Selection of tree species for cambium consumption by the Bornean orang-utan (*Pongo pygmaeus wurmbii*).

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Abstract

Cambium is a major fall-back food for orang-utans when fruit availability is low. Although recognised as a major source of food in these times, the motivation behind the preference for certain species is unclear. Energy content and nutritional composition of cambium was studied to see if there were differences between eaten and not-eaten species that might explain the choices made by Bornean orang-utans (*Pongo pygmaeus wurmbii*). Bark samples were collected from the Sabangau peat swamp forest, Central Kalimantan, and the cambium layer removed. Physical properties measurements were taken and nutritional analyses were performed to determine nutrient composition of the organic matter. Available energy was calculated and compared between eaten and not-eaten species. Due to small sample size and non-normal data distribution non-parametric tests were used to test for differences between species eaten and avoided. Cambium thickness and water content were both significantly different between eaten and not-eaten species, with not-eaten species being thicker ($p=0.001$) and containing more water ($p=0.010$). There were no significant differences between eaten and not-eaten species in terms of total available energy, the different fractions of organic matter or the energy gained from them. Eaten cambium is not chosen on the basis of energy content alone and it is probable that other factors, especially toughness, are important for limiting species eaten in this area. It is unlikely that hardness and secondary plant compounds play a role in cambium preference, but it is possible that essential fatty acid spectrum may also be important.

Introduction

One of the fall-back foods of orang-utans (*Pongo pygmaeus*) is the vascular phloem tissue found underneath the tough outer bark, i.e., the cambium. Bark is bitten and pulled from the tree using the hands, and the vascular tissue is scraped from the outer bark using the teeth and eaten or chewed and spat out, where orang-utans presumably derive nutrition from the fluid extracted (Vogel *et al*., in press, Caton *et al*., 1999). While the cambium of some species is eaten, others are not. The focus in this project is on the cambium on which orang-utans rely in times of poor fruit availability and how they might preferentially select the tree species from which they forage. Tree species selection may be dependent on expected energy intake, as shown by Leighton (1993) for fruit preference in Kutai National Park, East Kalimantan. However, the mechanisms underlying fruit selection may differ between sites, with fibre and protein the most important variables affecting preference in Sabangau (Harrison, in prep). Thus, I will be looking particularly at nutritional content and the possible differences between the eaten and not-eaten species. It may also be possible that the nature of the bark in terms of fibre content, toughness and hardness could be important. Energy expenditure through processing of the cambium may even prove prohibitive to consumption in some cases. The mode of selection of tree species for cambium consumption by Bornean orang-utans, unlike other food, has never been tested, but is important due to the reliance of orang-utans on cambium consumption when fruit availability is low.

Background

Orang-utans are only found on two islands, Borneo and Sumatra. *Pongo pygmaeus wurmbii*, the Bornean orang-utan is found in Kalimantan (Indonesia), and Sarawak and Sabah (Malaysia), with most individuals occurring in Kalimantan, where large areas of forest still exist, especially along the east coast and southern plains, but the dipterocarp forests of the Central and West Kalimantan forests are becoming more and more fragmented (WWF, 2006). The main component of an orang-utan's diet is fruit, but fruit availability in the forests of Borneo is variable. Variability in fruit availability is highest in the dry-land forests, like those in Kutai, East Kalimantan. In Sabangau peat-swamp forest, 2.2 to 7.1% of the orang-utan fruit trees bore fruit / month from July 2005 to June 2007 (Harrison in prep.). Fruit availability in Sumatra is greater and much more uniformly distributed over time (Knott, 1998). The Bornean orang-utans have been found to increase their fruit consumption during periods of higher fruit availability in the dry-land forests of Borneo (Leighton, 1993), but in Sabangau this is only seen with flanged males and may be because of the relatively low variability of fruit availability by comparison to dry-land forest. Bark consumption is negatively correlated with fruit availability in Sabangau (Harrison, in prep.). Periods of higher fruit availability are known as mast-fruiting episodes, which occur every two to ten years in the rain-forests of South-east Asia. Mast-fruiting is the intermittent and synchronous production of fruits by a population of plants at long intervals (Herrera *et al.* 1998, Kelly, 1994). This pattern of food availability is likely the result of the beginning of the El Niño Southern Oscillation 3 to 5 Mya, which is posited as the probable cause of mast fruiting in dipterocarp tree species. This, in turn, is thought to have driven the evolution of the orang-utan mating system (Harrison and Chivers, 2007). Threshold levels of drought and increased insolation (with resultant increase in photosynthetically-active radiation, (PAR) associated with El Niño years seem to coincide with mast-fruiting episodes in Malaysian tropical dipterocarp forests (van Schaik *et al*. 1993, Wright and van Schaik 1994). Thus, it seems likely that it may also play a role in Indonesian Borneo dry-land forest. This is primarily a phenomenon of dry-land dipterocarp forest, so peat-swamp forests like those found in Sabangau, containing far fewer dipterocarp species, do not mast on an appreciable scale, as described in Cannon *et al*. (2007).

At times of low fruit availability, Bornean orang-utans have been found to eat a diverse range of 'fall-back' foods, which include young leaves and shoots, as well as insects, mineral-rich soil, tree bark and woody lianas, and occasionally, eggs and small vertebrates. Much of their water is obtained from the fruit and other foods that make up their diet, but it is also drunk from tree holes (Macdonald 1984, 2001). In times of low fruit availability in Gunung Palung National Park, West Kalimantan, as little as 21% of the diet is composed of fruit, while 37% is bark (Knott, 1998). In the Sabangau population studied, bark was eaten for 3.87± 6.72% of total feeding time, for all age-sex classes combined, showing a monthly range of between 0 and 25% (Harrison, in prep.). The bark is stripped from the tree and it is usual for the orang-utans to scrape the phloem tissues from the outer bark with their incisors. The cambium may then be ingested or chewed and wadged, before the remaining fibrous wad is spat out. Bark from strangling figs is also sometimes eaten, but only from the ends of twigs (Rodman, 1977). Vogel *et al*. (in press), while observing chimpanzees and orang-utans, notes that the chimpanzees treated the cambium to molar occlusion and salivary softening but never fractured the fibrous material. They always extracted nutrients by wadging and spitting out the remains. In contrast, orang-utans masticated and consumed many of the more fracture-resistant foods like the cambium tissue. It is thought that adaptive features, such as enamel thickness, cusp architecture and mobility of the lips, evolved to tackle these tougher and harder foods (Vogel *et al*., in press).

Fluctuations in food availability have profound effects on the composition of the diet and, therefore, potential energy intake, as well as on the socio-ecology of the Bornean orang-utan. For example, Knott (1998) found that, during mast fruiting, orang-utan diets were composed of 100% fruit; they increased their daily food intake to above normal daily energy requirements, and more readily formed groups when fruiting occurred in large patches. Knott (1998) also looked at caloric intake of the orang-utans at the Gunung Palung National Park, from September 1994 through to September 1995. She found that in January, when the fruit consumption was highest, the caloric intakes of the males and females were estimated at 8422 kcal/day and 7404 kcal/day, respectively. In May, when fruit consumption was at its lowest, reflecting lower availability, caloric intake was much lower in both males and females. The intake for males was estimated at 3824 kcal/day, while for females it was 1793 kcal/day. Incidentally, bark consumption followed this pattern in reverse, being greatest in May and lowest in January. During periods of low fruit availability only, the orang-utans were found to go into ketosis, signifying use of fat stores built up during the fruit-rich periods. Females were found to have an overall greater ketone level in their urine during the fruit-poor period (March 1994 through September 1995), although both males and females showed ketosis. The females seemed, however, to cope less well and it is suggested that this may be due to increased metabolic demand during pregnancy and lactation and decreased foraging ability when a juvenile was in tow. Males may also be able to forage better than females (Knott, 1998). This pattern of variable energy intake with variability in fruit availability is not shared in Sumatra and only affects energy intake of flanged males in Sabangau. It has not been documented in chimpanzees (*Pan troglodytes)* in Kibale (Conklin-Brittain *et al.,* 2006) or eastern mountain gorillas (*Gorilla gorilla beringei*) in Bwindi either (Rothman *et al., 2007).* It has been suggested that this difference in dietary pattern may be a fundamental difference between the Sumatran

(*Pongo pygmaeus abelii*) and Bornean orang-utan (*Pongo pygmaeus wurmbii*), affecting aspects of their evolution (Wich *et al*., 2006), but Gunung Palung has the widest fluctuations in fruit availability of all these sites and so it is this that might be causing the variation in energy intake there.

The African apes have also been found to eat bark. The chimpanzee (*Pan troglodytes*) has been documented eating small amounts of bark, as demonstrated by finding fragments in sluiced faecal samples (Basabose, 2002). Gorillas typically eat less fruit than chimpanzees and survive on terrestrial herbaceous vegetation and bark. The eastern mountain gorilla (*Gorilla gorilla beringei)* has the most restricted diet of the African apes, consuming only leaves, pith, bark, terrestrial herbaceous vegetation, and bamboo when seasonally present (Watts, 1984, Taylor, 2002). *Gorilla gorilla beringei* in Uganda has been seen to eat a variety of species of tree bark (Stanford and Nkurunungi, 2003). The western lowland gorilla *(Gorilla gorilla gorilla)* is the most frugivorous of the gorillas, though it relies on fruit much less than the orang-utan, eating more terrestrial herbaceous vegetation and bark, especially when fruit is not available (Taylor, 2002). They typically survive on continuous resources of low quality, such as leaves, vines and bark with low selectivity (Taylor, 2002). Gorillas have long colons with many entodiniomorph ciliates, which aid in the digestion of cellulose. This allows them to survive on fibrous foods, such as some fruits, mature leaves, bark, and stems, when juicy fruit is scarce (Tutin *et al*., 1997). The similarities between gorillas and orang-utans in this respect may be another facet of the gorilla-like base from which the orang-utan is believed to have evolved, as is seen with the mating system and scheme of maturation (Harrison and Chivers, 2007).

Adaptations to diet

The diet of orang-utans is more resistant to deformation and fracture compared to the diet of chimpanzees. It is thought that orang-utans have evolved adaptations to this tougher diet and some suggest that it is the harder and tougher fall-back foods that have been selecting factors for these adaptations (Vogel *et al*., in press). The dental formula of orang-utans, like all other catarrhines, is $\frac{2123}{2123}$, but the morphology and structure of the teeth is adapted to their diet, having thick enamel comparable to humans, which is thicker than the enamel of African apes. This is argued to bear evidence for propensities to certain diets, with thicker enamel indicating a more fibrous and erosive diet (Schwartz, 2000). Thick enamel, high-cusped, crenellated teeth are probably adaptations to regular consumption of tough and hard foods with consumption of softer, riper fruits being aided by the very mobile lips and soft tissues of the mouth (Vogel *et al*., in press).

The digestive tract of the orang-utan, like other frugivores has a simple, single, globular stomach and, like chimpanzees, it is more elongated than other primates (Chivers and Hladik, 1980). The stomach makes up around 17 to 20% of the total gut volume in orang-utans (Milton, 1987). The small intestine makes up around 23 to 28% of the total gut volume and has two complete muscular coats in the tunica muscularis (Milton, 1987, Caton *et al*., 1999). The colon makes up the predominant part of the gut of orang-utans, comprising around 52 to 54% volume. It is very long with three muscular taeniae coli producing extensive haustration of the entire colon, which is important in the mixing of the digesta, aiding fermentation of fibre by gut microbes (Chivers and Hladik, 1980, Milton, 1987, Caton *et al*., 1999). The caecum is moderately sized in catarrhines, with a globular base, a sizeable body and a terminal vermiform appendix, but it probably acts no more than as an extension of the proximal colon (Chivers and Hladik, 1980, Caton *et al*., 1999).

