maturity stages during productivity surveys can be difficult, and is potentially unreliable (Vogel, pers. comm.).

Some species eaten occur at low density in the forest and did not appear in the productivity plots. For these species, a value of "one" (i.e., the lowest possible value) for availability was inserted for those months in which this item was eaten, and availability was recorded as zero in all other months. This differs from Leighton (1993) and McConkey *et al.* (2002), who included only tree species common in the forest in their

analyses. Assessing relative abundance of rare trees, as I have done, is prone to error and could artificially elevate preference values for these items, as (i) there will never be any months in which the item is recorded as available but not eaten and, hence, has a selectivity value of "zero", and (ii) the actual availability of this item in the forest will be < 1/ha. Despite this, retaining these species in the analysis was considered preferable as, if an item is both rare and eaten in any quantity then, by definition, it must be highly preferred. Hence, excluding these rare species from the analysis is likely to result in the exclusion of some of the most highly-preferred items present in the forest. Furthermore, it is unlikely that many rare items that are not preferred will have been eaten and, hence, included in the analysis. Thus, the amount of error introduced by using this approach should be negligible.

As the majority of species were unavailable in most months, it was necessary to calculate average selectivity for a food item based on the monthly values for which selectivity could be calculated. An average was not taken across all months as, obviously, if an item is not available, it cannot be eaten; hence, both availability and consumption are zero, and selectivity cannot be calculated. Monthly selectivity values also cannot be used as the dependent variable in analyses of selection criteria (i.e., if selectivity values for an item are calculated for six months, this item will be represented six times, once for each month). This is because the selectivity value for an item in a given month will depend on the other foods also available in that month. For example, a non-preferred food would normally have a low selectivity value, but might have a very high value if there were no more-preferred foods available in a month. Thus, including this high and atypical value

for this item in the analysis could confound results and an average over as many months as possible is preferable.

Due to the highly-plausible possibility of differences in selectivity between age-sex classes, due to differences in body size and reproductive demands, all analyses were conducted separately for each age-sex class. Analyses were not performed for unflanged males, due to small sample size (n = 11 months). This separation of age-sex classes is supported by comparisons of food-preference ranks between age-sex classes (see **Table 5.6** below and **Appendix II**).

5.2.2.2 Preference Indices

Preferred foods are eaten more than would be expected based on their availability. Thus, the simplest method for calculating preference/selectivity of a food item (S_i) is the ratio f_i / a_i, where f_i = the relative proportion of item i in the diet, and a_i = the relative proportion of item i in the environment (Ivlev, 1961, referred to hereafter as "Ivlev's forage ratio"). This index has been used for determining fruit preference in both orang-utans (Leighton, 1993) and gibbons (McConkey *et al.*, 2002).

Many other methods for calculating food item preference have also been developed, however, and, although most produce very similar results, certain methods are more suitable for certain datasets, and there are advantages and disadvantages to each method (Lechowicz, 1982; Vogel, pers. comm.). Ivlev's forage ratio, for example, takes a value

of 1 for random feeding (i.e., no selection and an item is eaten in direct proportion to its abundance), and has a range of 0-1 for unpreferred items and 1-∞ for preferred items. This asymmetry is undesirable, as, depending on the direction of the change, identical changes in f_i or a_i will produce changes in S_i of differing magnitudes. A further undesirable characteristic of this index, which is of great importance in this study, is that quantitative comparisons between forage ratios derived from samples differing in relative abundances (i.e., different months, when different numbers of food items are available) are inappropriate (Lechowicz, 1982). Thus, this index would also be unsuitable for use in inter-site comparisons of food selection.

An alternative, "Ivlev's electivity index" (*E*, Ivlev, 1961), has also been used by previous primate researchers, including those studying African apes (e.g., Malenky and Stiles, 1991; Takemoto, 2003; Ganas *et al.*, 2004, 2008). It is calculated as:

$$E_i = (f_i - a_i) / (f_i + a_i)$$

This method has an advantage over Ivlev's forage ratio in that it deviates symmetrically from 0 (no selection) and 1 to –1 for preferred and non-preferred items, respectively, but it suffers from the same disadvantage as the forage ratio, in that it is unstable under changes in the relative abundances of food types (Lechowicz, 1982). Although this is the case for the majority of selectivity indices developed, one index, "Chesson's α" or "Vanderploeg and Scavia's selectivity (*W*)" index (Chesson, 1978; Vanderploeg and Scavia, 1979), has been developed that allows for meaningful comparisons between

samples with differing abundances of food types. It is essentially an Ivlev forage ratio normalised so that the sum of all ratios in the sample equals one, and is calculated as follows:

$$\alpha_i = W_i = \frac{f_i / a_i}{\sum_i f_i / a_i}$$

This normalisation (a) represents the forager's perception of the value of the food item, in relation to both its own abundance and the abundance of other food items, and (b) means that the index is unaffected by changes in the relative abundances of food items (Lechowicz, 1982). Thus, this index was deemed most suitable for the current comparison, in which the relative abundances of different food items differed greatly between samples (months). This index is also being used by other orang-utan researchers currently performing similar work (Vogel, pers. comm.; Bastian, 2008).

In order to assess whether this choice of index is likely to cause differences between my results and those of previous ape researchers (Leighton, 1993; McConkey *et al.*, 2002; Takemoto, 2003; Ganas *et al.*, 2004, 2008), I calculated selectivity for adult females for fruit and flowers combined using Ivlev's forage ratio, Ivlev's electivity index and Chesson's α, and compared the results (**Table 5.1**). Correlations between indices, in particular Chesson's α and Ivlev's forage ratio (used for assessing orang-utan fruit preference by Leighton, 1993), were very strong. Thus, the choice of selectivity index

used here is unlikely to influence dramatically the results and the preferred Chesson's α index is used for all analyses hereafter.

Table 5.1 Correlations between different preference indices for fruit and flowers for adult females. Values are correlation coefficients[1]. n = 60 food items.

Index	Ivlev's electivity	Chesson's α
Forage ratio	0.873 ***	0.938 ***
Ivlev's electivity	X	0.843 ***

*** = $p < 0.001$.

1. Pearson's correlations performed on selectivity values and Spearman's correlations performed on selectivity rank were identical.

One consequence of this choice of selectivity index is that the difference in binomial-proportions technique used by McConkey *et al.* (2002), where relative consumption is compared directly to relative availability, in order to establish whether calculated selectivity values differ significantly from neutral selection, cannot be used. This is due to the nature of the two indices: Ivlev's forage ratio, used by McConkey *et al.* (2002), directly compares f_i and a_i, and, thus, is suitable for use with this technique, whereas Chesson's α does not. Nevertheless, this disadvantage is offset by the ability of Chesson's α to compare selectivity indices during periods of differing resource availability.

5.2.3 ASSESSING SELECTION CRITERIA

While the null hypothesis being tested here is that orang-utan food selection follows the predictions of optimal foraging theory (Stephens and Krebs, 1986, i.e., that food selection is geared towards maximising the rate of energy intake), as is thought to be the case in

Bornean mast-fruiting forests (Leighton, 1993), assessment of the truth of this hypothesis would not be complete without also considering the wide variety of other food properties that may also influence food preference. Thus, a wide spectrum of independent variables, covering most food properties that could potentially influence selectivity, were measured and incorporated into analyses of food selection criteria. These include most of the variables incorporated in Leighton (1993), McConkey *et al.* (2002) and Stevenson's (2004) analyses, in addition to a number of other variables, included here for the first time. Following Leighton (1993), all measures used were median values for the sample measured for a food item. Data collection techniques for nutritional components of foods are described in **Section 4.2**, and for food-patch density, crop-size measures and DBH in **Section 3.2.2.**

Physical and mechanical properties of foods, and anti-feedant levels were analysed using the physico-chemical field kit developed by Lucas *et al.* (2001, 2003a, b; please refer to these articles and http://www.gwu.edu/~hebdp/fieldtech/ for complete descriptions of methods used). These data were collected in collaboration with Dr S. M. Cheyne (both of us collected samples and processed them through the kit; I analysed the orang-utan data), using a kit donated by Dr P. W. Lucas. Due to the small amounts of sample required for analyses using this kit, it was possible to collect almost all samples from below feeding trees while the animal was feeding. The vast majority of samples collected in other ways were of foods that are not eaten. As far as possible, all samples were tested on the day of collection, as physical properties are not well preserved during storage. In all but a few cases, data were collected on > 1 sample and median values were used for analysis. Test

results were entered into custom-made computer programmes run on a LabVIEW 7.1 platform, which calculated the actual measurement (Lucas *et al.*, 2001).

5.2.3.1 Food Properties Analysed

The following independent variables were measured (* = recorded for fruits only; # = not recorded/measurable for bark; $ = categorical, all other variables were continuous):

1. *Food volume (cm^3)* #
2. *Wet weight of the part eaten (PE) (g)* #: fresh weight from nutritional samples.
3. *Dry weight of PE (g)* #: field-dry weight from nutritional samples.
4. *Number of seeds / fruit* *
5. *Seed volume / fruit (cm^3)* *: = seed volume x number of seeds/fruit.
6. *Pulp (and skin) volume / fruit (cm^3)* *: = (1) – (5). Although this includes the exocarp, this is broadly indicative of the amount of edible pulp in the fruit, as, for species lacking a thick exocarp, the skin is generally ingested along with the pulp.
7. *Percentage protein*: percentage organic matter (OM).
8. *Percentage lipid (OM)*
9. *Percentage total non-structural carbohydrate (TNC) (OM)*
10. *Percentage neutral detergent fibre (NDF) (OM)*
11. *Percentage water*: = (2) – (3)
12. *Percentage ash*: percentage dry matter (DM). Contains no energy, but includes inorganic minerals (e.g., calcium, copper, potassium, etc.). N.B., because ash contents

vary by > 5%, macro-nutrients have been reported, and included in selectivity analyses, as percentage OM, rather than DM (Conklin-Brittain *et al.*, 2006).

13. *Ratio protein / NDF*: e.g., Garber (1987), Whiten *et al.* (1991), Chapman *et al.* (2004).
14. *Available energy (kcal) / item #*: assuming high fibre digestibility (**Section 4.2.3**).
15. *Available energy (kcal) / 100g*: assuming high fibre digestibility.
16. *Energy available (kcal) / g NDF*: assuming high fibre digestibility.
17. *Protein intake rate (g/min)*
18. *Lipid intake rate (g/min)*
19. *TNC intake rate (g/min)*
20. *NDF intake rate (g/min)*
21. *Dry weight intake rate (g/min)*
22. *Energy intake rate (kcal/min)*: assuming high fibre digestibility (**Section 4.2.3**). In order for $H_0 5.3$ to be accepted, relationships between energy intake rate and food selectivity should be present and, ideally, stronger than relationships for any other independent variable.
23. *Hardness (Young's Modulus, YM,* E) *of PE (MPa) #*: a measure of the resistance of a substance to elastic deformation and one of the key attributes affecting the ability of primates to break into and process foods, and therefore food breakdown rate (Lucas et al., 2001). YM was determined from tests on small, measured sections of sample (ca. 4 mm^2 and 5 mm thick) using short cylinders in compression (**Figure 5.1.B2**) mounted on a portable universal tester (**Figure 5.1.B**), which recorded the data. YM data for *Mezzetia leptopoda / parviflora* were obtained from Lucas (2004).

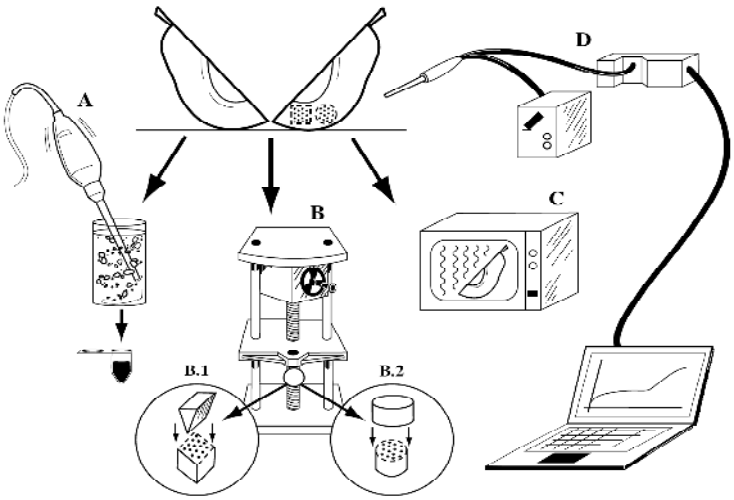


Figure 5.1 Measurement of food physical and chemical properties in the field. A portion (0.1 g) of the fruit is partitioned for extraction in 50% methanol with a portable homogeniser (**A**) for phenolic and tannin tests. A portable universal tester (**B**) is used to measure mechanical properties, such as fracture toughness (**B1**) and Young's modulus (**B2**). Remaining samples of the food can then be dried in an oven (**C**) for further nutritional analyses. Facilities for measuring colour also exist (**D**), but technical problems meant this was unavailable for use in this study. Figure courtesy of Nathaniel Dominy and Erin Vogel.

24. *Young's Modulus of outer skin (MPa)*: exocarp for fruits and outer layer of bark for bark; PE for other items.

25. *Fracture Toughness* (R) *of PE (J/m^2)*: this represents the work done in propagating a crack through a food item. A 15º-angle wedge was driven into small, measured rectangular-shaped specimens (**Figure 5.1.B1**). Toughness was calculated by dividing the area beneath the force-deformation curve by the product of crack depth (i.e., wedge displacement) and initial specimen width (Lucas *et al.*, 2001). To account for anisotropic variation within a tissue, particularly the fleshy mesocarp, a minimum of two measurements were generally taken and averages were used for analysis. For leaves and other thin foods, samples were fractured using cobalt scissors mounted on

the portable universal tester. Leaf samples were cut spanning both the petiole and leaf blade (Lucas *et al.*, 2001; Vogel *et al.*, 2008b).

26. *Fracture Toughness* (R) *of the outer skin (J/m^2)*

27. *pH*: recorded using either a pH metre or ColorpHast pH Test Strips, with a sensitivity of 0.5 pH units.

28. *Phenolics*: this test measures a mixture of phenolic compounds and water-soluble tannins (Lucas *et al.*, 2001). Phenolics may be lost during the drying process typically employed in primate studies (up to 20 mg/g in air-dried leaves, Orians, 1995) and, thus, chemical analysis of fresh samples is preferable (Lucas *et al.*, 2001). Levels of phenolic compounds were measured by the Prussian blue test (Price and Butler, 1977; Graham, 1992; see also Hagerman's website, http://mlavxl .muohio.edu/~hagermae). The test is performed as a micro-assay, using a 1.5-ml Eppendorf tube (i.e., 300 µl dH_2O + 10 µl sample + 100 µl 0.0016 *M* $K_3Fe(CN)_6$ + 100 µl 0.02 *M* $FeCl_3$ in 0.1 *M* HCl + 1 ml stabiliser). Phenolics present in the sample oxidise potassium ferricyanide to produce ferrous ions. These react with ferric chloride in HCl to produce a Prussian Blue complex, the concentration of which can be assessed by evaluating the absorbance of light at 700 nm using a spectrometer. Results are expressed as equivalents to six-point standard curves based on the gallic acid reference (see Lucas *et al.*, 2001 for details).

29. *Tannins.* To measure tannins more precisely, a radial diffusion assay for condensed tannins (which cannot be degraded by mammalian enzymes and, hence, are a greater deterrent to feeding than more easily-degraded hydrolysable tannins, Glander, 1982) was also performed. Using the portable homogeniser (**Figure 5.1.A**), extracts of the

sample were prepared and stored in 50% methanol. Some (0.1 g) sample was then homogenised and placed in 5 ml of methanol. This was filtered, leaving just the liquid extract, which could be stored indefinitely. As the composition of water used can influence results (Lucas *et al.*, 2001), deionised water was used for methanol dilution. Extracts were then inserted into 5-mm-diameter wells made in bovine serum albumin-containing agarose gels. The distance that the tannin diffused through the gel in 96 h at ambient temperature was then measured using calipers and the tannin content calculated on LabVIEW. Relative condensed-tannin measures were expressed as equivalents to six-point standard curves based on crude quebracho tannin (percentage quebracho tannin equivalent, %QTE). Full details of this procedure are given by Hagerman (1987), Hagerman *et al.* (1997), Lucas *et al.* (2001) and on Hagerman's website (http://mlavxl .muohio.edu/~hagermae).

30. *Food crop size*: fruit and flowers only. The number of fruits/flowers produced in a single patch, recorded from the productivity plots (**Section 3.2.3**).
31. *Food crop size (upper 50%)*: as above, except the median value was taken from the upper 50% of records (cf. Leighton, 1993).
32. *Dry weight of food (g) available / patch*: fruit and flowers only (**Section 3.2.3**).
33. *Energy of food (kcal) available / patch*: fruit and flowers only (**Section 3.2.3**).
34. *DBH (cm)*: average from all stems ≥ 10 cm DBH fruit, flower and bark species, and ≥ 6 cm DBH for leaf species.
35. *Pulp weight (g) / seed*
36. *Exocarp type* *: classified as "skin" or "peel" (definitions agreed by S. M. Cheyne and P. W. Lucas, pers. comm.). *Skin* was defined as "a closely-adhering outer layer

which cannot be peeled by the hands/teeth due to its hardness" and *peel* as "the outer protective layer of a fruit or vegetable which could be peeled off and contains the botanical exocarp". Thus, e.g., an orange would have peel and an apple skin.

37. *Colour $*: estimated visually and classified as black/mauve, blue, brown, green, orange, red, white or yellow (cf. McConkey *et al.*, 2002).
38. *Shape $*: estimated visually and classified as cone, ellipsoid, ellipse (i.e., leaves) or sphere.

5.2.3.2 Assessing Selection Criteria

Differences between real and non-foods, and different food types

In order to test $H_0 5.3a$ and *b* (i.e., that energy intake rate is greater for real than for non-foods and for preferred than FBFs, respectively), standard tests for differences were performed. Clearly, data on energy intake rates did not exist for non-foods and, thus, $H_0 5.3a$ was assessed based on comparisons of energy content/100 g. For $H_0 5.3b$, energy intake rates were compared between food types. Tests for differences in the other food properties listed above were also performed to (i) establish whether energy intake was the primary criterion underlying selection, (ii) provide alternative explanations should the null hypothesis be rejected, and (iii) to provide general information on food properties in Sabangau.

Samples of non-food species (see **Section 2.2.5** for definitions of "real" and "non-foods") were collected and data obtained on food properties in the same way as for foods eaten.

Samples of non-foods included both food species that are not eaten by orang-utans and non-eaten food parts from species in which another part is eaten (e.g., non-eaten leaves or fruit seed from a species in which fruit pulp is consumed). Non-food samples were processed in comparable fashion to those for foods eaten. Thus, for example, for a fruit species for which no part has ever been recorded as being eaten in Sabangau, if the skin and pulp were not easily separated from each other, but were easily separated from the seed, then the sample was processed as two parts: skin and pulp combined, and seed (as an orang-utan presented with such a fruit and intending to eat the fruit pulp would typically process it in this manner). For non-eaten parts (e.g., fruit skin and pulp, including aril) of food items that are eaten (e.g., fruit seed), unless the parts were easily separated, the non-eaten parts were typically analysed as one unit; i.e., in this case, as fruit skin and pulp, rather than separated into separate skin and pulp samples. In many cases, of course, there were only two "real" parts (as far as concerns feasible processing by orang-utans) to the food item, e.g., the cambium/phloem and outer bark layers of tree bark.

Assessing selection criteria within food types

Following Leighton (1993), selectivity ranks, not values, were used as the dependent variable in all analyses. Using selectivity ranks instead of selectivity values has the advantage that, while selectivity values may define an item as preferred using one index and avoided/non-preferred in another, preference ranks calculated using different indices are much more consistent (Lechowicz, 1982), thus facilitating comparisons between this study and Leighton's. Items were not ranked in classes (cf. Leighton, 1993), however, as,

while it is true that more inference can be made from a item's low preference the commoner it is, it was feared that this may introduce bias towards rarer species. All analyses were performed twice: once including real-food items (**Section 2.2.5**) that were available, but not eaten during the study period (and with avoided items assigned selectivity ranks based on their density, in reverse order of their values of a_i, cf. Leighton, 1993; intake rates obviously could not be assessed for these items) and once including only items that were actually eaten during the study period. I consider the latter to be the more reliable, as it only includes species for which selectivity is known and, thus, eliminates the risk of selectivity ranks being falsely assigned (i.e., a commoner taxon that is more preferred being assigned a lower selectivity value than a rarer taxon that is actually less preferred).

Unfortunately, testing of $H_0 5.3$ via simple bivariate correlations between energy intake rate and food selectivity rank for each food type is inadequate – if correlations are significant, this may be due merely to collinearity between energy intake and some other independent variable (or combination of independent variables/latent factor) that has greater explanatory power (James and McCulloch, 1990). Thus, bivariate analyses were performed primarily as initial exploratory analyses to identify likely determinants of selection and, as such, were not corrected for multiple comparisons (Roback and Askins, 2004). As in previous primate studies (Janson *et al.*, 1986; Leighton, 1993; McConkey *et al.*, 2002; Stevenson, 2004; Ganas *et al.*, 2008), greater inference was drawn herein from multi-variate analyses. Data were transformed prior to multi-variate analysis (using arcsine transformation for proportional variables and log transformation for all others, cf.

Leighton, 1993) to ensure normality. Some variables were not normally distributed even after transformation and these variables were excluded from the analysis (none of these excluded variables were significantly correlated with selectivity rank in the bivariate analyses). Categorical variables were transformed into dummy variables to allow inclusion in regression analyses. Step-wise regression techniques were not used, as this technique is regarded by many as being frequently unable to find the best model or alternative plausible models, and the order variables enter and leave the programme is often of no theoretical significance (Hocking, 1983; Wilkinson, 1987; James and McCulloch, 1990). Thus, predictive models were built manually.

While multiple regression allows the influence of many independent variables to be assessed, all variables cannot always be simply included in the analysis because, if high correlations between independent variables exist (collinearity/multi-collinearity), interpretation of results is hampered, as effects may be due to either true synergistic relationships, or spurious correlations (James and McCulloch, 1990; Zar, 1999; Graham, 2003). To overcome this problem, I first ran multiple regressions entering all the independent variables and looked at (a) the variance inflation factor (VIF) and partial correlations between the variables (VIFs ≥ 2 and $r \geq 0.6$ are commonly considered to be problematic, Graham, 2003), and (b) whether each independent variable provided any contribution to the model (based on the regression coefficients for individual independent variables). Independent variables that provided no contribution to the model were omitted and the procedure re-ran. Multiple regressions were then performed on all combinations of independent variables that contributed to this last model, in an attempt to find the

"best" model (i.e., that with the highest R^2 and the fewest explanatory variables). This improved the explanatory power of the models and removed some, but not all, of the collinearity problems between independent variables. When collinearity remained a problem, I adopted two approaches: (1) retention of the independent variable in a "set" of inter-correlated variables that contributed most to the model, and exclusion of all others in this set, and (2) principal components regression, in which PCA analysis was performed on all independent variables in a set in order to reduce the inter-correlated variables to un-correlated latent components (i.e., underlying latent variables that can be thought of as being responsible for the shared contributions); multiple regressions were then performed with all combinations of these components, and any other uncorrelated independent variables that contributed to the best model described above, as independent variables (Hocking, 1976; Graham, 2003, similar methods have also been used in studies of food selection in mountain gorillas, Ganas *et al.*, 2008). The best model that was not affected from collinearity of independent variables was then selected. All models were checked for violation of homogeneity of variance and linearity assumptions through analysis of plots of standardised residuals against standardised predicted values, and curvilinear regression between the dependent variable and all independent variables.

Leighton (1993) reports preference in orang-utans for fruit species with large crop size. Thus, in addition to including crop-size estimates and DBH as explanatory variables in the regression analyses described above, I also used Mann-Whitney tests to compare differences between trees fed on and average species' characteristics from productivity plots, to establish whether crop size and/or DBH in trees selected for feeding was larger

than that typically available in the environment. Species selected for this analysis were both highly preferred and important in terms of percentage time spent feeding, and $n > 10$ for all combinations (with the exception of tests for flowers).

5.3 RESULTS

5.3.1 IDENTIFICATION OF PREFERRED/FALL-BACK FOODS

As shown in **Chapter 4**, the consumption of different food types varied temporally. For all age-sex classes combined, fruit and flowers were eaten for an average 68.5 (± 26.8) % and 8.2 (± 16.8) % of total feeding time, compared to 9.9 (± 11.7) % and 3.9 (± 6.7) % for leaves and bark, respectively (**Table 4.4**). The density of fruit and flower patches with food, however, was much lower than that of bark and leaves ($mean_{fruit}$ = 2.15 patches/ha/month, $mean_{flower}$ = 1.22, $mean_{leaf}$ = 15.70, $mean_{bark}$ = 10.00; Kruskal-Wallis, $n = 70$, $p < 0.001$; Dunn's post-hoc, fruit and flowers both < leaves and bark, $p < 0.05$). A comparison of percentage time spent feeding (all age-sex classes combined) against the percentage of total food stems of each food type indicates that both fruit and flowers are eaten more than would be expected based on their availability (paired t-test, fruit: $t = 11.429$, $df = 22$, $p < 0.001$; flowers: $t = 2.104$, $df = 22$, $p = 0.047$), i.e., that they are preferred foods. Leaves ($t = -23.350$, $df = 22$, $p < 0.001$, based on the number of stems with new leaves) and bark ($t = -9.302$, $df = 22$, $p < 0.001$) were both eaten less than would be expected based on their availability and, hence, are not preferred foods. Tests for invertebrates, pith and "other" foods were not possible, due to a lack of data on their

environmental availability. As noted in **Tables 4.12** and **4.18**, consumption of both bark and leaves was negatively correlated with the availability of preferred foods (i.e., fruits and flowers), but consumption of pith and invertebrates was not. Thus, we can accept $H_0 5.1$ with respect to fruit, bark and leaves, but not with respect to flowers, invertebrates or pith.

5.3.2 ARE FIGS FALL-BACK FRUITS IN SABANGAU?

In order to test this hypothesis ($H_0 5.2$), the relative consumption of piths was compared to the availability of non-fig fruits during the study period. This was not significant (all age-sex classes lumped: $r_s = -0.118$, $n = 67$; all age-sex classes combined: $r_s = -0.098$, $n = 23$; adult females: $r_s = -0.062$, $n = 19$; nulliparous females: $r_s = 0.012$, $n = 18$; flanged males: $r_s = -0.237$, $n = 19$; unflanged males: $r_s = 0.027$, $n = 11$; p = NS in all cases) and, hence, $H_0 5.2$ must be rejected.

Having rejected $H_0 5.2$, it is now necessary to ask whether any FBF items can be identified within the preferred food types (*H5.2.1*: there are no fall-back fruits for orang-utans in Sabangau; *H5.2.2*: there are other, non-fig, fall-back fruits for orang-utans in Sabangau). Thus, the consumption of items with low preference rankings was compared to the availability of items with high preference rankings. Identification of fall-back fruits is not possible from mere inspection of preference indices, because, by definition, FBF consumption must be negatively correlated with preferred food availability and preference indices give no indication of whether this is the case.

Unfortunately, simple comparisons of the type detailed above (comparing less-preferred item consumption vs. most-preferred item availability) were also not possible, as this would require both food items to be available in a large sample of the same months, which was not generally the case. Thus, I sequentially added the availability of the most-preferred food items in **Appendix II** until "preferred-food" availability data existed for each month for which feeding data were obtained for an age-sex class (i.e., in each month, absolute availability of the most preferred item was added to that of the second-most, then the third-most, etc., until preferred-food availability > zero in all months). Consumption of fruits with low preference ranks that were available in a large number of months were then compared to this preferred-food availability index. As preference ranks differed between age-sex classes, the number of food items included in the preferred-food availability index also differed. Thus, to aid comparisons between age-sex classes, I also present results using the top-five preferred food items only. Results comparing consumption of less preferred fruits/flowers against the availability of two of the most commonly-eaten/available and highly-preferred foods in Sabangau, *Mezzetia leptopoda / parviflora* and *Diospyros bantamensis*, are also presented. The food items used to compose the preferred-food availability index are listed in **Table 5.2** and the results of correlations with less-preferred-fruit consumption in **Table 5.3**. All flowers had either a very high preference rank and/or were available in very few months and, hence, were unsuitable for inclusion in these analyses.

Based on these results, it appears that, in Sabangau at least, the distinction between preferred and FBFs stops at the level of food type and cannot be extended to food items;

Table 5.2 Species included in preferred-food availability index for different age-sex classes.

Age-sex Class	Species	Part	Analysis	Preference value	Preference rank	% diet[1]	Rank in diet[1]
Adult female	*Nephellium lappaceum*	Fruit pulp	Top-5/all months	0.31	1	1.17	19
	Palaquium cochlearifolium	Flowers	Top-5/all months	0.20	2	1.58	13
	P. ridleyii / xanthochymum	Fruit skin/pulp	Top-5/all months	0.17	3	7.00	3
	Mezzettia leptopoda / parviflora	Fruit seed	Top-5/all months	0.14	4	15.34	1
	Madhuca mottleyana	Flowers	Top-5/all months	0.13	5	4.63	4
	Ficus spp.[2]	Fruit skin/pulp	All months	0.13	6	2.75	9
Nulliparous female	*Gnetum* sp. 2	Fruit pulp	Top-5/all months	0.28	1	1.90	13
	M. mottleyana	Flowers	Top-5/all months	0.24	2	7.71	3
	Fibraurea tinctoria	Fruit pulp	Top-5/all months	0.18	3	1.82	16
	Diospyros bantamensis	Fruit pulp	Top-5/all months	0.14	4	8.97	1
	D. confertiflora	Fruit pulp	Top-5/all months	0.13	5	1.48	18
	Licania splendens	Fruit pulp	All months	0.13	6	0.46	39
	D. siamang	Fruit pulp	All months	0.12	7	4.83	7
Flanged male	*N. lappaceum*	Fruit pulp	Top-5/all months	0.45	1	3.76	6
	M. leptopoda / parviflora	Fruit seed	Top-5/all months	0.25	2	18.39	1
	Ficus cf. spathulifoli	Fruit skin/pulp	Top-5/all months	0.13	3	0.15	54
	Polyalthia hypoleuca	Fruit seed	Top-5/all months	0.11	4	1.68	15
	G. sp. 2	Fruit pulp	Top-5	0.10	5	0.32	41

Abbreviations: Top-5 = top-five preferred food items; all months = preferred food items sequentially combined until availability data existed for all months with diet data. See text for details.

1. Based on percentage time spent feeding on that item over the course of the study period.
2. Includes *Ficus cf. stupenda* and a number of other fig species that could not be differentiated reliably, but excludes *F. cf. spathulifolia*.

Table 5.3 Spearman's correlations between preferred-food availability[1] and percentage time spent feeding on less-preferred fruit items: (a) Adult females. Values are correlation coefficients. *n* = 19 months. See text for details.

		Preferred-food availability measure			
Food item consumed	**Preference ranking**	**Top (all months)**	**Top 5**	***M. leptopoda / parviflora***	***D. bantmensis***
P. leiocarpum	Low (45)	NS	NS	NS	NS
Xylopia cf. malayana	Low (43)	NS	NS	NS	NS
X. fusca	Low (39)	NS	NS	NS	NS

(b) Nulliparous females.

		Preferred-food availability measure			
Food type / item consumed	**Preferred?**	**Top (all months)**	**Top 5**	***M. leptopoda/ parviflora***	***D. bantmensis***
M. leptopoda / parviflora	Low (44)	0.495 *	0.566 *	**0.669 ****	0.612 **
P. leiocarpum	Low (61)	NS	NS	NS	0.488 *
X. cf. malayana	Low (45)	NS	NS	NS	NS
X. fusca	Low (59)	NS	NS	NS	NS

(c) Flanged males.

		Preferred-food availability measure			
Food item / type consumed	**Preferred?**	**Top (all months)**	**Top 5**	***M. leptopoda / parviflora***	***D. bantmensis***
P. leiocarpum	Low (38)	NS	NS	NS	NS
X. cf. malayana	Low (45)	NS	NS	NS	NS
Ficus spp.	Low (36)	NS	NS	NS	NS

* = $p < 0.05$; ** $p < 0.01$; NS = not significant. Boldface indicates *p*-values that remained significant post-Bonferroni correction.

1. Preference rankings for *M. leptopoda/parviflora* and *D. bantamensis* were, respectively: ADF 4, 11; NUF 44, 4; FLM 2, 9. Thus, *M. leptopoda/parviflora* was a very highly-preferred fruit for adult females and flanged males, but not for nulliparous females.

i.e., *H5.2.1* is supported and fall-back fruits do not exist. While some fruits and flowers are certainly more preferred than others, it would appear that even non-preferred fruits and flowers are preferred relative to the "true FBFs", leaves and bark. Indeed, the positive correlations between less-preferred fruit consumption and preferred-food availability in some cases suggest neutral, rather than negative, selection for these less-preferred fruits.

5.3.3 FOOD SELECTION

5.3.3.1 Differences Between Real Foods and Non-Foods

Before attempting to assess differences between preferred and FBF types, it is first necessary to identify whether any differences exist between real and non-foods (**Section 2.2.5**). Thus, I performed Mann-Whitney tests between real and non-foods within each food type for each food property listed in **Section 5.2.3.1** (**Table 5.4**). Corrections for multiple comparisons were not applied, as the aim of these tests was to screen for potential differences (Roback and Askins, 2004). Tests for bark were performed by Rothwell (2008; data were only available for comparison of chemical contents). These tests indicate a significant difference in energy content between real and non-foods for fruit pulp, but not for other food types. Thus, $H_0 5.3a$ can be accepted with respect to fruit pulp, but not with respect to other food types. For fruit pulp, dry weight and fibre content were lower, and carbohydrate content, water content and the weight and energy of food

available/tree higher, in real foods than non-foods. Toughness of eaten species was also lower than avoided species for both fruit pulp and flowers.

Table 5.4 Significant results of Mann-Whitney tests for differences between real and non-foods[1,2].