Gut transit time in colon fermenters is relatively long, being on average around 24hours but Caton *et al.* (1999) found that mean retention time for the particulate marker was 73.7hours in the orang-utans studied. The long, haustrated colon is where most of the fermentation of fibrous material, that is not digested elsewhere, takes place. In studies using different size markers (from dissolved solute to particulate in size), it has been shown that there are periods of peristalsis and anti-peristalsis, along with independent contraction in size of the haustra. The result of this is increased mixing of the gut microflora and the fibrous material, such as the structural polysaccharides found in all plant material, being particularly abundant in cambium material. There was also selective retention of different size particles, with the transit time being longer for the particulate markers. Presumably this serves to increase retention of larger masses to extract as much energy from them as possible, and is presumably very important for energy-needy animals like orang-utans (Caton *et al*., 1999).

Materials and Methods

Study Area

All samples were collected from the Natural Laboratory of Peat Swamp Forest (NLPSF) in the Sabangau Forest, Central Kalimantan. This forest covers an area of around 9200km^2, and is home to the largest known remaining orang-utan populations in the world, estimated at 6,900 in 2004 (Singleton *et al*., 2004). It covers almost the entire lowland river plains of southern Borneo. The Sabangau Forest is the largest area of lowland rainforest remaining in Borneo. The NLPSF is about 20 kilometres from the capital of Central Kalimantan, Palangkaraya (population ~100,000). The research area is located in the south part of Central Kalimantan Province, between the Sabangau, Katingan and Kahayan rivers in the old Pt. Setia Alam Jaya timber concession, which is now protected as a conservation area. Access to about 500 km^2 of the NLPSF is via the old timber extraction railway running south-west and then west into the peat-swamp forest (Morrogh-Bernard *et al*., 2003). All research carried out there is coordinated by the Centre for the International Cooperation in Management or Tropical Peatlands (CIMTROP), University of Palangka Raya and OuTrop.

Sample Design

Tree species used in the study were chosen based on orang-utan behavioural data collected by M. E. Harrison and H. Morrogh-Bernard, by separating them first into species that are eaten and those that are not eaten. Using phenology-plot data on species density collected by Simon Husson and Helen Morrogh-Bernard, common non-food species and less common food species were chosen for collection in this project. Nutritional analysis has been carried out on many of the foods that orang-utans eat, including a number of cambium species (Harrison, in prep.), but the data presented herein are the first on non-eaten cambium species, which is essential in order to understand why orang-utans choose or avoid certain species. Data on cambium species that are eaten have been collected by H. Morrogh-Bernard and M.E. Harrison from July 2003 to the present. The physical and nutritional data for the species they collected have been made available for the present comparison. In this project, samples were collected by me and processed for eaten species and not- eaten species of cambium, from the NLPSF from June to August 2007. I collected 21 samples of cambium from not-eaten species and 8 minor food species, which added to the 7 already collected by M. E. Harrison.

Methods

Samples were collected from the NLPSF directly and processed at the Setia Alam base camp; they were taken from the base of trees, using a parang, taking sections of bark with the underlying cambium from the tree. The intra-specific differences in cambium properties between the base and canopy level, from where orang-utans typically eat cambium, are unknown and may be considerable, but any inter-specific differences at the canopy level are probably reflected in any inter-specific differences seen at the base level and, thus, inter-specific comparisons using data collected in this way should still be valid (M. E. Harrison, pers. comm.).

Processing included measuring each piece of bark to get dimensions, so that area could be calculated and then scraping the cambium layer from the outer bark and measuring the thickness of the individual pieces (allowing volume to be calculated). Thickness was measured using a dial thickness gauge, sensitive to 0.01 mm (Mitutoyo Thickness Gage (Dial Type) Series No. 547,7305). Each sample was then weighed on scales sensitive to 0.01g, to attain a fresh wet weight for the sample. Samples were then placed in a paper envelope inside a kerosene-fuelled drying oven. The samples were weighed daily and were considered dry if the weight was the same on three consecutive days. Once dry, the samples were placed in individual sealable plastic bags with silica gel and then placed in a second sealable bag and stored in the dark. In order for the samples to be analysed nutritionally, a dry weight of 25g was required for each species of bark. Thus there were multiple samples for some species, but all were treated in the same way. Before they were finally packed they were weighed again to check that they were still dry.

It was initially considered to carry out physical-properties tests on the bark collected, including Young's modulus, toughness and hardness and some data on cambium species eaten were collected by M. E. Harrison and S. M. Cheyne, but, unfortunately, the necessary equipment (described in Lucas *et al*., 2001) experienced unfixable technical problems prior to the onset of this study, and so these data could not be collected. The fibre content of the cambium in the form of neutral detergent fibre (NDF) may give some indication of the importance of toughness in the food itself, but would not give full evidence. Lignin, which probably has a large influence on toughness, as well as digestibility, was not measured separately in the nutritional analyses (as acid detergent lignin), but makes up part of the NDF fraction. The procedures carried out were adapted from a protocol designed by M. E. Harrison and H. Morrogh-Bernard for food sample processing in collaboration with M. E Harrison.

The final samples were analysed nutritionally following Harrison (in prep, using methods similar to Knott ,1998) in the Laboratorium Pengujian Nutrisi Bidang Zoologi Pusat Penelitian Biologi (LIPI-Bogor Lab, Jakarta) under the supervision of Dr W. R. Farida. These nutritional analyses are for crude protein (CP), crude fat, ash, neutral detergent fibre (NDF) and water content of the individual cambium species. In order to find these different fractions there are a number of procedures. Simply, crude protein (CP) is measured using the Kjeldahl procedure for total nitrogen with the result multiplied by 6.25. The NDF was determined by the method described by Goering and van Soest (1970), modified by Robertson and van Soest (1980). Lipid content was measured using Soxhlet apparatus with a hexane solvent for six hours. Ash was found by heating at 550ºC until the sample had completely turned to ash. These techniques are standard practice and have been used in the study of the nutritional content of other foodstuffs.

The total non-structural carbohydrate (TNC) can be estimated using the fractions of CP, lipid, NDF and ash found by the nutritional analyses by subtraction from 100% (Knott, 1998, Conklin-Brittain *et al*., 2006; Harrison, in prep).

$$\%TNC = 100 - \%lipid - \%CP - \%total\ ash - \%NDF$$

These results can then be analysed in relation to factors that might affect preference:

- Available energy content (Kcal/ 100g organic matter (OM))[1];
- Average cambium thickness;
- Average dry weight of cambium/unit area bark;
- Water content;
- Available energy / unit surface area of bark;
- Available energy / unit volume cambium;
- Different fractions of the organic matter (CP, lipid, NDF, TNC);
- Percent of the total energy derived from these fractions;

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[1] Organic matter – if the ash values from the different cambiums vary by more than 5%, the non-mineral nutrients should be reported as a percentage of organic matter, instead of as a percentage of dry matter as the amount of ash in dry matter can be too variable resulting in potential confounding (Conklin-Brittain *et al*., 2006).

- Potential intake rates (dry weight cambium/minute and energy/min) were considered for use but average intake rates would need to be used for not-eaten species. Energy values / 100g will be used, making all measurements relative and useful. The energy content of the samples can be found for the organic part of the dried matter using the equations for metabolisable energy (ME).

$$ME\left(\frac{kCal}{100gOM}\right) = (4\ x\ \%TNC) + \ (4\ x\ \%CP) + \ (9\ x\ \%lipid) + (1.6\ x\ \%NDF)$$

The physiological fuel values used to gain the energy content of the organic matter are as follows:

- total non-structural carbohydrate (TNC) – 4kcal/g;
- crude protein (CP) - 4 kcal/g;
- lipid – 9 kcal/g;
- neutral detergent fibre (NDF) – This is a little more difficult, as fibre cannot be digested directly, but must first undergo microbial fermentation in the large intestine. From studies on chimpanzees (Milton and Demment, 1988), it was found that 54.3 % of the NDF fed to these chimpanzees was digested. Using data from Milton and Demment (1988), Knott (1998) suggests that this chimpanzee fibre digestion co-efficient value is adequate for female orang-utans, but may underestimate digestion capacity of male orang-utans, thus a higher value than 54.3% would be better. Orang-utans are considered to have a diet higher in NDF (lignin) content, but transit through the gut is slower and the large intestine is considerably longer in orang-utans, so we considered a figure of 54.3%

> for digestion coefficient to be adequate in these calculations (M. E. Harrison, pers. comm.). TNC yields 4kcal/g of energy when digested, similar to that released by the caeco-colic microbial fermentation of NDF, but gut microbes use around 1kcal/g of the energy released for their own metabolic processes, and only 3kcal/g is made available to the orang-utan. The result is a physiological fuel value of 1.6kcal/g (0.543 multiplied by 3kcal/g) (National Research Council, 1980).

If a lower digestion coefficient were to be used then 0.181 should be used, instead of 0.543, and the NDF part of the equation should be omitted completely, if it is assumed none of the structural fibre is digested (Conklin-Brittain *et al*., 2006).

Metabolisable energy with low NDF digestion can be calculated by:

$$ME\left(\frac{kCal}{100gOM}\right) = (4\ x\ \%TNC) + \ (4\ x\ \%CP) + \ (9\ x\ \%lipid) + (0.543\ x\ \%NDF)$$

If NDF were not digested, total metabolisable energy could be calculated by:

$$ME\left(\frac{kCal}{100gOM}\right) = (4\ x\ \%TNC) + \ (4\ x\ \%CP) + \ (9\ x\ \%lipid)$$

Different components of the cambium (CP, lipid, NDF and TNC) are calculated as percentages of organic matter (which does not contain ash), rather than dry matter (which contains ash), as Conklin-Brittain *et al*. (2006) suggest that, if the percentage of ash in the dry matter of the samples varies by more than 5%, it may confound the results.

I will also look at the different compositions making up the organic matter (the relative amounts of TNC, CP, lipid and NDF), as well as the potential energy gained from them in the different cambium species. This could also give an explanation of why some species are eaten while others are not.

The species of tree for which bark sample were collected are shown below (Table 1).

Table 1. Eaten and not-eaten tree species with regards to cambium consumption. Local name, Family, Genus and species are shown.

Family	**Latin Name**	**Local Name**	**Real OU food[2]?**
Anacardiaceae	*Campnosperma coriaceum*	Terantang	Yes
Anisophyllaceae	*Combretocarpus rotundus*	Tumeh	No
Annonaceae	*Xylopia fusca*	Jangkang Kuning	No
	Mezzettia leptopoda / parviflora	Pisang Pisang Besar	No
	Mezzettia umbellate	Pisang Pisang Kecil	No
Apocynaceae	*Dyera lowii*	Jelutong	Yes
Clusiaceae	*Garcinia bancana*	Manggis	No
	Callophyllum hosei	Mentangor	No
	Mesua sp. 1	Tabaras akar tinggi	No
Dipterocarpacae	*Shorea teysmanniana*	Meranti	No
Ebenaceae	*Diospyros siamang*	Ehang	Yes
	Diospyros bantamensis	Malam Malam	Yes
Euphorbiaceae	*Blumeodendron elateriospermum / kurzii*	Kenari	No
	Neoschortechinia kingie	Pupu Palanduk	No
Fabaceae	*Koompassia malaccensis*	Kempas	Yes
Fagaceae	*Lithocarpus sp. 1 cf. dasystachys*	Pampaning bitik	No
Hypericaceae	*Cratoxylon glaucum*	Geronggang	No
Icacinaceae	*Stemonorus scorpiodes / secundiflorus*	Tabaras yang tidak punya akar / pasir pasir	No
Lauraceae	*Litsea sp. 1 cf. resinosa*	Medang	No
Magnoliaceae	*Magnolia bintulensis*	Medang Limo	No
Meliaceae	*Sandoricum beccanarium*	Papong	No
Moraceae	*Parartocarpus venenosus*	Lilin Lilin	No
Myristicaceae	*Myristica lowiana*	Maha Darah Hitam	Yes
	Horsfieldia crassifolia	Mendarahan	Yes
	Gymnacranthera farquhariana	Mendarahan daun kecil	Yes

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[2] A food is defined as an item eaten at least twice and for at least six minutes during the duration of orang-utan behavioural research in Sabangau (Harrison, in prep; Harrison *et al*.,. submitted; Zweifel *et al*., 2008).