Food Type	Property	n_{real}	n_{non}	$Mean_{real}$		$Mean_{non}$	p
Fruit pulp[3]	Dry weight	47	37	0.74	<	3.15	0.014
	% NDF	39	27	55.24	<	65.51	0.015
	% TNC	39	27	31.67	>	23.17	0.041
	% water	43	16	76.09	>	65.69	0.003
	Energy/100 g	39	27	295.2	>	267.9	0.022
	Toughness PE	22	20	259.4	<	765.4	0.003
	Toughness skin	33	23	413.2	<	848.2	0.029
	Weight food/tree	37	21	186	>	70	0.043
	Energy food/tree	37	21	537	>	190	0.050
Flowers	Toughness PE	5	7	36.78	<	123.4	0.018
Leaves	DBH	33	11	9.68	<	15.8	0.003

Abbreviations: *n* = sample size (number of food items included in analysis); Non = non-food; real = real food; NDF = neutral-detergent fibre; TNC = total non-structural carbohydrate; PE = part eaten.

1. Tests not conducted due to insufficient data: flowers, independent variables 2-3 and 7-21.
2. Tests for bark for independent variables 7-11 and 14 were carried out by Rothwell (2008); all results were insignificant.
3. Includes fruit skin for items where skin and pulp are eaten together.

5.3.3.2 Differences Between Preferred and Fall-Back Food Types

As some differences between real and non-foods were found in the above analysis, tests for differences between food categories were restricted to real foods. Due to the non-normal distribution of some food property variables, Kruskal-Wallis tests were performed initially and, where significant, Dunn's non-parametric multiple comparison tests (Dunn,

1964) were performed with α set at 0.05, in order to identify which food types differed from which others. Corrections for multiple comparisons were not applied, as, again, the aim of these tests was to screen for potential differences. Descriptive statistics for each food type and the results of tests for differences are shown in **Table 5.5**. Energy intake rate did differ between food types, with energy intake rate from fruit > flowers > leaves > bark, but differences were only statistically different between the two extremes, fruit and bark. Thus, $H_0 5.3b$ (that energy intake rate is greater in preferred than in FBFs) can be accepted. Numerous other differences were found between food types, and these are detailed and discussed in **Section 5.4.2.2**.

5.3.3.3 Food Selection Criteria: Preferred Foods

Preference indices were derived from data from 19 months for adult females, 18 months for nulliparous females and 19 months for flanged males. Note that, in May 2007, no fruit or flowers were eaten by flanged males and, thus, preference ranks for all available fruit/flower species in that month were zero. Correlations of food-preference ranks between age-sex classes for fruits and flowers (**Table 5.6)** support the separation of age-sex classes for selectivity analyses. Although correlations do exist between adult females and the other age-sex classes, these are not exceptionally strong, and there was no significant correlation between flanged males and nulliparous females.

Table 5.5 Descriptive statistics and results of tests for differences in food properties between food types.

	Fruit			Flowers			Bark			Leaves			Test Results	
Food property	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Kruskal-Wallis**	**Dunn's post-hoc**
Food volume*	**128.0**	298.2	58	**11.7**	22.0	5	**N/A**	N/A	N/A	**7.7**	6.4	21	<0.001	FR > FL FR > LS
Wet weight*	**3.6**	9.7	56	**1.1**	2.0	4	**N/A**	N/A	N/A	**0.3**	0.2	20	0.001	FR > LS
Dry weight*	**0.7**	1.4	57	**0.2**	0.3	4	**N/A**	N/A	N/A	**0.1**	0.1	20	<0.001	FR > LS
% protein	**8.3**	5.0	47	**8.8**	2.8	4	**7.1**	3.3	6	**13.7**	6.8	19	0.002	NS
% lipid	**5.1**	6.5	47	**3.8**	0.6	4	**4.1**	6.1	6	**1.5**	1.1	19	NS	N/A
% TNC	**30.5**	19.9	47	**32.2**	18.8	4	**27.6**	11.0	6	**36.8**	20.1	19	NS	N/A
% NDF	**56.1**	20.3	47	**55.2**	18.0	4	**61.3**	14.1	6	**48.3**	18.0	19	NS	N/A
% water	**72.2**	16.8	55	**79.2**	9.4	4	**N/A**	N/A	N/A	**68.4**	25.1	20	NS	N/A
% ash	**3.45**	1.69	47	**3.88**	1.61	4	**6.19**	3.35	6	**3.14**	0.97	19	NS	N/A
Protein / fibre	**0.21**	0.23	47	**0.17**	0.07	4	**0.12**	0.06	6	**0.32**	0.17	19	0.002	LS > FR
Energy / item*	**2.3**	4.5	47	**0.4**	0.8	4	**N/A**	N/A	N/A	**0.3**	0.1	19	0.005	FR > LS
Energy / 100g	**292.4**	63.8	47	**288.4**	42.5	4	**275.2**	56.5	6	**294.8**	39.3	19	NS	N/A
Energy / g NDF	**7.6**	7.9	47	**5.9**	2.9	4	**4.9**	2.2	6	**7.4**	4.0	19	NS	N/A
Protein intake	**0.14**	0.10	47	**0.11**	0.11	4	**0.02**	0.02	4	**0.15**	0.10	6	0.031	FR > B
Lipid intake	**0.10**	0.13	47	**0.05**	0.05	4	**0.02**	0.03	4	**0.02**	0.01	6	0.049	NS
TNC intake	**0.61**	0.57	47	**0.31**	0.15	4	**0.07**	0.06	4	**0.16**	0.14	6	0.011	NS
NDF intake	**1.36**	1.37	47	**0.84**	1.01	4	**0.18**	0.18	4	**0.52**	0.36	6	NS	N/A
Weight intake	**2.21**	1.98	47	**1.32**	1.18	4	**0.29**	0.23	4	**0.83**	0.41	6	0.018	FR > B
Energy intake	**6.11**	5.24	47	**3.55**	2.66	4	**0.82**	0.70	4	**2.21**	0.92	6	0.009	FR > B
Young's Modulus PE*	**3.1**	2.3	22	**1.2**	2.4	5	**N/A**	N/A	N/A	**6.4**	5.7	12	NS	N/A
Young's Modulus skin	**8.5**	38.1[1]	38[1]	**1.2**	2.5	5	**12.0**	4.73	9	**6.4**	5.7	12	0.002	B > FL B > FR
Toughness PE*	**258.7**	158.2	24	**36.8**	36.5	5	**N/A**	N/A	N/A	**688.6**	439.8	8	<0.001	LS > FL
Toughness skin	**488.2**	669.1	39	**36.8**	36.5	5	**1,595.9**	673.7	6	**688.6**	439.8	8	<0.001	B > FL B > FR FR > FL LS > FL

	Fruit			Flowers			Bark			Leaves			Test Results	
Food property	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Kruskal-Wallis**	**Dunn's post-hoc**
PH	**4.5**	1.1	58	**4.6**	.5	6	**4.6**	.2	9	**4.3**	.6	21	NS	N/A
Phenolic	**0.094**	0.105	45	**0.113**	0.100	5	**0.094**	0.053	7	**0.169**	0.149	15	NS	N/A
Tannin	**1.579**	1.508	52	**0.032**	0.072	5	**0.441**	0.793	8	**1.436**	1.113	17	0.001	FR > B FR > FL LS > B LS > FL
Stem density	**15**	22	54	**11**	4	6	**10**	6	10	**26**	31	35	NS	N/A
DBH	**13.8**	5.7	53	**14.3**	7.1	6	**16.1**	7.1	10	**9.6**	5.2	33	NS	N/A

* = excluding bark (as analyses not appropriate).

Abbreviations: B = bark; FL = flowers; FR = fruit; K-W = Kruskal-Wallis; LS = leaves; NDF = neutral detergent fibre; PE = part eaten; TNC = total non-structural carbohydrate.

1. Including *M. leptopoda/parviflora* seed case (205 MPa, Lucas, 2004).

Table 5.6 Pearson's correlations (one-tailed) between food-preference rankings for different age-sex classes (fruits and flowers). Values are: correlation coefficient (*n*).

	Adult female	**Flanged male**
Nulliparous female	0.401** (50)	NS (44)
Adult female	X	0.444** (43)

** = $p < 0.01$; NS = not significant.

In this section, I look at the determinants of food selectivity rank among the preferred foods, fruit and flowers. Analyses were repeated for: (i) fruit and flowers combined, (ii) fruits only (all parts), and (iii) fruit pulp only, and (a) including avoided items, and (b) excluding avoided items. Insufficient sample size existed to assess flowers only. Prior to analysis, Spearman's correlations between all the independent variables were performed (**Appendix III**).

The results of bivariate analyses of selectivity are shown in **Table 5.7**. These tests reveal that, in most cases, there was no relationship between selectivity rank and energy intake rate. Furthermore, flanged male fruit pulp selectivity was actually *negatively* correlated with energy intake rank, in direct contrast to expectations. A number of correlations existed between selectivity rank and other independent variables, however; these were most numerous for adult females and point towards a potentially important influence of number of seeds, protein, lipid and energy content, protein/fibre ratio, fibre intake and pulp weight/seed. Correlations were far fewer for flanged males and these indicate a possible influence of number of seeds, protein content, protein/fibre ratio, and fibre and weight intake rate. Even fewer correlations were found for nulliparous females and these indicate a possible influence of number of seeds, ash and phenolic content and pulp

Table 5.7 Spearman's correlations between fruit and flower selectivity rank and food properties. Values are correlation coefficients (note that a negative correlation coefficient denotes a positive correlation, due to the inverse order of selectivity ranks).

Property	Adult female				Flanged male				Nulliparous female			
	FR + FL (inc. avoided)	FR + FL (exc. avoided)	Fruit (exc. avoided)	Pulp (exc. avoided)	FR + FL (inc. avoided)	FR + FL (exc. avoided)	Fruit (exc. avoided)	Pulp (exc. avoided)	FR + FL (inc. avoided)	FR + FL (exc. Avoided)	Fruit (exc. avoided)	Pulp (exc. avoided)
Food volume	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Wet Weight	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Dry Weight	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
No. seeds	NS	-0.282*	-0.282*	-0.348*	-3.16*	NS	NS	NS	NS	NS	NS	-0.296*
Seed volume	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Seed volume/fruit	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Volume skin + pulp	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% Protein	NS	-0.349*	-0.329*	-0.366*	-0.277*	NS	NS	-0.361*	NS	NS	NS	NS
% lipid	NS	-0.335*	-0.357*	NS	NS	NS	NS	NS	NS	NS	NS	NS
% TNC	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% NDF	0.272*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% ash	NS	NS	NS	NS	NS	NS	NS	NS	-0.296*	NS	NS	NS
Protein / fibre	-0.327*	-0.384*	-0.336*	-0.441**	-0.304*	NS	NS	-0.360*	NS	NS	NS	NS
Energy / item	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Energy / 100g	-0.296*	-0.311*	NS	-0.363*	NS	NS	NS	NS	NS	NS	NS	NS
Energy / g NDF	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Protein intake	N/A	NS	NS	NS	N/A	NS	NS	NS	N/A	NS	NS	NS
Lipid intake	N/A	NS	NS	NS	N/A	NS	NS	NS	N/A	NS	NS	NS
TNC intake	N/A	NS	NS	NS	N/A	NS	NS	NS	N/A	NS	NS	NS
NDF intake	N/A	0.340*	0.312*	0.421*	N/A	NS	NS	0.359*	N/A	NS	NS	NS
Weight intake	N/A	NS	NS	0.345*	N/A	NS	NS	0.371*	N/A	NS	NS	NS
Energy intake	N/A	NS	NS	NS	N/A	NS	NS	0.358*	N/A	NS	NS	NS

Property	Adult female				Flanged male				Nulliparous female			
	FR + FL (inc. avoided)	**FR + FL (exc. avoided)**	**Fruit (exc. avoided)**	**Pulp (exc. avoided)**	**FR + FL (inc. avoided)**	**FR + FL (exc. avoided)**	**Fruit (exc. avoided)**	**Pulp (exc. avoided)**	**FR + FL (inc. avoided)**	**FR + FL (exc. Avoided)**	**Fruit (exc. avoided)**	**Pulp (exc. avoided)**
Young's Modulus PE	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Young's Modulus skin	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Toughness PE	NS	0.546**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Toughness skin	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
PH	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Phenolic	NS	NS	0.362*	NS	NS	NS	NS	NS	0.515***	0.370*	NS	NS
Tannin	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Food crop size	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Food crop size (top 50%)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Weight food available/tree	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Energy food available/tree	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
DBH	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Pulp weight/seed	NS	0.333*	0.333*	0.333*	NS	NS	NS	NS	0.338*	NS	NS	NS
Variation in *n*	28-66	20-53	16-53	14-45	27-65	19-48	16-48	14-39	29-64	21-53	20-53	17-46

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N/A = not applicable (intake rates not available for species not eaten during the study period, see **Section 5.2.3.2**); NS = not significant.
Abbreviations: FL = flower; FR = fruit; *n* = sample size (number of items included in analysis); NDF = neutral detergent fibre; PE = part eaten; TNC = total non-structural carbohydrate.

weight/seed. As noted above, while these analyses give an initial insight into the factors most likely to influence selection, the results are difficult to interpret, especially when viewed together with those in **Appendix III**. Thus, further analysis through multiple regression is required to enable accurate interpretation of the observed relationships.

Multiple regression analyses successfully predicted selectivity rank in adult females (**Table 5.8** and **Figure 5.2**), but no significant predictive models could be built for either flanged males or nulliparous females. For adult females, the model with the highest predictive power with fruit/flower preference rank (excluding avoided species and that did not suffer from problems of collinearity) as the dependent variable that could be built from the original independent variables contained only protein/fibre ratio and energy/100g (R^2 = 0.158, df = 46, p = 0.025). Removal of energy/100g resulted in only a very small loss in predictive power (R^2 = 0.157, df = 46, p = 0.006); thus, protein/fibre ratio alone is the best model with the fewest explanatory variables that can be built based upon the original independent variables. A model containing fibre/protein ratio, energy/100g, protein content, and fibre, weight and energy intake rate had the highest predictive value (R^2 = 0.269, df = 40, p = 0.082), but suffered from a high degree of multi-collinearity between fibre/protein ratio, protein content, and fibre, weight and energy intake rate (VIF > 2). PCA reduced these five variables to just one component, explaining 77.4% of the variance of the original variables (this component was justified; Kaiser-Maier-Olkin measure of sampling adequacy = 0.624; Bartlett's test of sphericity: χ^2 = 339.13, df = 10, p < 0.001). Regression of this component and the remaining uncorrelated independent variable, energy/100g, produced a model with predictive power

Table 5.8 "Best" models from multiple regression analyses for predicting selectivity rank of fruit pulp, fruit (all parts), and fruit and flowers combined for adult females. No significant models could be constructed for flanged males and nulliparous females. See text for details.

Food type	Variables included[a]	R^2	p	df	Slope[b]
Fruit pulp (exc. av.)	Protein / fibre only	0.155	0.023	31	-0.410
Fruit (all parts, exc. av.)	Protein / fibre only	0.139	0.015	40	-0.377
Fruit + flowers (exc. av.)	Protein / fibre only	0.157	0.006	46	-0.403
Fruit + flowers (inc. av.)	Protein / fibre only	0.094	0.027	51	-0.306

a. Protein/fibre ratio was not normally distributed, even after transformation, and, thus, fibre/protein ratio was used in its place and the direction of the effect reversed for protein/fibre. This substitution is valid, as protein/fibre and fibre/protein ratios are perfectly correlated across all food items (r_s = -1.000, n = 157, p < 0.001).

b. Standardised regression coefficient, giving the expected change, in standard deviations, in selectivity rank for each standard deviation change in the variable.

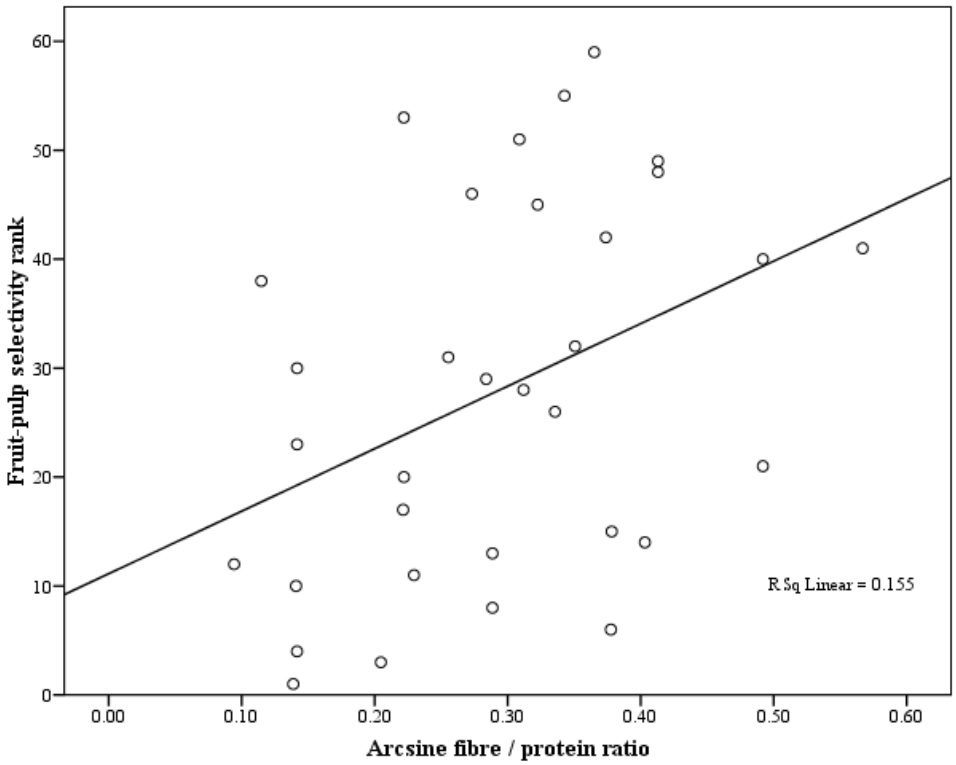


Figure 5.2 Regression of adult female fruit-pulp selectivity rank (excluding avoided species) against fibre/protein ratio. Fibre/protein ratio was used in place of protein/fibre ratio (see legend to **Table 5.8**).

only very slightly greater than did protein/fibre ratio alone (R^2 = 0.159, df = 40, p = 0.037). Similarly, a component derived from the two variables contributing most to the five-variable model above, fibre/protein ratio and fibre intake, which explained 86.5% of the original variation in these variables (Kaiser-Maier-Olkin measure of sampling adequacy = 0.500; Bartlett's test of sphericity: χ^2 = 32.602, df = 1, p < 0.001), also provided no substantial improvement in predictive power when regressed against fruit/flower preference rank (R^2 = 0.164, df = 40, p = 0.009). Inclusion of dummy variables for shape, colour and exocarp type (**Section 5.2.3.2**) did not improve the model.

These analyses indicate that protein/fibre ratio is the best sole predictor of fruit/flower preference rank (excluding avoided species) in adult females and that the addition of extra variables results in no substantial improvement to the model. The same results were found when assessing preference rank for fruits/flowers (including avoided species), just fruit and for fruit pulp (both excluding avoided species): the best model contained only protein/fibre ratio as the predictor variable. Thus, we can reject $H_0 5.3c$ (that food energy returns are the primary determinant of food preference rankings within food types) with respect to the preferred food types, fruits and flowers.

Categorical Analyses

Significant differences were found in DBH, crop size, and dry weight and energy of food available/tree between trees fed on and average environmental availability (as determined from the productivity plots) for selected food items (**Table 5.9**). These data support the

hypothesis that orang-utans preferentially select larger trees with more food available, as observed in the masting forests of Kutai (Leighton, 1993).

Table 5.9 Results of Mann-Whitney tests for differences between trees fed on and environmental availability[1]: (a) DBH (cm).

Part	Species	n_E	n_{No}	$Mean_E$		$Mean_{No}$	p
Fruit	*Blumeodendron elateriospermum / tokbrai*	131	17	17.5		16.4	NS
	Diospyros bantamensis	380	54	28.7	>	25.5	**0.001**
	D. siamang	132	13	28.7	>	22.7	**<0.001**
	Mezzetia leptopoda / parviflora	491	39	24.3	>	20.4	**<0.001**
Flower	*Madhuca mottleyana*	207	8	31.4	>	26.8	0.019
	Palaquium pseudorostratum	15	6	36.7		33.4	NS

(b) Crop size (number of fruits/tree)

Part	Species	n_E	n_{No}	$Mean_E$		$Mean_{No}$	p
Fruit	*Blumeodendron elateriospermum / tokbrai*	30	17	187	>	89	0.040
	Diospyros bantamensis	344	53	473		649	NS
	D. siamang	56	13	332	>	179	0.022
	Mezzetia leptopoda / parviflora	376	38	289	>	170	**<0.001**
Flower	*Madhuca mottleyana*	18	6	12,611	>	3,429	**0.007**
	Palaquium pseudorostratum	14	5	9,821		4,165	NS

(c) Energy of food available (kcal/tree)

Part	Species	n_E	n_{No}	$Mean_E$		$Mean_{No}$	P
Fruit	*Blumeodendron elateriospermum / tokbrai*	30	17	722	>	343	0.040
	Diospyros bantamensis	344	53	543		744	NS
	D. siamang	56	13	929	>	501	0.022
	Mezzetia leptopoda / parviflora	376	38	165	>	97	**<0.001**
Flower	*Madhuca mottleyana*	18	6	181	>	49	**0.007**
	Palaquium pseudorostratum	14	5	149		63	NS

E = eaten; No= not eaten (data from productivity plots); *n* = number items included in the analysis. Boldface indicates results that remained significant post-Bonferroni correction.

1. Data from all age-sex classes combined; no minimum follow limit imposed; juveniles and infants excluded.

5.3.3.4 Food Selection Criteria: Fall-Back Foods

Bark

The number of bark species that were consumed, and that could be ranked for preference, was very small (7 for nulliparous females, 4 for adult females and 3 for flanged males, **Appendix II**) and, hence, avoided real-food species were also included in the analysis. Despite this, sample size was still low for all bivariate correlations attempted (n = 3-9). No correlations were significant, with the following exception: flanged males preferred species with higher lipid contents ($r_s = -1.0$, $p < 0.001$, $n = 5$). Multi-variate analyses were not attempted due to the small sample size. Thus, $H_0 5.3c$ can be neither accepted nor rejected with respect to bark.

Leaves

Unfortunately, due to the great difficulty involved in identifying accurately leaf species eaten by orang-utans in the field, in a large proportion of leaf-eating bouts, the species eaten could not be identified, and these bouts had to be excluded from the analysis (e.g., "unknown leaf" feeding represented 47% of all time spent feeding on leaves by adult females). Thus, the analyses presented herein for leaves should be regarded as preliminary. When calculating leaf selectivity ranks using the density of stems with new leaves, months where no leaf eating was recorded were excluded from the index, as leaves are FBFs (i.e., their consumption is negatively correlated with the availability of preferred foods, fruits and flowers, **Section 5.3.1, Tables 4.12** and **4.18**). Hence, including these months (and the accompanying "zeroes" for species with new leaves),

where leaves were clearly not part of the optimal diet, could lead to "unfairly" reduced selectivity ranks for those species available in months when no leaves were consumed. Thus, these selectivity indices were composed of 16 months for adult females, 12 months for nulliparous females and 11 months for flanged males (**Appendix II**). When calculating leaf selectivity using stem density, all months were included as, with this measure, all species are available in all months and, hence, no bias would be introduced in months when no leaves were consumed. For all age-sex classes, both selectivity ranks calculated from total stem density and density of stems with new leaves were highly correlated ($r_s \geq 0.886$, $p \leq 0.009$ in all cases, $n = 6$ for flanged males, 12 for adult females and 13 for nulliparous females).

Results of bivariate correlations on selectivity rank are shown in **Tables 5.10** and **5.11**. As for preferred foods, corrections for multiple comparisons were not made, as the aim in these tests was to provide preliminary information on the independent variables likely to influence leaf preference rankings in multi-variate analyses. For adult females, these tests indicate only one likely influence; that of pH on selectivity rank (including avoided species) based on the density of stems with new leaves (preference for more alkaline leaves). For flanged males, a similar correlation for pH was found when avoided species were included. In addition, significant correlations in flanged males were also found for wet weight (preference for lighter leaves) and DBH (preference for smaller trees). For nulliparous females, similar correlations with wet weight were found when avoided species were included, but more significant correlations were found when avoided species were excluded. Surprisingly, in these analyses, significant correlations were

Table 5.10 Results of Spearman's correlations between selectivity rank (calculated using total stem density) and food properties for leaves. Values are correlation coefficients.

	Adult females		Flanged males		Nulliparous females	
Food Property	**Inc. avoided**	**Exc. avoided**	**Inc. avoided**	**Exc. avoided**	**Inc. avoided**	**Exc. avoided**
Food volume	NS	NS	NS	NS	NS	NS
Wet weight	NS	NS	0.504*	NS	0.534*	NS
Dry weight	NS	NS	NS	NS	NS	NS
% protein	NS	NS	NS	NS	NS	NS
% lipid	NS	NS	NS	NS	NS	NS
% TNC	NS	NS	NS	NS	NS	0.578*
% NDF	NS	NS	NS	NS	NS	NS
% water	NS	NS	NS	NS	NS	NS
% ash	NS	NS	NS	NS	NS	NS
Protein / fibre	NS	NS	NS	NS	NS	NS
Energy / item	NS	NS	NS	NS	NS	NS
Energy / 100g	NS	NS	NS	NS	NS	NS
Energy / g NDF	NS	NS	NS	NS	NS	NS
Protein intake	N/A	NS	N/A	NS	N/A	NS
Lipid intake	N/A	NS	N/A	NS	N/A	NS
TNC intake	N/A	NS	N/A	NS	N/A	NS
NDF intake	N/A	NS	N/A	NS	N/A	NS
Dry weight intake	N/A	NS	N/A	NS	N/A	NS
Energy intake	N/A	NS	N/A	NS	N/A	NS
Young's Mod. PE	NS	NS	NS	NS	NS	NS
Toughness PE	NS	NS	NS	NS	NS	NS
pH	NS	NS	-0.797*	NS	NS	NS
Phenolic	NS	NS	NS	N/A	NS	NS
Tannin	NS	NS	NS	NS	NS	NS
DBH	NS	NS	0.380*	NS	NS	NS
Variation in *n*	5-32	4-11	5-32	4-8	5-34	5-16

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N/A = data deficient/analyses not possible, NS = not significant.

Table 5.11 Results of Spearman's correlations between selectivity rank (calculated using density of stems with new leaves) and food properties for leaves. Values are correlation coefficients.

	Adult females		Flanged males		Nulliparous females	
Food Property	**Inc. avoided**	**Exc. avoided**	**Inc. avoided**	**Exc. avoided**	**Inc. avoided**	**Exc. avoided**
Food volume	NS	NS	NS	NS	NS	NS
Wet weight	NS	NS	NS	0.900*	NS	NS
Dry weight	NS	NS	NS	NS	NS	NS
% protein	NS	NS	NS	NS	NS	NS
% lipid	NS	NS	NS	NS	NS	NS
% TNC	NS	NS	NS	NS	NS	0.796**
% NDF	NS	NS	NS	NS	NS	-0.758*
% water	NS	NS	NS	NS	NS	NS
% ash	NS	NS	NS	NS	NS	NS
Protein / fibre	NS	NS	NS	NS	NS	NS
Energy / item	NS	NS	NS	NS	NS	0.648*
Energy / 100g	NS	NS	NS	NS	NS	0.685*
Energy / g NDF	NS	NS	NS	NS	NS	0.733*
Protein intake	N/A	NS	N/A	NS	N/A	NS
Lipid intake	N/A	NS	N/A	NS	N/A	NS
TNC intake	N/A	NS	N/A	NS	N/A	NS
NDF intake	N/A	NS	N/A	NS	N/A	NS
Dry weight intake	N/A	NS	N/A	NS	N/A	NS
Energy intake	N/A	NS	N/A	NS	N/A	NS
Young's Mod. PE	NS	NS	NS	NS	NS	NS
Toughness PE	NS	NS	NS	NS	NS	NS
pH	-0.499*	NS	-0.503*	NS	NS	NS
Phenolic	NS	NS	NS	NS	NS	NS
Tannin	NS	NS	NS	NS	NS	NS
DBH	NS	NS	0.446**	NS	NS	NS
Variation in *n*	5-32	4-11	5-32	4-8	5-35	5-14

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N/A = data deficient/analyses not possible; NS = not significant.

found for NDF content (positive), TNC content, energy/item, energy/100g and energy/g NDF (all negative).

The only significant multi-variate model for leaf selection that could be built using either method for calculating selectivity rank and any combination of independent variables was for nulliparous females. Excluding avoided species and based on the density of stems with new leaves, the best model comprised energy/100 g and energy/item (R^2 = 0.719, *df* = 9, *p* = 0.012), both of which were associated with *decreased* preference rank (standardised regression coefficients = 0.555 and 0.354, respectively). Thus $H_0 5.3c$ can clearly be rejected with respect to leaves. As noted above, due to the large number of leaf feeding bouts in which the species eaten was unknown and the low degree of freedom in the above analysis, this result should be treated with extreme caution and it is quite possible that the correlation observed above is spurious and/or the result of some unmeasured variable (see **Section 5.4.2.3).**

5.4 DISCUSSION

5.4.1 PREFERRED AND FALL-BACK FOODS

The results of this study – that fruit and flowers are the preferred foods, and leaves and bark are FBFs – support the contentions of numerous other ape researchers (e.g., Galdikas, 1988; Leighton, 1993; Knott, 1998; Conklin-Brittain *et al.*, 2001; Knott, 2005; Yamagiwa and Basabose, 2006a, b; Vogel *et al.*, 2008b). Though formal tests to establish

whether invertebrates and pith are preferred foods could not be conducted, it seems improbable that they are preferred foods, and most likely that they are neither preferred nor FBFs in Sabangau, but instead are eaten relatively constantly year-round (**Tables 4.12-13** and **4.18-19**, **Figures 4.4** and **4.6).** Of note, although abundance and, hence, preference, of caterpillars was not assessed, anecdotal observations indicate that they are highly preferred, being eaten in large quantities whenever available, and with individual orang-utans even being seen outside of their normal range in order to feed on caterpillars in areas of abundance (pers. obs.). Thus, our null hypothesis ($H_0 5.1$) can be only partially accepted: as in masting forests in Borneo (Leighton, 1993; Knott, 1998, 1999), fruit is a preferred food, and bark and leaves are FBFs, but, unlike masting forests, flowers are also preferred foods, and invertebrates and pith are not FBFs, for orang-utans in Sabangau.

Figs are commonly considered to be FBFs for apes (e.g., chimpanzees: Wrangham *et al.,* 1991, 1993, 1996; Malenky *et al.*, 1994; Tweheyo and Lye, 2003, but see also Newton-Fisher, 1999; gibbons: Marshall, 2004; Marshall and Leighton, 2006; Sumatran orang-utans: Wich *et al.*, 2006b), but appear to be relatively preferred foods for orang-utans in Sabangau (**Appendix II**), and are also not FBFs for eastern lowland gorillas in Kahuzi-Biega National Park, Congo (Yamagiwa *et al.*, 2005). Although some non-fig fruits have been recognised as FBFs for chimpanzees (e.g., *Musanga leo-errerae*, Furuichi *et al.*, 2001) and western lowland gorillas (e.g., *Duboscia macrocarpa* and *Klainedoxa gabonensis*, Remis *et al.*, 2001; Doran *et al.*, 2002, see also Rogers *et al.*, 1990), it would appear that fall-back fruits do not exist for orang-utans in Sabangau; thus, $H_0 5.2$ must be rejected.

One possible reason for these observations could be lower availability of high-quality fruits in Borneo. Leaves in Borneo have been documented as being of lower quality than mainland Malaysian, Indian and African forests (Waterman *et al.*, 1988), and it has been suggested that Bornean fruits are also of lower quality (Knott, 2005). A comparison of fruit-pulp energy contents between chimpanzee foods in Kanyawara, and orang-utan foods in Gunung Palung (listed in Conklin-Brittain *et al.*, 2006; using high digestibility values for fibre, **Section 4.2.3**) and Sabangau supports this (**Table 5.12**): CV of fruit energy contents in Borneo appears less than in Uganda, and maximum energy contents are also much lower. Thus, I propose an alternative hypothesis, whereby less variation in, and overall lower, fruit quality might result in a relative increase in the preference rank of figs and a lack of fall-back fruits in Borneo, especially in peat-swamp forest.

Table 5.12 Comparison of food-energy contents (kcal/100 g; high fibre digestibility) between Kanyawara, Gunung Palung and Sabangau[1].

Site	Mean	SD	CV	Min.	Max.	*n*
Kanyawara	308	91	0.29	233	644	30
Gunung Palung	320	62	0.19	211	434	15
Sabangau	297	65	0.22	209	436	42

1. Kanyawara and Gunung Palung data from Conklin-Brittain *et al.* (2006).

5.4.2 FOOD PREFERENCE

5.4.2.1 Differences Between Foods and Non-Foods

Clear differences in macro-nutrient levels between eaten and non-eaten foods were found for fruit pulp in Sabangau (similar findings have also been made for African apes, e.g., chimpanzees and bonobos, Hohmann *et al.*, 2006). Eaten fruit pulp had higher energy, carbohydrate and water content, and lower fibre content, than avoided fruit pulp (**Table 5.4**), though these differences were not found for other food types. Thus, $H_0 5.3a$ (that the energy content of eaten foods is greater then non-eaten foods) can be accepted for fruit pulp, but not for other food types. Tellingly, toughness was also lower for eaten fruit pulp and flowers than for non-eaten species of these food types. Higher toughness of avoided foods has also been observed for orang-utans in the peat swamps of Tuanan (Vogel *et al.*, 2008b), indicating that toughness plays a key role in orang-utan food selection, at least in peat swamps. The higher water content of real-fruit pulps could be due to the generally more fleshy nature of primate fruits (Leighton and Leighton, 1983). Higher water content in eaten than non-eaten chimpanzee and bonobo fruits has also been documented (Hohmann *et al.*, 2006). With the exception of fruit pulp and flowers, however, there are no differences in food properties between eaten and avoided foods, indicating that the key variable/s influencing whether items of these food types are eaten may not have been measured in this study (e.g., the presence of some unmeasured toxin, or lignin contents), or that small sample size may have led to Type II errors.

Another potential explanation is that, due to the often conservative feeding behaviour of herbivores in general (e.g., Freeland and Janzen, 1974) and orang-utans in particular (Rijksen, 1978; Grundmann *et al.*, 2001; Russon, 2002; Jaeggi *et al.*, 2007), orang-utans may not have learnt all of the potential food items in the area. This may be particularly true for less profitable food types, which may comprise a great many potential food items of relatively low quality. This suggestion is boosted by previous observations of geographical differences in orang-utan feeding behaviour that appear to be inexplicable on ecological grounds and, hence, are interpreted as potential cultural differences (i.e., that orang-utans at all sites have not learnt all of the potential food items/feeding techniques consumed/used by orang-utan at other sites, van Schaik and Knott, 2001; van Schaik *et al.*, 2003a; Fox *et al.*, 2004; van Schaik, 2004; Bastian, 2008; Zweifel, 2008). Similar observations have been made for chimpanzees (Whiten *et al.*, 1999, 2001) and white-faced capuchins (*Cebus capucinus*, Panger *et al.*, 2002).

5.4.2.2 Differences Between Preferred and Fall-Back Foods

Based on the results in **Table 5.5** (see also **Appendix I**), it is possible to compose a general description of the four main orang-utan food types (**Table 5.13**). From these descriptions, which are similar to those derived from other ape studies (e.g., Calvert, 1985; Rogers *et al.*, 1990; Knott, 1999; Matsumoto-Oda and Hayashi, 1999; Remis *et al.*, 2001; Remis, 2003; Vogel *et al.*, 2008b; see also Lambert *et al.*, 2004), orang-utan preference for fruit and flowers, and relative avoidance of leaves and bark, are easily understandable. Fruit provides the highest energy intake rates, supporting $H_0 5.3b$ (that

Table 5.13 Generalisations of properties of different major food types[1].

Item	Desirable characteristic	Undesirable characteristic
Fruit (P)	Large size and consequent energy/ item, highest energy/lipid/TNC intake rates, relatively low toughness	Highest weight intake[2], high tannin content[3] and YM.
Flowers (P)	Lowest toughness/YM, low tannins, energy/nutrient intake rates generally higher than leaves and bark	Smaller size, and consequent energy/item, than fruit
Leaves (F)	Highest % protein and protein/ fibre ratio	High toughness, smaller size (and consequent energy/item) than fruit
Bark (F)	None	High toughness and YM, lowest energy/weight/protein/TNC intake

Abbreviations: F = fall-back food; P = preferred food.

1. Not all of these differences between food types were significant, but sample size for flowers and bark was often very small ($n < 5$ in some cases) and so there is a high probability of Type II errors in these cases.
2. Considered an undesirable characteristic here due to negative correlations with selectivity rank in bivariate analyses (**Table 5.7**).
3. Compared to other food types in Sabangau, but not compared to other studies.

preferred foods yield higher rates of energy intake than FBFs), though it is clear that energy intake rate is not the only factor potentially influencing food type preference. Fruit also offers the highest intake rates for all macro-nutrients (with the exception of protein, which is slightly, but non-significantly, higher in leaves), supporting the suggestion that fruit can be a valuable source of protein for orang-utans (Hamilton and Galdikas, 1994). In common with gorilla foods in Bai Hokou (Remis, 2003), fruits also contain more tannins than any other food type (though this was not significant), suggesting that tannins do not discourage orang-utan feeding at the relatively low levels found in Sabangau. Flowers provide slightly (non-significantly) lower intake rates than fruit, but are soft and easy to process, and contain low amounts of tannins. Leaves have the highest protein

content and protein/fibre ratio, but these advantages are presumably offset by difficult processing (due to high toughness) and/or high phenolic levels. Leaves may also contain more toxic compounds not measured in this study, such as alkaloids and terpenes (Ganzhorn, 1988; Iaconelli and Simmin, 2002), which have previously been reasoned to influence negatively food selection in orang-utans (Leighton, 1993; Hamilton and Galdikas, 1994) and other primates (e.g., baboons: Whiten *et al.*, 1991; lemurs: Ganzhorn, 1988). Bark is difficult to process and gives very low rates of energy/nutrient intake and, hence, should be expected to be eaten in large quantities only when absolutely necessary.

This would appear to be true in Sabangau, with orang-utans seemingly turning to leaves as their first-choice FBF, and only consuming large quantities of bark when fruit/flower availability and, hence, consumption, reaches very low levels (i.e., March-June 2007, **Figures 3.3** and **4.4**, **Table 4.13**). Leaves are much more nutritious than bark, however, and so why eat bark at all? One reason could be limited availability of new leaves for consumption, but this seems unlikely, considering that new leaves of most real-leaf species were available in most months. Another reason could be a maximum tolerance level for phenolic and/or other toxic compounds, e.g., alkaloids, which are generally present in higher concentrations in leaves, and especially young leaves (McKey, 1974; Oates *et al.*, 1980; Ganzhorn, 1988; Iaconelli and Simmin, 2002; this study). This may place a maximum limit on the amount of leaves that can be eaten, especially as orang-utans lack the detoxifying/digestion-inhibitor-neutralising gut microflora of the more folivorous colobines (Oates *et al.*, 1977; Oates *et al.*, 1980; van Schaik, 2004). Once this

limit is reached, orang-utans may then be forced to consume the only other food available to them in large quantities, i.e., bark (observations of food switching due to high toxin ingestion associated with certain foods have been made in a large number of studies, e.g., Freeland and Janzen, 1974; Westoby, 1978; Milton, 1979; Moss, 1991; Altmann, 1998). Observations of maximum tolerance thresholds for anti-feedants have been made in other species (*Microcebus murinus*: Iaconelli and Simmin, 2002; *Lemur catta* and *Propithecus verreauxi verreauxi*: Yamashita, 2008), boosting the plausibility of this explanation.

5.4.2.3 Differences in Selection Criteria Between Preferred and Fall-Back Foods

Overall, the analyses in this chapter suggest that the expected rate of energy intake is not the best predictor of food preference rankings within any food type and, hence, $H_0 5.3c$ must be rejected (field studies on mountain gorillas have also indicated a lack of influence of energy content on food selectivity rank, Ganas *et al.*, 2008). Although many significant bivariate correlations were found between food properties and selectivity ranks in different age-sex classes, such analyses are difficult to interpret and inconclusive, due to inter-correlations between independent variables. Few significant multi-variate models could be constructed, but these suggest that (i) preference rank among preferred food types (i.e., fruits and flowers) is positively related to the protein/fibre ratio of foods in adult females, and (ii) leaf selectivity rank in nulliparous females is *negatively* related to energy content. Similar conclusions regarding the importance of protein/fibre ratios in primate food selection have been made for other primate species (e.g., baboons, Whiten *et al.*, 1991; Barton and Whiten, 1994), but

protein/fibre is generally considered to be most important in leaf selection by folivorous primates (Milton, 1980; McKey *et al.*, 1981; Garber, 1987; Fashing *et al.*, 2007), including mountain gorillas (Ganas *et al.*, 2008), though it is unclear whether these findings also apply to the more frugivorous lowland gorillas. Asides from the absence of any plausible theoretical reason to explain the latter observation in nulliparous females, the small sample size and fact that leaf species eaten could not be identified in many feeding bouts suggests that this observation should be treated with extreme caution and is most probably spurious.

Among the preferred foods, fruit and flowers, selection appears to be for quality (high protein/fibre ratio) over quantity (energy/nutrient intake), at least for adult females. In fact, selectivity rank of adult females and flanged males was negatively affected by NDF, weight or energy intake from a food item in at least one bivariate analysis (all trends were also in the same direction). NDF, weight and energy intake are all very highly correlated between items ($r_s > 0.910$ and $p < 0.001$ in all cases, **Appendix III**). Thus, it is likely that the negative bivariate correlations between preferred-food selectivity rank and energy intake in some cases are a result of the strong correlations between these variables, and selection against items that involve the consumption of large amounts of relatively indigestible fibre, rather than selection against foods that yield high energy returns *per se*.

In this context, these results are not surprising. Not only does fibre offer lower energy returns/unit weight than other macro-nutrients (NRC, 2003) and, hence, occupy space in the gut that could be occupied by more energy-rich nutrients, but consumption of large

amounts of dietary bulk also leads to increased food passage rates through the gut, decreasing the efficiency with which energy and nutrients can be extracted from the food (Milton and Demment, 1988; van Soest, 1994; Lambert, 1998). Thus, unless fibre contents of foods are very low or foods are very energy rich, consuming large amounts of food bulk in order to maximise energy intake is probably not an optimum strategy. This selection for high-quality foods over large quantities of food intake, in addition to a large colon surface area (Chivers and Hladik, 1980) and long transit time (Caton *et al.*, 1999), classifies Sabangau orang-utans (or at least adult females) as maximisers of digestive efficiency, rather than food intake (see Milton, 1981a). Similar conclusions have also been reached for gorillas, which have been reported as selecting foods with high digestibility (Calvert, 1985; Plumptre, 1995).

Accepting the significant model of a negative influence of energy content on leaf selectivity rank in nulliparous females as probably spurious, the properties influencing the selectivity rank of FBFs – leaves and bark – remain unclear. In contrast to preferred foods (and the findings of Hamilton and Galdikas, 1994 for orang-utans and Takemoto, 2003 for chimpanzees, which suggest important roles for protein and tannin content in determining leaf choice, similar to findings for more folivorous primates, see above), nutritional quality seems relatively unimportant in determining selectivity rank of FBFs in Sabangau. With the exception of the probably spurious significant model for nulliparous females mentioned above, no other significant multi-variate model for explaining leaf selectivity rank could be built, suggesting that some unmeasured variable, such as critical stress intensity (Vincent and Saunders, 2002; Agrawal and Lucas, 2003),

lignin content/digestibility or some type of toxin may explain orang-utan leaf preference in Sabangau.

Sample size for bark species was small and, hence, multi-variate models of selectivity could not be built. The only significant bivariate correlation indicated a preference for species with high lipid contents for flanged males. If this effect is true, this would not be surprising as, although bark lipid content is not particularly high, bark eaten by orang-utans has been shown to have a complex fatty-acid profile, including linoleic, alpha-linoleic, palmitic, stearic and oleic acid, indicating that orang-utans can obtain essential fatty acids through consuming bark (Heller *et al.*, 2002). As bark is also the toughest food item available, it would also not be surprising if more complete future analyses found toughness to be an important influence on bark selectivity.

The apparent reduced effects of food properties on selectivity for FBFs could also have a cultural explanation. Cultural differences in feeding behaviour might be expected to be greater for less preferred/profitable food types, as items within these food types all yield relatively low rewards (Knott, 1998, 1999; this study). Thus, little stands to be gained from continually seeking out and testing new items of this food type, compared to more profitable items, such as fruit (Bastian *et al.*, 2008). A comparison of orang-utan diets between Tuanan and Sungai Lading (two neighbouring, ecologically-similar sites in Central Kalimantan, separated by an impassable river) supports this: dietary overlap between sites was greatest for fruit than for less-preferred food items (Bastian, 2008; Zweifel, 2008). Similar results have also been found between chimpanzee populations in Mahale Mountains and Gombe National Parks, Tanzania (Nishida *et al.*, 1983). Thus, as

a community, orang-utans in Sabangau could have learnt a suite of FBF species that are not too toxic and yield reasonable returns and, due to their natural conservatism and unwillingness to try lots of novel, potentially toxic, foods with likely meagre rewards, have never incorporated other, potentially better, FBF species into their diet.

5.4.2.4 Alternative Explanations

Unfortunately, despite my intention to incorporate as many variables as possible into these selectivity analyses, some food properties that could influence orang-utan food selection were not included in this study. The most notable of these are other types of toxin, specifically alkaloids, and lignin, sugar and micro-nutrient contents. Numerous authors have demonstrated that alkaloids (a very heterogeneous group, including a whole variety of toxic compounds, including terpenoids) are important in determining primate food choice (e.g., lemurs: Ganzhorn, 1988; baboons: Whiten *et al.*, 1991; orang-utans: Hamilton and Galdikas, 1994), although this does not appear to be the case for colobines, whose forestomach microflora have considerable alkaloid-detoxification capabilities (Oates *et al.*, 1977, 1980). Although the results of some bivariate analyses appear to indicate preference for more alkaline leaves by some age-sex classes, and pH did not differ between eaten and avoided foods, avoidance of alkaloids and/or other toxins remains a distinct possibility. This is especially likely in light of the prediction that there may be ca. 400,000 plant secondary compounds, many of which will likely be toxic (Swain, 1977).

Lignin is included in the NDF fraction, but is composed of insoluble, polyphenolic fibres, and is essentially unfermentable and indigestible (Conklin-Brittain *et al.*, 2006). Lignin levels in orang-utan diets in Gunung Palung were 16% and, hence, formed almost half of the fibre fraction (which averaged 34% of dietary intake, Knott, 1999; Conklin-Brittain *et al.*, 2006). Unfortunately, analysis of lignin contents could not be performed at the LIPI-Bogor laboratory, but, as the mean NDF fraction of the orang-utan diet in Sabangau (31.7% of dry weight, **Table 4.8**) is very similar to Gunung Palung, it is likely that the proportion of lignin is also similar. The amount of lignin in chimpanzee (Conklin-Brittain *et al.*, 1998) and mountain gorilla (Rothman *et al.*, 2007) diet is known to decrease when preferred fruits are more available/consumed, and both lignin content and digestibility of foods have been shown to influence food selectivity in gorillas (Calvert, 1985; Plumptre, 1995). Thus, lignin/digestibility is highly likely to be important in determining orang-utan food preferences, especially considering the apparent importance of fibre on orang-utan fruit/flower selectivity in Sabangau.

Soluble sugars (fructose, sucrose and glucose) are highly digestible and a good source of energy. Studies of captive gorillas and chimpanzees indicate a preference for sweeter solutions, which may act as a criterion for food selection (Remis, 2002; Remis and Kerr, 2002), corroborating earlier suggestions regarding wild gorillas (Rogers *et al.*, 1990; Remis *et al.*, 2001) and chimpanzees (Conklin-Brittain *et al.*, 1998). Recent studies on wild mountain gorillas also show selection for sugars in leaves and pith, which may even over-ride the presence of condensed tannins in some foods (Ganas *et al.*, 2008). The same authors also suggest that the apparent preference of one group for fruits high in fibre and

condensed tannins may be due to simultaneous ingestion of relatively high amounts of sugar. Sugars form part of the TNC fraction, but, unfortunately, were not analysed directly in this study. Thus, the lack of influence of TNC content on orang-utan selectivity generally observed in this study is not necessarily indicative of a lack of preference for high sugar levels.

Various micro-nutrients, e.g., calcium, copper, iron, potassium, sodium and zinc, have been shown to influence primate food selection (e.g., calcium, potassium and sodium have been suggested to be important in feeding selectivity of western lowland gorillas in clearings, Magliocca and Gautier-Hion, 2002) and/or have even been postulated as important determinants of primate density for some species (McKey *et al.*, 1981; Waterman *et al.*, 1983; Takemoto, 2003; Chapman *et al.*, 2004; Rode *et al.*, 2006). For example, Rode *et al.* (2006) found copper and sodium intake levels to be very low and potentially limiting for red-tail monkeys, *Cercopithecus ascanius*, due to the fact that these minerals are not essential for plants and, hence, occur at very low concentrations (McDowell, 2003). Unfortunately, analysis of micro-nutrient contents was not possible in this study and, although the ash residue contains a whole variety of inorganic minerals, its composition remains unknown and an influence of minerals on orang-utan food selection cannot be discounted.

Consumption of plants for medicinal purposes (Huffman *et al.*, 1996; Huffman, 1997; Huffman, 2003; Huffman and Hatoshi, 2004) also cannot be discounted. Plants of the genus *Commelina* are chewed and rubbed into the fur in Sabangau, and this is thought to

be a form of self medication, most probably as an anti-bacterial or anti-inflammatory agent (Morrogh-Bernard, 2008). While this may explain selection for a small number of items, however, it is unlikely to explain selection for the majority of food items, which are much more likely to be eaten for nutritive reasons.

It could be argued that, being as leaves and bark are not preferred foods, the concept of preference and, hence, the selectivity analysis performed herein, do not apply to these food types. Few would argue, however, that just because a food type is not preferred, all food items within that food type are perceived as equal by the forager. This is supported by the large degree of variation in selectivity values for both leaves and bark (**Appendix II**), where selectivity values of the most-preferred species are orders of magnitude higher than for the least-preferred species.

As the data on relative consumption of food items by an age-sex class were not obtained from the same individual/s each month, it is possible that some error could have been introduced due to different individuals within an age-sex class having different food preferences. This is assumed not to be the case here, but could certainly be addressed in future analyses.

5.4.3 BROADER IMPLICATIONS

5.4.3.1 Differences Between Age-Sex Classes

Various authors have hypothesised that, due to the large differences in body size between sexes, flanged male orang-utans should consume a lower- (Rodman, 1977, 1979; Hamilton and Galdikas, 1994) or higher-quality diet than adult females (Wheatley, 1987). As demonstrated in **Section 4.3.2** (and by Knott, 1999 for orang-utans in Gunung Palung), the nutrient composition of flanged male and adult female diets was not significantly different, and time spent feeding on the top-four most important dietary items was highly correlated and did not differ between the two age-sex classes. Based on the analyses in this chapter, fruit selectivity rank was not influenced by expected rate of energy intake in either sex, but a role for fibre and protein (i.e., protein/fibre ratio and fibre intake) in diet selection cannot be discounted for both sexes (i.e., significant bivariate correlations existed for both protein/fibre ratio and fibre intake in males and females, though multiple regression models were significant only for adult females, for which protein/fibre ratio alone best predicted fruit selectivity rank). Thus, it is likely that both age-sex classes attempt to maximise dietary quality with respect to protein/fibre ratio and fibre intake and, though this effect appears greater in adult females, this does not result in flanged males consuming a lower-quality diet.

As expected, the greatest disparity in selectivity between age-sex classes was between the two size extremes: nulliparous females and flanged males (**Table 5.6**). For fruit and

flowers (excluding avoided species), nulliparous female selectivity rank was significantly (negatively) correlated only with phenolic content, which did not affect the other age-sex classes. This could be due to lower tolerance of phenolics by nulliparous females, due to their smaller size and, hence, smaller gut and reduced dilution of phenolic compounds. Nulliparous female food-selection criteria are more difficult to interpret than for other age-sex classes; i.e., fruit/flower selectivity rank is not affected by any of the chemical properties that appear important in other age-sex classes and leaf selectivity is negatively associated with energy content. Why should this be?

Four possible explanations could be put forward: (1) these results are due to chance/are spurious and, hence, are not a true reflection of reality, (2) nulliparous females are small (all the individuals included in this study were immature) and are not hampered by the demands of reproduction and, hence, have less difficulty in meeting their energetic/nutritional requirements, and so do not need to select the most nutritious foods, (3) nulliparous females are younger and, consequently, are less experienced foragers and have a less complete knowledge of food quality and/or try more new foods, and (4) that selectivity is influenced by some other factor not recorded here. For leaves, in which sample size was small and identification of species consumed in the field was not possible in many bouts, the first explanation is probably most likely. For fruits and flowers, the second explanation is plausible, but, as a result of their smaller body and gut size, immature nulliparous females should also be less efficient at digesting fibre (e.g., Chivers and Hladik, 1980; Demment, 1983; Cork and Foley, 1991; Remis, 2000) and, hence, should be expected to avoid fibrous foods, as do adult females (and probably also

flanged males). Although, unfortunately, the last explanation cannot be dismissed, this leaves the third explanation as potentially the most likely, with respect to fruits and flowers.

5.4.3.2 Are Orang-utans Foraging Optimally?

While previous studies have indicated that fruit selection in orang-utans (Leighton, 1993) and chimpanzees (Matsumoto-Oda and Hayashi, 1999, though the authors of this study actually assessed importance, rather than preference, see definitions in **Section 5.1**) matches the predictions of classic optimal foraging theory (OFT, Stephens and Krebs, 1986), that is, that fruits are selected based on expected rate of energy intake, the results of this study are more equivocal. In agreement with OFT, eaten fruit pulp had higher energy content than avoided fruit pulp and the preferred food types (fruits and flowers) yielded higher energy intake rates than FBFs, though it is likely that macro-nutrients, and especially toughness, have at least as great an influence as energy content/intake in these regards. Furthermore, quality appears more important than quantity in determining fruit/flower selectivity rank, with selection based primarily on protein/fibre ratio (at least for adult females), and energy intake/content was actually *negatively* correlated with selectivity rank in some analyses, in direct disagreement with OFT's energy maximising predictions.

Many studies on other primate species, whilst not setting out to test explicitly optimal foraging models, have also found that their subjects either select foods with (1) high

protein/fibre ratio (e.g., howler monkeys, *Allouatta* sp.: Milton, 1979), (2) high digestibility, low lignin and high protein (e.g., gorillas: Calvert, 1985; Plumptre, 1995), (3) high protein content and low fibre/toxin levels (e.g., lemurs: Ganzhorn, 1988; black colobus, *Colobus satanus*: McKey *et al.*, 1981; mountain gorillas: Ganas *et al.*, 2008), or (4) that their subject just does not behave as OFT models predict (e.g., patch residence times: Grether *et al.*, 1992; Kamil *et al.*, 1993).

Does this mean, then, that orang-utans in Sabangau are "sub-optimal foragers" or that OFT is of limited/no use to primatologists (e.g., Post, 1984)? Not necessarily. On a general level, it must be remembered that OFT is more than just rate maximisation (Stephens and Krebs, 1986). In addition, not only can many different alternative "currencies" be envisaged, but selection can also be for minimising (e.g., toxin intake), as well as maximising a currency, and selection can be towards maximising or minimising within certain constraints (e.g., maximising energy intake within the constraint of a maximum tolerance for certain toxins).

Furthermore, as these models enable hypotheses concerning design and constraint to be tested, they can indicate why the animal's behaviour does not comply with the model's predictions, which is often the question of real interest anyway (Foley, 1985; Stephens and Krebs, 1986; Grether *et al.*, 1992). This is particularly relevant here: although orang-utan fruit selectivity in Sabangau was negatively correlated with the expected rate of energy intake in some bivariate analyses, energy intake among fruits was very strongly correlated with both dry weight (r_s = 0.980, n = 47, p < 0.001) and fibre intake (r_s =

0.911, $n = 47$, $p < 0.001$) (**Appendix III**). Thus, in attempting to maximise energy intake while eating fruit, orang-utans would also be maximising their consumption of relatively indigestible, nutrient-poor bulk. This would result in decreased digestion efficiency and, hence, possibly a reduced level of energy absorption (Milton and Demment, 1988; van Soest, 1994). Thus, orang-utans may optimise the amount of fibre intake compared to gut passage time (Knott, 1999). Furthermore, energy intake was also negatively correlated with percentage protein, protein/fibre ratio and phenolic content (**Appendix III**).

Thus, in adult females at least (and possibly also in flanged males), the optimal strategy for selecting fruits appears to be to maximise nutritional quality, rather than maximising food/energy intake. Presumably, this strategy must result in increased rates of energy/nutrient *absorption*. This also seems to be the case for gorillas, whose foods are also high in fibre and which appear to select foods primarily for low fibre and high protein content, and high digestibility (Calvert, 1985; Rogers *et al.*, 1990; Plumptre, 1995; Remis, 2002; Ganas *et al.*, 2008; though fruit selectivity in one group in this latter study was actually positively related to fibre content, but this is though to be a result of simultaneously ingesting large amounts of sugar). In agreement with OFT and Leighton (1993), however, orang-utans in Sabangau did prefer trees with a large crop size of fruit (i.e., a large expected meal size, **Table 5.9**).

Although foraging strategies and dietary preferences within primate species are generally conservative, it is possible that inter-site differences in selection criteria may exist, depending on local phenological patterns and nutritional contents of foods available

(Garber, 1987; Ganas *et al.*, 2004; Yamagiwa and Basabose, 2006b; see also Chapman *et al.*, 2003). Considering the large differences in orang-utan food availability, diet composition and energy intake between orang-utan research sites (see **Chapters 3** and **4** and references therein), this is eminently plausible for orang-utans. Indeed, this would appear to explain the differences in fruit-selection criteria between Kutai (Leighton, 1993) and Sabangau.

When "primate fruits" are compared between the two sites, it is apparent that variation in protein, lipid and fibre contents of fruits is greater, and variation in carbohydrate contents lower, in Sabangau (**Table 5.14**). Furthermore, mean TNC content of primate fruits in Kutai is greater than Sabangau, and mean NDF content lower. Thus, the respective influences of protein and fibre on fruit selection in Sabangau, and carbohydrate in Kutai, are not surprising. Similarly, the more nutritious nature of primate fruits in Kutai may favour a strategy of maximising food intake, rather than food quality, as seen in adult females (and probably also flanged males) in Sabangau. In addition, Kutai is a masting forest (Leighton, 1993) and, hence, orang-utan energy intake in Kutai is probably also tightly related to fruit availability, as in the masting forests of Gunung Palung (Knott, 1998, 1999). Thus, greater selectivity for food energy content and maximising energy intake may be expected in Kutai, and the differences in fruit selection criteria between Sabangau and Kutai are most likely a product of different ecological conditions between the sites, in particular the more fibrous nature of fruits and the lack of mast-fruiting, and consequent lack of very high-energy fruits available during masts in Sabangau (energy

Table 5.14 Comparison of nutrient contents (percentage dry matter) of "primate fruits" eaten by orang-utans in Kutai[1] and Sabangau.

	Sabangau			Kutai	
Variable	**Median**	**Range[2]**	**Difference**	**Median**	**Range[2]**
% protein	7.0	3.4-15.7	>	6.4	2.4-10.6
% lipid	5.5	0.5-20.7	>	1.5	0-5.0
% fibre[3]	42.4	13.8-64.1	>	21	10-38
% TNC	41.3	19.4-72.0	<	61.7	32.8-86.4
n	29			23-30	

1. Data from Leighton (1993).
2. Range between 10th and 90th percentiles.
3. NDF for Sabangau; acid-detergent fibre (ADF) for Kutai. Based on Appendix I in Knott (1999), the conversion factor for ADF to NDF is 1.34. Thus, NDF in Leighton's sample would have been roughly 28.1, with a range of 13.4-50.9, still substantially lower than Sabangau.

content of fruits available during masts in Gunung Palung is greater than during inter-mast periods, and is higher than in Sabangau, Knott, 1998, 1999, **Table 4.23**).

OFT also predicts that the consumption of non-preferred foods should depend not on their own availability, but on the availability of more preferred/profitable items; i.e., only when items with high profitability are rare or unavailable should less profitable items be included in the diet (Stephens and Krebs, 1986). This prediction is certainly borne out in Sabangau, at least at the level of food type.

5.5 SUMMARY

1. The availability of different food types was compared to their consumption during the study period. These analyses indicate that fruit and flowers are the preferred foods (i.e., are eaten in relatively greater proportions than they are available), and leaves and bark are fall-back foods (FBFs, i.e., consumption is negatively correlated with availability of preferred foods) in Sabangau, as in mast-fruiting habitats in Borneo.
2. The distinction between preferred and FBFs appears to stop at the level of food type, i.e., fall-back fruits do not exist. This is in contrast to findings at other ape research sites, where certain species of fruit (frequently figs) are used as FBFs during lean periods. This is interpreted as being due to the relatively low quality, and relatively low variation in quality, of fruit in Borneo, and especially peat-swamp forest, compared to Sumatran and African forests.
3. Data were collected on 38 chemical and non-chemical properties of orang-utan foods. These properties were compared between real and non-foods, between food types and between food items of each major food type (fruit and flowers, leaves and bark), in order to assess the determinants of food selection.
4. Differences in food properties between real and non-foods indicate higher energy and carbohydrate, and lower fibre, content in eaten than avoided fruit pulps, and lower toughness in consumed fruit pulps and flowers. All differences in food properties between eaten and avoided food items were not significant for other food types. An alternative, cultural, explanation is invoked as a possible reason for this, especially for non-preferred foods of lesser quality.

5. Preferred food types (fruits and flowers) appear to be selected largely on the basis of expected rates of energy/nutrient gain, in agreement with the predictions of optimal foraging theory.
6. For fruits and flowers, significant multi-variate models of selection could only be built for adult females, for which protein/fibre ratio alone was the best predictor of selectivity rank (protein/fibre ratio was also positively correlated with fruit-pulp selectivity rank in bivariate analyses for flanged males). Selectivity rank of adult females and flanged males was negatively affected by fibre, weight or energy intake in at least one bivariate analysis. This is suggested to represent selection against ingestion of large amounts of relatively indigestible fibre and maximisation of food nutritional quality and digestive efficiency, rather than selection against foods yielding high energy returns *per se*.
7. Nutritional quality seems less important in selection of FBFs, leaves and bark. Significant multi-variate models predicting leaf selectivity rank could only be built for nulliparous females, for which the best model comprised energy content/100 g and energy content/item, which both negatively influenced preference. It is considered most likely that this result is spurious, as a result of low sample size and the large proportion of leaf-feeding bouts for which species identifications could not be made. Multi-variate models of selectivity could not be built for bark, due to small sample size, and the only significant bivariate correlation was for flanged males, which preferred species with higher lipid contents.
8. Potential alternative explanations and methodological issues affecting the analyses are discussed.

9. Adult females appear to be more sensitive to food quality than flanged males, but both age-sex classes appear averse to the consumption of high amounts of fibre and the proportion of fibre in the diet was not significantly different between them, refuting the hypothesis that flanged males have lower dietary quality than adult females. Unsurprisingly, the greatest disparity in selectivity between age-sex classes was between the two size extremes, nulliparous females and flanged males.
10. Differences between orang-utan fruit selection criteria in Sabangau and Kutai National Park (where selection is towards high carbohydrate content and is indicative of attempts to maximise energy intake rate) are interpreted as being a result of ecological differences between sites. Higher variability in protein and fibre contents, and higher absolute fibre and lower carbohydrate contents, in fruits and the lack of mast-fruiting in Sabangau are the most likely explanations for the observed differences.
11. Thus, orang-utans in Sabangau are not "sub-optimal" foragers, and what constitutes "optimal foraging" may differ depending on the foraging decision in question, and between sites (and species), due to differences in prevailing ecological conditions, and individual/specific demands.

6. FOOD AVAILABILITY, ENERGY INTAKE AND BEHAVIOUR

6.1 INTRODUCTION

In the last two chapters, I have assessed the effects of fruit/flower availability on diet composition and energy intake (**Chapter 4**), and food-selection criteria (**Chapter 5**). It is now pertinent to ask how food availability and dietary composition/intake affect orang-utan behaviour, and how this can be interpreted in terms of orang-utan foraging strategies in Sabangau. Thus, there are three main aims in this chapter: (1) to present basic data on orang-utan activity profiles during the study period, (2) to identify how variations in fruit/flower availability, diet composition and energy intake influence behaviour, (3) to identify the foraging strategy in Sabangau, and (4) to compare these observations to those made in other orang-utan and African ape studies.

As discussed in Section **4.4.1**, adult female orang-utans should strive to maintain a positive energy balance virtually continuously, in order to continue normal ovarian cycling, and, when pregnant/lactating, maintain a continual supply of energy to the developing young (Wasser and Barash, 1983; Ellison, 1990; Ellison *et al.*, 1993; Knott, 1999, 2001; Ellison, 2003; Emery Thompson, 2005; Emery Thompson and Wrangham, 2008). Male gamete production is very insensitive to acute changes in energetic status, although testosterone production, and, consequently, behavioural mating effort and

various physiological correlates, such as muscle mass, can vary depending on energetic state (humans: Ellison, 2003; chimpanzees: Muller and Wrangham, 2005). These effects in males, however, are likely to be much less than for females. Unfortunately, due to the small number of reproductively-active females in this study (n = 3, two of which would not have cycled during the study period), the effects of changes in energy intake and fruit/flower availability on female reproduction could not be assessed. One adult female had a small infant throughout, one gave birth in September 2005, and one had no offspring and so was potentially cycling, but very rarely entered the study area and was only found during the first month of the study. The female with a small infant was observed to mate once, in February 2007, but this was a forced copulation with an unflanged male. It is unlikely she was cycling, as the infant was only 5-6 years old, and no new offspring or signs of pregnancy had been seen by assistants following this orang-utan from the cessation of fieldwork for this study until the time of writing. The effects on behaviour could be assessed, however, and the likely effects of these observations and those in **Chapter 4** are discussed in **Chapter 7**.

Based on a comparison of orang-utan activity budgets at ten research sites, including Sabangau, it has been suggested that orang-utans employ one of two foraging strategies (Morrogh-Bernard *et al.*, 2009). In the "*sit-and-wait*" strategy, energy expenditure is minimised during periods of low fruit availability, by spending long periods of time resting and relatively short periods feeding and travelling, and energy intake is maximised during the brief periods of high fruit availability. In the *"search-and-find'* strategy, energy intake is maintained at a relatively constant level by continuously

feeding and moving in search of food. The same authors suggest that orang-utans adopt the former strategy in mixed-dipterocarp forests characterised by mast-fruiting events and irregular fruit availability (e.g., Gunung Palung, Kutai), and the latter strategy in swamp forests with a regular supply of fruit (e.g., Suaq Balimbing, Sabangau), or in dryland forests with high strangling-fig density (e.g., Ketambe). In **Chapters 4** and **5**, it is shown that the effects of fluctuations in orang-utan fruit/flower availability on diet composition and energy intake, and food-selection criteria, are not always consistent between age-sex classes. Thus, while it is possible to distinguish broadly between sites in this way, it is also possible that foraging strategies could differ between age-sex classes.

Another useful distinction regarding foraging strategies is that of "*energy maximising*" and "*time minimising*" (Schoener, 1971). If an age-sex class is pursuing a strategy of maximising energy intake, then we should expect that increased preferred-food availability will lead to, in order of importance: (1) increased energy intake, and (2) increased day range (DR, the distance travelled in one day), as patch density is lower for preferred foods (Mann-Whitney, fruits/flowers *vs.* new leaves/cambium, $n = 105$, $p < 0.001$). Increased feeding and decreased resting are not necessarily expected, as energy intake will be increased by these activities regardless of the amount of preferred foods available (although the increase in energy intake derived from these activities will be greater when preferred foods are more available).