Myrtaceae	*Syzygium garcinfolia*	Jambu Burung 0/2	No
	Syzygium sp.3 or 4	Jambu Burung kecil	No
	Syzygium havilandii	Tatumbu / JJ1	No
Rutaceae	*Tetractomia tetrandra*	Rambangun	Yes
Sapotaceae	*Palaquium leiocarpum*	Hangkang	No
	Madhuca mottleyana	Katiau	Yes
	Palaquium ridleyii / xanthochymum	Mark Mark UN	Yes
Sapotaceae	*Palaquium pseudorostratum*	Nyatoh Babi	Yes
	Palaquium cochlearifolium	Nyatoh Gagas	Yes
Simaroubaceae	*Quassia borneensis*	Takang (sometimes sp. Teras Bamban/Prupuk Keras)	Yes
	unknown	NEW BARK	Yes

Rather excitingly, whilst in Central Kalimantan, an orang-utan was seen eating bark from a tree, the species of which could not be identified at the time; since it has not yet been identified this could mean that it is a new species. This species, included within the eaten-species data, is designated as ‘NEW BARK’. The sample for this species was taken from the same tree from which the orang-utan was eating and was treated to the same processing protocol, physical measurements and nutritional analysis.

Data entry and statistical analyses

The data entry for the physical properties, cambium thickness, area, wet weights and dry weights was carried out on site and the nutritional data were received on the 30th January 2008. Non-statistical calculations were made using Microsoft Excel TM, as were all graphical representations of data in the results section. Statistical analyses were undertaken using Minitab for WindowsTM with instruction provided by Ryan and Joiner (1994). Approximation to the normal distribution was tested on all data sets used by Anderson-Darling tests. Some of the data set approximated well to the normal distribution, whilst others did not. As the sample sizes for the eaten and not-eaten species were relatively small anyway, it was decided that non-parametric statistical analyses were more appropriate, although less powerful, being less likely to produce Type II errors. Mann-Whitney U tests were used to test for differences between eaten and non-eaten species. P-values <0.05 were taken to indicate statistical significance.

Results

The bark from a total of 36 tree species, 15 eaten and 21 not-eaten species were collected, processed and analysed in the study. The results in raw data form are detailed in the Appendix including physical data (cambium thickness, area and volume) and nutritional analysis data.

Physical Properties

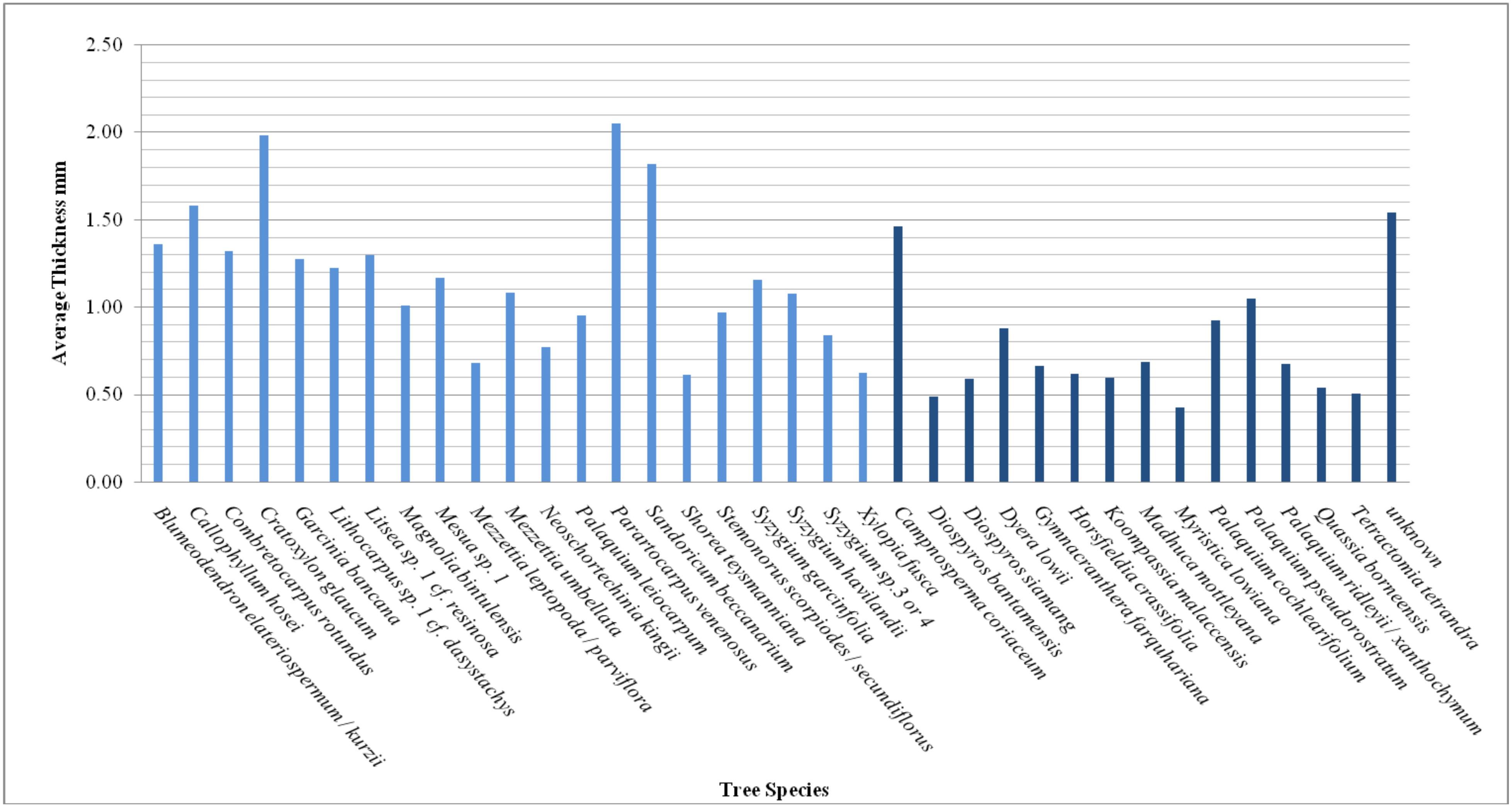

Figure 1. The average thicknesses of the cambium layer (mm). The not-eaten species are shown in the light blue (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*), the eaten species are shown in dark blue (*Campnosperma coriaceum* to unknown). The tree species marked as 'unknown' refers to NEW BARK described previously.

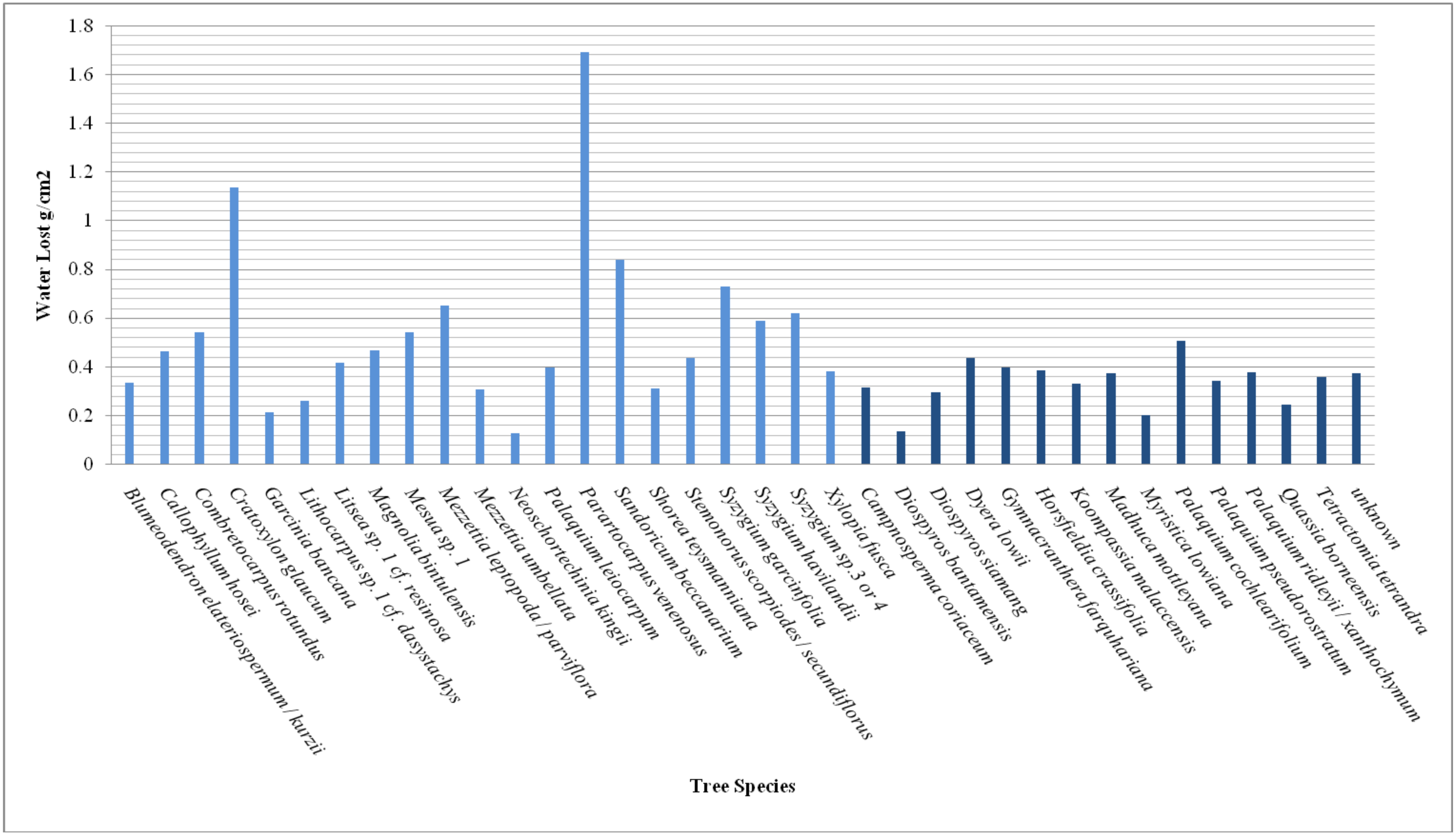

Figure 2. The average water loss from the cambium layer during drying (g/cm^2). The not-eaten species are shown in the light blue (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*), the eaten species are shown in dark blue (*Campnosperma coriaceum* to unknown). The tree species marked as 'unknown' refers to NEW BARK described previously.

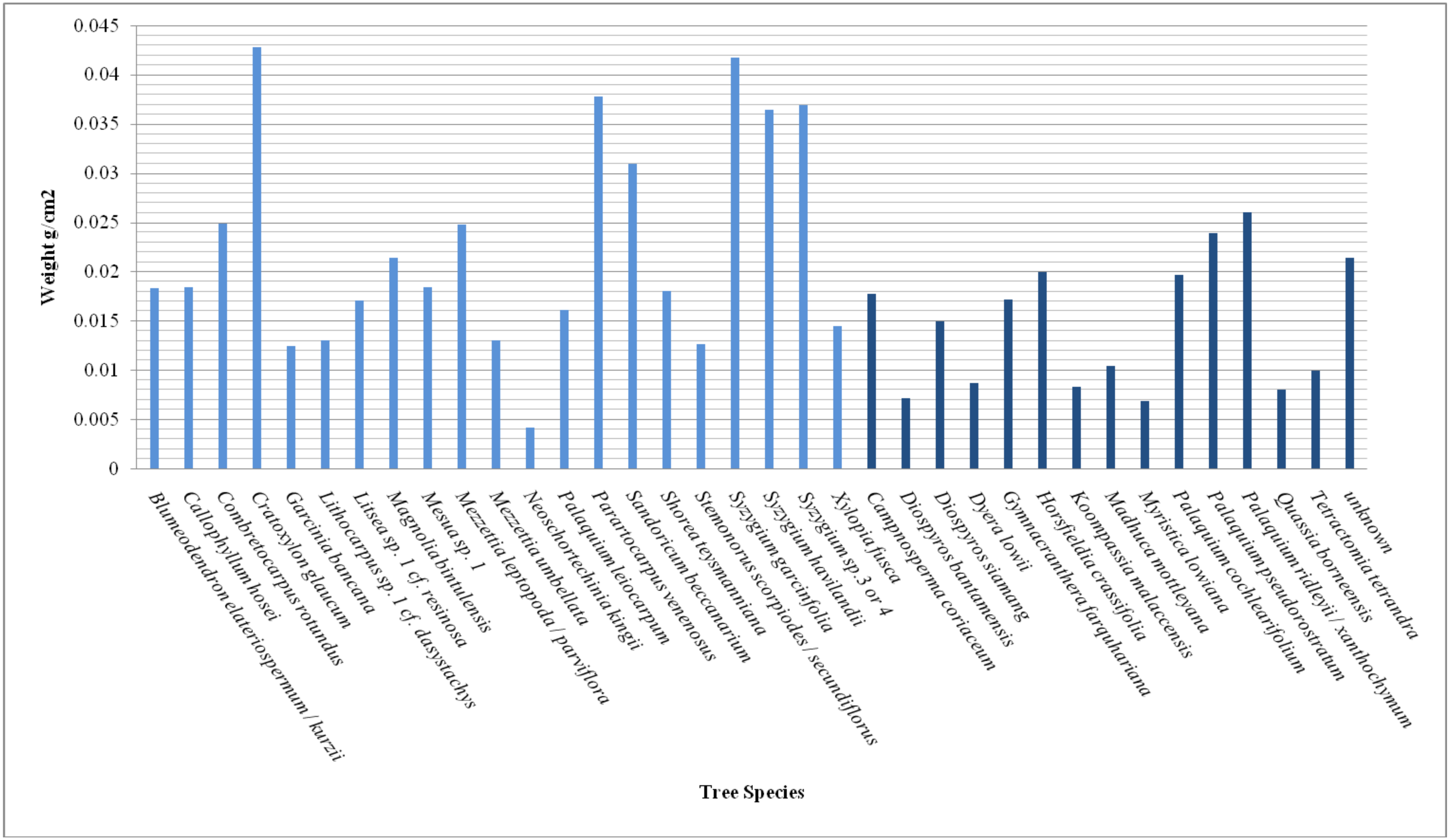

Figure 3. The dry weight of the cambium layer of the different species (g/cm^2). The not-eaten species are shown in the light blue (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*), the eaten species are shown in dark blue (*Campnosperma coriaceum* to unknown). The tree species marked as 'unknown' refers to NEW BARK described previously.

The physical properties of the bark species were examined and are shown graphically for eaten and not-eaten species in Figures 1 to 3. The result of the Mann-Whitney U tests for the average thickness of the cambium was that the not-eaten species had significantly thicker cambium than the eaten species (p= 0.001, mean for eaten species = 0.78, mean for non-eaten species = 1.18mm), with a difference between the mean values of 0.40mm. The water content of the cambium was also examined by finding the water lost during the drying process. The not-eaten species lost significantly more water than the eaten species (p=0.0096), shown in Figure 2. The field dry weight (g/cm^2) of the not-eaten species was also significantly greater than the eaten species (p=0.026), shown in Figure 3. Thus, contrary to the prediction that orang-utans might select those species providing greatest food bulk, cambium from a not-eaten species was more likely to be thicker, contain more water and have a greater dry mass for equivalent area compared to the cambium of eaten species.

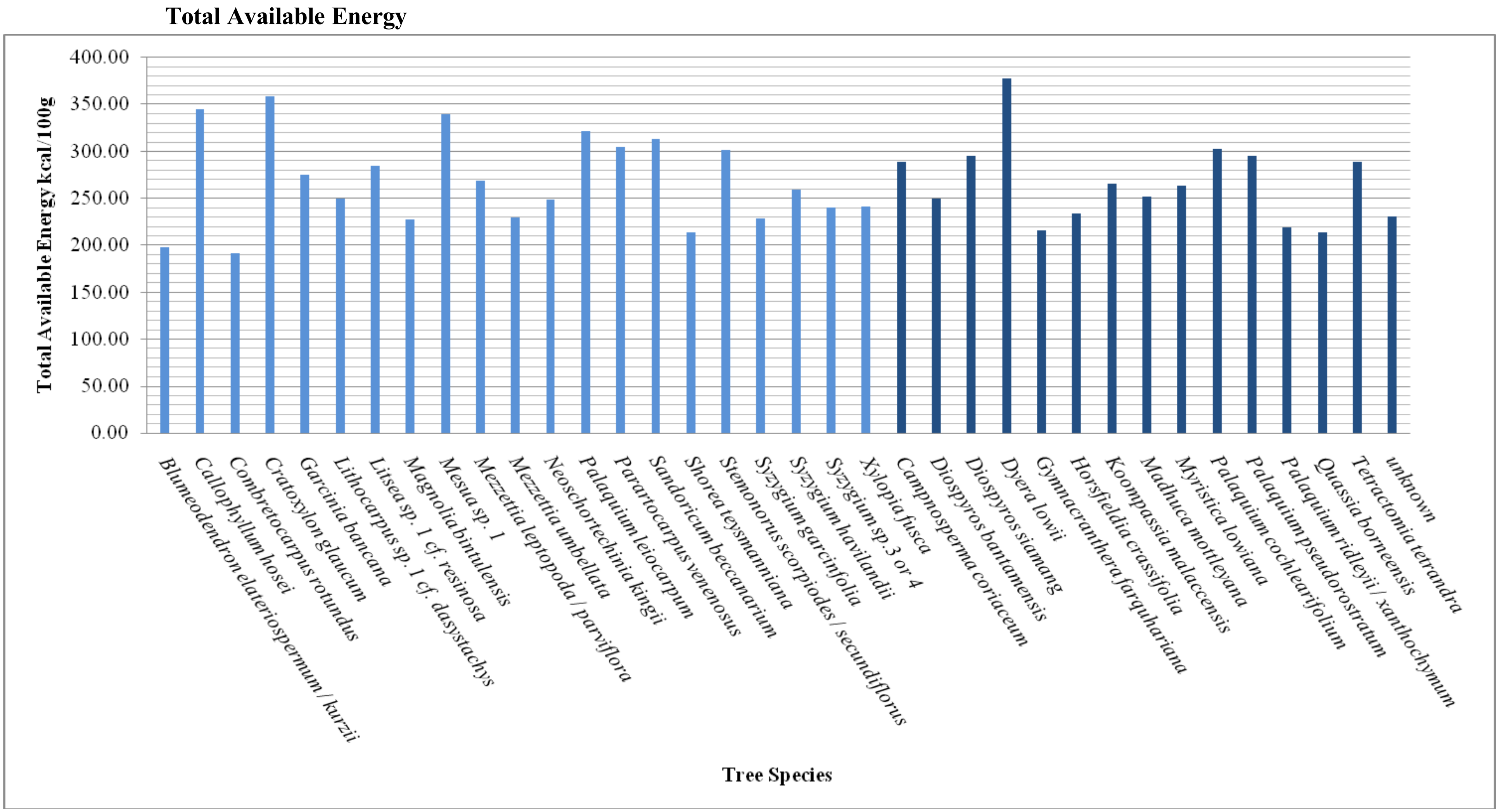

Figure 4. Available energy kcal/100g for all tree species. The available energy is also calculated with different digestion coefficients for NDF reflecting the energy derived with different digested amounts. Species that are not eaten (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*) are in the lighter blue while those that are eaten (*Campnosperma coriaceum* to unknown) are presented in the darker blue. The tree species marked as ‘unknown’ refers to NEW BARK described previously.

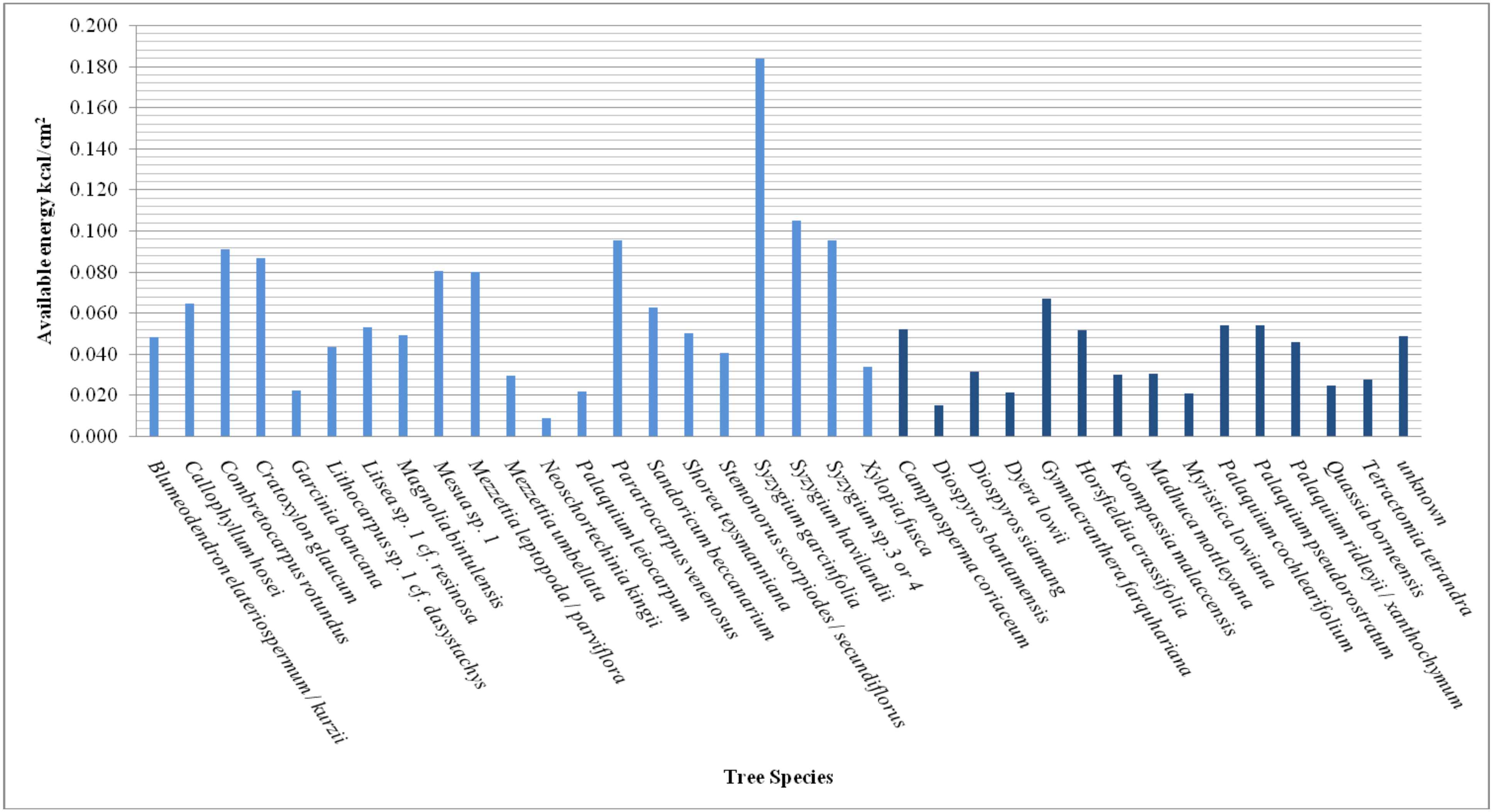

Figure 5 Available energy kcal/cm^2 for all tree species. The available energy is also calculated with different digestion coefficients for NDF reflecting the energy derived with different digested amounts. Species that are not eaten (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*) are in the lighter blue while those that are eaten (*Campnosperma coriaceum* to unknown) are presented in the darker blue. The tree species marked as 'unknown' refers to NEW BARK described previously.