In contrast, a time minimiser will attempt to satisfy dietary requirements as quickly as possible, in order to either conserve energy by resting, or allow more time for other

activities, e.g., socialising (Schoener, 1971). Thus, increased fruit/flower availability should lead to: (1) no change in energy intake, and (2) decreased time feeding, as energy can be obtained more quickly from preferred foods (**Table 5.5**). Increased time resting, and decreased ranging and active period (AP, the amount of time spent awake, see **Section 6.2.1**), would indicate time minimising to conserve energy, whereas increased sociality would indicate time minimising to allow more time for social activities. Increased consumption of preferred foods would be expected with both strategies, as this increases energy intake rate, thereby allowing animals to either consume more energy throughout the day (energy maximising), or feed for less time before satisfying their requirements (time minimising).

Thus, in order to achieve the aims in this chapter, and in light of the over-arching null hypothesis in this thesis (i.e., that observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats, **Section 1.1**), the following hypotheses were tested:

Effects of fluctuations in food availability

$H_0$6.1: Orang-utans in Sabangau respond to decreases in fruit availability in the same ways as do orang-utans in masting habitats (MacKinnon, 1971, 1974; Rodman, 1977; Mitani and Rodman, 1979; Knott, 1999), by: (a) spending less time socialising (adult females), (b) decreasing DR (also seen in Tanjung Puting, Galdikas, 1979), (c) decreasing time spent travelling (flanged males, also seen in Ketambe, Morrogh-Bernard *et al.*, 2009), (d) increasing time spent feeding

(flanged males), and (e) increasing AP. No change in time spent resting is observed (f).

$H_0$6.2: Increased availability of preferred foods leads to an increase in their consumption, which allows orang-utans to increase daily energy intake.

$H_0$6.3: Socialising is energetically costly for orang-utans, because: (a) it results in increased energy expenditure, and/or (b) it results in decreased energy intake. Energy expenditure is not estimated here, as collection of data with sufficient detail to accurately estimate energy expenditure (cf. Knott, 1999) was not possible, due to restricted visibility and mobility in Sabangau, but behavioural changes associated with increased sociality, which indicate increased energy expenditure (i.e., increased AP, decreased time feeding and resting, and increased time travelling and DR), were recorded (cf. Galdikas, 1988; Mitani, 1989; van Schaik, 1999; Wich *et al.*, 2006a). DR is particularly important, as travelling accounts for the largest proportion of energy expenditure in apes (Leonard and Robertson, 1997; Knott, 1999; Pontzer and Wrangham, 2004; Knott, 2005; Lehmann *et al.*, 2007).

$H_0$6.4: Increased energy intake enables increased sociality. This is likely if sociality is energetically costly to orang-utans (*$H_0$6.3*), and energy balance is close to zero or negative (i.e., orang-utans are energetically stressed, which would seem to be the case in Sabangau, **Chapter 4**).

If these hypotheses are supported, this would indicate that orang-utan behaviour and, hence, energy expenditure, in Sabangau is influenced by fruit/flower availability, diet composition and, ultimately, energy intake.

Orang-utan forging strategies

$H_0$6.5: Orang-utans in Sabangau follow an "energy-maximising" foraging strategy. This hypothesis will be supported by the acceptance of *$H_0$6.1b* (that DR increases when feeding more on preferred foods) and, crucially, *$H_0$6.2* (that energy intake increases when the availability and consumption of preferred foods increases).

Comparisons with orang-utans in mast-fruiting forests in Borneo

$H_0$6.6: Orang-utan activity profiles in Sabangau are similar to those in masting habitats in Borneo. Tests of this hypothesis have recently been performed by Morrogh-Bernard *et al.* (2009), and the data collected during this study are compared to those presented by Morrorgh-Bernard *et al*. to assess whether their conclusions hold with the inclusion of my data.

$H_0$6.7: DR is similar for orang-utans in Sabangau and masting habitats.

$H_0$6.8: Orang-utans in Sabangau spend a similar amount of time socialising as do orang-utans in masting habitats.

$H_0$6.9: The following differences in activity profiles exist between age-sex classes, as in mast-fruiting habitats in Borneo (Mitani, 1989; Knott, 1999; Morrogh-Bernard *et al.*, 2009): (a) adult female time socialising > flanged males, (b) adult female DR > flanged males, (c) flanged male time travelling < all other age-sex classes, (d)

adult female and unflanged male time resting < flanged males, and (e) flanged male time feeding < adult females and unflanged males.

In addition, I test one final hypothesis, based on the observation that, across primates as a whole, resting time is positively correlated with the percentage of leaves in the diet (Dunbar, 1988). This is thought to be a consequence of the fact that the fibre fermentation process requires the animal to be resting (van Soest, 1982), which imposes constraints on the amount of time available for other activities, e.g., socialising (Dunbar, 1988).

$H_0$6.10: Increased fibre intake necessitates: (a) increased time spent resting for colic fermentation, and, hence, (b) decreased time spent travelling and DR, and (c) decreased sociality, as less time is available for these activities.

6.2 METHODS

Methods for estimating food availability and diet composition/energy intake are described in **Sections 3.2** and **4.2**, respectively (see also **Table 3.1** for definitions of terms for food availability). Details on the sampling regime, data excluded from analyses and calculation of basic statistics for inclusion in analyses are furnished in **Chapter 2**. In order to ensure consistency with the feeding data, behavioural data was also limited to follows ≥ 6 h on habituated individuals. A 3-h limit has been used in previous studies in Sabangau (Morrogh-Bernard *et al.*, 2009; Morrogh-Bernard, submitted), but, although the minimum follow length included in analyses can influence mean values for activity

profiles (Harrison *et al.*, in press), the results presented herein should still be broadly comparable with these earlier studies (of the significant differences reported by Harrison *et al.*, in 81% of cases the difference between means was < 2% and in 54% of cases < 1%). As orang-utan fruit/flower availability was found to have the strongest influence of all the estimates of orang-utan food availability on dietary composition/energy intake (**Chapter 4**), this estimate was used in all analyses incorporating food availability in this chapter. Due to space restrictions, results of analyses have been reported using only the high physiological fuel value (PFV) for fibre (**Section 4.2.3**; analyses using the low PFV yielded virtually identical results).

Behavioural observation methods were based on methods established in Sabangau in 2003 and recommended as standard for orang-utan studies (see Morrogh-Bernard *et al.*, 2002; Morrogh-Bernard, submitted for full descriptions; see also van Schaik, 1999 for social methods). These methods were suitable for the data collection requirements of this study, and also had the advantages that all the research assistants were fully trained and competent in their use from the outset, and that long-term standardised data for Sabangau could be collected during the course of this study. Using these methods, instantaneous scan samples of behaviour (Altmann, 1974) were collected at five-minute intervals. Shorter intervals between scans proved impractical, due to the thick undergrowth of *Pandanus* and other species, and the poor visibility in Sabangau.

6.2.1 ACTIVE PERIOD

Active-period (AP) duration was defined as "the length of time in minutes between the start of daily activity (i.e., the time of day when the animal first sits up at the edge of the nest, or performs a behaviour other than reclining) and end of daily activity (i.e., the time of day when the animal reclines in the nest and performs no other observed behaviours)" (Morrogh-Bernard *et al.*, 2002). Thus, AP was calculated from the difference between the start and end times (recorded to the nearest minute) of daily activity in full-day follows.

6.2.2 ACTIVITY PROFILES

Orang-utan behaviour was recorded at five-minute intervals and categorised according to the definitions in **Table 6.1**. From these data, percentage time spent engaged in different activities by each individual *a* in month *x* was calculated as:

(Count of activity $i_{a,x}$ recorded / total count of all activities$_{a,x}$) x 100

From this, total minutes/day spent engaged in each activity was also calculated as:

Percentage time engaged in activity $i_{a,x}$ x mean $AP_{a,x}$

Table 6.1 Activity definitions used for categorising orang-utan behaviour[1].

Activity	Definition
Feeding	The harvesting/processing of food, including travel within a food patch[2].
Food searching	Searching for food, such as termites or other animals, while not actively engaged in feeding. Distinguished from "Feeding" as the orang-utan has yet to begin feeding.
Co-feeding	Feeding in the same patch as another *independent* individual (**Section 2.2.3**), regardless of whether or not the other individual is feeding.
Nest building	Actively making a new nest, or rebuilding or reusing an old nest.
Auto-play	When alone, engaging in any behaviour that is judged by the observer to represent play. This behaviour is very rare.
Socialising	*Interacting* with another individual < 50 m from the focal animal. Excludes interactions between mothers and dependent offspring.
Travelling	Travelling, in trees or on the ground, to another feeding patch or area. Includes travelling with another individual and prolonged pursuits (> 1 min), but excludes movement within a feeding patch.
Aggression towards observer	Actively engaged in aggression (kiss squeak, charge, snag crash etc.) towards the observer, but not aggression towards another orang-utan. This is useful for assessing habituation.
Resting	Not moving and not engaged in any other primary activity (the default option).

1. These definitions are based on those devised by Morrogh-Bernard *et al.* (2002), Morrogh-Bernard (submitted) and van Schaik (1999), to which the reader is referred for full descriptions.
2. A *food patch* is defined as an "individual food tree or liana in which the individual is feeding (if the crowns of two or more separate trees of the same food species are totally inter-digitated then this is considered a single patch)" (Morrogh-Bernard *et al.*, 2002).

When mean AP values for an individual were not available, mean values for that age-sex class in that month were used and, when these were not available, mean values for the population as a whole were used. Levels of "aggression towards observer" were very low, as data on unhabituated individuals was excluded, and habituated individuals very rarely threatened observers. Periods when the focal was lost or not visible were excluded.

6.2.3 DAY RANGE

The distance travelled by the orang-utan between each five-minute scan was estimated to the nearest metre and recorded. Accuracy was ensured by (a) following the route taken by the orang-utan, where possible, and pacing the distance, (b) training with all observers to estimate distances between markers at known distances apart, to ensure accuracy when following the route taken by the orang-utan was not possible and travel distance was estimated visually, and (c) tracing a map of the daily travel route onto a map of the study grid, and checking the accuracy of distances recorded when marked transects were crossed (**Figure 2.4**). In order to incorporate distances travelled during partial follows into the dataset, DR for individual *a* in month *x* was calculated as:

$$DR_{a,x} = \left(\sum D_{a,x} / T_{a,x}\right) \times AP_{a,x}$$

where *D* is the total distance travelled between all five-minute scans by individual *a* in month *x* and *T* is the total time followed in that month. A Wilcoxon-signed ranks test indicated that there was no difference in DR calculated using the above formula and the 6-h minimum follow limit, compared to estimates derived from full-day follows only (all age-sex classes lumped: $n = 45$, p = NS), validating the inclusion of partial follows in this analysis.

6.2.4 SOCIALITY

Following previous researchers (van Schaik, 1999; Morrogh-Bernard *et al.*, 2002; Wich *et al.*, 2006a; Morrogh-Bernard, submitted), the presence of independent con-specifics within a 50-m radius of the focal animal was recorded at each five-minute interval. This distance is thought to be the distance within which orang-utans react to one another (van Schaik, 1999). The number and identity of all con-specifics was recorded. Three measures of sociality were calculated based on these data: percentage time in a party, average mins/day in a party and average party size (PS, van Schaik, 1999; Wich *et al.*, 2006a). Average PS was calculated as:

$$PS_{a,x} = 1 + \left(\sum t_{aj,x} / T_{a,x}\right)$$

where $\sum t_{aj,x}$ is the time t in month x that focal a spent in association with other, independent individuals j, summed for all j's (van Schaik, 1999), and T is the total time followed in that month.

Following Morrogh-Bernard (submitted), additional data on in-depth activity profiles (i.e., resting positions, travel mode employed, etc.), ranging and social interactions were also collected, as part of the long-term Sabangau orang-utan dataset. These data will be included in future publications, but are not presented here, due to space restrictions and limited relevance to the aims in this chapter.

6.2.5 DATA EXPRESSION AND STATISTICAL ANALYSIS

Statistical analysis techniques used in this chapter were similar to those described in the previous two chapters. General linear models (GLM/ANCOVA) and binomial logistic regression were used to test for the effects of fluctuations in orang-utan fruit/flower availability and age-sex class on behavioural variables, as described in **Sections 4.2.5** and **4.3.2**. The latter test was used in instances where the dependent variable was not normally distributed and the range of values was low. While these tests were informative in assessing the causes of variations in the data, they were insufficient to assess the effects of fluctuations in food availability on individual age-sex classes, and further analyses were therefore performed separately on each age-sex class.

Initial assessment of hypotheses pertaining to the effects of fluctuations in preferred food availability ($H_0 6.1\text{-}5$) and fibre intake ($H_0 6.10$) on orang-utan behaviour was performed through bivariate correlations between all variables. These correlations were one-tailed, as hypotheses were directional, and no corrections were made for multiple comparisons, in keeping with the exploratory nature of this analysis (Roback and Askins, 2004). While these bivariate analyses allowed for the rejection of hypotheses reliant on significant correlations and the acceptance of hypotheses reliant on a lack of correlation, further tests were needed to determine whether crucial hypothesis-confirming significant correlations were spurious and whether the independent variable in question explained a significant amount of variation in the dependent variable, after eliminating the effects of other independent variables. Thus, multiple regression techniques were used (cf. **Chapter 5**).

A large number of significant bivariate correlations existed between the different variables (see **Appendix IV**), suggesting that caution is needed when attempting multiple regression analyses, to avoid serious collinearity problems (cf. **Section 5.2.3.2**). Additionally, in most cases, there are plausible theoretical reasons why more than one independent variable (e.g., food availability and PS) may affect the dependent variable in question (e.g., DR, which may increase when feeding more on preferred foods, which are rarer in the environment, $H_0 6.1b$, and/or when spending more time socialising, $H_0 6.3a$). This is further complicated in the present example, when one considers that food availability may also affect average PS ($H_0 6.1a$). Thus, in order to circumvent these problems, measures to eliminate the effects of multi/collinearity of independent variables were taken, as in **Section 5.2.3.2**, and hierarchical regression procedures were used.

When using hierarchical regression, independent variables that were correlated significantly with the dependent variable in bivariate analyses for that age-sex class were inserted into block one (variables that did not provide a significant contribution to the model in test runs were removed), and the independent variable of interest inserted into block two. This enabled the effect of the independent variable of interest to be judged via the significance of the F test for R^2 change, with the effects of the other explanatory variables in block one removed (Tabachnick and Fidell, 1996; Graham, 2003). As such, the decision as to whether the independent variable of interest should remain in the model did not depend on the presence of the other variables and model composition was not affected by the use of marginal statistics (Graham, 2003). If the independent variable of interest significantly improved the model, then it was considered to have a significant

effect. This method differs from the multiple regression methods used in **Chapter 5** as, in this chapter, the aim was to establish whether a particular variable has a significant effect, rather than to build the best predictive model.

In instances where food availability was the independent variable of interest, percentage time spent feeding on preferred foods was not included as a controlling variable in block one of the regression analysis, because time spent feeding on preferred foods is a function of their availability (see **Chapters 4** and **5**). Similarly, as time spent in the three major activities (feeding, travelling and resting) was generally highly correlated in all age-sex classes (**Appendix IV**) and as there are plausible theoretical arguments as to why any one of these may be the underlying cause of these correlations, time spent in other major activities was not included in block one of analyses in which another major activity was the dependent variable of interest.

6.3 RESULTS

Before testing the above hypotheses, I first provide a general description of orang-utan behaviour in Sabangau, for use in comparisons with other sites and previous studies in Sabangau (Morrogh-Bernard, submitted).

6.3.1 ORANG-UTAN BEHAVIOUR: GENERAL DESCRIPTION

6.3.1.1 Active Period

Average AP by age-sex class is shown in **Table 6.2**. These data show that orang-utans in Sabangau spend around 11 h awake each day.

Table 6.2 Average active period (minutes) from July 2005 – June 2007.

Age-sex class	Mean	SD	Min.	Max.	*n* (months)
Adult females	**653**	50	547	758	17
Nulliparous females	**649**	64	528	774	16
Flanged males	**642**	70	395	778	15
Unflanged males	**684**	41	610	770	4

6.3.1.2 Activity Profiles

Summary statistics for percentage time and minutes/day spent engaged in different activities are given in **Table 6.3**. During the study period, orang-utans in Sabangau spent an average of at least half, and generally two-thirds or more, of their time feeding. Travelling (14-19%) and resting (11-17.5%) occupied similar amounts of time, with

Table 6.3 Average percentage time and minutes/day spent engaged in different activities from July 2005 – June 2007. Minutes/day corrected to full-day follow length (see text for details).

		All feeding[1]		Travelling		Resting		Nesting		Socialising	
Age-sex class (*n* mo)	**Statistic**	**Mins**	**%**	**Mins**	**%**	**Mins**	**%**	**Mins**	**%**	**Mins**	**%**
Adult females (19)	**Mean**	**434**	**65.3**	**103**	**15.5**	**116**	**17.5**	**11**	**1.7**	**1**	**0.1**
	SD	77	11.0	37	5.6	48	7.5	10	1.5	1	0.2
	Min	220	36.3	53	8.3	53	7.7	5	0.8	0	0
	Max	562	81.7	200	28.6	229	37.8	50	7.5	5	0.7
Nulliparous females (18)	**Mean**	**434**	**65.7**	**127**	**19.0**	**87**	**12.9**	**12**	**1.8**	**5**	**0.7**
	SD	50	9.2	37	4.6	45	5.7	5	0.8	11	1.5
	Min	353	45.9	65	10.8	32	4.6	5	0.8	0	0
	Max	538	79.0	184	25.4	229	29.8	22	3.4	45	6.6
Flanged males (19)	**Mean**	**444**	**68.7**	**92**	**14.2**	**96**	**14.9**	**10**	**1.6**	**4**	**0.6**
	SD	68	9.5	30	4.6	46	7.0	7	1.0	4	0.5
	Min	294	46.6	24	3.9	25	4.2	4	0.6	0	0
	Max	573	85.7	141	21.0	199	31.5	36	4.9	13	1.8
Unflanged males (11)	Mean	**474**	**71.1**	**114**	**17.0**	**73**	**11.0**	**6**	**0.9**	**0**	**0.0**
	SD	51	7.1	30	4.1	32	5.1	7	1.0	0	0.0
	Min	391	60.8	67	11.2	22	3.7	0	0.0	0	0
	Max	550	85.0	169	26.0	130	20.3	18	2.7	0	0.0

1. Time "feeding", "co-feeding" and "food-searching" (**Table 6.1**) combined; i.e., total time spent feeding.

nesting and socialising generally taking up < 2% of the active period. Minimum time nesting is recorded as "zero" for unflanged males; this is not a true reflection, as no full-day follows were obtained in these months and, hence, no nest-building was witnessed (orang-utans generally construct one "night nest" a day, though day nests are also made frequently, Johnson *et al.*, 2005; Prasetyo *et al.*, 2009). Considering the small proportion of an orang-utan's daily activity budget allocated to nest building, the inclusion of months where no full-day follows were obtained is likely to have a negligible effect on the activity profiles derived. Indeed, including these months probably improves the accuracy of the dataset, considering the temporal influence (of food availability) identified below (**Section 6.3.2)**. Auto-play was only observed on four scans throughout the study, and so has not been listed here.

6.3.1.3 Day Range

Average DRs for each age-sex class over the course of the study are shown in **Table 6.4**. Adult females and flanged males generally travel < 1 km/day, whereas nulliparous females and unflanged males generally travel > 1 km/day. The shortest DR recorded was 280 m (flanged male), and the longest almost 3 km (2,834 m, unflanged male).

Table 6.4 Average day range (m) by age-sex class from July 2005 – June 2007.

Age-sex class	Mean	SD	Min.	Max.	*n* (months)
All combined	**989**	275	540	1,626	23
Adult female	**858**	246	517	1,318	19
Nulliparous female	**1,058**	365	662	2,218	18
Flanged male	**897**	315	280	1,505	19
Unflanged male	**1,149**	628	590	2,834	11

6.3.1.4 Sociality

Average statistics for orang-utan sociality are given in **Table 6.5.** The three measures were all very highly correlated ($r \geq 0.995$, $p < 0.001$ in all cases, $n = 18$ for NF, 19 for AF and FLM and 11 for UFM). Thus, in all subsequent analyses, only average PS is used. All age-sex classes spent the majority of their time alone, with the exception of adult females (mean PS = 1.52).

Table 6.5 Average sociality statistics from July 2005 – June 2007.

Measure	Statistic	Adult females (inc. own)[1]	Adult females (exc. own)[2]	Nulliparous females	Flanged males	Unflanged males
Percentage Time	**Mean**	**52.6**	**8.4**	**16.3**	**3.8**	**2.9**
	SD	34.8	15.9	20.3	6.4	5.1
	Min.	0	0	0	0	0
	Max.	98.4	49.1	63.0	22.4	15.6
Minutes / day	**Mean**	**352**	**108**	**111**	**25**	**21**
	SD	228	114	140	42	38
	Min.	0	0	0	0	0
	Max.	655	370	434	150	120
Average party size	**Mean**	**1.52**	**1.08**	**1.16**	**1.04**	**1.03**
	SD	0.35	0.16	0.20	0.06	0.05
	Min.	1.00	1.00	1.00	1.00	1.00
	Max.	1.98	1.49	1.60	1.22	1.16

1. Including time spent in association with own independent offspring.
2. Excluding time spent in association with own independent offspring.

6.3.2 THE INFLUENCE OF AGE-SEX CLASS AND FLUCTAUTAIONS IN FOOD AVAILABILITY ON BEHAVIOUR

As for diet (**Chapter 4**), it is evident from the average statistics that there is much variation in non-feeding behaviours in Sabangau. Thus, the influence of the two obvious

potential causes of this variation – fluctuations in food availability and differences between age-sex classes – were assessed. The influence of age-sex class and fluctuations in food availability were assessed through GLM for the percentage time spent engaged in the three major activities (feeding, travelling and resting), DR and AP, and through binomial logistic regression for PS (coded as "0" when average PS for an age-sex class in a month = 1, and "1" when PS > 1), as these data were not normally distributed and the range of values was low (**Table 6.6**). Monthly variations in adult female and flanged male activity profiles are shown in **Figure 6.1**.

Table 6.6 Results of tests for effects of age-sex class and fluctuations in orang-utan fruit/flower availability on behaviour: (a) General linear models (ANCOVA). Dependent variables are in *italics*.

	df	***F***	***p***
Active period			
Age-sex class[1]	2, 48	1.896	NS
Orang-utan fruit/flower availability	1, 48	1.945	NS
Percentage time total feed			
Age-sex class	3, 67	1.429	NS
Orang-utan fruit/flower availability	1, 67	1.573	NS
Percentage time resting			
Age-sex class	3, 67	2.757	0.050
Orang-utan fruit/flower availability	1, 67	0.179	NS
Percentage time travelling			
Age-sex class	3, 67	4.116	0.010
Orang-utan fruit/flower availability	1, 67	8.222	0.006
Day range			
Age-sex class	3, 67	1.880	NS
Orang-utan fruit/flower availability	1, 67	1.484	NS

(b) Binomial logistic regression

	df	*Wald*	*p*
Average party size (including time spent with own infant for adult females)[2]			
Age-sex class	3	10.612	0.014
Orang-utan fruit/flower availability	1	7.117	0.008
Average party size (including time spent with own infant for adult females)[3]			
Age-sex class	3	7.998	0.046
Orang-utan fruit/flower availability	1	5.862	0.015

1. Excluding unflanged males, as data on AP duration in unflanged males were only obtained in four months.
2. Omnibus test of model coefficients and Hosmer and Lemeshow tests indicate that the overall model adequately fits the data (Omnibus: χ^2 = 18.046, *df* = 4, *p* = 0.001; Hosmer and Lemeshow: χ^2 = 8.376, *df* = 8, *p* = NS).
3. Omnibus test of model coefficients and Hosmer and Lemeshow tests indicate that the overall model adequately fits the data (Omnibus: χ^2 = 12.589, *df* = 4, *p* = 0.013; Hosmer and Lemeshow: χ^2 = 7.924, *df* = 8, *p* = NS).

The results of these tests indicate that there was no influence of either age-sex class or orang-utan fruit/flower availability on AP, DR and percentage time spent feeding. Significant effects of age-sex class are apparent for percentage time spent resting and travelling, and for PS, and significant effects of orang-utan fruit/flower availability for percentage time spent travelling and PS. Further testing revealed that percentage time spent resting was greater for adult females than unflanged males; differences between the other age-sex classes were not significant (ANOVA: $F_{3, 63}$ = 2.817, *p* = 0.046; Tukey's $HSD_{ADF/UFM}$: *p* = 0.049; *p* = NS in all other pair-wise comparisons).

As significant effects of orang-utan fruit/flower availability were also found for percentage time spent travelling and PS, paired tests matched by month were performed between each age-sex class combination and Bonferroni corrections performed to correct

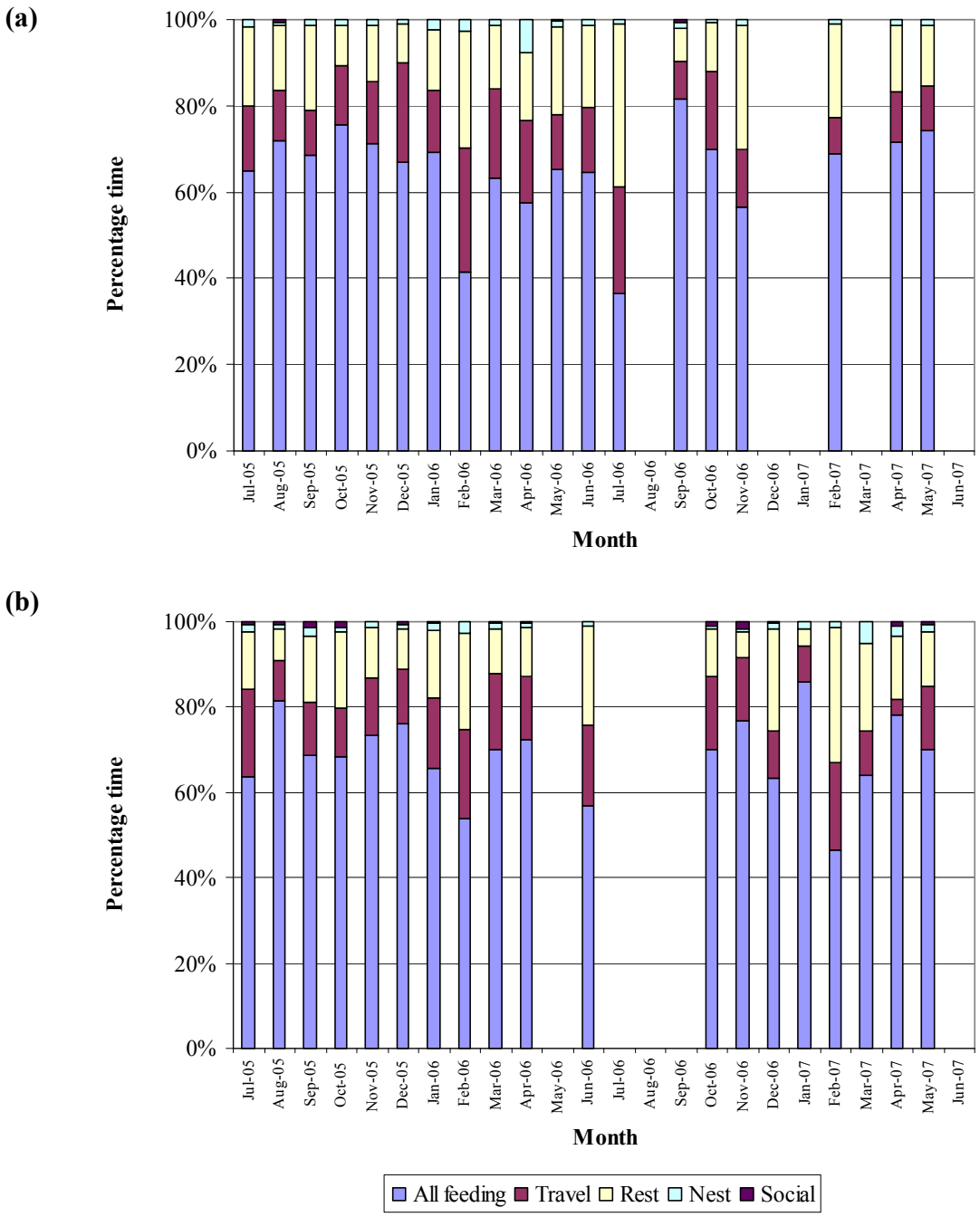


Figure 6.1 Orang-utan activity budgets (percentage time) by month: (a) adult females, and (b) flanged males. "All feeding" = time "feeding", "co-feeding" and "food-searching" (**Table 6.1**) combined; i.e., total time spent feeding.

for multiple comparisons (Hochberg, 1988). These tests indicate that nulliparous females spent significantly more time travelling than flanged males (t = 3.235, df = 15, p = 0.006). Trends (i.e. $p < 0.05$, but not significant post-Bonferroni correction) also existed for the following comparisons: nulliparous females > adult females (t = 2.847, df = 13, p = 0.014) and unflanged males (t = 2.392, df = 8, p = 0.044), and unflanged males > flanged males (t = 2.469, df = 8, p = 0.039). These tests also revealed that adult female PS was significantly higher than both flanged (t = 4.582, df = 15, $p < 0.001$) and unflanged (t = 4.800, df = 8, p = 0.001) males, though comparison with nulliparous females revealed only a trend for higher PS in adult females (t = 2.19, df = 13, p = 0.047). There was also a trend for nulliparous females to have higher PS than flanged males (t = 2.994, df = 15, p = 0.009). When time spent in association with a females' own offspring was excluded, adult female PS was significantly less than when their own infants were included (Wilcoxon signed rank: n = 19, p = 0.002), and was not different from all other age-sex classes (NUF: n = 14; FLM: n = 16; UFM: n = 9; p = NS in all cases). Differences between adult females (excluding time spent in association with their own independent offspring) and flanged males were significant on a minutes/day (paired t-test, t = 3.107, df = 15, p = 0.007) and percentage time (t = -3.093, df = 15, p = 0.007) basis, however, and trends also indicated higher sociality than unflanged males (minutes/day: t = -2.578, df = 8, p = 0.033; percentage time: t = -2.727, df = 8, p = 0.026).

The results of these tests provide some support for the hypotheses that decreased fruit/flower availability results in less time socialising in adult females ($H_0 6.1a$), decreased time spent travelling in flanged males ($H_0 6.1c$) and no change in time spent

resting (*$H_0$6.1f*), that adult females are more social than flanged males (*$H_0$6.9a*) and that flanged males spend the least time travelling (*$H_0$6.9c*). Hypotheses *$H_0$6.9b* (adult female DR > flanged males), *d* (adult female and unflanged male time resting < flanged male) and *e* (flanged males spend less time feeding than adult females and unflanged males) were not supported. Although these analyses indicate broad differences between age-sex classes, it is necessary to analyse the data separately for each age-sex class, in order to provide full assessments of the effects of fluctuations in food availability on individual age-sex classes (*$H_0$6.1-5*, cf. **Chapter 4**). Analysis of age-sex class differences in Sabangau in relation to those observed in mast-fruiting habitats is given in **Section 6.3.4**.

6.3.2.1 Effects of Fluctuations in Food Availability: Exploratory Analyses

In order to assess whether *$H_0$6.1-5* are supported in all age-sex classes, I first performed bivariate correlations between all the variables described above. The resulting correlation matrices for each age-sex class are shown in **Appendix IV.**

These correlations reveal many relationships between the different variables, and support some, but not all, of the hypotheses in **Section 6.1**. For all age-sex classes, percentage time spent feeding on preferred foods (fruit and flowers combined) was positively correlated with orang-utan fruit/flower availability. Orang-utan fruit/flower availability was also positively correlated with PS in adult females (including own, independent offspring) and flanged males, energy intake in flanged males, time spent travelling in nulliparous females and unflanged males, AP in nulliparous females, and time spent

resting in unflanged males. Percentage time feeding on preferred foods was negatively correlated with percentage time feeding on fall-back foods (FBF) in all age-sex classes (cf. **Table 4.12**), and positively correlated with PS in adult and nulliparous females, DR in adult females, AP in nulliparous females, energy intake in flanged males, and travel time in nulliparous females and unflanged males (correlations are very similar for percentage FBF, but in the opposite direction). Daily energy intake was negatively correlated with time spent resting in adult females, and positively correlated with minutes spent feeding in nulliparous females and flanged males, and AP in flanged males. In nulliparous females, AP was positively correlated with PS, DR, and time travelling, which was also positively correlated with PS. Daily fibre intake was not significantly correlated with time spent resting and travelling, DR or PS for any age-sex class.

As in the preceding chapter, interpretation of these bivariate relationships is difficult, due to inter-correlations between dependent variables (see **Section 6.2.5**). Thus, additional testing via multi-variate techniques was performed when significant correlations were found between the dependent variable and the independent variable of interest.