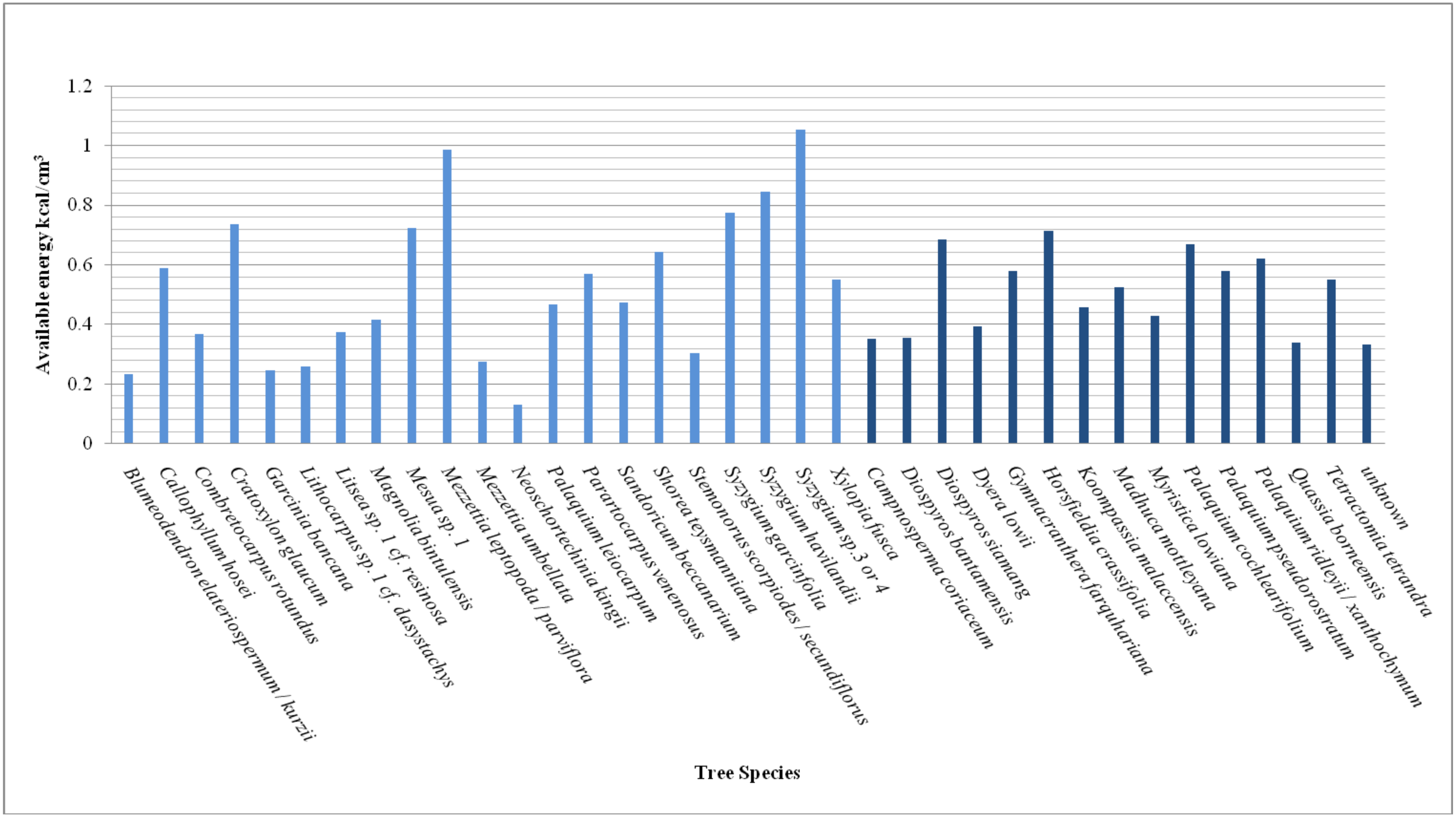

Figure 6 Available energy kcal/cm^3 for all tree species. The available energy is also calculated with different digestion coefficients for NDF reflecting the energy derived with different digested amounts. Species that are not eaten (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*) are in the lighter blue while those that are eaten (*Campnosperma coriaceum* to unknown) are presented in the darker blue.The tree species marked as 'unknown' refers to NEW BARK described previously.

The energy available / 100g (energy density) from the cambium was also determined and analysed (Figure 4[3].). The available energy in the cambium, if a high NDF digestion coefficient is considered, was not statistically significant different between eaten and not-eaten species (p=0.8979). Differences using a low and zero digestibility estimate for NDF were also not significant (p=0.9233 and 0.8852, respectively).

In order to relate energy availability to the physical data of thickness and area, the energy available / unit area and volume was calculated for the cambium of each species. The eaten and not-eaten species were then compared. The value of total available energy / unit area was found for each individual bark species by calculating the fresh cambium area that produced 100g when dried and dividing the available energy in kcal / 100g by it. This was calculated using the available energy values attained using both the high and low NDF digestion coefficients, as well as the total energy available if the NDF fraction was excluded (Figure 5[3]). This time, the high digestion coefficient value was significantly higher in the not-eaten species than the eaten species (p = 0.0171), which was not expected. The low and zero NDF digestion coefficient energy available / cm^2 were both insignificant (p=0.0645 and p=0.1304 respectively). Thus, for a cambium sample of any species, it was unlikely that there was any difference in the energy density based on whether it was eaten or not.

The available energy / cm^3 (volume of fresh cambium) for each species was found by calculating the fresh volume that produces 100g dry sample for each individual species and dividing the available energy / 100g by it. Again this was calculated using the available energy values / 100g with high, low and zero NDF digestion coefficients (Figure 6[3].). The differences were not significant (p= 1, p=0.9488 and p=1 respectively).

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[3] Figures 4,5 and 6 only detail total available energy (kcal/100g), total available energy / cm^2 and total available energy / cm^3 respectively for high NDF digestion coefficients since the same pattern was shown at all three NDF digestions coefficients. The only major difference was the absolute energy values (highest with high NDF digestion coefficient, lowest when no NDF digestion was included and in between for low NDF digestion coefficient values.

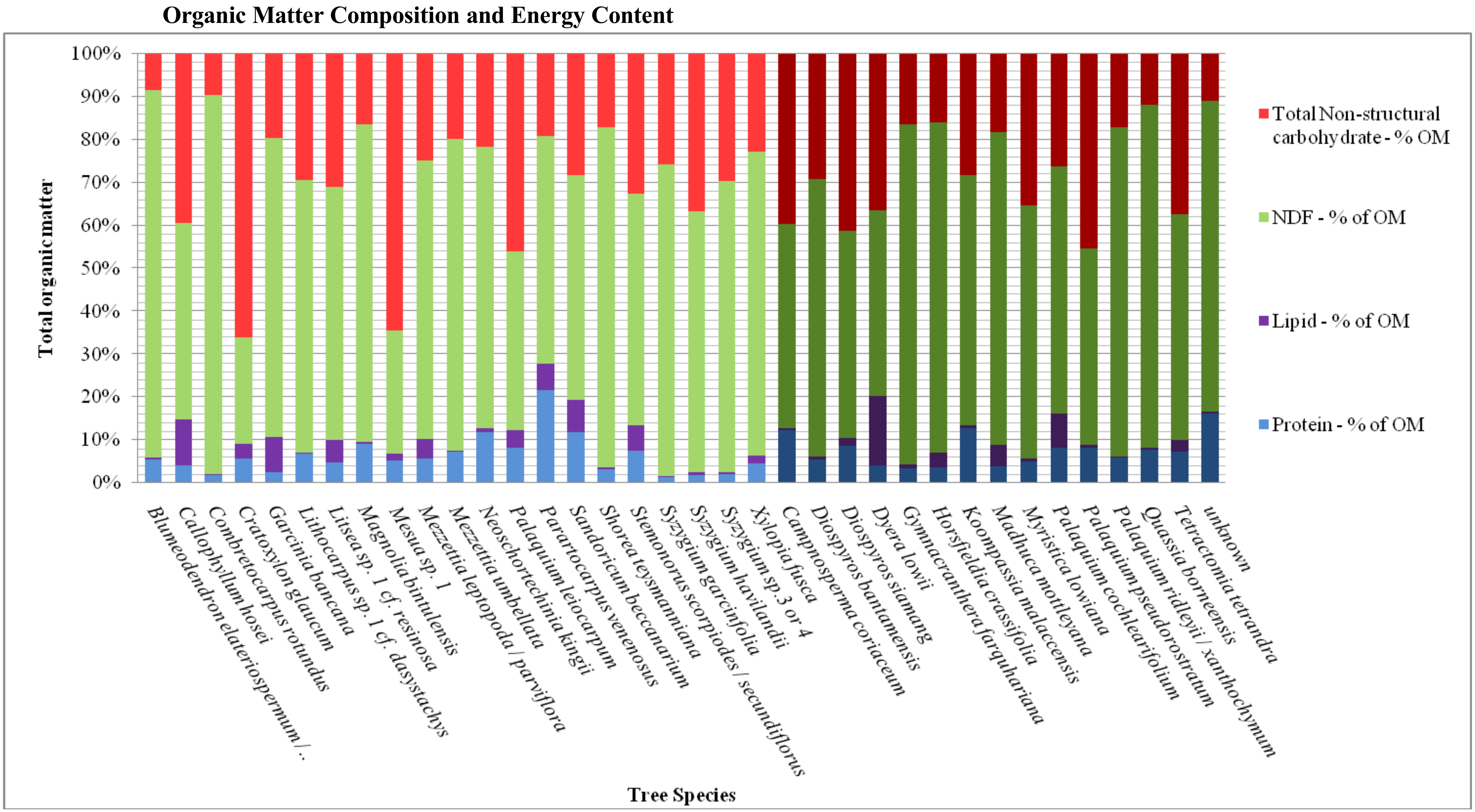

Figure 7 The individual fractions of the total organic matter (OM). Species that are not eaten (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*) are in the lighter colours while those that are eaten (*Campnosperma coriaceum* to unknown) are presented in the darker colours. The tree species marked as 'unknown' refers to NEW BARK described previously.

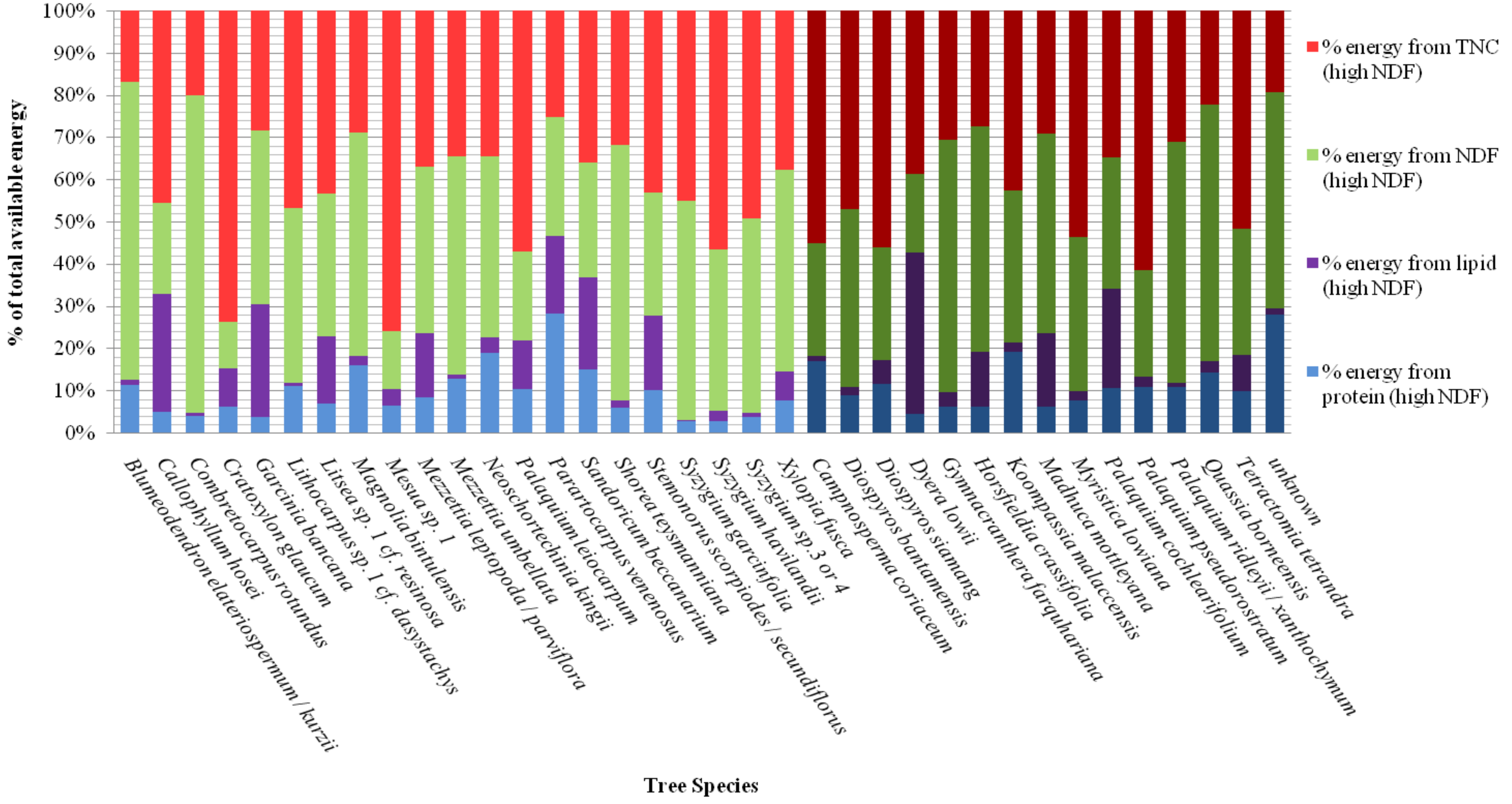

Figure 8 Energy gained from the individual fraction of the total Available energy. Species that are not eaten (*Blumeodendron elateriosperum/kurzii* to *Xylopia fusca*) are in the lighter colours while those that are eaten (*Campnosperma coriaceum* to unknown) are presented in the darker colours. The tree species marked as 'unknown' refers to NEW BARK described previously.

In order to test the composition of the organic matter in different species, the separate fractions of organic matter, namely protein, lipid, NDF and TNC content, were also compared between the eaten and not-eaten species (Figure 7.). The protein fractions of the organic matter between eaten and not-eaten species were not significantly different (p=0.2352), though the eaten species mean was greater than the not-eaten species, but this could be an artefact due to many of the cambiums from eaten species being around 7% OM or more . The lipid fraction of the organic matter was also not significantly different between the eaten and not-eaten species (p=1), but the eaten species showed greater variances in the lipid content, the only fraction to do so. The NDF fraction of the organic matter was not significantly different between the eaten and not-eaten species (p=1), nor was the TNC fraction (p=0.9233). The TNC and NDF fractions formed the bulk of the organic matter for both the eaten and not-eaten species.

Finally, the energy provided by these fractions of the organic matter, was also compared between eaten and not-eaten species (Figure 8). The percentage of energy from protein was not found to be significantly different between the eaten and not-eaten species (p=0.2228). The energy provided by lipid was also not significantly different between the eaten and not-eaten species (p=0.9488). The percentage of total energy derived from NDF was also not significantly different between eaten and not-eaten species (p=1). Finally, the percentage of the total energy derived from TNC was not significantly different between the eaten and not-eaten species (p=0.9234). The bulk of the energy derived from digestion of the organic matter came from the TNC and NDF fractions, as expected from the fractions of the organic matter. This was the same for all eaten and not-eaten species except *Parartocarpus venenosus* (not-eaten), where the greatest energy was derived from the protein fraction (28.25%) and NDF fraction (28.35%).

A summary of the results from the Mann-Whitney U tests can be found in Table 2, below.

Table 2. Mann-Whitney U Test results for all variables. Two-tailed tests shown and where results significant, appropriate one-tailed test result is also shown. Statistical significance indicated by p<0.05. Significant results indicated by *.

Mann-Whitney U Test Statistics

	P-value	
	not-eaten≠eaten	not-eaten>eaten
Average thickness	0.002*	0.001*
Water lost during drying	0.019	0.010*
Field Dry Wt	0.043	0.022*
Available energy kcal/100g (High NDF)	0.898	
Available energy kcal/100g (Low NDF)	0.885	
Available energy kcal/100g (excluding NDF)	0.923	
Fresh Area yielding 100g - energy content (kcal/cm2) (High NDF)	0.034*	0.017*
Fresh Area yielding 100g - energy content (kcal/cm2) (Low NDF)	0.064	0.032*
Fresh Area yielding 100g - energy content (kcal/cm2) (excluding NDF)	0.130	
Fresh Volume yielding 100g - energy content / cm3 (High NDF)	1.0	
Fresh Volume yielding 100g - energy content / cm3 (Low NDF)	0.949	
Fresh Volume yielding 100g - energy content / cm3 (excluding NDF)	1.0	
Protein %OM	0.235	
Lipid %OM	1.0	
NDF %OM	1.0	
TNC %OM	0.923	
% energy from Protein	0.223	
% energy from Lipid	0.949	
% energy from NDF	1.0	
% energy TNC	0.923	

Discussion

The aim in this project was to investigate orang-utan food preferences for cambium, an important fall-back food for orang-utans. Data were collected on certain physical properties including thickness, area, volume and weight, as well as the nutritional content of eaten and not-eaten cambium samples from different tree species. The nutritional content found was in terms of crude protein, lipid, TNC and NDF. In many respects, the cambiums from the eaten and not-eaten species are similar, but there were some significant differences. It is these results that will be looked at in more detail.

Physical Properties

I expected that the eaten cambium would be thicker than the not-eaten cambium layers, but it was found that the not-eaten species were significantly thicker, so perhaps thicker cambium takes greater effort to eat. Consumption of large quantities of relatively indigestible and energy-poor cambium may be undesirable for orang-utans, as this adds considerable roughage to the diet, decreasing gut passage time and food digestibility, and takes up room in the gut that could be filled with more energy-rich foods. The not-eaten species also had greater water content, when compared to the eaten species of cambium. As orang-utans are gaining water from eating the cambium, as well as gaining nutrients, this seems a little surprising, but, if much water is contained within the dietary fibre matrix, this can decrease the transit time of food through the gut and increase faecal output. Thus, this decreases the time for fermentation by the caeco-colic microbial flora and decreases the efficiency of the digestion of the fibre in the large intestine. As a result, the amount of energy gained from the food would be decreased (Burrows *et al*., 1982). Eating food with very large water content would also cause the stomach to fill more rapidly, wasting space, which could otherwise be filled with food containing energy (Burrows *et al*., 1982). This is not efficient for an energy-needy animal like the orang-utan (Wrangham, 1971).

Total Available Energy

When the total available energy was calculated for each cambium species using a high NDF digestion coefficient, it was expected that the energy values would be greater in the eaten species. This was not the case. This could possibly be due to the fact that bark has very high lignin content when compared to other foods eaten and it is almost completely indigestible. The NDF fraction found in nutritional analyses includes hemicellulose, cellulose and lignin (Rothman *et al*., 2006). As a result, the lignin content of each sample cannot be determined from the data collected in this study. The nutritional analyses did not detect acid-detergent fibre (ADF) or acid-detergent lignin (ADL), which would have allowed detection of lignin content. It has also been shown that, as the lignin content of a food increases, the nutritional content of the food decreases (Rothman *et al*., 2006) by making a greater proportion of the nutrients unavailable, especially lipid (Burrows *et al*., 1982). In order to get an idea of how this could possibly be affecting the results, I looked at the available energy using the different NDF digestion coefficients. Presumably, if the lignin content was high and affecting the energy content, then significant differences might be seen with high NDF digestion values, as it assumes a greater contribution made to the energy content of the food by lignin. If NDF digestion is excluded, then lignin should not influence the results and the lower NDF digestion coefficient value might fall in the middle. This is what is suggested by the results in Table 2. despite no significant differences being found. Thus, lignin content could be confounding the results. There is considerable inter-specific variation in the available energy.

Energy content related to physical properties

I then decided to look at energy content related to area and volume of cambium. The total available energy (kcal/100g dry cambium) could be related to the fresh cambium area which yields

100g dry cambium to give energy/cm^2 for each cambium species. All values were therefore specific to the individual bark species and given in kcals/cm^2 for comparison. This was done using the available energy values for each level of NDF digestion. With the high NDF digestion energy values, there was no significant difference between eaten and not-eaten species. This was the case for both the low digestion of NDF and no digestion of NDF energy values / cm^2, but, when a one-tailed Mann-Whitney U test was performed on the available energy (high and low digestion of NDF) for not-eaten cambium, being of higher energy density than eaten cambium, the results were significant ($p=0.017$ and $p=0.032$ respectively). These results seem unlikely, but perhaps there are some explanations.

As discussed before, the NDF fraction of the nutritional analyses includes hemicellulose, cellusose and lignin fractions, and lignin content is known to be particularly high in cambium, compared to other foods (Rogers *et al*., 1990, Rothman *et al*., 2006). Woody plants in particular, which include bark and bamboo, are regarded as having an ‘effective plastic intra-cellular collapsing mechanism in their secondary cell walls, rendering these plants exceptionally tough’ (Lucas *et al*., 2000).

The calculations for energy including NDF digestion assume that all the NDF is fermentable and so energy is derivable from it when the products of fermentation, produced by the caeco-colic microbes, are absorbed. If lignin is higher in the not-eaten species, which is plausible, if not likely, it might appear as an artefact of the results that the species which are not eaten have greater total metabolisable energy contained in a given area of cambium, thereby giving these results. They may not contain any greater amount of metabolisable NDF, or possibly less, since the results show that the NDF fractions for eaten and not-eaten species are not significantly different. This idea is supported by the fact that there are no significant differences in the available energy /

cm^2 between eaten and not-eaten species when the NDF fraction is not included in the energy calculations. The difference is also not significant when available energy calculated with low NDF coefficients is used. This could be because the overall total energy seeming to be gained from the NDF fraction is lower and affects the total available energy values less.

When total available energy was looked at, compared to the volume of fresh cambium, there were no significant differences between the eaten and not-eaten species. This was the case for all three levels of NDF digestion calculated. The high NDF value for available energy in a given area was significantly different ($p=0.017$) between the eaten and not-eaten species, but the energy in a given volume is not. This may be because, in the energy / given volume, an extra dimension is factored in, thickness. Thickness of the cambium is affected by its structural properties, but it is also presumably affected by the water content. It was shown that there was a significantly greater amount of water contained within the not-eaten species cambium than the eaten. Since the cambium is a vascular tissue, this may therefore affect the overall thickness of the cambium layer. As a result the energy / given volume of cambium is probably a better measure of the energy concentration, since it takes into account the extra dimension, which is subject to other factors, such as water content, as well as structural fibre. Differences using this measure were not significant.