6.3.2.2 Multi-variate Analyses and Hypothesis Testing

$H_0$6.1 Orang-utans in Sabangau respond to decreases in fruit availability in the same ways as do orang-utans in masting habitats.

a) In the bivariate analysis, a significant positive correlation was found between orang-utan fruit/flower availability and PS in adult females when time spent in association with their own independent offspring was included, but not when time spent in association with their own offspring was excluded (**Appendix IV**). Regression of adult female PS including their own offspring against orang-utan fruit/flower availability revealed a significant positive relationship (R^2 = 0.226, *df* = 18, *p* = 0.040, **Figure 6.2**), in agreement with this hypothesis. No relationship between PS and orang-utan fruit/flower availability was found for any other age-sex class. Thus, this hypothesis was supported when including time spent by adult females in association with their own independent offspring.

b) This hypothesis was not supported; no significant correlations between DR and orang-utan fruit/flower availability were found for any age-sex class.

c) This hypothesis was also not supported; no significant correlations between percentage time spent travelling and orang-utan fruit/flower availability were found for flanged males, though significant positive correlations were found for both nulliparous females and unflanged males. Based on hierarchical regression models, there was no significant effect of orang-utan fruit/flower availability on travel time in nulliparous females (after removing the effects of DR, *overall model* R^2 = 0.549, *df* = 17, *p* = 0.003; R^2 *change from addition orang-utan fruit/*

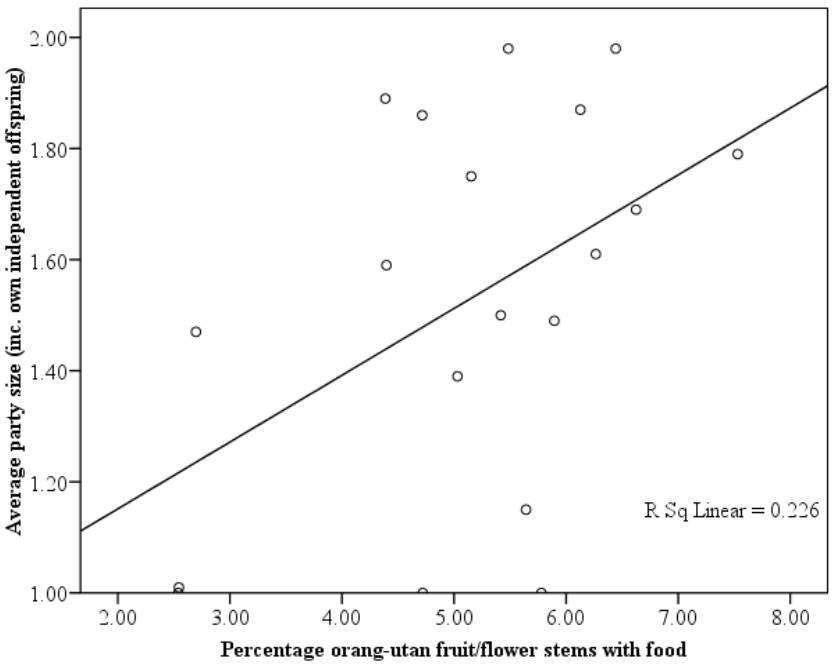


Figure 6.2 Regression of average party size of adult females (including time spent in association with their own offspring) against orang-utan fruit/flower availability.

/flower availability = 0.055, *p* = NS), but there was a significant positive relationship between the two variables in unflanged males (orang-utan fruit/flower availability only, R^2 = 0.430, *df* = 10, *p* = 0.028, **Figure 6.3**).

d) This hypothesis was not supported; no significant correlation between percentage time spent feeding and orang-utan fruit/flower availability was found for flanged males (or any other age-sex class).

e) No significant correlations were found between AP and orang-utan fruit/flower availability for adult females and the two male morphs, but a significant positive correlation was found for nulliparous females. A hierarchical regression between these two variables was significant (after removing the effects of percentage time spent resting, *overall model* R^2 = 0.635, *df* = 17, *p* = 0.002; R^2 *change from*

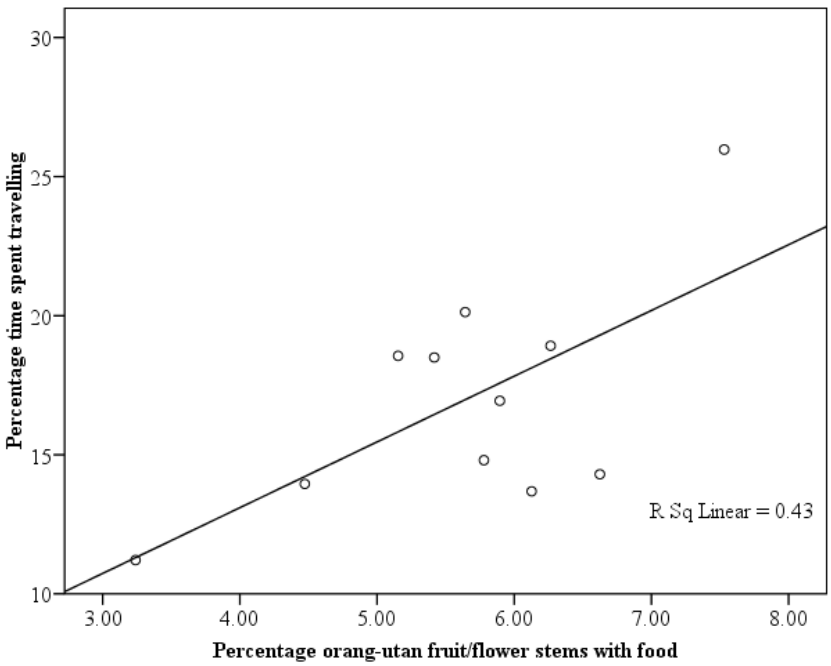


Figure 6.3 Regression of percentage time spent travelling by unflanged males against orang-utan fruit/flower availability.

addition orang-utan fruit/flower availability = 0.148, p = 0.040; orang-utan fruit/flower availability: β = 0.408, t = 2.282, p = 0.040). Thus, this hypothesis was supported only in nulliparous females.

f) No correlations were found between percentage time spent resting and orang-utan fruit/flower availability for any age-sex classes, supporting this hypothesis.

$H_0$6.2 Increased availability of preferred foods leads to an increase in their consumption, which allows orang-utans to increase daily energy intake.

With the exception of unflanged males, the first part of this hypothesis is supported by the analyses in **Section 4.3.2**. The second part of this hypothesis is supported only in

flanged males (after removing the effects of AP, *overall model* R^2 = 0.597, *df* = 13, *p* = 0.007; R^2 *change from addition percentage time feeding on preferred foods* = 0.343, *p* = 0.011; percentage time feeding on preferred foods: β = 0.587, *t* = 3.061, *p* = 0.011).

$H_0$6.3 Socialising is energetically costly for orang-utans.

a) The results of the correlation tests provided no support for the hypothesis that increased PS results in increased energy expenditure (as assessed through increases in AP and DR) for adult females or the two male morphs. A significant positive correlation between AP and PS was found for nulliparous females, but this had no effect beyond that of DR and orang-utan fruit/flower availability (*overall model* R^2 = 0.661, *df* = 15, *p* = 0.004; R^2 *change from addition PS* = 0.030, *p* = NS). Thus, this hypothesis was not supported.
b) The hypothesis that increased sociality results in decreased energy intake was not supported; no significant correlation between daily energy intake and PS was found for any age-sex class.

$H_0$6.4 Increased energy intake enables increased sociality.

This hypothesis was not supported; no significant correlation between daily energy intake and PS were found for any age-sex class.

6.3.3 ORANG-UTAN FORAGING STRATEGIES

In $H_0 6.5$, it was hypothesised that orang-utans in Sabangau follow an "energy-maximising" foraging strategy, as indicated by increased DR ($H_0 6.1b$) and, crucially, energy intake ($H_0 6.2$) when the availability/consumption of preferred foods increases. $H_0 6.1b$ is not satisfied in any age-sex class, but $H_0 6.2$ is satisfied for flanged males, indicating that they are "energy maximisers". In **Section 6.1**, it was predicted that a "time minimiser" would respond to an increase in fruit/flower availability by (1) no change in energy intake, and (2) decreased minutes spent feeding. The first of these conditions is satisfied in all the three remaining age-sex classes, but the second condition is not satisfied for any age-sex class. Thus, flanged males can be classified as energy maximisers, but the remaining age-sex classes cannot be classified as either energy maximisers or time minimisers.

6.3.4 COMPARISONS WITH MAST-FRUITING FORESTS

$H_0 6.6$: Orang-utan activity profiles in Sabangau are similar to those observed in masting habitats in Borneo.

Tests of this hypothesis have recently been performed by Morrogh-Bernard *et al.* (2009), using data from seven Bornean sites (non-masting: Sabangau (using data collected prior to the onset of this study by H. Morrogh-Bernard), Tuanan and Tanjung Puting; masting: Gunung Palung, Kutai, Kinabatangan and Danum Valley). The authors found that activity budgets differed between habitat types, with orang-utans in non-masting habitats

spending, on average, more time feeding and travelling, and less time resting, than in masting habitats. The percentage time spent engaged in different activities in Sabangau during 2003-05 (Morrogh-Bernard *et al.*, 2009) and 2005-07 (**Table 6.3** and **Figure 6.1**) were similar and, hence, this hypothesis can be rejected.

$H_0$6.7: Day range is similar for orang-utans in Sabangau and masting habitats.

Day ranges of orang-utans in Sabangau and other non-masting habitats in Borneo are compared to those from other sites in **Table 6.7**. These data indicate that adult female DR is similar for Bornean and Sumatran orang-utans in non-masting peat-swamp forests (PSF), and in the mast-fruiting forests of Gunung Palung (except during periods of low fruit availability, when DR becomes substantially lower), but appear higher than Kutai (though these data are difficult to interpret as they represent a mean of flanged males and adult females). Flanged male DR is also higher for orang-utans in Bornean PSF than in the mast-fruiting forests of Gunung Palung and Kutai. Thus, this hypothesis must be rejected.

$H_0$6.8: Orang-utans in Sabangau spend a similar amount of time socialising as do orang-utans in masting habitats.

Van Schaik (1999) and Wich *et al.* (2006a) compared adult female average PS in five different sites, three of which are in Borneo (mast-fruiting: Kutai and Gunung Palung; non-masting: Tanjung Puting). Average PS in Kutai and Gunung Palung and Tanjung Puting was 1.2, 1.0 and 1.2, respectively. When socialising with their own, independent individuals was excluded, average PS for adult females in Sabangau was 1.08 (**Table**

6.5). In Sabangau, flanged males spent 3.8% of their time in association with another orang-utan (**Table 6.5**), compared to 16.5% in Kutai and 0% in Gunung Palung (Mitani *et al.*, 1991). Thus, this hypothesis can be accepted.

Table 6.7 Day ranges (m) by orang-utans at different research sites.

Site	Island	Masting?	Adult female[1]	Nulliparous female	Flanged male	Unflanged male
Sabangau 2005-07	Borneo	No	858	1,058	897	1,149
Sabangau 2003-05	Borneo	No	809	857	754	1,037
Tuanan	Borneo	No	766	NA	NA	NA
Tanjung Putting	Borneo	No	711	NA	850	NA
Gunung Palung	Borneo	Yes	802 (high fruit) 524 (low fruit) 690 (average)	NA	570 (high fruit) 273 (low fruit)	NA
Kutai	Borneo	Yes	305[2]	NA	305[2]	NA
Suaq Balimbing	Sumatra	No	833	1,150	NA	NA
Ketambe	Sumatra	Yes	675	675	590	865

1. Figures for adult female mothers.
2. Mean value for flanged males and adult females.

References: Sabangau 2005-07, this study; Sabangau 2003-05, Morrogh-Bernard (submitted), Singleton *et al.* (2009); Tuanan, Singleton *et al.* (2009); Tanjung Puting, Galdikas (1988); Gunung Palung, Knott (1999), Singleton *et al.* (2009); Kutai, Rodman (1977); Suaq Balimbing, van Schaik (1999), Singleton *et al.* (2009); Ketambe, Wich *et al.* (2006a), Singleton *et al.* (2009). NA = published data not available.

$H_0$6.9: Differences in activity profiles exist between age-sex classes are consistent between Sabangau and mast-fruiting habitats in Borneo.

Behavioural differences between age-sex classes in Sabangau orang-utans during 2005-07 were assessed in **Section 6.3.2** and these differences are compared to those found in other sites (and in Sabangau during Morrogh-Bernard's study in 2003-05) in **Table 6.8**.

Table 6.8 Age-sex class differences in activity budgets in masting and non-masting habitats in Borneo. Adapted from Morrogh-Bernard *et al.* (2009).

Site	Masting?	Feeding	Travelling	Resting
Sabangau 2005-07	No	NS	NULF > FLM	ADF > UFM
Sabangau 2003-05	No	NS	NULF > FLM	NS
Tuanan	No	NUF > UFM	NUF > ADF UFM > ADF UFM > FLM	NUF > all others
Tanjung Putting	No	NS	NS	NS
Gunung Palung	Yes	NS	NUF > FLM	NS
Kutai	Yes	ADF > FLM UFM > FLM	ADF > FLM UFM > FLM	FLM > ADF FLM > UFM

Abbreviations: ADF = adult female; FLM = flanged male; NUF = nulliparous females; UFM = unflanged males; NS = differences between age-sex classes not significant.
References: Sabangau 2005-07, this study; Sabangau 2003-05, Morrogh-Bernard *et al.* (2009); Tuanan, Morrogh-Bernard *et al.* (2009); Tanjung Puting, Galdikas (1988); Gunung Palung, Morrogh-Bernard *et al.* (2009); Kutai, Mitani (1989).

Based on this table and **Section 6.3.2**, the following conclusions can be drawn:

a) As in mast-fruiting forests, adult females in Sabangau spend more time socialising than flanged males, supporting this hypothesis.

b) Unlike in mast-fruiting forests, adult female DR in Sabangau was not statistically longer than flanged males'; hence, this hypothesis must be rejected.

c) Similar to mast-fruiting forests, flanged male travel time in Sabangau < other age-sex classes (though differences post-correction for multiple comparisons were significant only when compared with nulliparous females, all trends were in the expected direction) and, consequently, this hypothesis can be tentatively accepted.

d) No differences in time spent resting were found between age-sex classes. Thus, the hypothesis that adult females and unflanged males spend less time resting than flanged males, as in masting forests, must be rejected.

e) Similarly, the hypothesis that flanged males in Sabangau spend less time feeding than adult females and unflanged males, as in masting forests, must also be rejected: differences in time feeding between age-sex classes were not significant.

6.3.5 THE EFFECT OF FIBRE INTAKE ON ACTIVITY PROFILES

Finally, inspection of the correlation matrices in **Appendix IV** indicate that daily fibre intake is not significantly correlated with time spent resting ($H_0 6.10a$), time spent travelling ($H_0 6.10b$) or PS ($H_0 6.10c$) in any age-sex class. In contrast to the predictions of this hypothesis, fibre intake is significantly *positively* correlated with DR in adult females and flanged males. Thus, it appears that fibre intake does not influence orang-utan activity profiles and $H_0 6.10$ must be rejected.

6.4 DISCUSSION

6.4.1 BEHAVIOURAL DIFFERENCES BETWEEN AGE-SEX CLASSES

When considering average figures, the behavioural profiles of the different age-sex classes in Sabangau are fairly similar, and differences between age-sex classes were generally not significant. Some differences between age-sex classes were apparent, however, and these show that (a) adult females were more social than flanged males, with similar trends for comparisons with unflanged males, (b) nulliparous females spent more time travelling than flanged males, and (c) adult females spent more time resting than unflanged males.

Including time spent in association with their own independent infant, adult females were much more social than any other age-sex class, spending, on average, over half of their time in parties. This was mostly due to time spent in association with their own infants; adult females spent only 8.4% of their time in association with other individuals. Nevertheless, adult females were still more social than males, even with their own infants excluded (**Section 6.3.2**). These observations are not surprising in light of recent genetic data collected in Sabangau, which indicate female philopatry and male dispersal (Morf, 2008; Morrogh-Bernard, submitted). As a result of this, females may benefit more from close social networks of related individuals (Morf, 2008; Morrogh-Bernard, submitted). On the other hand, males should gain greatest benefit from socialising, and attempting to mate with, unrelated sexually-receptive females. As none of the females followed during

the course of this study were sexually receptive (i.e., they all had dependent infants or were still immature), males may have concentrated their social efforts on receptive females in other parts of the forest, which would obviously not have been detected.

It might be expected that unflanged males would travel more than flanged males, considering the much larger size, and consequently higher travel costs, of flanged males, and the differences in the two morphs' mating strategies: "call-and-wait" for flanged males *vs.* "sneak-and-rape" for unflanged males (Galdikas, 1981, 1985a, c; Schurmann and van Hooff, 1986; van Schaik and van Hooff, 1996; Delgado and van Schaik, 2000; Utami *et al.*, 2002; Harrison and Chivers, 2007). Mean DR for unflanged males was greater than for flanged males and, though no statistically significant differences in DR were found between age-sex classes, sample size was low and a trend for higher time spent travelling in unflanged males than flanged males was found, indicating that unflanged males probably do travel further than flanged males.

Although all tests were not statistically significant, it appears that nulliparous females spent more time travelling than any other age-sex class. This may be because nulliparous females are less energetically constrained and/or less efficient foragers than the other age-sex classes, as suggested in **Section 5.4.3.1**. Thus, they may either be freer (energetically speaking) to travel further in search of food/social interactions, and/or need to travel further to find large patches of good food, due to lower search efficiency. As for diet (**Chapter 4)**, important differences also existed between age-sex classes in their behavioural responses to fluctuations in fruit/flower availability.

6.4.2 THE INFLUENCE OF DIET COMPOSITION AND FOOD AVAILABILITY ON BEHAVIOUR

Increases in the availability of preferred foods (fruits and flowers, **Section 5.3.1**) led to an increase in their consumption, but only in flanged males did this result in increased daily energy intake. Of the various behavioural responses to reductions in preferred food availability expected, based on observations of orang-utans in mast-fruiting forests in Borneo (MacKinnon, 1971, 1974; Rodman, 1977; Mitani and Rodman, 1979; Knott, 1999), most were not seen in this study, with the exceptions of decreased PS in adult females and increased AP in nulliparous females (though this increase was associated with increased time spent travelling, resting and socialising, but not feeding, as seen in flanged males in Gunung Palung).

Furthermore, there was no relationship between daily energy intake and PS in any age-sex class, in contrast to hypotheses suggesting an energetic cost of socialising in terms of decreased feeding efficiency. Increased sociality also did not lead to changes in behaviour associated with increased energy expenditure (increased DR or AP), suggesting either that (i) there are no energetic costs to sociality in Sabangau and, hence, that the suggestion that orang-utans can only socialise when fruit availability is high, as this enables these costs to be overcome (van Schaik, 1999) does not apply to orang-utans in this forest, or, more likely, (ii) that Sabangau orang-utans spend so little time in association with one another that such costs are not apparent in this analysis. This latter suggestion is supported by the positive relationship observed between adult female PS

(including associations with their own independent offspring) and preferred food availability in this study and in Gunung Palung (Knott, 1999), in addition to observations of increased time spent travelling, and decreased time spent feeding and resting, when socialising reported in other studies (Galdikas, 1988; Mitani, 1989), higher orang-utan sociability in Sumatra, where food availability is higher, than in Borneo (van Schaik, 1999; Wich *et al.*, 2006a; Marshall *et al.*, 2009a), and evidence that scramble competition for food resources does impose costs on female orang-utans (Knott *et al.*, 2008).

The decrease in adult female sociality reported when preferred food availability/ consumption decreases may be the result of decreased co-feeding with their own infants in large fruit/flower patches: it may simply be harder to feed together in small leaf trees/ while eating cambium. Additionally, leaf/cambium species are commoner in the forest than fruit/flower patches (**Sections 5.3.1** and **6.1**) and, hence, presumably, are easier to find, which may lead independent infants to feed and range further from their mother when preferred foods are scarce. Unfortunately, data are not currently available to test these hypotheses.

Thus, generally, the results in this study are *not* consistent with the suggestion that orang-utan behaviour in Sabangau is heavily influenced by preferred food availability, with the exception of time spent in association with their own independent offspring by adult females. This general lack of behavioural flexibility exhibited in response to fluctuations in preferred food availability suggests that either (i) fluctuations in fruit/flower

availability are of an insufficient magnitude to elicit behavioural responses, and/or (ii) the demands of living in peat-swamp forest are such that lowering energy expenditure to attain neutral/positive energy balance is not possible (in light of the energetic shortfalls documented in **Chapter 4**, it is highly unlikely that such adjustments are not necessary).

The observations of low sociality in flanged males compared to females is at odds with the hypothesis expounded in **Section 4.4.1** that differences in relative energetic and social demands exist between the sexes, with females focussing on attempting to maintain a positive/neutral energy balance, in order to ensure survival/growth of their dependent offspring, and males focussing on social considerations, with the intention of recouping any energetic losses incurred when food availability is low during periods of high food abundance. Three reasons suggest, however, that this hypothesis cannot be rejected based on this observation. Firstly, much flanged male social behaviour may be undetectable with the methods used in this study, because many social interactions likely take place over distances considerably greater than 50 m. Flanged male long calls, which are thought to be unique to different individuals and distinguishable by other members of the population (Delgado, 2003a, b, c), are also thought to be important for regulating social relationships, facilitating intra-sexual spacing/aggression and attracting females (Galdikas, 1983; Mitani, 1985b; Fox, 2002; Delgado, 2006; Utami Atmoko *et al.*, 2009). These calls can be heard up to 1 km away (Delgado, 2006; pers. obs.) and, hence, much flanged male social behaviour is clearly played out over long distances. Furthermore, call frequency is not affected by fruit availability in Sumatra (Delgado, 2003b). Flanged males doubtless also spend a large portion of their time chasing/running away from other

males and searching for sexually-receptive females> 50 m away. These behaviours could not be detected in this study, but it is unlikely that their frequency will be related to fruit/flower availability (cf. Delgado, 2003b). Secondly, adult females responded to decreased preferred food availability by spending less time in association with their own dependent offspring, which may lower their energetic costs (see above) and, hence, enable them to direct more resources to dependent offspring in times of need. Further data collection is needed in this area, to establish whether this observation holds with a larger dataset, or whether it is merely a consequence of the maturation of the independent offspring during the course of the study. Finally, orang-utan fruit/flower availability during the period included in this study is thought to have been unusually low (Morrogh-Bernard, submitted; **Section 3.2.2**). If this is the case, then it may be that the inclusion of periods of higher fruit/flower availability in the analysis would lead to more significant results between fruit/flower availability, energy intake and orang-utan behaviour.

There was no support for the hypothesis that daily fibre intake influences activity profiles, because, given that fibre digestion is only possible while resting (van Soest, 1994), increased resting is required when fibre intake increases, imposing constraints on the amount of time available for other activities (Dunbar, 1988). There were no significant correlations between fibre intake and time spent resting or travelling, DR or PS in any age-sex class, indicating that, even during periods of relatively high fibre intake, orang-utans in Sabangau have sufficient resting time for fibre digestion during the typical 1-2 h of resting time/day and the 13 h or so spent inactive in the night nest outside of the daily AP.

6.4.3 ORANG-UTAN FORAGING STRATEGIES IN SABANGAU

In agreement with Morrogh-Bernard *et al.* (2009), with the exception of flanged males, orang-utans in Sabangau appear to allocate a fairly constant amount of effort to feeding and travelling in search of food. Furthermore, DR in Sabangau during 2003-2005 was 100-200 m/day lower on average for each age-sex class than in 2005-2007 (see **Table 6.7**). Orang-utan fruit/flower availability during this study was also lower than 2003-2005 (Morrogh-Bernard, submitted; **Section 3.2.2**), supporting Morrogh-Bernard *et al.*'s (2009) suggestion that orang-utans in PSF will travel further when fruits and flowers are scarce to obtain more food.

Based on the analyses in **Section 6.3.3**, flanged males can be considered energy maximisers, but adult females, nulliparous females and unflanged males cannot be distinguished as adopting either an energy-maximising or time-minimising strategy. Instead, the observations in these age-sex classes may be better explained by some alternative strategy, e.g., nutrient balancing (Randolph and Cameron, 2001). Thus, not only do broad differences in activity profiles exist between sites (Morrogh-Bernard *et al.*, 2009), but feeding strategies may also differ between age-sex classes within a site.

6.4.4 COMPARISONS WITH ORANG-UTAN STUDIES IN MASTING HABITATS AND AFRICAN APES

6.4.4.1 Comparisons with Orang-utans in Mast-fruiting Habitats

Based on the analysis herein, orang-utan behaviour and responses to fluctuations in preferred food availability clearly differ between masting and non-masting habitats within Borneo. Orang-utan activity budgets and AP in Sabangau are compared with those from other sites by Morrogh-Bernard *et al.* (2009, to which the reader is referred for a detailed discussion of this topic). These authors conclude that orang-utans in Sabangau spend more time feeding and travelling, and less time resting, than orang-utans in masting habitats such as Gunung Palung, but that these time allocations are similar to those in other non-masting sites and Ketambe, where fruit availability is relatively consistent, due to high fig densities (Morrogh-Bernard *et al.*, 2009). Orang-utan DR in Sabangau and other non-masting forests is relatively long compared to masting forests. This is in agreement with Morrogh-Bernard *et al.*'s analysis, based on time spent travelling, which indicated that orang-utans in habitats where fruit availability is more constant travel more than those in masting habitats, where fruit availability is less predictable and, hence, searching is less likely to yield rewards.

Unlike the masting forests of Gunung Palung (Knott, 1999) and Ketambe (Morrogh-Bernard *et al.*, 2009), where orang-utans responded to decreased fruit availability by decreasing DR, orang-utans in Sabangau did not adjust their DR in response to

fluctuations in fruit/flower availability. This is unexpected, as it could be hypothesised that (a) decreased fruit/flower availability should lead to decreased DR, on the basis that that fruit/flower consumption increases when these foods are more available (**Section 4.3.2** and **Appendix IV**) and that these foods are rarer in the environment than FBFs (leaves and bark, **Section 5.3.1**), and/or to reduce energy expenditure (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Boinski, 1987; Knott, 1999, 2005), or (b) that decreased preferred food availability should lead to increased DR, as animals travel further in search of more preferred, and sparsely distributed, foods (Barton *et al.*, 1992; Overdorff, 1993). It is, however, in agreement with Morrogh-Bernard *et al.*'s (2009) suggestion that orang-utans in PSF adopt a search-and-find foraging strategy, in which orang-utans continually travel in search of food.

In contrast, orang-utans in Sabangau spent a similar amount of time socialising as orang-utans in the masting forests of Gunung Palung and Kutai, and, in common with these other Bornean sites, spent less time in the company of others than do Sumatran orang-utans (van Schaik, 1999; Wich *et al.*, 2006a). Furthermore, unlike the Sumatran sites of Suaq (van Schaik, 1999) and Ketambe (Wich *et al.*, 2006a), but in common with Gunung Palung (Knott, 1999), adult female sociality in Sabangau was positively associated with preferred food availability. The apparent lack of effect of orang-utan fruit/flower availability on PS in other age-sex classes in Sabangau may be a consequence of the low amounts of time spent socialising by these age-sex classes in all months. In itself, this could be a consequence of overall low fruit availability in Sabangau compared to other orang-utan study sites (see **Section 3.4.3.1**) curtailing orang-utan sociality in all months,

in addition to the relatively low density of orang-utans in the study area (Husson *et al.*, 2009), which is probably also the result of low fruit availability. Thus, it appears that levels of fruit availability as low as those found in Sabangau (overall) and Gunung Palung (between masts) do limit PS in orang-utans, as has been suggested previously (Delgado and van Schaik, 2000).

In this study, as in mast-fruiting forests in Borneo (Mitani, 1989; Knott, 1999; Morrogh-Bernard *et al.*, 2009), adult females were more social than flanged males and flanged males spent less time travelling than other age-sex classes (though differences post-correction for multiple comparisons were not quite significant when compared with adult females and unflanged males). These differences appear to hold across both masting and non-masting forests in both Borneo and Sumatra (Delgado and van Schaik, 2000; Morrogh-Bernard *et al.*, 2009; this study). In contrast to masting forests, however, differences in DR, and time spent resting and feeding were not significant between age-sex classes. This indicates that (i) flanged males in Sabangau travel faster than adult females (this could be due to increased terrestrial travel by flanged males, Galdikas, 1988; Delgado and van Schaik, 2000; pers. obs.), and (ii) that, in PSF, all age-sex classes need to spend as much time feeding as possible, in order to attempt to meet their metabolic requirements (Morrogh-Bernard *et al.*, 2009). As a consequence of this, resting time is reduced in all age-sex classes and the activity profiles of the different age-sex classes become more aligned. This suggestion is supported by observations of more time spent feeding by orang-utans in PSF than masting forests (Morrogh-Bernard *et al.*, 2009)

and of energy shortfall in Sabangau (**Chapter 4**), which indicates that orang-utans in Sabangau need to spend as much time feeding and obtaining energy as possible.

6.4.4.2 Comparisons with African Apes

The influence of fluctuations in fruit availability on African ape behaviour has been studied by numerous researchers (see recent summaries by Yamagiwa, 2004 and Knott, 2005). A number of responses to periods of fruit scarcity are seen, and these are documented below.

Chimpanzees

Chimpanzees typically exhibit a positive correlation between fruit availability and DR (Wrangham, 1977; Hasegawa, 1990; Doran, 1997; Boesch and Boesch-Achermann, 2000), though this has not been seen in all studies (Yamagiwa, 1999). Fruit consumption generally decreases, and bark, terrestrial herbaceous vegetation (THV), figs and pith are typically consumed as FBFs, though this change is less marked than in gorillas and orang-utans, and, in many sites, fruit consumption and availability are not correlated, indicating that chimpanzees continue to search for this preferred food even when it becomes scarce (Nishida, 1976; Nishida and Uehara, 1983; Kuroda *et al.*, 1996; Yamagiwa *et al.*, 1996; Newton-Fisher, 1999; Stanford and Nkurunungi, 2003; Knott, 2005; Yamagiwa and Basabose, 2006a, b). Reduced PS and gregariousness in response to fruit shortage are typically seen (Chapman *et al.*, 1995; Wrangham *et al.*, 1996; Doran, 1997; Matsumoto-Oda *et al.*, 1998; Hashimoto *et al.*, 2003), though not in all

studies, e.g., the highly productive forests of Budongo (Newton-Fisher *et al.*, 2000). The effect on time feeding is variable, with both increases and decreases reported in response to fruit scarcity (Knott, 2005). Risk-prone behaviours, such as hunting, may also be less likely during low-fruit periods (Gilby and Wrangham, 2007).

Bonobos

Fewer studies have been conducted on bonobos than chimpanzees, but available evidence indicates that bonobos respond to periods of fruit shortage by continuing to search for fruit and using THV as FBF. Bonobos show even less pronounced dietary switching than chimpanzees, however (Kano, 1992; Yamagiwa, 2004), and some authors have reported a complete lack of seasonal dietary switching (White, 1998). There is generally no effect of fruit availability on DR (Kano, 1992; Yamagiwa, 2004). When an effect is seen on PS and gregariousness, animals become less social when fruit is scarce (White, 1996; White, 1998).

Gorillas

Mountain gorillas are habitual folivores and live in environments where fruit is absent or rare, and, hence, show very little response to changes in fruit availability (Watts, 1984, 1996; Yamagiwa, 2004). On the other hand, lowland gorillas are much more frugivorous and respond to reduced fruit availability by decreasing fruit consumption, and increasing consumption of bark and THV as FBFs (Goodall, 1977; Sabater Pí, 1977; Rogers *et al.*, 1988; Williamson *et al.*, 1990; Tutin and Fernandez, 1993; Remis, 1994; Yamagiwa and Mwanza, 1994; Remis, 1997a; Goldsmith, 1999; Remis, 2003; Cipolletta, 2004; Doran-

Sheehy *et al.*, 2004; Yamagiwa *et al.*, 2005; Yamagiwa and Basabose, 2006a, b; Masi *et al.*, in press). As in orang-utans and most chimpanzee populations studied, lowland gorillas decrease DR and time spent travelling when fruit is less abundant (Goodall, 1977; Mwanza *et al.*, 1992; Yamagiwa and Mwanza, 1994; Goldsmith, 1999; Cipolletta, 2004; Doran-Sheehy *et al.*, 2004; Masi *et al.*, in press). Increases in time spent feeding during periods of low frugivory have been reported in western lowland gorillas, but frugivory had no effect on time spent resting (Masi *et al.*, in press). Unlike mountain gorillas, in which groups are generally very cohesive, groups of the more frugivorous western lowland gorillas are less cohesive, with sub-groups even sleeping apart occasionally; behaviour thought to reflect differences in frugivory between the species (Mitani, 1992; Goldsmith, 1996; Remis, 1997b). Studies of energy expenditure in western gorillas have documented a lack of seasonal change in response to fruit availability, mirroring the lack of relationship between energy intake and fruit availability (Masi, 2007).

These observations in African apes are in general agreement with the comparative observations made in previous chapters; i.e., across species, the more variable and unpredictable the fruit supply, the greater the influence of fluctuations in fruit availability on behaviour (see, e.g., Newton-Fisher *et al.*, 2000 for a similar conclusion). Furthermore, the general observation across great apes of decreased sociability during periods of fruit scarcity in most habitats indicates that socialising is energetically costly in most apes (though the nature of costs may vary and costs may not always be apparent), but that these costs can be offset or weathered in habitats with high and/or predictable

fruit availability (e.g., bonobos, Sumatran orang-utans) (van Schaik, 1999). Only in more folivorous mountain gorilla populations, where fruit is not available and the only suitable alternative, vegetative plant parts, is abundant and easily found year-round, does high sociability appear not to be energetically costly (e.g., Watts, 1998).

6.5 SUMMARY

1. Data on orang-utan active period (AP), activity profiles, day range (DR) and sociality were collected at five-minute intervals, using standard methods. These data were used to test hypotheses regarding the effects of fruit/flower availability, diet composition, and energy and fibre intake on orang-utan behaviour, and to infer foraging strategies.
2. Average party size (PS) in adult females was significantly more than flanged and unflanged males. Most of this time spent "socialising" by adult females was spent in association with their own independent offspring, however, and differences in PS between age-sex classes were not significant when time spent with their own independent offspring was excluded (though adult females were still more social than males on a minutes/day and percentage-time-in-association basis).
3. No differences in time spent feeding or resting were found between age-sex classes, with the exception that adult females spent more time resting than flanged males. Nulliparous females spent more time travelling than flanged males, and trends also indicated that time spent travelling by nulliparous females > adult females and unflanged males, and unflanged males > flanged males. Differences in DR between age-sex classes were not significant, however, suggesting that the above results are due to faster terrestrial travel by flanged males. Longer time spent travelling in nulliparous females could be because they have more 'free energy' and/or are less efficient at finding foods in the forest than other age-sex classes, whereas the shorter time spent travelling in flanged males is probably a consequence of their respective reproductive strategies ("call-and-wait" *vs.* "sneak-and-rape" for unflanged males).