When looking at the particular fractions that made up the organic matter, including crude protein, lipid, NDF and TNC, there were no significant differences between the eaten and not-eaten species. The main bulk of the organic matter was TNC and NDF for all, as expected, especially for NDF, since this contains the structural components giving cambium its fibrous nature. There was also no significant difference between the energy derived from each of the four fractions, when eaten and not-eaten species were compared. The bulk of the energy derived from these foods tends, it seems, to be derived from the TNC fraction of the organic matter in most cases, although, as has already been described, *Parartocarpus venenosus* contains most energy within the protein and NDF fractions. On the basis of these results, it appears that orang-utans, in this area at least, are not selecting cambium species for consumption based on energy or nutrient content. The water content, thickness and fibre content may play a role in deciding the preferences for these foods. It has also been found that orang-utans make some food choices based on protein and fibre content with reference to fruit and flowers but this does not seem to be the case with cambium (Harrison, in prep). For eaten cambium species, preference rank is correlated with lipid contents for flanged-males, but not for any other age-sex class (Harrison, in prep.).

It has been found in other orang-utan foods, and in foods of other great apes, that other factors are important in modelling dietary selectivity. When looking at fruits, it is suggested that crop-patch size, fruit pulp weight as compared to the total fruit weight, sugar and total phenolics are important and significantly-related to selectivity rankings in orang-utans in Kutai (Leighton, 1993). Leighton (1993) found that differences in these four variables were the cause of variation in selectivity ranking of fruits (r^2=0.86). Perhaps, where cambium consumption is concerned, the most salient feature affecting consumption to consider is phenolic content, shown to influence preference of fruits and flowers in orang-utans in Sabangau (Harrison, in prep). Crop-patch size may be irrelevant, or perhaps related to tree size; analogues of fruit pulp to whole fruit ratio could be suggested to be cambium thickness compared to the thickness of the entire bark, but this seems unlikely, considering that the eaten cambiums tend to be thinner. Western lowland gorillas have a varied diet, which changes seasonally with changes in fruit availability and includes, besides fruit; seeds, leaves, bark and stems (Rogers *et al*., 1990). Food selection by Western lowland gorillas (*Gorilla gorilla gorilla*) is thought to be most governed by lignin content, digestibility and crude protein (Calvert, 1985). The fruits, seeds and leaves eaten may all contain high concentrations of total phenols and condensed tannins, thus suggesting that gorillas are able to cope with them (Rogers *et al*., 1990).

Secondary Plant Compounds

In contrast to gorillas, the presence of total phenolics (plant toxins and anti-feedants from many chemical groups, including tannins) and condensed tannin (anti-feedants that bind protein, reducing digestibility) concentrations of foods are major factors affecting ingestion of foods by orang-utans, as has already been described. It seems also that orang-utans make choices between species for food by using information about quality of individual items and distribution of food patches. For fruit, these qualities include tannins, digestible carbohydrate and energy content in Kutai (Leighton, 1993), and protein, fibre and phenolics in Sabangau (Harrison, in prep). Since orang-utans do not seem to be choosing cambium from species for consumption based on energy content or digestible carbohydrate, it may be possible that phenolics or tannins may play a role. Tannins are found in most plant tissues predominating in the woody parts (Vellayan, 1981). One role of phenols like condensed tannins seem to be as anti-feedants, both in the fruits (figs predominantly) and seeds studied (Leighton, 1993). It was found that orang-utans choose preferentially unprotected seeds lower in condensed tannins or other phenolic compounds than uneaten seeds by comparison. Thus, despite being rich in energy and protein and available in fruits when general fruit availability was poor, they were likely avoided due to the tannin content.

Potential reasons suggested for tannin avoidance were unpalatability, giving a bitter taste to food (Rogers *et al*., 1990), their ability to bind protein making the protein unavailable for digestion by proteolysis (Vellayan, 1981), or the potential toxic effects of hydrolysable tannins but toxic effects seem unlikely (Leighton, 1993). Foods containing other compounds such as terpenes and alkaloids were strongly avoided by orang-utans despite high energy content and Caton *et al*. (1999)

suggest that the greatest deterrent to feeding is low levels of alkaloids, more than phenols and tannins, as they are toxic. It has been found with lar gibbons (*Hylobates lar*), that the foods eaten lack alkaloids completely. Hominoids do not produce uricase enzyme which breaks alkaloids down, a loss that is thought to have occurred due to a mutation early in the hominoid evolution during the Miocene (Watanabe *et al*., 2002).

The highest tannin concentration in the diet of the lar gibbon (*Hylobates lar*) is 5.33% (Vellayan, 1981). In Leighton's (1993) data, the highest concentration of tannin in figs eaten by orang-utans was 1.44%, while total phenolics was 3.44% with a positive correlation between total phenol concentration and selectivity rank (r_s= 0.49, $P<0.05$). The phenomenon of astringency is found only if the tannin concentration is greater than 5% (Oates *et al*., 1980). Perhaps this means that orang-utans avoid tannins at lower concentrations, compared to the lar gibbon. In Vellayan (1981), the known 'tanniferous families' were listed. Of the samples taken, 8 of these are found in some of these families, which are: Anarcardiceae, Lauraceae, Sapotaceae, and Simaroubaceae. Of these 8 tree species in these families, 6 are eaten species with 4 of them being part of the Sapotaceae family (Table 1.). Perhaps, the cambium of these eaten species do not contain levels of tannins above the threshold for feeding deterrence as it is known that secondary plant compound concentrations are found in different concentrations in different parts of the plant and at different times (Leighton, 1993).

From bark samples taken by Cheyne and Harrison, it was found that the phenolic content of eaten cambium was low, being less than that found in mature leaves, but not significantly different from leaf shoots. Tannin content was also low in eaten cambiums, being significantly less than the levels found in fruit pulp, which is the preferred food of orang-utans (Harrison, in prep; Cheyne and Harrison, unpubl. data). It was thought that this could potentially be a factor affecting the species from which cambium is eaten, as those eaten are not significantly different from those not eaten, in terms of energy and nutrient composition. This would then parallel the seeds that are eaten and not eaten by orang-utans mentioned in Leighton (1993), where a major difference was phenolics concentrations, especially condensed tannins, but based on these data, phenolics seem unlikely deterrence factors.

Toughness and Hardness

Physical properties of different foodstuffs eaten by orang-utans and gorillas have also been tested and investigated, including leaves, fruits, seeds and cambium/bark. Eastern mountain gorillas (*Gorilla gorilla beringei*) eat a considerable amount of plant structural material and less fruit. The amount eaten is variable between different populations with 30% of the Bwindi gorilla population diet consisting of bark, while only 6.9% of the Mgahinga gorilla population diet was made up of bark (Elgart-Berry, 2004). In the study by Elgart-Berry (2004), the plant foods of two eastern mountain gorilla populations in Uganda were tested for fracture toughness. These were in gorilla groups found in the Bwindi-Impenetrable National Park (BINP) and the Mgahinga Gorilla National Park (MGNP). Fracture toughness is the work required to break a unit area of tissue. It was found that the tree barks were the toughest food items of all those tested, ranging from 0.23 to 8.2kJ/m^2. Those in the BINP were tougher than those in the MGNP, with also a greater range in toughness, but the most-eaten species were those with the lower toughness. The species eaten most was *Mimulopsis,* which constituted 10% of the bark diet and was lowest in toughness (0.23±0.06 kJ/m^2). This was based on 10 species of bark from BINP, where it was a greater part of the diet and 3 species of bark from MGNP, where it was less important.

Vogel *et al*. (in press) also found that the cambium species eaten by orang-utans were considerably tougher than the other foods, being 2.38±0.860 kJ/m^2, surpassed in toughness only by the structural elements of leaves, the primary and secondary veins. It was also found that, in general, the diet of orang-utans was more resistant to deformation and fracture than the diet of chimpanzees. Orang-utan cambium consumption in the Tuanan Research Station, Central Kalimantan was found to range from 0 to 42% of the total diet from month to month with the average consumption being 10% (Vogel *et al.*, in press). This is higher than the consumption rates found in NLPSF, Sabangau, where the monthly range was between 0 and 25%, with an average of 3.87±6.72% (Harrison, in prep). In Tuanan, Central Kalimantan, eaten cambium was two to four times tougher than leaves and orang-utans tended to avoid or reject very tough tissues (Vogel *et al.*, in press).

The outer bark is far harder, however, than the cambium layer, so, while the toughness and hardness of the cambium layer is probably important, it is the properties of the outer-bark layer that is likely the greater factor in deterring consumption of particular species. The average hardness, or Young's Modulus, of the outer bark of some eaten species from the NLPSF is 15.77MPa (Harrison, in prep). This is far higher than the hardness of foods tested in Vogel *et al.* (in press), which range from 1.34±0.61MPa for ripe fruit to 5.06±2.00MPa for ripe endosperm. Orang-utans have been found to reject particularly resistant foods and so this provides some evidence that the toughness of the outer bark may have some bearing on the preferences of orang-utans for certain species for cambium consumption (Vogel *et al.*, in press). The mean Young's Modulus value for the outer-bark layer of samples from NLPSF was found to be intermediate, and less than the values for leaf shoots, fruit skin and fruit pulp (Cheyne and Harrison, unpubl. data) and thus probably has little bearing on cambium choice.

It is described in Knott (1998) how the physical properties of food may affect the extent to which they are eaten by certain age-sex classes. For example, the *Neesia* fruit is very large and hard with irritating hairs protecting the seeds inside. The fruit must be ripped open to gain access to the seeds and it is suggested that the greater consumption of these seeds by adult male orang-utans may be due to them being better able to open and process them (Knott, 1998). Based on data from Harrison (in prep), there are no sex-age class differences in *Dyera lowii* cambium consumption, with 2.12% of the total feeding time being spent by adult females eating this species, and 2.66% and 2.02% being spent by adolescent females and flanged males respectively. *D. lowii* was the most-eaten bark species by orang-utans, ranking 11th for adult females, and 12th, for both adolescent females and flanged males. The sap of *D. lowii* is used in the manufacture of chewing gum and is very commonly eaten by orang-utans. Looking more closely at *D. lowii* cambium nutritional data, it contained the most available energy / 100g dry mass of all the species collected. This might make it seem that the *D. lowii* was very rich in energy, but it was not the most energy dense which, may be due to its high water content (2nd highest of the eaten species collected, Figure 2) perhaps giving it a low dry mass. Looking at the fractions of organic matter composition, the NDF fraction was low, compared to other eaten species (43.34% compared to 62.40% average for eaten and 61.72% average for not-eaten species). The lipid content of the cambium is also far greater than the other species studied (16.01% compared to the 2.79% average for eaten and 3.00% average for not-eaten species). As a result, the lipid fraction yields a large proportion of the energy derived from the cambium (38.19%), which is almost equal to that derived from the TNC fraction (38.71%). This is the greatest amount of energy yielded from the lipid fraction, for all the species collected, eaten and not-eaten.

The most-eaten food across all age and sex classes, apart from adolescent females, is also the toughest and hardest and is the *Mezzetia parviflora/ leptopoda* fruit. On average, between 15 and 28% of the feeding time is spent eating this food in all age and sex classes, but adolescent females only eat this food for 1.15% of feeding time, so that it ranks 21st in terms of time spent eating it. This is probably due to problems in processing the food for consumption by adolescent females, because it is too hard (Harrison, in prep). This supports the suggestions that less time may be spent eating barks where processing is difficult, or particularly hard work, in favour of trees with softer outer bark. When collecting samples, some species, notably *Neoschortechinia kingii*, were very difficult to remove bark sections any larger than 5 cm in either length or breadth as the outer bark was very brittle and crumbly. Perhaps difficulty in removing appreciable sections of bark might also be a deterrent to orang-utans eating them.

The mean toughness value for the outer-bark layer was the highest of any other food part and significantly higher than the toughness for fruit husks and skins and mature leaves. With fruit pulp and skin combined the toughness value for the outer-bark was not significantly greater (Cheyne and Harrison, unpubl. data). These data indicate that bark is the toughest food consumed and suggest that this is the most likely reason limiting the species which can be eaten, as mentioned in Vogel *et al*. (in press). This fits in with other observations also mentioned in Knott (1998). Since no differences were found in the nutritional and energy data between eaten and not-eaten species, it is possible that this could be the overriding factor affecting consumption in this area, though comparison between eaten and not-eaten species is needed.