4. Generally, the results in this chapter are *not* consistent with the suggestion that orang-utan behaviour in Sabangau is heavily influenced by fruit/flower availability or energy intake. Of the various behavioural responses to reductions in preferred food availability expected, based on observations of orang-utans in mast-fruiting forests in Borneo, most were not seen in this study, with the exceptions of decreased PS in adult females and increased AP in nulliparous females. Similarly, no relationships were found between energy intake and PS, or fibre intake and behavioural profiles.
5. The general lack of behavioural flexibility exhibited by Sabangau orang-utans in response to fluctuations in preferred food availability suggests that (a) fluctuations in fruit/flower availability in Sabangau are of an insufficient magnitude to elicit behavioural responses, and/or that the demands of living in this continually fruit-poor habitat are such that (b) orang-utans continually need to maximise time feeding, in an attempt to meet their metabolic requirements (a suggestion supported by the observations of energy shortfall documented in Chapter 4) and, consequently, (c) that lowering energy expenditure to attain neutral/positive energy balance is not possible in peat-swamp forest (PSF). This suggestion is in agreement with the observation that orang-utans in PSFs spend more time feeding and travelling, and less time resting, than orang-utans in masting habitats.
6. In contrast to expectations, socialising did not appear to be energetically costly for orang-utans in Sabangau, either in terms of increased day range or active period, or decreased energy intake. It is likely that this is a result of the typically low levels of sociality in Sabangau orang-utans, in agreement with the above suggestion.

7. With the exception of flanged males, these findings concur with previous suggestions (Morrogh-Bernard *et al.*, 2009) that orang-utans in Sabangau employ a search-and-find strategy, whereby energy intake is kept relatively constant through consistently high time spent feeding and travelling in search of food.
8. The results also support the classification of flanged males as pursuing an "*energy maximising*" foraging strategy. Adult females, nulliparous females and unflanged males cannot be reliably categorised as either energy maximisers or time minimisers.
9. Orang-utan DR in Sabangau was relatively long compared to masting forests, and was not affected by fluctuations in fruit/flower availability, in agreement with the search-and-find strategy proposed for orang-utans in PSFs. In contrast, orang-utans in Sabangau spent a similar amount of time socialising as orang-utans in Bornean masting forests, and less time socialising than in the more consistently-productive Sumatran forests, supporting the suggestion that levels of fruit availability as low as those found in Sabangau and in masting forests between masts do limit party size in orang-utans.
10. It is suggested that the relative lack of differences in activity profiles between age-sex classes in Sabangau compared to masting forests is a result of all orang-utans in PSF needing to spend as much time feeding as possible, resulting in different age-sex classes' activity profiles becoming more aligned.
11. Comparisons with other orang-utan populations and African apes are in general agreement with the comparative observations made in previous chapters; i.e., across species, the more variable and unpredictable the fruit supply, the greater the influence of fluctuations in fruit availability on behaviour.

7. CONCLUDING DISCUSSION

7.1 INTRODUCTION

Detailed studies of feeding behaviour (energy/nutrient acquisition and food selection) have been completed for both African apes (Calvert, 1985; Conklin-Brittain *et al.*, 1998; Reynolds *et al.*, 1998; Wrangham *et al.*, 1998; Conklin-Brittain *et al.*, 2006; Hohmann *et al.*, 2006; Rothman *et al.*, 2006, 2007; Masi, 2007; Rothman *et al.*, 2008b) and orang-utans in mast-fruiting habitats (Leighton, 1993; Knott, 1998, 1999), which experience short periods of very high fruit availability, punctuated by long periods of low fruit availability (see **Chapter 3**). These studies point towards differences in diet composition and nutrient/energy intake (**Chapter 4**), food selection (**Chapter 5**) and behavioural responses to fluctuations in fruit availability (**Chapter 6**) between orang-utans in mast-fruiting habitats and African apes. To date, no detailed studies on energy/nutrient acquisition and food selection in orang-utans have been completed in non-masting habitats, however, which have more muted fluctuations in fruit availability. As a result, studies on orang-utans in non-masting habitats may be instructive in understanding whether previous observations on orang-utans in masting habitats are specific to orang-utans, or to orang-utans in masting habitats.

Thus, the main aim in this study was to provide information on feeding behaviour from an orang-utan population in a non-masting habitat, in an attempt to answer this question. To do this, I collected data over two years (July 2005-June 2007) from the non-masting

Sabangau peat-swamp forest (PSF), Central Kalimantan, on orang-utan fruit/flower availability (**Chapter 3**), dietary composition and food-energy intake, and the effects of fluctuations in food availability on this (**Chapter 4**), food-selection criteria (**Chapter 5**), and the effects of changes in diet composition/intake and food availability on non-feeding behaviours (**Chapter 6**). I then compared these data to observations on orang-utans in other sites (focussing particularly on contrasts between masting and non-masting habitats within Borneo) and on African apes. The null hypothesis throughout was that observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats, and different facets of this hypothesis were tested in the different chapters.

In this chapter, I summarise my main results and assess whether the available evidence is more consistent with acceptance or rejection of this hypothesis. Finally, I discuss the implications of this for understanding orang-utan and ape ecology, orang-utan and hominoid evolution, and for orang-utan conservation.

7.2 SUMMARY OF MAIN RESULTS

7.2.1 FOREST PRODUCTIVITY AND FOOD AVAILABILITY

In common with other forests, the availability of orang-utan fruits and flowers in Sabangau varied between months, with the percentage of orang-utan fruit stems bearing fruit ranging from 2.2-7.1% (mean 4.6%), and orang-utan fruit/flower stems bearing food

ranging from 2.5-7.5% (mean 4.9%). The weight and energy of orang-utan fruits and flowers available was highly correlated with these measures, although the magnitude of fluctuations in weight and energy of available orang-utan foods was much greater. When compared to other orang-utan sites, it is clear that, not only is mean orang-utan fruit availability in Sabangau relatively low, but fluctuations in fruit availability are much lower than in the masting habitats of Gunung Palung, where orang-utan energetics has been studied previously (Knott, 1998, 1999). Similarly, in most African ape sites, fruit availability appears to be generally higher and less variable than that experienced by orang-utans. Fruit availability for chimpanzees in Kanyawara during the period for which published data on chimpanzee energetics exists (Wrangham *et al.*, 1998; Conklin-Brittain *et al.*, 2006), appears slightly higher and more variable than orang-utan fruit availability in Sabangau, but lower and less variable than orang-utan fruit availability in Gunung Palung (Knott, 1998, 1999). Thus, three-way comparisons between these sites should be particularly informative in interpreting inter-specific differences in the effects of fluctuations in food availability on diet composition, energy intake and behaviour.

7.2.2 DIET COMPOSITION AND ENERGY INTAKE

As in Bornean masting habitats, fruit was the orang-utan's main dietary component in Sabangau, comprising an average 69% of total feeding time and 77% of total calories obtained. Similar to Bornean masting habitats, the proportion of fruit and other food types in the diet varied temporally, with fruit and flowers preferred when available, and bark and leaves rising in importance when fruit was scarce. Orang-utans in Sabangau

gained a similar proportion of their energy from protein as did those in the masting forests of Gunung Palung (Knott, 1999), but gained less energy from lipids and carbohydrates, and more from fibre, indicating a poorer-quality diet in Sabangau. The percentage of total energy intake obtained through the different nutritional fractions was generally not affected by orang-utan fruit/flower availability, and orang-utans in Sabangau appeared to meet requirements for both protein and fibre.

Despite this, daily energy intake was low in comparison to estimated requirements. This was especially true for flanged males, which did not meet energy requirements in any of the months for which data were available. Daily energy intake was similar to Gunung Palung during periods of very low fruit availability between masts and ketones were detected regularly in urine, indicating regular periods of starvation (i.e., metabolism of fat reserves). Orang-utan fruit availability during the study period was also similar to inter-mast periods in Gunung Palung. Furthermore, fruit-availability data and extrapolations for energy intake during 2003-2005 (based on diet composition data collected by Morrogh-Bernard, submitted) indicate that both fruit availability and orang-utan energy intake in 2003-2005 were higher than during this study (Harrison *et al.*, in prep). Thus, the low energy intake rates documented herein are probably due primarily to unusually low fruit/flower availability during the study period. This is supported by anecdotal observations, which indicate increasingly poor flanged male condition throughout the period included in this study, followed by consequent improvement between the cessation of this study and the time of writing (**Section 4.4.3**). Orang-utans are suggested to have coped with this low level of energy intake by metabolising fat reserves, and reducing

energy expenditure through decreased body weight and "non-exercise activity", and increased ergonomic efficiency.

When controlled for fluctuations in food availability, differences in food types consumed, the nutritional composition of the diet and energy intake between age-sex classes were not significant, thereby refuting hypotheses that flanged male and adult female dietary quality differs, due to differences in body size. In contrast to Gunung Palung, where energy intake is positively associated with fruit availability for both sexes (Knott, 1998, 1999), significant correlations between fruit/flower availability and energy intake in Sabangau orang-utans were detected for flanged males, but not for any other age-sex class. This is interpreted as being a result of either differing abilities to find fruit in the forest and/or, possibly more likely, differences in relative energetic and social demands between the sexes. To date, observations on Sumatran orang-utans (inferred from the absence of ketones detected in urine, Wich *et al.*, 2006b) and African apes (Conklin-Brittain *et al.*, 2006; Masi, 2007; Rothman *et al.*, 2007; K. Potts, pers. comm.) indicate that, generally, daily energy intake in these apes is not significantly influenced by fluctuations in fruit availability. Thus, available data are consistent with the hypothesis that the magnitude of fruit-availability fluctuations determines the strength of the relationship between fruit availability and energy intake, and that effects on females are seen only in habitats with very large fluctuations in fruit availability, whereas effects may be seen on males in habitats where food availability fluctuates less widely, especially if mean fruit availability is low.

7.2.3 FOOD SELECTION

Similar to mast-fruiting habitats in Borneo, comparisons of the relative availability and consumption of different food types identified fruit and flowers as preferred foods, and leaves and bark as fall-back foods (FBFs), in Sabangau. Previous studies on orang-utan fruit selection in masting habitats (Kutai, Leighton, 1993) had indicated that orang-utans choose fruits based largely on crop size and carbohydrate content, in agreement with the predictions of optimal foraging theory (OFT, Stephens and Krebs, 1986). OFT appears to explain well orang-utan selection criteria in Sabangau when comparing energy contents of eaten and avoided fruit pulps, and different food types: FBFs – leaves and bark – offer lower rates of return than preferred foods – fruit and flowers, though not all differences were statistically significant. It does not appear, however, to hold for selection among fruits and flowers in Sabangau: energy content and energy intake rate were not significant predictors of fruit/flower selectivity rank. Instead, multi-variate selectivity modelling showed that adult female fruit/flower selectivity rank in Sabangau was best predicted by the protein/fibre ratio of foods, which was positively associated with selectivity rank. Although multi-variate models were not significant for other age-sex classes, protein/fibre ratio was also significantly positively correlated with selectivity rank in bivariate analyses for flanged males, pointing towards an important role of protein/fibre ratio in orang-utan fruit and flower selection in Sabangau. Furthermore, adult female and flanged male fruit selectivity was negatively affected by fibre, weight or energy intake in at least one bivariate analysis. This is suggested to represent selection against ingestion of large amounts of relatively indigestible fibre, and maximisation of food nutritional

quality and digestive efficiency, rather than selection against foods yielding high energy returns *per se*.

This difference in fruit selectivity between Sabangau and Kutai is interpreted as a result of ecological differences between sites, namely: (1) higher variability in protein and fibre content, and lower variability in carbohydrate contents, of fruits in Sabangau, (2) higher absolute fibre, and lower carbohydrate, contents in fruits in Sabangau, and (3) the lack of mast-fruiting in Sabangau. Kutai is a masting forest (Leighton, 1993) and, hence, orang-utan energy intake in Kutai is probably also tightly related to fruit availability, as in the masting forests of Gunung Palung (Knott, 1998, 1999). Thus, greater selectivity for food-energy content (and maximising energy intake) may be expected in Kutai, selection for quality over quantity may be expected in Sabangau, due to lower overall fruit quality, and what constitutes "optimal foraging" may differ between sites, depending on prevailing ecological conditions. Similarly, the apparent preference for flowers and lack of "fall-back fruits" identified in Sabangau is probably a result of the uniformly low quality of fruits in Sabangau. This is supported by comparison of the nutritional content of fruit pulps between Sabangau and Kanyawara, where figs are FBFs for chimpanzees.

7.2.4 FOOD AVAILABILITY, ENERGY INTAKE AND BEHAVIOUR

Contrary to expectations based on research on orang-utans in masting habitats in Borneo, fluctuations in orang-utan fruit/flower availability generally did not induce changes in non-feeding behaviours. The only exceptions were that adult females were less social and

nulliparous females spent more time awake when fruit/flower availability decreased. Similarly, no relationships were found between energy intake and average party size (PS), or fibre intake and behavioural profiles. Thus, it appears that orang-utan behaviour in Sabangau is not heavily influenced by fruit/flower availability or energy intake. This may be a consequence of the relatively low variations in fruit availability in Sabangau compared to masting forests, and/or the energetic demands of living in the relatively continually fruit-poor Sabangau PSF. Two lines of evidence support this latter suggestion. Firstly, it is clear that the period included in this study was a period of extreme energetic hardship for Sabangau orang-utans. Secondly, in a recent comparison of orang-utan activity budgets between masting and non-masting habitats, it was concluded that orang-utans in non-masting habitats spend more time travelling and feeding, and less time resting, than in masting habitats and that these differences are related to the relatively more consistent fruit supply in non-masting forests (Morrogh-Bernard *et al.*, 2009). Thus, orang-utans in Sabangau appear to need to continually maximise their time spent feeding in an attempt to satisfy their metabolic requirements, which, in turn, may reduce their ability to modify their activity profiles (and, hence, energy expenditure) in response to changes in fruit availability. The relative lack of differences in activity profiles between age-sex classes in Sabangau, in comparison to Bornean masting forests, adds further support to this suggestion.

Orang-utan day range was high in comparison to that recorded in Bornean masting forests, giving further support to the suggestion that orang-utans in PSF travel continuously in search of food (Morrogh-Bernard *et al.*, 2009). Average PS in Sabangau

was similar to that observed in Bornean masting habitats, however, but lower than that observed in the more productive habitats in which Sumatran orang-utans have been studied, supporting the suggestion that levels of fruit availability as low as those found in Sabangau and in masting forests between masts do limit PS in orang-utans. Assessment of these findings in relation to reported behavioural responses to fluctuations in fruit availability in gorillas, chimpanzees and bonobos is in line with observations in previous chapters, i.e., the more variable and unpredictable the fruit supply, the greater the influence of fluctuations in fruit availability on behaviour.

7.3 DOES ORANG-UTAN FEEDING BEHAVIOUR DIFFER BETWEEN MASTING AND NON-MASTING HABITATS WITHIN BORNEO?

Based on these findings, it can be concluded that (i) the availability and nutritional quality of orang-utan fruits in Sabangau during this study was less variable than recorded in the masting forests of Gunung Palung, and similar to periods of low fruit availability between masts in this habitat, (ii) correspondingly, dietary quality and energy intake in Sabangau were low, and similar to low-fruit periods in Gunung Palung, (iii) fruit selection criteria in Sabangau are not consistent with observations from the masting forests of Kutai, and observed differences are consistent with differences in the typical quality and availability of fruits between the two habitat types, and (iv) that orang-utans in Sabangau exhibit relatively few behavioural responses to fluctuations in preferred-food availability, compared to orang-utans in Bornean masting forests. Thus, the over-arching null hypothesis in this thesis – that observations on orang-utan feeding behaviour in

Sabangau are consistent with those made on Bornean orang-utans in masting habitats – cannot be accepted.

7.4 IMPLICATIONS FOR UNDERSTANDING APE ECOLOGY: THE GRADED-RESPONSE HYPOTHESIS

The detailed data provided herein on the inter-relationships between orang-utan diet composition, energy intake, food selection, behaviour and food availability in the non-masting PSF of Sabangau bridge an important gap between orang-utans in mast-fruiting habitats, which are only found in South-east Asia (van Schaik and Pfannes, 2005), and African apes. In bridging this gap, it is apparent that (i) differences in feeding behaviour exist between Bornean orang-utans in masting and non-masting forests, and (ii) these differences, in addition to observations made on other orang-utan and African ape populations, are consistent with the hypothesis that mean fruit availability and quality, and the magnitude of variations in fruit availability and quality, in a site are key in invoking inter-site differences in ape diet composition, energy intake, food selection and behaviour, plus their relationship with fruit availability (cf. Newton-Fisher *et al.*, 2000; Knott, 2001, 2005; Russon *et al.*, 2009; van Schaik *et al.*, 2009b). This is in agreement with previous observations across primates that fruit resources (which are relatively energy rich compared to other food types, Knott, 1998, 1999; this study) are tracked more closely, and behavioural responses more extreme, in habitats with higher variability in fruit availability and longer dry seasons, respectively (Hemingway and Bynum, 2005). Put simply, it appears that, the lower and more variable the supply and quality of fruit in

a habitat (i.e., the less predictable the availability of high-energy fruit), the stronger the relationship between fruit availability, fruit consumption and energy intake, the more food is selected based on energy content, and the stronger the influence of fluctuations in fruit availability on behaviour.

Within apes, three non-mutually-exclusive potential causes of differences in feeding behaviour exist: (i) innate differences, as a result of differing geno/phenotypes, (ii) ecological differences between sites, i.e., flexible responses of the same genotype to varying environments, and (iii) cultural differences (see, e.g., Whiten *et al.*, 2001; Laland and Hoppitt, 2003; van Schaik *et al.*, 2003a and references therein). While cultural differences certainly appear important in explaining behavioural plasticity between conspecific ape populations (e.g., Whiten *et al.*, 1999; van Schaik and Knott, 2001; Whiten *et al.*, 2001; van Schaik *et al.*, 2003a; Whiten *et al.*, 2007; Whiten and van Schaik, 2007; Bastian, 2008; Bastian *et al.*, 2008; van Schaik *et al.*, 2009a), in theory, such cultural traditions should arise at random in all species and, hence, no obvious patterns should be seen between species/populations.

Innate differences in feeding behaviour between great apes clearly exist, as illustrated by comparisons of sympatric gorillas and chimpanzees (Tutin and Fernandez, 1985, 1993; Kuroda *et al.*, 1996; Yamagiwa *et al.*, 1996; Stanford and Nkurunungi, 2003; Stanford, 2006; Yamagiwa and Basabose, 2006a, b). While these studies do report various differences, particularly in the use of FBFs and range use, it is now recognised that inter-generic differences between African apes are not as vivid as was previously believed,

based on comparisons of chimpanzees with mountain gorillas (see Stanford, 2006 and references therein). Furthermore, western lowland gorilla diet is reported as being more similar to that of sympatric chimpanzees than mountain gorillas (Rogers *et al.*, 1990; Tutin and Fernandez, 1993). In this study, I show that the effects of fluctuations in fruit availability on orang-utan energy intake in the non-masting PSFs of Sabangau appear as similar to that of chimpanzees in Kanyawara (Conklin-Brittain *et al.*, 2006) and lowland gorillas in Bai Hoku (Masi, 2007), as to orang-utans of the same sub-species in the masting forests of Gunung Palung (Knott, 1998, 1999). Similarly, the scale of differences in food selection and behavioural responses to changes in fruit availability between orang-utans in Sabangau and mast-fruiting forests in Borneo also appear comparable to differences between Sabangau orang-utans and African apes (**Chapters 5** and **6**). This provides further support for the importance of ecological differences in the determination and evolution of inter-specific differences in ape feeding behaviour and supports the graded-response hypothesis proposed herein.

A graded effect of geographic variations in the predictability of fruit availability on ape behaviour is not surprising, given that all extant great apes are preferential ripe-fruit eaters (e.g., Knott, 2005), that fruits yield the highest rates of energy return (Knott, 1999; this study), and observations in humans (Ellison, 1990; Ellison *et al.*, 1993; Ellison, 2003), chimpanzees (Anderson *et al.*, 2006; Emery Thompson and Wrangham, 2008; see also review in Knott, 2001) and orang-utans (Knott, 1999, 2001) that female reproduction is suppressed by negative energy balance during periods of low fruit availability (see also

Wasser and Barash, 1983; van Schaik and van Noordwijk, 1985; Lee, 1991; Takahashi, 2002 for discussions on other species).

On this basis, it should be expected that, in the face of fluctuations in fruit availability, female apes will attempt to maintain energy intake at levels sufficient for the maintenance of positive energy balance, and that, only in habitats where mean fruit availability is low and fluctuations in fruit availability are so great as to make the continual maintenance of neutral/positive energy balance impossible, should we expect to see a positive relationship between energy intake and fruit availability (e.g., Knott, 2005). Because male fecundity is much less influenced by short-term changes in energy balance (humans: Ellison, 2003; chimpanzees: Muller and Wrangham, 2005), male reproductive success probably hinges more on maintaining their position in the dominance hierarchy and social relationships with females than proximate energy balance. Hence, positive relationships between fruit availability and energy intake might be expected in habitats with lower fluctuations in fruit availability, where similar relationships are not found for females. To date, the available data (reviewed below) are in agreement with this hypothesis (an extension of the "Ecological Energetics" hypothesis proposed by Knott, 1999, 2001, 2005). Further, we should also expect that apes in habitats with more extreme fluctuations in fruit availability, and/or variation in food quality/calorie content, would be more likely to use energy returns as their primary selection criteria than apes in habitats where fruit availability and quality are more uniform.

Although, unfortunately, it was not possible to monitor the production of female orang-utan reproductive hormones in this study (as performed by Knott, 1999, 2001 in Gunung Palung and Emery Thompson, 2005, and Emery Thompson and Wrangham, 2008 for chimpanzees in Kanyawara), the lack of a positive relationship between fruit/flower availability and energy intake in adult female orang-utans in Sabangau implies that female orang-utan reproduction in Sabangau *may* not be as tightly governed by fruit/flower availability as in the masting forests of Gunung Palung (Knott, 1998, 1999, 2001). This suggestion is *very* preliminary, however, especially in light of the generally low levels of energy intake observed for adult females in this study, and long-term data on reproductive-hormone production (cf. Knott, 1999, 2001) is necessary before it can be verified (collection of these data has recently begun in Sabangau under the coordination of C. D. Knott and H. Morrogh-Bernard).

Data collected on chimpanzees in Kanyawara over a 12-yr period indicate that, as in orang-utans in Gunung Palung (Knott, 1999, 2001) and humans (Ellison, 2003), female chimpanzee reproduction is contingent upon energetic status: sexual swellings, oestrogen levels and conceptions were all positively correlated with the consumption of drupe fruits (Emery Thompson and Wrangham, 2008). Similar findings have also been made in the Taï National Park, Côte d'Ivore: both the number of females in oestrus and the timing of first sexual swellings were positively related to food abundance (Anderson *et al.*, 2006). In orang-utans in Ketambe, however, no relationship between conception rate and monthly or annual (i.e., mast-fruiting vs. non-mast-fruiting years) fruit availability was found (Wich *et al.*, 2006a). If the very preliminary suggestion made herein that female

orang-utan reproduction in Sabangau may be less constrained by fluctuations in fruit availability than in Gunung Palung, due to greater variability in fruit availability at the latter site, is found to be true, this would be in agreement with the hypothesis that energetic differences, caused by varying local ecologies (i.e., the degree of variability in fruit production) are major determents of reproductive parameters in female apes (Knott, 2001).

To my knowledge, similar data on wild female gorilla and bonobo reproduction are not available, but available evidence suggests that reproduction in these species is less affected by fluctuations in fruit availability, due to more consistent and predictable fruit availability in these species' habitats (Knott, 2001; see also Tutin, 1994). In fact, variations in the predictability of food availability are considered to be a key cause of differences in life history between ape species: inter-birth interval and other life-history variables are generally longest in orang-utans, which have the least predictable food supply, become progressively shorter in chimpanzees and bonobos, and are shortest in gorillas, mirroring the increased predictability of food supply typically experienced by these species (Knott, 2001; see also Wich *et al.*, 2004b; Knott *et al.*, 2009).

Thus, although innate inter-specific differences in feeding behaviour, responses to fluctuations in fruit availability and, ultimately, the effects of these fluctuations on behaviour, reproduction and life history certainly exist, available evidence indicates that ecological differences between the habitats in which the different species live are also important in inducing the observed inter-specific differences. Put another way, apes

appear to exhibit a *graded response* to fluctuations in food (fruit) availability, which may depends as much on the predictability of its supply, as the species of ape in question.

This hypothesised response may occur at the proximate level (short-term behavioural responses by individuals depending on prevailing conditions, e.g., increased feeding responses to fluctuations in fruit availability during periods of highly-variable fruit availability, compared to that during more stable periods, as suggested by the Kanyawara example, Potts, 2008, pers. comm.; see **Section 4.4.4**), and/or, probably more importantly, at the ultimate level (i.e., the evolution of characters fitting populations/ species to niches, depending on prevailing conditions over generations). Thus, it is possible that, while ultimate-level mean responses may differ between species, ranges may overlap, due to flexibility around this mean, depending on the predictability of the local fruit supply.

An ultimate-level response could be in terms of "classic" genetic evolution, but could also represent population-level cultural evolution, where the population develops a fast-and-feast feeding culture in highly variable environments, with individuals learning to take maximum advantage of periods of plenty from their mother and other conspecifics (this may be difficult to distinguish from a proximate-level response). Being as translocations of apes from one habitat into another are clearly not feasible, testing of these hypotheses will rely on comparative long-term data collected from as many different ape habitats covering as wide a range of conditions and variations in fruit availability as possible.

7.5 IMPLICATIONS FOR ORANG-UTAN AND HOMINOID EVOLUTION

Based on the results of this study and a review of the literature, it would appear that great apes, including orang-utans, exhibit a graded response to fluctuations in fruit availability, depending on the degree of uncertainty and the magnitude of fruit-availability fluctuations. Thus, it is easy to imagine that, over time, continued exposure to different degrees of unpredictability in high-energy fruit availability in different ape species could have led to the evolution of the observed differences in feeding behaviour and myriad other characteristics between species (cf. Dunbar, 1988; Yamagiwa, 1999; Knott, 2001; Yamagiwa, 2004; Knott, 2005; Harrison and Chivers, 2007). For example, inter-site differences in the predictability of fruit supply could lead to changes in sociality at different sites, with animals at sites where fruit availability is less predictable becoming typically less social, which, over extended periods, could lead to fundamental changes in social structure (Harrison and Chivers, 2007). Similarly, such differences in the predictability of fruit availability between sites could lead to inter-site differences in individual energetic status and mortality risk, which, over time, could lead to changes in reproductive parameters and life history (Knott, 2001; Wich *et al.*, 2004b; Knott, 2005; Knott *et al.*, 2009).

7.5.1 THE EVOLUTION OF THE ORANG-UTAN MATING SYSTEM

Recently, we proposed that the evolution of the orang-utan's unique social and mating system (i.e., adult male dimorphism, and delayed development and the attainment of

paternity in unflanged males) most probably evolved from a uni-male polygynous mating system, similar to that of the modern-day gorilla (Harrison and Chivers, 2007). We suggested that the trigger for the change to the present system was an increase in the length and severity of fruit-poor periods, which came about as a result of the development of supra-annual mast-fruiting in dipterocarp forests in South-east Asia and/or "orang-utans" moving into these forests, when climatic changes caused a southerly and easterly contraction of wet tropical forests and, consequently, arboreal primates (Jablonski, 1997, 1998; Jablonski *et al.*, 2000). We contended that this change in food availability would have meant that full-time gregariousness was no longer energetically tolerable for the orang-utan's ancestor and, as a result, females dispersed more widely in search of preferred fruits and adult/flanged males were no longer able to guard effectively a harem of females. A niche for a quiet, quick, opportunistic ''sexual predator'' (i.e., the unflanged male) then became available. Much of the reasoning in this paper was based on Knott's (1998, 1999, 2001) observations of orang-utans in Gunung Palung.

Comparisons of the data collected in this study on orang-utans in PSF with that collected on orang-utans in Gunung Palung (Knott, 1998, 1999, 2001), in addition to observations on Sumatran orang-utans (van Schaik, 1999; Wich *et al.*, 2006a, b), might appear to contradict our hypothesis. Available evidence suggests that Gunung Palung (i.e., mast-fruiting forests in Borneo) represents an extreme case, and that the strong relationships between fruit availability, energy intake and, possibly, female reproduction seen in orang-utans in Gunung Palung do not exist in non-masting forests, and even in mast-fruiting dipterocarp forests in Sumatra (e.g., Ketambe, Wich *et al.*, 2006a, b). Other evidence is

also apparently contradictory. The most recent and complete analysis of genetic data collected on Sumatran and Bornean orang-utans (Steiper, 2006), suggests that genetic diversity is higher in Sumatra than Borneo, and that extensive gene flow between Sumatran and Bornean orang-utans probably did not occur during the Pleistocene. This is supported by Harrison *et al.*'s (2006) recent synthesis of genetic, palaeoclimatic, palaeontological and zoo-archeological data, which supports a model in which "orang-utans" enter Sundaland at ca. 2.7 Mya, with population fragmentation at ca. 1.8 Mya. Although the Sunda Shelf was cyclically exposed at this time, it is thought that major river systems and drier more seasonal woodland and grassland ecosystems, largely unsuitable for arboreal primates, between Borneo and Sumatra curtailed gene flow between the two islands, though gene flow was maintained between Sumatra and the mainland via intermittent land bridges (Harrison *et al.*, 2006). This suggests that, due to more recent mingling with the ancestral mainland population, the Sumatran orang-utan, in which sociality, energy intake and female reproduction are likely influenced little, if at all, by fruit availability is the best model for the ancestral orang-utan.

The observations made herein suggest, however, that the response of apes to fluctuations in fruit availability may be dependent as much on the ecology of the habitat in which they live as on inter-specific differences. Thus, we probably stand to gain greatest insight into the pressures that shaped orang-utan evolution by examining contemporary orang-utans in habitats most similar to those that were probably inhabited by their ancestors. Despite the probably closer genetic affinity of Sumatran orang-utans to the common orang-utan ancestor, there is reason to believe that greater inference can be drawn from observations

on Bornean orang-utans in masting habitats, such as Gunung Palung and Kutai (Leighton, 1993; Knott, 1998, 1999), than from orang-utans in Bornean PSFs and Sumatra.

Firstly, Sumatran forests in general, and particularly Sumatran forests in which orang-utan behaviour has been studied (i.e., Ketambe and Suaq Balimbing), are more productive than both Bornean forests (Marshall *et al.*, 2009a; see also **Section 3.4.3**) and probably also those in Peninsular Malaysia. Sumatra is composed mainly of young, volcanic and, hence, nutrient-rich rocks, compared to the older sedimentary rocks of Borneo and, especially, mainland Asia (where rocks in many regions date back to the Palaeozoic era 540-248 Mya, e.g., Steinshouer *et al.*, 1997; Whitten *et al.*, 1997). Although the probability of mast-fruiting events occurring in any given year in Sumatra (average 0.25), Borneo (0.24) and Peninsular Malaysia/Singapore (0.22) does not differ (Wich and van Schaik, 2000), forest productivity in lowland dipterocarp forests, as measured through total litter-fall, appears slightly higher in Sumatra (Ketambe: mean 9.58 t/ha/yr, calculated from all 17 plots in van Schaik and Miranto, 1985), compared to Borneo (Gunung Mulu National Park: 8.8 t/ha/yr, Proctor *et al.*, 1983b) and Peninsular Malaysia (Pasoh Forest Reserve: 8.9 t/ha/yr, Lim, 1978). The percentage of trees with fruit during both mast and non-mast periods (Medway, 1972; Sakai *et al.*, 1999; Intachat *et al.*, 2001; Sakai, 2002; Frederiksson *et al.*, 2006; Brearley *et al.*, 2007; Cannon *et al.*, 2007a, b) and above-ground plant biomass (Kato *et al.*, 1978; Kira, 1978; Yamakura *et al.*, 1986) are also very similar in Borneo and Peninsular Malaysia (as far as I am aware, similar published data are not available from Sumatra). Thus, if Sumatran forests are more productive in terms of orang-utan fruits than Borneo (Marshall *et al.*, 2009a), then

orang-utan fruit availability in Miocene/Pliocene Peninsular Malaysia would probably also have been lower than in Sumatra. Other comparisons reveal a similar picture: for example, hylobatid biomass in Ketambe, Sumatra (98 kg/km^2) is much higher than both Peninsular Malaysia (mean 43.7 kg/km^2) and Borneo (mean 35.4 kg/km^2, Mather, 1992, see also Chivers, 2001; O'Brien *et al.*, 2004).

Secondly, numerous lines of evidence indicate that the orang-utan probably underwent most of its evolution in lowland dipterocarp forests in Peninsular Malaysia, which, as argued above, were probably more similar in terms of productivity to present-day dipterocarp forests in Borneo than Sumatra. Even though orang-utans are thought to have entered Sundaland ca. 2.7 Mya (Harrison *et al.*, 2006), the eruption of the Toba volcano ca. 75,000 ya would have decimated most of the Sumatran orang-utan population (Muir *et al.*, 2000) and, hence, the Sumatran population was most probably replenished quite recently by large immigrations from Peninsular Malaysia after this event.

Today, PSF is unevenly distributed throughout South-east Asia, with the vast majority occurring in Indonesia (ca. 206,950 km^2, 82% of total area of PSF in SE Asia) and, particularly, Borneo and Sumatra (Rieley *et al.*, 1996; Hooijer *et al.*, 2006; Page *et al.*, 2007, 2008). Although large relatively-flat expanses, on which swamps might be expected to form, do occur in Thailand, Myanmar and Cambodia, the amount of PSF in these areas is very low (ca. 394, 500 and 0 km^2, 0-1%, Lappalainen, 1996; Page *et al.*, 2008; see also maps in Stibig *et al.*, 2002, 2004). The topography of the remaining parts of the region indicates that large swathes of PSF probably did not occur in mainland Asia

during last few million years. It is probable that some swamp forest did occur on the Sunda Shelf when this was exposed, but the shelf was only exposed during brief inter-glacial periods, and the majority of evidence indicates that the climate was generally drier during such periods and that vegetation cover on the exposed shelf was probably mostly savannah/open woodland (Harrison *et al.*, 2006).

Furthermore, dipterocarp pollen has been found in Pleistocene marine cores from the Banda Sea on the Sunda Shelf (van der Kaars *et al.*, 2000; Hope *et al.*, 2004). Dipterocarps tend to dominate in most contemporary SE Asian forests in which they occur (Ashton, 1989), indicating that areas of dipterocarp-dominated forest probably also existed on the Sunda Shelf. Finally, dipterocarp forests span most of the lowland areas of contemporary SE Asia (Ashton, 1989) and, although the extent of these forests during the last few million years almost certainly expanded and contracted in response to climatic changes (Jablonski, 1997, 1998; Jablonski *et al.*, 2000), it is likely that dipterocarp forests persisted throughout in southern Peninsular Malaysia and, hence, that these were key habitats for orang-utans during these times. In summary, therefore: (a) the orang-utan's ancestor underwent the majority of its evolution on mainland SE Asia, where dipterocarp forests were most probably the dominant forest type, and (b) the source of any orang-utan's dispersing from the mainland (i.e., Peninsular Malaysia) was most probably dominated by evergreen dipterocarp forests, similar in character to those found on Borneo today, for most, if not all, of the last 5 Myrs.

Thus, although detailed comparisons of forest productivity between Sumatra, Borneo and Peninsular Malaysia (cf. Marshall *et al.*, 2009a) are needed in order to confirm this suggestion, the available data indicate that orang-utan fruit availability in dipterocarp forests in mainland Malaysia before the extinction of orang-utan populations there would probably have been more similar to contemporary Bornean forests than the highly-productive Sumatran sites (Ketambe and Suaq Balimbing), in which orang-utans have been studied to date. Consequently, orang-utans in Bornean masting forests may be the best model of the ancestral orang-utan.

7.5.2 THE EVOLUTION OF LARGE BODY SIZE IN ORANG-UTANS

It has been proposed that the orang-utan's large body size enables (a) increased digestive efficiency and, hence, consumption of lower-quality food sources in times of food shortage, (b) greater absolute and relative fat storage, allowing excess calories consumed during periods of food abundance to be converted to fat, which can be drawn upon in periods of food shortage, and (c) that, as energy and protein requirements scale to 0.762 body weight (Lloyd *et al.*, 1978; Robbins, 1983; Nagy, 1994), a larger animal can live for longer from its bodily reserves (Wheatley, 1982, 1987; Leighton, 1993; Knott, 1998). The observations of large variations in energy intake between months, regular ketolysis and a positive correlation between energy intake and fruit/flower availability in flanged males made in this study are in agreement with this hypothesis. The lack of a significant relationship between energy intake and fruit/flower availability in females runs counter to this hypothesis, but, as noted above, greater inference of the importance of such

adaptations during orang-utan evolution can probably be drawn from orang-utans in mast-fruiting habitats, such as Gunung Palung, where strong correlations between energy intake and fruit availability in female orang-utans were found (Knott, 1998, 1999). A more complete reassessment of Wheatley's (1987) hypotheses will form the subject of a future analysis.

7.6 IMPLICATIONS FOR CONSERVATION

7.6.1 THE FUTURE OF THE SABANGAU ORANG-UTANS

The data presented in this study are potentially worrying from a conservationist's viewpoint. I observed mean orang-utan energy intake to be below estimated requirements for all age-sex classes, and flanged male energy intake was below estimated requirements in each month followed. This observation was made using the higher estimate for fibre digestibility (see **Section 4.2.3)** and, thus, probably represents the 'best-case scenario' for the orang-utan population during this period. As noted above, however, the low energy intake rates documented are probably due to low fruit/flower availability during the study period. Thus, although orang-utans (and particularly flanged males) in Sabangau clearly walk an "energetic tightrope", where the struggle to maintain an adequate energy balance is ever present, it may be premature to conclude that the population is on the cusp of death via starvation.

The observations of very low energy intake in flanged males and the positive relationship observed between flanged male energy intake and fruit/flower availability, in addition to anecdotal observations on body condition, suggests that flanged male orang-utans in Sabangau are susceptible to any loss of feeding trees through logging disturbance. The observation that adult female energy intake was not affected by fruit/flower availability in this study does not, however, necessarily indicate that adult females are insusceptible to reductions in food availability due to logging disturbances. Firstly, similar to flanged males, adult female energy intake during this study was below requirements in most months, indicating that adult female orang-utans in Sabangau also balance precariously on the "energetic tightrope". Secondly, the extreme fluctuations in fruit availability seen in Bornean mast-fruiting habitats do result in a positive relationship between fruit availability and energy intake in adult females (Knott, 1998, 1999), and similar responses may be seen in Sabangau over the long term, when greater fluctuations in fruit availability will occur. Finally, as discussed above and in **Section 4.4.1**, due to the ever-present demands of reproduction, adult females may need to maintain a relatively constant energy balance compared to males. Thus, removal of food trees from the habitat may push mean food availability below a threshold level, beyond which point females can no longer maintain mean energy intake above requirements in the long term. Though speculative, these considerations merit caution. Furthermore, adult female home ranges are smaller and more fixed than males' (Singleton and van Schaik, 2001; Morrogh-Bernard, submitted), adult females are reported to be less efficient at travelling through disturbed forest (Rao and van Schaik, 1997) and are more vulnerable to ground predators (Galdikas, 1988) and, hence, are probably more likely to avoid areas with large canopy

discontinuities (Felton *et al.*, 2003). These reasons are thought to have resulted in sex-biased effects of logging disturbance in orang-utans, with females suffering more severe declines following disturbance than males (Felton *et al.*, 2003; Husson *et al.*, in prep).

The length of time that orang-utans can exist in varying degrees of negative energy balance, and the speed with which they can recover and replenish reserves in times of plenty are not known, and can only be established through long-term studies. Nevertheless, the data presented herein should ring some alarm bells and remind us that complacency is not a luxury we can afford.

7.6.2 LONG-TERM MONITORING OF THE SABANGAU ORANG-UTANS

Recently, my colleagues and I have argued for the importance of long-term monitoring of orang-utan populations, without which the effectiveness of conservation efforts, which frequently require large amounts of financial and other resources, cannot be assessed and adapted to increase their effectiveness (Harrison *et al.*, 2007a; Husson *et al.*, 2007, see also, e.g., Hockings *et al.*, 2000; Carignan and Villard, 2001; Dale and Beyeler, 2001). In Sabangau, it has been shown that, following the formation of the CIMTROP (Centre for the International Cooperation in Management of Tropical Peatlands) Patrol Team, charged with preventing illegal logging in the Natural Laboratory of Peat-Swamp Forest (NLPSF) where this study was conducted, in 2004, both orang-utan density and mean tree basal area/ha in NLPSF increased up until mid-2007 (Husson *et al.*, 2007). This demonstrates the importance of effective law enforcement for conservation in the area.

Thus, a subsidiary aim in this study was to attempt to develop easy, quick, cost-effective techniques for monitoring orang-utan population viability in the area, to complement on-going density surveys, which suffer from the problem of delayed response (i.e., where problems are only detected after the event, Harrison *et al.*, 2007a).

Energy intake and balance (assessed through ketone production in urine) are useful in this regard, as female orang-utan reproduction is dependent on energetic status (Knott, 1999, 2001) and, thus, prolonged low energy intake/negative energy balance may indicate future population declines (Harrison *et al.*, 2007a). The main obstacle preventing wide-spread usefulness of energy intake as a monitoring technique is the large investment of time and money required to obtain nutritional data for plant species eaten (Harrison *et al.*, 2007a). These data have been provided during the course of this study, which will enable long-term monitoring of energy intake to be conducted from basic ongoing observations of diet composition.

Long-term monitoring of orang-utan fruit/flower availability is also important, because (i) flanged male energy intake in Sabangau is shown here to be dependent on fruit/flower availability, and (ii) to establish whether similar trends exist for females over the long term, when wider fluctuations in fruit availability will occur. Unfortunately, total litter-fall (LF), which is very easy and cheap to collect, was found not to correlate with any plot-derived measure of orang-utan fruit/flower availability or orang-utan energy intake, and, thus, cannot be used for long-term monitoring in this sense. It remains to be established, however, whether longer-term relationships between these measures exist

between sites (i.e., comparing mean values for sites collected over a number of years). Available evidence suggests that orang-utan and gibbon population density is higher in habitat sub-types in Sabangau with greater LF production (Morrogh-Bernard *et al.*, 2003; Sulistiyanto *et al.*, 2004; Cheyne *et al.*, 2008), suggesting that (a) LF may be a useful indicator of ape population density in relatively undisturbed PSF, and (b) future studies will substantiate the suggestion that long-term mean LF, and ape fruit availability and density are related across habitats/sites.

7.7 SUMMARY – FINAL CONCLUSIONS

1. The main findings in this study were that:
    a. mean orang-utan fruit/flower availability, and variation in this, in Sabangau were low, consistent with the lack of mast-fruiting in Sabangau,
    b. mean orang-utan energy intake was low and requirements were not met in most months, particularly for flanged males,
    c. orang-utan energy intake was positively related to fruit/flower availability in flanged males, but not in females or unflanged males,
    d. orang-utans tended to select food types based largely on expected rates of energy return, but selection within fruits may depend more on fruit quality (the best model predicting adult female fruit selectivity rank contained only protein/fibre ratio),
    e. orang-utans in Sabangau exhibit a relative lack of alterations in non-feeding behaviours in response to reductions in preferred-food availability and energy intake.
2. These results contrast with those of previous researchers on Bornean orang-utans in masting habitats, suggesting that the null hypothesis that "observations on orang-utan feeding behaviour in Sabangau are consistent with those made on Bornean orang-utans in masting habitats" should be rejected. In turn, this implies that previous observations on orang-utans in masting habitats cannot necessarily be considered representative of all orang-utan populations.

3. When compared with findings on orang-utans at other (mast-fruiting) sites and African apes, these findings are consistent with a *graded-response* hypothesis, in which the less predictable the availability of (high-energy) fruit, the stronger the relationship between energy intake and fruit availability, the more food is selected based on energy content, and the stronger the influence of fluctuations in fruit availability on behaviour and, ultimately, probably also female reproduction.
4. It is hypothesised that positive relationships between fruit availability and energy intake might be expected in males in habitats with lower fluctuations in fruit availability, where similar relationships are not found for females, due to differing energetic (providing for offspring in females) and social (maintaining dominance and ensuring mating opportunities are not missed in males) demands between the sexes.
5. The findings in this study suggest that orang-utans in Sabangau struggle to meet their daily energetic needs and, hence, should be very sensitive to reductions in fruit/flower availability due to logging disturbance. The data collected in this study will also enable long-term monitoring of orang-utan energy intake in Sabangau, which will aid in predicting/interpreting future population trends.

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APPENDIX I – NUTRIENT AND ENERGY CONTENT DATA

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Adenanthera pavonina	Yes	SD	Yes	0.29	90	17	7	24	49	3	87	22	9	30	39	322	338	372
Adenanthera pavonina	No	SK	Yes	0.99	89	8	0	30	60	2	87	10	1	38	51	249	270	312
Aglaia rubiginosa	No	PL	Half	0.85	93	9	15	35	39	3	91	10	18	42	30	321	344	389
Aglaia sp. 1	Yes	PL	Yes	0.17	82	5	1	43	47	3	79	8	2	66	24	143	179	251
Aglaia sp. 1	No	SD	Yes	1.25	92	10	1	24	64	1	90	12	1	29	58	290	306	337
Aglaia sp. 1	No	SK	Yes	0.37	91	11	10	55	18	5	87	14	13	70	3	187	225	301
Alyxia sp. 1	Yes	LS	No	0.09	95	6	2	55	32	5	90	6	2	64	27	155	190	259
Baccaurea bracteata	No	PL/SK	Yes	0.45	92	3	0	53	41	3	90	3	1	64	32	146	181	251
Blumeodendron elateriospermum / kurzii	Yes	AR	Half	0.31	93	6	1	42	44	6	88	8	1	52	39	197	225	282
Blumeodendron elateriospermum / kurzii	Yes	SD	Half	2.25	94	8	9	55	26	2	92	9	11	63	17	202	236	305
Blumeodendron elateriospermum / kurzii	No	SK	Half	-	96	2	1	73	23	2	93	2	1	81	16	78	122	211

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Blumeodendron elateriospermum / kurzii	No	SK	No	3.03	95	1	0	68	28	2	93	2	0	77	21	96	137	220
Blumeodendron elateriospermum / kurzii	Yes	LS	No	0.09	91	10	1	32	55	3	88	13	1	40	47	245	266	310
Buchanania cf. arborescens	Yes	WH	Yes	0.10	91	5	3	69	20	2	89	6	4	86	3	77	123	217
Calamus sp. 1	No	SD	Yes	0.09	89	6	1	67	24	2	88	7	1	86	6	63	110	203
Calamus sp. 1	No	SK	Yes	0.03	91	3	1	71	19	5	87	4	1	90	5	43	92	190
Callophyllum hosei	Yes	PL/SK	No	0.23	96	4	5	68	20	2	94	5	5	76	15	122	164	246
Callophyllum hosei	Yes	PL/SK	Yes	0.36	91	4	5	55	34	3	89	5	6	67	22	163	199	272
Callophyllum hosei	No	SD	No	0.21	91	5	2	68	23	2	89	6	3	83	8	80	125	216
Callophyllum hosei	No	SD	Yes	0.83	98	7	0	79	11	2	95	7	0	85	7	60	106	198
Callophyllum hosei	Yes	LS	No	0.03	92	7	4	36	51	2	90	8	4	44	44	245	269	317
Callophyllum sclerophyllum	Yes	PL/SK	Yes	0.36	94	4	8	40	46	2	92	4	9	47	39	259	284	335

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter					Organic Matter	Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash		Crude Protein	Lipid	NDF	TNC			
Callophyllum sclerophyllum	No	SD	Yes	1.80	94	3	6	52	38	1	93	3	7	59	31	200	232	296
Campnosperma coriaceum	Yes	PL/SK	No	0.06	88	6	0	59	30	4	85	9	0	79	12	86	129	215
Campnosperma coriaceum	No	SD	No	0.05	91	6	4	69	21	1	90	7	4	83	5	87	133	223
Campnosperma squamatum	Yes	PL/SK	Yes	0.31	92	3	1	41	51	4	89	4	1	50	45	202	229	284
Castanopsis foxworthyii	Yes	SD	No	0.38	91	5	1	45	47	2	89	6	1	56	38	180	211	271
Castanopsis foxworthyii	No	SK	No	0.65	92	4	1	68	24	3	89	5	1	84	10	69	114	205
Castanopsis foxworthyii	Yes	LS	No	0.08	93	11	1	20	65	4	90	13	1	23	62	312	325	350
Combretocarpus rotundus	Yes	WH	Yes	0.02	92	11	2	61	25	2	90	13	3	73	11	119	159	239
Cratoxylon glaucum	No	LS	No	0.02	94	16	3	23	55	3	91	19	3	27	52	309	323	352
Ctenolophon parvifolius	No	PL	No	0.03	89	11	2	16	71	1	88	14	3	20	64	334	345	366
Ctenolophon parvifolius	Yes	SD	No	0.06	90	6	0	19	71	4	87	8	1	24	68	307	320	346

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Ctenolophon parvifolius	No	SK	No	0.14	94	6	0	69	24	1	93	7	0	79	13	85	128	214
Ctenolophon parvifolius	Yes	LS	No	0.04	91	18	0	35	44	3	88	22	0	43	34	227	251	298
Dialium patens	Yes	LS	No	0.16	93	8	0	32	58	2	91	9	0	37	53	251	271	312
Diospyros bantamensis	Yes	CA	-	-	93	4	0	51	36	7	86	5	1	65	29	144	179	249
Diospyros bantamensis	Yes	PL	Yes	0.49	92	10	1	52	23	14	79	14	1	71	14	119	157	235
Diospyros bantamensis	No	SD	No	3.99	89	4	0	65	28	2	87	6	0	84	10	65	111	202
Diospyros bantamensis	No	SD	Yes	4.96	90	4	0	61	32	2	88	6	0	77	17	93	135	219
Diospyros bantamensis	No	SK	No	8.11	92	3	1	69	26	2	91	3	1	82	14	77	121	210
Diospyros bantamensis	No	SK	Yes	11.36	95	3	1	73	22	2	94	3	1	82	15	77	121	210
Diospyros bantamensis	Yes	LS	No	0.07	93	19	2	63	12	4	89	23	2	77	0	113	155	238
Diospyros confertiflora	Yes	PL	Yes	0.07	92	4	0	9	84	3	89	5	0	11	84	359	365	377
Diospyros confertiflora	Yes	SD	Yes	0.14	91	6	1	21	69	3	88	7	1	26	66	300	314	342

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Diospyros confertiflora	No	SK	Yes	0.24	93	4	1	44	48	3	90	5	1	52	42	198	226	283
Diospyros siamang	Yes	CA	-	-	93	6	1	37	43	12	81	9	2	48	41	216	242	295
Diospyros siamang	Yes	PL	Yes	0.68	89	9	6	8	74	4	86	11	8	10	71	398	403	414
Diospyros siamang	No	SD	Yes	1.90	87	7	0	42	47	4	84	10	1	57	33	174	205	267
Diospyros siamang	No	SK	Yes	5.08	94	3	1	64	29	3	91	4	1	75	20	104	145	227
Diospyros siamang	Yes	LS	No	0.10	92	11	1	34	51	3	89	13	1	42	44	237	260	306
Dyera lowii	Yes	CA	-	-	93	3	13	36	43	5	88	4	16	43	37	307	330	377
Dyera lowii	No	BK	-	-	94	1	1	71	26	1	93	2	1	82	15	79	123	212
Dyera lowii	No	SK	No	16.71	92	3	3	66	26	2	90	3	4	79	14	101	144	230
Dyera lowii	No	SK	Yes	21.14	94	2	3	66	27	2	91	3	3	77	17	109	151	235
Dyera lowii	No	LS	No	0.18	93	8	0	32	58	2	91	9	0	37	53	251	271	312
Dyera lowii	Yes	PI		1.78	95	3	16	23	53	4	91	3	19	27	51	385	400	429
Elaeocarpus mastersii	No	PL/SK	No	0.07	90	3	1	29	66	2	88	4	1	37	58	257	277	317
Elaeocarpus mastersii	Yes	PL/SK	Yes	0.05	87	4	0	58	36	2	86	5	1	78	17	92	134	218

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Elaeocarpus mastersii	No	SD	No	0.06	92	5	8	65	20	1	91	6	10	79	6	136	179	264
Elaeocarpus mastersii	No	SD	Yes	0.05	92	5	12	66	15	1	91	6	15	80	0	156	200	286
Elaeocarpus mastersii	Yes	LS	No	0.04	91	7	1	21	70	2	89	9	1	26	65	303	317	345
Euphorbiaceae sp. 2	Yes	LS	No	0.05	91	24	1	36	36	4	88	30	1	45	23	228	252	301
Fibraurea tinctoria	Yes	PL	Yes	0.08	80	11	1	14	72	2	79	17	2	23	58	316	329	354
Fibraurea tinctoria	No	SD	Yes	0.73	94	4	3	82	11	1	93	5	3	93	-1	43	94	195
Fibraurea tinctoria	No	SK	Yes	0.31	90	8	3	46	36	7	84	10	4	60	25	180	212	278
Ficus cf. spathulifolia	Yes	PL/SK	Yes	0.21	95	5	1	43	44	7	88	7	1	51	41	201	229	285
Ficus sp.	No	SD	Yes	0.22	96	6	1	71	17	5	91	7	1	80	12	86	129	216
Freycinetia sp. 1	No	Blade	Yes	0.16	93	5	0	72	19	4	90	6	0	85	8	61	107	200
Freycinetia sp. 1	Yes	PI	Yes	0.02	93	8	0	47	36	8	86	10	0	60	30	163	196	260
Fungi (kulat bango)	Yes	-	-	0.31	92	21	0	53	22	3	89	26	1	66	8	141	176	247
Garcinia bancana	No	PL	No	3.63	85	2	3	44	51	1	84	2	4	61	33	174	207	273

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter					Organic Matter	Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash		Crude Protein	Lipid	NDF	TNC			
Garcinia bancana	Yes	PL	Yes	1.40	88	2	8	44	44	1	87	3	10	58	29	220	251	315
Garcinia bancana	No	SD	Yes	0.97	95	7	28	62	0	3	92	8	32	71	-11	277	316	392
Garcinia bancana	No	SK	Yes	2.46	88	3	15	52	28	2	86	3	19	68	9	224	261	335
Garcinia bancana	Yes	LS	No	0.07	91	10	1	37	49	3	88	12	2	46	40	225	250	300
Garcinia sp. 11	Yes	PL/SK	Yes	0.04	85	3	2	33	61	1	84	5	2	46	47	225	250	300
Garcinia sp. 11	No	SD	Yes	0.07	95	6	37	46	10	1	94	7	41	51	1	401	429	484
Garcinia sp. 5	No	SK	Yes	4.26	84	2	10	29	58	2	82	2	14	41	42	304	326	371
Gnetum sp. 1	No	PL/SK	No	0.20	97	10	1	71	14	4	94	11	2	77	10	98	140	224
Gnetum sp. 1	Yes	PL/SK	Yes	0.18	96	12	1	57	26	5	92	13	1	65	21	149	184	254
Gnetum sp. 1	No	SD	Yes	0.62	95	8	2	43	46	1	93	9	2	49	40	215	242	295
Gnetum sp. 2	Yes	PL	Yes	0.05	86	10	0	47	37	6	81	14	1	67	18	135	171	244
Gnetum sp. 2	No	SD	Yes	0.52	92	7	2	37	53	2	90	8	2	45	45	229	254	303
Gnetum sp. 2	No	SK	Yes	0.20	91	6	0	57	33	4	88	8	0	71	21	117	156	233
Gymnacranthera farquhariana	No	LS	No	0.12	94	14	1	43	40	2	93	16	1	50	33	208	235	289
Honey	Yes	-	-	-	95	35	32	34	-5	4	91	41	37	39	0	500	521	564
Horsfieldia crassifolia	Yes	LS	No	0.15	92	18	1	38	39	4	89	22	2	47	30	221	247	297

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Koompassia malaccensis	Yes	CA	-	-	92	10	1	47	38	5	87	13	1	58	28	170	202	265
Koompassia malaccensis	No	BK	-	-	93	4	0	67	23	5	88	5	1	83	12	72	117	207
Koompassia malaccensis	No	LS	No	0.02	92	10	0	14	74	2	90	12	0	17	70	333	342	361
Licania splendens	No	PL/SK	No	0.06	95	5	1	65	22	6	89	6	1	77	15	96	138	222
Licania splendens	No	SD	No	0.10	97	7	1	78	11	3	95	7	1	85	7	69	115	207
Licania splendens	No	SD	Yes	0.16	98	7	0	79	11	2	95	7	0	85	7	60	106	198
Lithocarpus conocarpus	Yes	SD	Half	1.27	90	3	1	66	29	1	89	4	1	81	14	78	122	211
Litsea sp. 1 cf. resinosa	Yes	PL/SK	No	0.10	90	6	12	41	38	3	87	7	15	52	25	269	297	353
Litsea sp. 1 cf. resinosa	Yes	PL/SK	Yes	0.21	87	4	0	58	36	2	86	5	1	78	17	92	134	218
Litsea sp. 1 cf. resinosa	No	SD	No	0.14	91	5	11	58	24	2	89	7	14	71	9	185	224	301
Litsea sp. 1 cf. resinosa	No	SD	Yes	0.43	96	10	16	49	23	2	94	12	17	55	16	269	298	358

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Madhuca mottleyana	Yes	CA	-	-	93	3	4	61	28	4	89	4	5	73	18	132	172	251
Madhuca mottleyana	Yes	FLB	No	0.01	97	10	5	69	12	4	93	11	5	77	8	119	161	244
Madhuca mottleyana	Yes	FL	Yes	0.00	97	11	3	42	38	6	91	13	4	48	36	226	252	305
Madhuca mottleyana	No	FL stalk	Yes	0.01	97	8	5	66	16	5	92	9	6	74	11	135	175	256
Madhuca mottleyana	Yes	LS	No	0.10	92	13	2	15	65	5	87	16	3	19	62	338	349	370
Memecylon sp. 3	Yes	PL/SK	Yes	0.02	92	5	2	30	58	7	86	6	2	37	55	261	281	322
Mesua sp. 1	Yes	PL/SK	No	0.54	92	5	0	37	53	4	88	6	1	46	47	220	245	294
Mesua sp. 1	Yes	PL/SK	Yes	0.68	92	5	1	26	65	3	89	7	1	32	61	276	294	328
Mesua sp. 1	No	SD	No	0.44	92	3	0	9	85	2	90	4	0	11	85	356	362	375
Mesua sp. 1	No	SD	Yes	1.20	91	6	4	65	24	1	90	8	5	78	9	111	154	239
Mezzettia leptopoda / parviflora	Yes	PL	Yes	0.13	92	16	21	31	29	3	89	19	25	38	17	374	394	436
Mezzettia leptopoda / parviflora	No	SD	Yes	15.74	94	2	2	74	21	1	93	2	2	85	11	70	116	208

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter					Organic Matter	Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash		Crude Protein	Lipid	NDF	TNC			
Mezzettia leptopoda / parviflora	No	SK	Yes	6.70	96	4	1	68	23	4	92	5	1	78	16	92	135	219
Mezzettia leptopoda / parviflora	Yes	LS	No	0.12	92	10	2	51	35	2	90	11	2	62	25	164	197	264
Mezzettia umbellata	No	SD	Yes	1.27	97	4	4	70	22	1	96	4	4	75	17	121	162	244
Mezzettia umbellata	No	SK	Yes	0.44	96	9	2	68	15	6	90	11	2	78	9	97	139	224
Mezzettia umbellata	No	LS	No	0.10	95	15	2	25	56	3	92	17	2	28	53	297	312	343
Myristica lowiana	Yes	CA	-	-	94	4	1	51	42	3	91	5	1	59	35	167	199	263
Myristica lowiana	Yes	PL/SD	Yes	3.78	95	6	7	32	52	2	93	7	8	36	48	296	316	355
Myristica lowiana	No	LS	No	0.45	91	10	1	66	19	3	88	13	2	83	3	78	123	213
Neoschortechinia kingii	Yes	PL	Yes	0.16	90	5	1	62	26	7	84	7	1	82	11	76	120	209
Neoschortechinia kingii	Yes	SD	Yes	0.50	86	9	2	43	44	2	84	13	2	59	26	177	209	273

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter					Organic Matter	Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash		Crude Protein	Lipid	NDF	TNC			
Neoschortechinia kingii	No	SK	Yes	0.35	92	13	1	62	19	5	87	16	1	78	5	96	138	223
Nephellium lappaceum	Yes	PL	Yes	0.07	90	7	2	14	72	5	86	9	2	18	70	341	351	370
Nephellium lappaceum	No	SD	Yes	0.93	92	6	6	37	35	16	77	9	9	52	30	234	262	319
Nephellium lappaceum	No	SK	Yes	1.20	92	3	0	47	44	6	87	4	0	58	37	170	202	265
Nephellium maingayi	No	SD	Half	0.27	97	11	44	31	13	2	96	12	47	33	8	504	522	558
Nephellium maingayi	Yes	LS	No	0.04	91	11	1	17	70	2	89	13	1	21	65	321	332	355
Palaquium cochlearifolium	Yes	FL	Yes	0.02	90	5	3	27	62	2	88	6	4	34	55	283	301	339
Palaquium cochlearifolium	No	FL stalk	Yes	0.09	93	5	4	36	53	3	90	6	4	43	47	251	274	321
Palaquium cochlearifolium	Yes	PL/SK	Half	1.94	92	2	6	17	72	2	90	3	7	21	69	355	366	389
Palaquium leiocarpum	Yes	PL/SK	No	0.49	97	6	1	62	26	4	93	7	2	68	23	134	172	246
Palaquium leiocarpum	No	LS	No	0.21	93	8	3	22	63	4	89	9	4	27	60	312	327	356

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Palaquium pseudorostratum	Yes	FL	Yes	0.01	89	6	2	48	41	3	87	7	3	62	28	169	203	269
Palaquium pseudorostratum	Yes	PL/SK	No	0.59	95	5	4	52	35	4	90	5	5	61	29	181	214	280
Palaquium pseudorostratum	No	LS	No	0.10	92	7	3	42	44	4	89	8	4	52	37	211	239	296
Palaquium ridleyii / xanthochymum	Yes	PL/SK	Half	0.04	90	7	2	38	50	3	87	9	2	49	40	215	242	295
Palaquium ridleyii / xanthochymum	Yes	PL/SK	No	0.04	90	8	2	23	65	3	87	10	3	29	58	297	313	344
Palaquium ridleyii / xanthochymum	Yes	PL/SK	Yes	0.03	89	10	2	40	44	4	85	13	2	53	32	198	227	285
Palaquium ridleyii / xanthochymum	No	SD	Half	0.02	94	10	26	41	20	3	91	11	31	48	10	359	385	438
Palaquium ridleyii / xanthochymum	Yes	LS	No	0.11	92	7	3	42	44	4	89	8	4	52	37	211	239	296
Pandanus sp. 1	Yes	PL/SD	Half	4.83	91	7	4	44	39	7	85	10	5	57	29	195	226	288
Pandanus sp. 1	No	SK	Half	8.97	92	3	1	72	20	4	89	4	1	89	7	49	97	193

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Pandanus sp. 1	No	Blade	-	-	91	6	0	71	18	6	86	7	1	90	3	44	93	190
Pandanus sp. 1	Yes	PI	-	0.15	90	8	0	63	19	10	82	11	0	86	3	59	106	199
Parartocarpus venenosus	Yes	FL	Yes	0.70	93	8	4	63	22	5	88	9	4	76	10	116	158	241
Parartocarpus venenosus	Yes	PL	Yes	4.63	93	4	1	52	40	3	89	5	1	63	31	151	186	254
Parartocarpus venenosus	No	SD	Yes	4.09	94	12	13	35	38	2	92	14	15	40	31	315	337	380
Parartocarpus venenosus	No	SK	Yes	14.91	93	5	7	56	28	5	88	6	8	69	17	165	202	277
Polyalthia hypoleuca	Yes	SD	No	0.23	94	11	4	64	19	2	92	12	4	74	10	125	165	245
Polyalthia hypoleuca	No	LS	No	0.12	93	9	1	45	41	3	90	11	2	54	33	192	221	280
Quassia borneensis	Yes	CA	-	-	92	6	0	65	25	3	89	8	1	80	12	83	127	214
Sandoricum beccanarium	No	SD	No	0.34	90	8	2	61	27	2	88	10	2	77	11	102	144	227
Sandoricum beccanarium	No	SK	No	0.39	89	6	8	67	15	3	86	7	11	88	-6	103	151	246
Stemonorus scorpiodes / secundiflorus	Yes	LS	No	0.12	91	12	1	59	25	4	87	14	1	74	10	107	147	228

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter						Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Crude Protein	Lipid	NDF	TNC			
Syzigium sp. 15	Yes	PL/SK	Yes	0.05	91	4	2	48	44	2	89	4	3	59	34	179	211	275
Syzigium sp. 15	No	SD	Yes	0.08	93	3	0	68	28	1	92	3	0	79	18	85	128	214
Syzygium garcinfolia	Yes	PL/SK	No	0.76	95	4	1	61	31	4	91	4	1	70	25	126	164	239
Syzygium garcinfolia	Yes	PL/SK	Yes	0.91	97	2	1	71	23	2	95	3	1	76	20	99	141	224
Syzygium garcinfolia	No	SD	No	0.33	94	2	0	57	37	3	91	2	0	67	30	134	170	243
Syzygium garcinfolia	No	SD	Yes	0.79	94	2	1	47	48	3	92	2	1	55	43	184	214	273
Syzygium garcinfolia	No	LS	Yes	0.19	91	5	1	57	33	3	88	7	1	72	21	120	159	237
Syzygium garcinfolia	Yes	LS	No	0.02	91	7	1	26	64	3	89	8	1	32	59	280	297	332
Syzygium havilandii	Yes	PL/SK	No	0.44	95	4	0	56	34	5	90	5	0	66	29	140	176	247
Syzygium havilandii	Yes	PL/SK	Yes	0.70	95	5	1	55	36	4	91	5	1	63	30	150	184	253
Syzygium havilandii	No	SD	No	0.22	91	2	0	36	61	2	89	2	0	44	53	224	248	296
Syzygium havilandii	No	SD	Yes	0.58	92	2	0	45	52	2	90	2	0	54	44	186	215	274
Syzygium sp. 2	Yes	PL/SK	Yes	0.08	93	5	0	63	28	4	89	6	0	77	17	92	134	218

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter					Organic Matter	Percentage of Organic Matter				Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
						Crude Protein	Lipid	NDF	TNC	Ash		Crude Protein	Lipid	NDF	TNC			
Syzygium sp. 2	No	SD	Yes	0.10	91	3	0	46	48	2	89	3	0	57	40	176	207	268
Ternstroemia magnifica	No	PL	Yes	1.74	93	1	21	9	68	1	92	1	25	11	63	479	485	497
Ternstroemia magnifica	No	SK	Yes	13.37	91	2	0	66	30	3	89	2	0	81	17	76	120	209
Tetractomia tetrandra	Yes	CA	-	-	91	5	2	40	43	9	83	7	3	53	37	203	232	289
Tetractomia tetrandra	Yes	LS	No	0.14	90	10	1	26	59	4	87	13	2	33	53	276	294	330
Tetramerista glabra	Yes	PL/SK	No	0.89	95	4	1	58	34	3	92	4	1	66	29	140	176	248
Tetramerista glabra	No	PL/SK	Yes	1.04	91	3	1	46	48	3	89	4	1	56	39	182	212	273
Tetramerista glabra	Yes	LS	No	0.17	91	7	1	31	57	5	86	8	1	39	51	250	271	313
Willughbeia sp. 1	Yes	PL/SK	Half	8.61	89	6	11	56	24	3	87	8	14	72	6	182	221	300
Willughbeia sp. 1	No	SD	Half	5.33	89	4	3	48	43	1	88	5	4	62	29	173	206	274
Willughbeia sp. 1	No	SD	Yes	26.39	90	2	0	64	32	1	89	3	0	79	17	84	127	214
Xanthophyllum cf. ellipticum	Yes	LS	No	0.02	93	22	1	63	8	5	88	27	1	77	0	118	160	243
Xerospermum laevigatum / noronhianum	Yes	LS	No	0.09	92	8	0	22	68	2	90	9	0	27	64	296	310	339

Latin Name	Real Food?	Part	Ripe?	Field DW (g/item)	Dry Matter	Percentage of Dry Matter: Crude Protein	Lipid	NDF	TNC	Ash	Organic Matter	Percentage of Organic Matter: Crude Protein	Lipid	NDF	TNC	Kcal/100g (zero NDF)	Kcal/100g (low NDF)	Kcal/100g (high NDF)
Xylopia fusca	No	PL/SK	No	0.95	95	4	1	61	31	4	91	4	1	70	25	126	164	239
Xylopia fusca	No	PL/SK	Yes	1.67	95	4	1	68	23	3	92	5	2	78	16	96	138	223
Xylopia fusca	Yes	SD	Yes	0.91	96	7	8	69	15	2	94	8	9	76	7	142	183	265

Nutrients: NDF = neutral detergent fibre; TNC = total non-structural carbohydrate
Parts: AR = aril; BK = outer bark; CA = cambium; FL = mature/open flower; FLB = flower bud; LS = leaf shoot; PI = pith; PL = fruit pulp; SD = fruit seed; SK = fruit skin/husk; WH = whole fruit.
Energy contents calculated as described in Section **4.X.** Low NDF assumes available energy of 0.543 kcal/g fibre; high NDF assumes available energy of 1.6 kcal/g fibre.

APPENDIX II – FOOD PREFERENCE RANKINGS (CHESSON'S α INDEX)

FRUITS AND FLOWERS (PREFERRED FOODS)

			Adult females				Nulliparous females				Flanged males			
Species	**Part**	**Density / ha[1]**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**
Adenanthera pavonina	Fruit	1.1	0	=61	68	Avoided	0	=66	68	Avoided	0.0020	48	48	No
Aglaia sp. 1	Fruit	< 1	0.0833	13	13	Yes	0.0012	58	58	No	0	=54	54	Avoided
Ampelocissus sp. 1	Fruit	< 1	0	=61	61	Avoided	0.0143	34	34	Yes	0	=54	54	Avoided
Antidesma coriaceum	Fruit	< 1	0	=61	61	Avoided	0.0216	27	27	Yes	0	=54	54	Avoided
Artobotrys cf. roseus	Fruit	< 1	0.0148	30	30	Yes	0.0141	35	35	Yes	0.0289	22	22	Yes
Artobotrys suaveolins	Fruit	2.2	0.0360	18	18	Yes	0.0533	15	15	Yes	0.0341	19	19	Yes
Blumeodendron elateriospermum / kurzii	Fruit	18.9	0.0408	16	16	Yes	0.0264	24	24	Yes	0.0803	8	8	Yes
Buchanania cf. arborescens	Fruit	< 1	0.1128	7	7	Yes	0.0124	38	38	Yes	0	=54	54	Avoided
Callophyllum hosei	Fruit	68.9	0.0004	59	59	No	0	=66	82	Avoided	0.0047	42	42	No
Callophyllum sclerophyllum	Fruit	6.7	0.0188	26	26	Yes	0	=66	75	Avoided	0	=54	70	Avoided
Calophyllum soulattri	Fruit	25.6	0	=61	83	Avoided	0.0234	26	26	Yes	0.0087	39	39	No
Campnosperma coriaceum	Fruit	38.9	0.0026	51	51	No	0.0028	48	48	No	0.0039	43	43	No
Campnosperma squamatum	Fruit	3.3	0.0087	42	42	No	0.0119	40	40	No	0	=54	65	Avoided

			Adult females				Nulliparous females				Flanged males			
Species	**Part**	**Density / ha[1]**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**
Castanopsis foxworthyii	Fruit	2.2	0.0025	52	52	No	0.0199	29	29	Yes	0.0002	53	53	No
Combretocarpus rotundus	Fruit	11.1	0	=61	78	Avoided	0	=66	78	Avoided	0	=54	74	Avoided
Ctenolophon parvifolius	Fruit	2.2	0.0028	50	50	No	0.0292	22	22	Yes	0.0080	41	41	No
Cyathocalyx biovulatus	Fruit	7.8	0.0022	54	54	No	0.0014	56	56	No	0	=54	71	Avoided
Diospyros bantamensis	Fruit	23.3	0.0968	11	11	Yes	0.1379	4	4	Yes	0.0793	9	9	Yes
Diospyros cf. evena	Fruit	4.4	0.0186	27	27	Yes	0	=66	70	Avoided	0	=54	67	Avoided
Diospyros confertiflora	Fruit	3.3	0.0988	10	10	Yes	0.1316	5	5	Yes	0.0181	29	29	Yes
Diospyros siamang	Fruit	3.3	0.0906	12	12	Yes	0.1244	7	7	Yes	0.0758	10	10	Yes
Dyera lowii	Flowers	15.6	0	=61	82	Avoided	0	=66	80	Avoided	0	=54	79	Avoided
Dyera lowii	Fruit	15.6	0.0136	34	34	Yes	0.1035	9	9	Yes	0.0244	24	24	Yes
Elaeocarpus mastersii	Flowers	5.6	0	=61	72	Avoided	0	=66	73	Avoided	0.0016	51	51	No
Elaeocarpus mastersii	Fruit	5.6	0.0031	48	48	No	0.0017	54	54	No	0.0696	13	13	Yes
Fibraurea tinctoria	Fruit	< 1	0.0101	38	38	No	0.1831	3	3	Yes	0.0099	37	37	No
Ficus cf stupeda + other spp.	Fruit	2.2	0.1290	6	6	Yes	0.1160	8	8	Yes	0.0106	36	36	No
Ficus cf. spathulifolia	Fruit	3.3	0.0175	29	29	Yes	0.0370	19	19	Yes	0.1321	3	3	Yes
Fragreaea sp. 1	Fruit	3.3	0	=61	71	Avoided	0	=66	69	Avoided	0.0020	49	49	No
Garcinia bancana	Fruit	7.8	0.0257	21	21	Yes	0.0333	21	21	Yes	0.0179	30	30	Yes
Garcinia cf. parvifolia	Fruit	< 1	0	=61	61	Avoided	0	=66	66	Avoided	0.0033	44	44	No
Garcinia sp. 11	Fruit	< 1	0	=61	61	Avoided	0.0834	13	13	Yes	0.0593	14	14	Yes

			Adult females				Nulliparous females				Flanged males			
Species	**Part**	**Density / ha[1]**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**
Garcinia sp. 5	Fruit	< 1	0.0089	40	40	No	0	=66	66	Avoided	0.0007	52	52	No
Gnetum sp. 1	Fruit	6.7	0.0271	20	20	Yes	0.0907	11	11	Yes	0.0243	25	25	Yes
Gnetum sp. 2	Fruit	< 1	0.0023	53	53	No	0.2753	1	1	Yes	0.1016	5	5	Yes
Horsfieldia crassifolia	Fruit	72.2	0.0002	60	60	No	0	65	65	No	0	=54	82	Avoided
Ilex hypoglauca	Fruit	8.9	0	=61	75	Avoided	0.0130	36	36	Yes	0.0020	47	47	No
Isonandra lanceolata	Fruit	3.3	0.0020	56	56	No	0.0068	42	42	No	0	=54	66	Avoided
Licania splendens	Fruit	< 1	0	=61	61	Avoided	0.1250	6	6	Yes	0.0310	20	20	Yes
Lithocarpus spp.	Fruit	22.2	0.0034	47	47	No	0	=66	81	Avoided	0.0306	21	21	Yes
Litsea cf. rufo-fusca	Fruit	5.6	0	=61	73	Avoided	0.0011	60	60	No	0	=54	69	Avoided
Litsea sp. 1 *cf. resinosa*	Fruit	8.9	0.0030	49	49	No	0.0529	16	16	Yes	0.0120	34	34	No
Madhuca mottleyana	Flowers	8.9	0.1326	5	5	Yes	0.2363	2	2	Yes	0.0356	17	17	Yes
Madhuca mottleyana	Fruit	8.9	0.0216	25	25	Yes	0	=66	76	Avoided	0.0016	50	50	No
Magnolia bintulensis	Flowers	14.4	0	=61	81	Avoided	0	=66	79	Avoided	0	=54	78	Avoided
Magnolia bintulensis	Fruit	14.4	0	=61	80	Avoided	0.0016	55	55	No	0	=54	77	Avoided
Memecylon sp. 3	Fruit	1.1	0.0148	31	31	Yes	0.0198	30	30	Yes	0.0121	33	33	No
Mesua sp. 1	Fruit	17.8	0.0396	17	17	Yes	0.0126	37	37	Yes	0.0119	35	35	No
Mezzettia leptopoda / parviflora	Fruit	21.1	0.1376	4	4	Yes	0.0056	44	44	No	0.2521	2	2	Yes
Mezzettia umbellata	Fruit	5.6	0.0250	23	23	Yes	0.0514	17	17	Yes	0.0122	32	32	Yes
Microcos sp. 1	Fruit	< 1	0.0334	19	19	Yes	0.0036	47	47	No	0.0027	46	46	No

			Adult females				Nulliparous females				Flanged males			
Species	**Part**	**Density / ha[1]**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**
Myristica lowiana	Fruit	5.6	0.0217	24	24	Yes	0	=66	72	Avoided	0	=54	68	Avoided
Neoschortechinia kingii	Fruit	38.9	0	=61	84	Avoided	0.0043	46	46	No	0	=54	81	Avoided
Nephellium lappaceum	Fruit	1.1	0.3072	1	1	Yes	0.0026	49	49	No	0.4518	1	1	Yes
Nephellium maingayi	Fruit	2.2	0	=61	69	Avoided	0.0026	50	50	No	0.0844	7	7	Yes
Palaquium cochlearifolium	Flowers	5.6	0.1970	2	2	Yes	0	=66	71	Avoided	N/A	N/A	N/A	N/A
Palaquium cochlearifolium	Fruit	5.6	0.0049	46	46	No	0.0100	41	41	No	0.0393	16	16	Yes
Palaquium leiocarpum	Fruit	126.7	0.0049	45	45	No	0.0010	61	61	No	0.0093	38	38	No
Palaquium pseudorostratum	Flowers	16.7	0.0138	33	33	Yes	0.0003	64	64	No	0.0747	11	11	Yes
Palaquium pseudorostratum	Fruit	16.7	0.0020	55	55	No	0.0005	62	62	No	0	=54	80	Avoided
Palaquium ridleyii / xanthochymum	Flowers	13.3	0	=61	79	Avoided	0.0021	52	52	No	0	=54	75	Avoided
Palaquium ridleyii / xanthochymum	Fruit	13.3	0.1652	3	3	Yes	0.0175	31	31	Yes	0.0209	27	27	Yes
Parartocarpus venenosus	Flowers	< 1	0.0252	22	22	Yes	0.0538	14	14	Yes	0.0345	18	18	Yes
Parartocarpus venenosus	Fruit	< 1	0.0482	15	15	Yes	0.0439	18	18	Yes	0.0249	23	23	Yes
Polyalthia glauca	Fruit	2.2	0	=61	70	Avoided	0.0359	20	20	Yes	0	=54	64	Avoided
Polyalthia hypoleuca	Fruit	1.1	0.1016	9	9	Yes	0.0148	33	33	Yes	0.1145	4	4	Yes
Sandoricum beccanarium	Fruit	22.2	0.1031	8	8	Yes	0.0862	12	12	Yes	0.0982	6	6	Yes

			Adult females				Nulliparous females				Flanged males			
Species	**Part**	**Density / ha[1]**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**	**Pref. value**	**Pref. rank**	**Rank (inc. avoided)**	**Preferred?**
Sterculia rhoiidifolia	Fruit	< 1	0	=61	61	Avoided	0.0013	57	57	No	0	=54	54	Avoided
Syzigium sp. 13	Fruit	< 1	0	=61	61	Avoided	0.0124	39	39	Yes	N/A	N/A	N/A	N/A
Syzigium sp. 15	Fruit	< 1	0.0114	36	36	Yes	0.0174	32	32	Yes	0	=54	54	Avoided
Syzygium cf. valevenosum	Fruit	< 1	0.0132	35	35	Yes	0.0018	53	53	No	0	=54	54	Avoided
Syzygium garcinfolia	Fruit	16.7	0.0087	41	41	No	0.0062	43	43	No	0.0233	26	26	Yes
Syzygium havilandii	Fruit	18.9	0.0141	32	32	Yes	0.0215	28	28	Yes	0.0083	40	40	No
Syzygium sp. 2	Fruit	14.4	0.0006	58	58	No	0.0005	63	63	No	0	=54	76	Avoided
Syzygium sp. 5 *cf. E. spicata*	Fruit	10.0	0	=61	76	Avoided	0	=66	77	Avoided	0	=54	72	Avoided
Tetramerista glabra	Fruit	3.3	0.0740	14	14	Yes	0.0961	10	10	Yes	0.0500	15	15	Yes
Willughbeia sp. 1	Flowers	10.0	0	=61	77	Avoided	0.0026	51	51	No	0	=54	73	Avoided
Willughbeia sp. 1	Fruit	10.0	0.0176	28	28	Yes	0.0288	23	23	Yes	0.0716	12	12	Yes
Xanthophyllum sp. 2	Fruit	< 1	0.0107	37	37	No	N/A	N/A	N/A	N/A	0	=54	54	Avoided
Xerospermum laevigatum / noronhianum	Fruit	1.1	0.0008	57	57	No	N/A	N/A	N/A	N/A	0	=54	63	Avoided
Xylopia cf. malayana	Fruit	3.3	0.0085	43	43	No	0.0045	45	45	No	0.0030	45	45	No
Xylopia coriifolia	Fruit	5.6	0	=61	74	Avoided	0	=66	74	Avoided	0.0127	31	31	Yes
Xylopia fusca	Fruit	32.2	0.0094	39	39	No	0.0011	59	59	No	0.0186	28	28	Yes
Zyzyphus angustifolius	Fruit	< 1	0.0077	44	44	No	0.0254	25	25	Yes	0	=54	54	Avoided

N.B. For Cheeson's α index, the expected value for random feeding is a function of the number of food items included in the dataset: $1/n$, where n is the number of food items in the sample. Items with a preference value > $1/n$ are preferred. Items with a value of 0 are avoided. Thus, the "preferred food threshold value" is 0.0119 for adult females, and 0.0122 for nulliparous females and flanged males.

1. Density of stems ≥ 10 cm.

LEAVES

Species	Density / ha[1]	Adult females						Nulliparous females						Flanged males					
		Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)	Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)	Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)
Alyxia sp. 1	1.1	0.2506	2	2	0.3720	1	1	0.2592	2	2	0.2150	2	2	0.3378	2	2	0.4357	1	1
Artobotrys suaveolins	2.2	0	-	17	0	-	17	0	-	19	0	-	18	0	-	12	0	-	=11
Blumeodendron elateriospermum / kurzii	80.0	0	-	34	0	-	33	0.0006	13	13	0.0048	11	11	0	-	35	0	-	34
Callophyllum hosei	124.4	0	-	35	0	-	34	0	16	16	0	-	35	0.0001	8	8	0	-	35
Castanopsis foxworthyii	4.4	0	-	20	0	-	20	0	-	23	0	-	22	0	-	17	0	-	16
Ctenolophon parvifolius	2.2	0.0945	4	4	0.0420	9	9	0.0410	3	3	0.0241	7	7	0	-	12	0	-	=11
Cyathocalyx biovulatus	15.6	0	-	25	0	-	24	0	-	27	0	-	26	0	-	22	0	-	21
Dialium patens	1.1	0.1947	3	3	0.3489	3	3	0	-	=17	0	-	=16	0	-	=9	0	-	=8
Diospyros bantamensis	51.1	0.0028	9	9	0.0428	8	8	0.0111	8	8	0.1148	5	5	0.0050	5	5	0.0487	5	5
Diospyros cf. evena	7.8	0	-	23	0	-	22	0.0022	11	11	0.0029	12	12	0	-	20	0	-	19
Diospyros siamang	8.9	0.0276	5	5	0.0821	5	5	0.0099	9	9	0.0148	9	9	0.0468	3	3	0.1083	4	4
Elaeocarpus mastersii	21.1	0.0035	8	8	0.0483	7	7	0.0063	10	10	0.0185	8	8	0	-	26	0	-	25
Ficus cf. spathulifolia	3.3	0	-	=18	0	-	=18	0	-	=20	0	-	=19	0	-	=14	0	-	=13
Ficus cf. stupenda + other spp.	3.3	0	-	=18	0	-	=18	0	-	=20	0	-	=19	0	-	=14	0	-	=13
Fragreaea sp. 1	3.3	0.0027	10	10	0.0028	10	10	0	-	=20	0	-	=19	0	-	=14	0	-	=13
Garcinia bancana	24.4	0	-	28	0	-	27	0	-	29	0	-	28	0	-	27	0	-	26
Gnetum sp. 1	6.7	0	-	=21	0	-	=21	0	-	=24	0	-	=23	0	-	=18	0	-	=17
Lithocarpus spp.	40.0	0	-	30	0	-	29	0.0007	12	12	0.0028	13	13	0	-	29	0	-	28
Litsea sp. 1 *cf. resinosa*	38.9	0	-	29	0	-	28	0	-	30	0	-	29	0	-	28	0	-	27

Species	Density / ha[1]	Adult females						Nulliparous females						Flanged males					
		Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)	Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)	Pref. Value (stem)	Rank (exc. av. stem)	Rank (inc. av. stem)	Pref. Value (shoots)	Rank (exc. av. shoots)	Rank (inc. av. shoots)
Magnolia bintulensis	17.8	0	-	27	0	-	26	0	-	28	0	-	27	0	-	24	0	-	23
Mezzettia leptopoda / parviflora	58.9	0	-	33	0	-	32	0	-	34	0	-	33	0	-	33	0	-	32
Neoschortechinia kingii	63.3	0.0001	13	13	0.0004	12	12	0	-	35	0	-	34	0	-	34	0	-	33
Nephellium maingayi	6.7	0.0244	6	6	0.0722	6	6	0.0123	7	7	0.0087	10	10	0.0008	7	7	0.0066	7	7
Palaquium ridleyii / xanthochymum	16.7	0	-	26	0	-	25	0.0003	14	14	0.0011	14	14	0	-	23	0	-	22
Quassia borneensis	1.1	0	-	=14	0	-	=14	0	-	=17	0	-	=16	0	-	-9	0	-	=8
Sandoricum beccanarium	54.4	0.0004	12	12	0.0002	13	13	0	-	33	0	-	32	0	-	32	0	-	31
Santiria cf. griffithi	6.7	0	-	=21	0	-	=21	0	-	=24	0	-	=23	0	-	=18	0	-	=17
Shorea teysmanniana	147.8	0	-	36	0	-	35	0	-	36	0	-	36	0	-	36	0	-	36
Stemonorus scorpiodes / secundiflorus	48.9	0	-	32	0	-	31	0	-	32	0	-	31	0	-	31	0	-	30
Sterculia rhoïdifolia	1.1	0	-	=14	0	-	=14	0.0144	6	6	0.5846	2	2	0.0034	6	6	0.0119	6	6
Syzygium sp.	1.1	0	-	=14	0	-	=14	0.0287	4	4	0.0879	6	6	0	-	9	0	-	=8
Tetramerista glabra	20.0	0.0010	11	11	0.0028	11	11	0.0002	15	15	0.0001	15	15	0	-	25	0	-	24
Willughbeia sp. 1	10.0	0	-	24	0	-	23	0	-	26	0	-	25	0	-	21	0	-	20
Xanthophyllum cf. ellipticum	1.1	0.3800	1	1	0.3498	2	2	0.5898	1	1	0.5982	1	1	0.5713	1	1	0.3689	2	2
Xerospermum laevigatum / noronhianum	8.9	0.0179	7	7	0.1341	4	4	0.0230	5	5	0.1656	4	4	0.0347	4	4	0.1806	3	3
Xylopia fusca	45.6	0	-	31	0	-	30	0	-	31	0	-	30	0	-	30	0	-	29

1. Density of stems ≥ 6 cm.

Abbreviations: exc. av. stem/shoot = excluding avoided species (i.e., species that were not eaten and that were ranked based on their availability); inc. av. stem/shoot = including avoided species. See **Section 5.2.1.1** for details.

BARK

Species	Density / ha[1]	Adult Females			Nulliparous females			Flanged males		
		Pref. Value	Rank (exc. av.)	Rank (inc. av.)	Pref. Value	Rank (exc. av.)	Rank (inc. av.)	Pref. Value	Rank (exc. av.)	Rank (inc. av.)
Diospyros bantamensis	23.3	0	-	11	0	-	11	0	-	11
Diospyros siamang	3.3	0.1309	4	4	0	-	8	0	-	4
Dyera lowii	15.6	0.2845	2	2	0.6736	1	1	0.2911	1	1
Koompassia malaccensis	5.6	0.3998	1	1	0.0133	6	6	0	-	7
Madhuca mottleyana	8.9	0	-	7	0.0084	7	7	0.0400	3	3
Myristica lowiana	5.6	0.1848	3	3	0.0728	3	3	0.6689	2	2
Palaquium pseudorostratum	17.8	0	-	10	0	-	10	0	-	10
Palaquium ridleyii	13.3	0	-	9	0	-	9	0	-	9
Tetramerista glabra	4.4	0	-	6	0.0416	5	5	0	-	6
Willughbeia sp. 1	10.0	0	-	8	0.1194	2	2	0	-	8
Xylopia cf. malayana	3.3	0	-	5	0.0710	4	4	0	-	4

1. Density of stems ≥ 10 cm.

APPENDIX III – SPEARMAN'S CORRELATIONS BETWEEN FOOD PROPERTIES; REAL-FRUITS

Characteristic	No	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Food volume	1	X																																	
Wet weight	2	0.824 ***	X																																
Dry Weight	3	0.702 ***	0.923 ***	X																															
No. seeds	4	0.519 ***	0.440 **	0.425 **	X																														
Seed volume / fruit	5	0.822 ***	0.671 ***	0.556 ***	0.355 **	X																													
Volume skin + pulp	6	0.984 ***	0.807 ***	0.712 ***	0.547 ***	0.743 ***	X																												
% protein	7	NS	-0.389 **	-0.433 **	NS	NS	NS	X																											
% lipid	8	0.404 **	NS	NS	0.456 **	0.388 *	0.408 **	NS	X																										
% TNC	9	NS	NS	NS	NS	NS	NS	NS	NS	X																									
% NDF	10	NS	NS	NS	NS	NS	NS	NS	NS	-0.851 ***	X																								
% water	11	0.297 *	0.344 *	NS	NS	NS	NS	NS	NS	NS	NS	X																							
% ash	12	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X																						
Fibre / protein	13	NS	-0.348 *	-0.399 **	NS	NS	NS	0.830 ***	NS	0.325 *	-0.620 ***	NS	NS	X																					
Energy / item	14	0.748 ***	0.928 ***	0.989 ***	0.545 ***	0.576 ***	0.752 ***	-0.399 **	NS	NS	NS	NS	NS	-0.321 *	X																				
Energy / 100g	15	0.307 *	NS	NS	0.324 *	NS	NS	NS	0.559 ***	0.611 ***	-0.904 ***	NS	NS	0.534 ***	NS	X																			
Energy / g NDF	16	NS	NS	NS	NS	NS	NS	NS	0.368 *	0.787 ***	-0.979 ***	NS	NS	0.566 ***	NS	0.961 ***	X																		
Protein intake	17	NS	0.477 **	0.527 ***	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.504 **	NS	NS	X																	
Lipid intake	18	0.415 **	0.496 **	0.571 ***	0.377 **	0.340 *	0.401 **	NS	0.764 ***	NS	NS	NS	NS	NS	0.613 ***	NS	NS	0.660 ***	X																
TNC intake	19	0.309 *	0.593 ***	0.568 ***	NS	NS	0.302 *	-0.498 **	NS	0.574 ***	-0.326 *	NS	NS	0.585 ***	NS	NS	NS	0.679 ***	0.498 ***	X															
NDF intake	20	NS	0.495 **	0.573 ***	NS	NS	NS	-0.566 ***	NS	NS	0.478 **	NS	-0.692 ***	-0.501 **	-0.384 *	NS	-0.435 **	0.786 ***	0.673 ***	0.631 ***	X														
Dry weight intake	21	NS	0.577 ***	0.653 ***	NS	NS	NS	-0.536 ***	NS	NS	NS	NS	-0.327 *	-0.569 ***	0.615 ***	NS	NS	0.857 ***	0.719 ***	0.787 ***	0.959 ***	X													
Energy intake	22	0.325 *	0.637 ***	0.696 ***	NS	0.328 *	NS	-0.537 ***	NS	NS	NS	NS	NS	-0.500 **	0.690 ***	NS	NS	0.842 ***	0.765 ***	0.845 ***	0.911 ***	0.980 ***	X												
Young's PE	23	NS	0.467 *	NS	NS	0.565 **	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.506 *	NS	NS	0.619 *	NS	X											
Young's SK	24	0.337 *	NS	NS	NS	NS	NS	NS	0.374 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.997 ***	X										
Tough PE	25	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X									
Tough SK	26	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.789 **	X							
pH	27	NS	NS	NS	NS	NS	NS	0.508 ***	NS	NS	NS	NS	NS	0.423 **	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X						
Phenolic	28	NS	NS	NS	NS	NS	NS	-0.512 **	NS	NS	NS	NS	NS	-0.446 **	0.413 *	-0.364 *	NS	NS	NS	0.448 **	0.518 **	0.466 **	0.421 *	NS	NS	NS	NS	NS	NS	X					
Tannin	29	NS	NS	NS	NS	NS	NS	NS	-0.359 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X				
Crop size	30	-0.538 **	NS	-0.432 *	NS	-0.464 **	-0.557 **	NS	NS	NS	NS	NS	NS	NS	-0.452 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X			
Crop size (top 50%)	31	-0.432 *	NS	-0.366 *	NS	-0.364 **	-0.463 **	NS	NS	NS	NS	NS	NS	NS	-0.377 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X		
Weight food / tree	32	NS	NS	NS	NS	NS	NS	-0.443 *	NS	NS	NS	NS	NS	0.422 *	0.387 *	NS	NS	NS	NS	0.560 **	0.463 **	0.496 **	0.525 **	NS	NS	NS	NS	NS	NS	0.515 **	NS	0.585 ***	0.648 ***		
Energy food / tree	33	NS	NS	NS	NS	NS	NS	-0.419 *	NS	NS	NS	NS	NS	0.393 *	0.383 *	NS	NS	NS	NS	0.563 **	0.413 **	0.457 **	0.497 **	NS	NS	NS	NS	NS	NS	0.500 **	NS	0.588 ***	0.655 ***	0.992 ***	X
DBH	34	NS	NS	NS	-0.310 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.395 *	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X
Pulp weight / seed	35	0.523 *	0.694 ***	0.734 ***	NS	0.436 **	0.521 **	-0.502 **	NS	0.658 ***	NS	NS	-0.413 *	-0.417 **	0.415 *	0.496 **	NS	NS	NS	0.526 **	0.613 ***	0.637 ***	0.634 ***	NS	NS	0.456 *	0.398 *	NS	0.398 *	NS	NS	NS	NS	NS	NS

* p < 0.05, ** p <0.01, *** p < 0.001, NS = not significant.

APPENDIX IV - CORRELATION MATRICES SHOWING RELATIONSHIPS BETWEEN ORANG-UTAN FRUIT/FLOWER AVAILABILITY, DIET COMPOSITION[1], INTAKE, AND BEHAVIOURAL VARIABLES

Values are (Pearson) correlation coefficients. Spearman's correlations, in *italics*, were performed on non-normally distributed variables[1].

Adult Females

Variable	% preferred[2]	% FBF[2]	Energy intake	Fibre intake	AP length	Average PS (inc. own)	*Average PS (exc. own)*[3]	DR	% T	Min T	% F	Min F	% total feed	Min total feed	% R	Min R
OU FR/FL availability	0.759***	-0.810***	NS	NS	NS	0.475*	*NS*	NS	NS	NS	NS	NS	NS	NS	NS	NS
% Preferred[2]	X	-0.897***	NS	NS	NS	0.430*	*0.537***	0.414*	NS	NS	-0.469*	-0.478*	NS	NS	NS	NS
% FBF[2]		X	NS	NS	NS	-0.579**	*NS*	-0.462*	NS	NS	0.482*	0.479*	NS	NS	NS	NS
Energy intake			X	0.754***	NS	NS	*NS*	NS	NS	NS	NS	NS	NS	NS	-0.452*	-0.475*
Fibre intake				X	NS	NS	*NS*	0.522*	NS	NS	NS	NS	NS	NS	NS	NS
AP length					X	NS	*NS*	0.503*	NS	NS	NS	NS	NS	NS	NS	NS
Average PS (inc. own)						X	*NS*	NS	NS	NS	-0.631**	-0.610**	NS	NS	NS	NS
Average PS (exc. own)							X	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
DR								X	0.686**	0.759***	-0.631**	-0.591**	-0.467*	NS	NS	NS
% T									X	0.988***	-0.788***	-0.802***	-0.772***	-0.743***	NS	NS
Min T										X	-0.797***	-0.792***	-0.742***	-0.682**	NS	NS
% F											X	0.988***	0.809***	0.731***	-0.575**	-0.588**
Min F												X	0.828***	0.787***	-0.594**	-0.590**
% total feed													X	0.969***	-0.854***	-0.845***
Min total feed														X	-0.835***	-0.795***
% R															X	0.988***

Nulliparous females

Variable	% preferred^2	% FBF^2	Energy intake	Fibre intake	AP length	Average PS	DR	% T	Min T	% F	Min F	% total feed	Min total feed	% R	Min R
OU FR/FL availability	0.589**	-0.688**	NS	NS	0.594**	NS	NS	0.454*	0.524*	-0.427*	NS	NS	NS	NS	NS
% preferred^2	X	-0.856***	NS	NS	0.565*	0.422*	NS	NS	0.408*	-0.407*	NS	NS	NS	NS	NS
% FBF^2		X	NS	NS	-0.740**	-0.428*	NS	NS	-0.493*	0.430*	NS	NS	NS	NS	NS
Energy intake			X	0.679**	NS	NS	NS	NS	NS	NS	NS	NS	0.453*	NS	NS
Fibre intake				X	NS	NS	NS	NS	NS	NS	NS	NS	0.416*	NS	NS
AP length					X	0.435*	0.651**	0.677**	0.803***	-0.628**	NS	NS	NS	0.461*	0.568*
Average PS						X	NS	NS	0.406*	-0.842***	-0.823***	-0.483*	NS	NS	NS
DR							X	0.703**	0.777***	-0.639**	-0.525*	-0.880***	-0.684**	0.817***	0.862***
% T								X	0.973***	-0.658**	-0.553**	-0.806***	-0.603**	NS	0.428*
Min T									X	-0.715***	-0.567**	-0.837***	-0.542*	0.468*	0.527*
% F										X	0.959***	0.858***	0.659**	-0.618**	-0.640**
Min F											X	0.796***	0.744***	-0.592**	-0.580**
% total feed												X	0.744***	-0.830***	-0.842***
Min total feed													X	-0.782***	-0.728***
% R														X	0.990***

Flanged males

Variable	% preferred^2	*% FBF*^{2}	Energy intake	Fibre intake	AP length	Average PS	DR	% T	Min T	% F	Min F	% total feed	Min total feed	% R	Min R
OU FR/FL availability	0.598**	*-0.461**	0.537**	NS	NS	0.407*	NS	NS	NS	NS	NS	NS	NS	NS	NS
% preferred^2	X	*-0.665***	0.399*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% FBF^2		X	*-0.538**	*-0.290**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Energy intake			X	0.790***	0.496*	NS	NS	NS	NS	NS	0.390*	NS	0.435*	NS	NS
Fibre intake				X	NS	NS	0.426*	NS	NS	NS	NS	NS	0.409*	NS	NS
AP length					X	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Average PS						X	NS	NS	NS	-0.441*	-0.430*	NS	NS	NS	NS
DR							X	NS	NS	NS	NS	NS	NS	NS	NS
% T								X	0.980***	-0.691**	-0.622**	-0.703***	-0.618**	NS	NS
Min T									X	-0.678**	-0.529**	-0.692**	-0.519*	NS	NS
% F										X	0.903***	0.954***	0.838***	-0.850***	-0.834***
Min F											X	0.863***	0.959***	-0.775***	-0.699***
% total feed												X	0.883***	-0.906***	-0.891***
Min total feed													X	-0.808***	-0.727***
% R														X	0.986***

Unflanged males

Variable	% preferred[2]	% FBF[2]	Energy intake	Fibre intake	Average PS	DR	% T	Min T	% F	Min F	% total feed	Min total feed	% R	Min R
OU FR/FL availability	0.747**	-0.638*	NS	NS	NS	NS	0.656*	0.642*	-0.770**	NS	-0.724**	NS	NS	0.540*
% preferred[2]	X	-0.652*	NS	NS	NS	NS	0.538*	0.540*	NS	NS	NS	NS	NS	NS
% FBF[2]		X	NS	NS	NS	NS	-0.631*	-0.719**	0.554*	NS	NS	NS	NS	NS
Energy intake			X	0.726**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Fibre intake				X	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Average PS					X	NS	NS	NS	NS	NS	NS	NS	NS	NS
DR						X	NS	NS	NS	NS	NS	NS	NS	NS
% T							X	0.966***	-0.742**	NS	-0.718**	NS	NS	NS
Min T								X	NS	NS	NS	NS	NS	NS
% F									X	0.746**	0.986***	0.679*	-0.804**	-0.824**
Min F										X	0.813**	0.989***	-0.804**	-0.754**
% total feed											X	0.768**	-0.844**	-0.854***
Min total feed												X	-0.785**	-0.729**
% R													X	0.994***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant.

Abbreviations: AP = active period; DR = day-journey length; F = feeding (excluding co-feeding and food search); FBF = fall-back food; Min = minutes spent in activity *i*/day; OU FR/FL = orang-utan fruit/flower; PS = party size; R = resting; T = travelling; total feed = total time spent feeding (including co-feeding and food search). See **Tables 3.1** and **6.1** for definitions.

1. Percentage time spent feeding on preferred and FBFs for adult females, and average PS for flanged males were arcsine-transformed to normality. Variables on which non-parametric correlations were performed were non-normally distributed, even after transformation.
2. Preferred foods were fruit and flowers, and FBFs leaves and cambium, for all age-sex classes (see **Chapter 5**).
3. Average PS, excluding parties involving a female's own, independent offspring.