Essential Fatty Acids

Finally, it has been found that, although the overall lipid content of cambiums is low (average 2.91% of OM for eaten and not-eaten species combined), and not significantly different between eaten and not-eaten species, the profile of fatty acids may be important. As a fall-back food it may provide several essential fatty acids, such as, palmitic, stearic, oleic and linoleic acids, which are the commonest. It is unknown whether cambium provides these in any physiologically-useful quantity but it may provide another dimension on which selectivity is based (Heller *et al*., 2002).

Conclusion

The data collected and analysed for the cambium of different tree species, eaten and not-eaten, presented no obvious evidence to suggest orang-utans were choosing species for food based on energy content alone in this area, as it was similar but variable between eaten and not-eaten species. It was expected that energy content might be the primary factor influencing selection of food species, since orang-utans are very energy "needy", but this was not the case.

From other studies, it is known that orang-utans take other factors into account when selecting different foods for consumption (Leighton, 1993) and so this is probably likely to be the case for cambium. It is possible that digestion inhibitor concentrations could have been important factors affecting cambium consumption, as is the case with fruit and seeds, for example (Leighton, 1993). Data collected by Cheyne and Harrison (unpubl. data) on phenolic and tannin content of the cambiums of certain eaten species only, suggest this is not important in cambium species selection. Alkaloids were not tested and may provide another dimension on which dietary selectivity is based, as suggested by Caton *et al*. (1999), but if other secondary compounds are in low concentrations in cambium, this might suggest toxins may also be low.

Bark is obviously very fibrous, and this may be also be a contributing factor affecting which species are eaten and which are not, as the tough outer layer may prevent or discourage orang-utans from eating it. The lignin content is known to be much higher than any other food eaten by orang-utans (Vogel *et al*., in press) and so is the toughness (Harrison, in prep). The fact that orang-utans are known to reject certain foods based on whether they are particularly resistant, might suggest that species of tree with a very tough outer bark are not eaten. Perhaps this needs to be looked at in more detail, comparing eaten with not-eaten species to look for significant differences.

Orang-utans are suggested to be particularly adapted to tougher and harder foods with specific reference to fall-back foods, based on diet comparison with chimpanzees *(Pan troglodytes)* and tooth and cranial robustness and morphology and gut morphology (Vogel *et al*., in press). These features better enable fracture of cell walls allowing greater access to cellular contents and thus increase the nutrient content available. The toughness and hardness of the actual cambium layer might also affect preferences for certain cambiums as foods, but it seems that the outer-bark layer is of greater consequence, the toughness of which seems to be limiting which species can be consumed or at least, consumed profitably in this area.

Thus, while energy content does not seem to be the overriding factor affecting cambium consumption in the Sabangau Forest, toughness of the outer layer seems to be a major factor. Perhaps data on phenolics and toughness and hardness of not-eaten species could be collected for comparison with the eaten species data to give a firmer conclusion to what these preliminary data suggest. Multi-variate analysis of all of these characteristics, as well as species density, might also be useful, to try to determine foraging strategy for cambium, as it is probably a more complicated relationship than simply the toughness of the outer-bark layer explicitly determining whether species are eaten or not eaten. Leighton (1993) states, with reference to fruits and seeds, that it is unlikely that any single characteristic is likely to cause a change from eaten to not-eaten based on specific threshold values and so this is surely the case for other orang-utan foods, including cambium, though toughness of the outer-bark layer does seem to be important.

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Appendix

Raw Data table can be found below (Tables 3-5).

Table 3. Raw Physical Properties data including area collected, average thickness, volume, dry weight, field dry weight, wet weight, water lost, wet weight and dry weight of cambium (PE). MR = M. Rothwell, MEH = M. E. Harrison.

Latin Name	**Collected by**	Food?	Total Area PE mm^2	Av Thickness PE mm	Volume PE mm^3	Wet Weight PE g	Dry Weight PE g	Field Wet weight PE g/cm^2	Field Dry Weight PEg/cm^2
Blumeodendron elateriospermum /	MR	No	170175	1.36	244608	59.89	28.94	0.35	0.02
Callophyllum hosei	MR	No	110047	1.58	173874	52.68	29.64	0.48	0.02
Combretocarpus rotundus	MR	No	109685	1.32	144784	61.94	27.89	0.56	0.02
Cratoxylon glaucum	MR	No	94480	1.99	187542	111.34	38.49	1.18	0.04
Garcinia bancana	MR	No	225137	1.28	287049	50.38	25.71	0.22	0.01
Lithocarpus sp. 1 cf. dasystachys	MR	No	267555	1.23	32775	72.39	33.85	0.27	0.01
Litsea sp. 1 cf. resinosa	MR	No	195977	1.30	254770	84.30	33.40	0.43	0.02
Magnolia bintulensis	MR	No	197327	1.01	199300	95.95	36.37	0.49	0.02
Mesua sp. 1	MR	No	192777	1.17	238969	107.57	50.90	0.56	0.02
Mezzettia leptopoda / parviflora	MR	No	98744	0.68	67145	66.57	24.67	0.67	0.02
Mezzettia umbellata	MR	No	200687	1.09	217745	63.88	26.22	0.32	0.01
Neoschortechinia kingii	MR	No	726666	0.77	561955	94.14	29.61	0.13	0.00
Palaquium leiocarpum	MR	No	286425	0.96	226682	117.58	32.93	0.41	0.02
Parartocarpus venenosus	MR	No	80970	2.05	165988	139.89	31.03	1.73	0.04
Sandoricum beccanarium	MR	No	92231	1.82	167860	80.26	25.42	0.87	0.03
Shorea teysmanniana	MR	No	161706	0.61	98640	52.68	29.64	0.33	0.02
Stemonorus scorpiodes /	MR	No	248363	0.97	403597	110.68	40.65	0.45	0.01
Syzygium garcinfolia	MR	No	244937	1.16	390144	188.42	132.66	0.77	0.04
Syzygium havilandii	MR	No	155360	1.08	167012	96.62	54.28	0.62	0.04
Syzygium sp.3 or 4	MR	No	80325	0.84	67473	52.68	29.64	0.66	0.04
Xylopia fusca	MR	No	193990	0.62	121387	76.36	27.72	0.39	0.01
Campnosperma coriaceum	MR	Yes	158876	1.46	231958	52.53	28.22	0.33	0.02
Diospyros bantamensis	MEH	Yes	482808	0.49	235932	67.99	33.57	0.14	0.01
Diospyros siamang	MEH	Yes	234787	0.59	138232	72.56	32.12	0.31	0.01
Dyera lowii	MEH	Yes	339687	0.88	298385	150.39	30.97	0.44	0.01

Gymnacranthera farquhariana	MR	Yes	168499	0.67	112051	69.53	30.02	0.41	0.02
Horsfieldia crassifolia	MR	Yes	142345	0.62	96497	57.66	29.43	0.41	0.02
Koompassia malaccensis	MEH	Yes	455782	0.59	270365	153.49	46.53	0.34	0.01
Madhuca mottleyana	MEH	Yes	568626	0.69	390702	217.86	81.53	0.38	0.01
Myristica lowiana	MEH	Yes	441525	0.42	187500	91.20	30.39	0.21	0.01
Palaquium cochlearifolium	MR	Yes	158626	0.93	146729	83.43	32.49	0.53	0.02
Palaquium pseudorostratum	MR	Yes	143856	1.05	151048	52.68	29.64	0.37	0.02
Palaquium ridleyii /	MR	Yes	254216	0.68	165891	102.43	47.08	0.40	0.03
Quassia borneensis	MEH	Yes	444059	0.54	239606	112.05	38.06	0.25	0.01
Tetractomia tetrandra	MEH	Yes	356822	0.50	179038	131.43	34.02	0.37	0.01
unknown	MR	Yes	133237	1.54	205184	52.68	29.64	0.40	0.02

Table 4. Dry and Organic Matter data for eaten and not-eaten species. MR = M. Rothwell, MEH = M. E. Harrison.

Latin Name	Real OU food?	Collected by	Water (%)	Ash (%)	Protein (%)	Lipid (%)	NDF	TNC	Dry Matter	Ash - % of DM	Protein - % of DM	Lipid % of DM	NDF - % of DM	TNC - % of DM	Organic Matter	Protein - % of OM	Lipid - % of OM	NDF - % of OM	TNC- % OM
Blumeodendron elateriospermum / kurzii	No	MR	7.45	10.2	4.64	0.26	71.92	12.98	92.55	9.44	4.29	0.24	66.56	19.46	83.81	5.54	0.31	85.81	8.34
Callophyllum hosei	No	MR	9.57	2.53	3.71	9.46	40.37	43.93	90.43	2.29	3.35	8.55	36.51	49.30	88.36	4.20	10.71	45.69	39.41
Combretocarpus rotundus	No	MR	9.36	2.32	1.7	0.13	78.39	17.46	90.64	2.10	1.54	0.12	71.05	25.19	88.73	1.92	0.15	88.34	9.59
Cratoxylon glaucum	No	MR	11.39	1.84	4.88	3.07	21.62	68.59	88.61	1.63	4.32	2.72	19.16	72.17	87.17	5.60	3.52	24.80	66.08
Garcinia bancana	No	MR	11.45	3.29	2.24	6.99	59.96	27.52	88.55	2.91	1.98	6.19	53.09	35.82	85.97	2.61	8.13	69.75	19.52
Lithocarpus sp. 1 cf. dasystachys	No	MR	8.96	9.59	5.7	0.16	52.88	31.67	91.04	8.73	5.19	0.15	48.14	37.79	83.09	6.86	0.19	63.64	29.31
Litsea sp. 1 cf. resinosa	No	MR	8.75	3.57	4.29	4.46	52.22	35.46	91.25	3.26	3.91	4.07	47.65	41.11	88.28	4.86	5.05	59.15	30.93
Magnolia bintulensis	No	MR	8.67	5.78	7.79	0.51	63.94	21.98	91.33	5.28	7.11	0.47	58.40	28.74	86.51	9	0.59	73.91	16.49
Mesua sp. 1	No	MR	7.32	5.68	4.66	1.35	25.23	63.08	92.68	5.26	4.32	1.25	23.38	65.78	87.80	5.31	1.54	28.74	64.42
Mezzettia leptopoda / parviflora	No	MR	9.19	4.57	4.89	3.95	56.61	29.98	90.81	4.15	4.44	3.59	51.41	36.41	87.04	5.62	4.54	65.04	24.81
Mezzettia umbellata	No	MR	8.22	7.93	6.27	0.21	61.72	23.87	91.78	7.28	5.75	0.19	56.65	30.13	85.10	7.37	0.25	72.53	19.86
Neoschortechinia kingii	No	MR	9.66	8.91	9.8	0.8	54.57	25.92	90.34	8.05	8.85	0.72	49.30	33.08	83.07	11.80	0.96	65.69	21.55
Palaquium leiocarpum	No	MR	9.21	5.13	7.12	3.56	36.05	48.14	90.79	4.66	6.46	3.23	32.73	52.92	86.56	8.23	4.11	41.65	46.02
Parartocarpus venenosus	No	MR	9.23	3.59	18.92	5.44	46.62	25.43	90.77	3.26	17.17	4.94	42.32	32.31	87.81	21.55	6.20	53.09	19.17

Sandoricum beccanarium	No	MR	9.28	6.19	10.09	6.47	44.93	32.32	90.72	5.62	9.15	5.87	40.76	38.60	85.63	11.78	7.56	52.47	28.19
Shorea teysmanniana	No	MR	9.34	3.46	2.79	0.33	69.71	23.71	90.66	3.14	2.53	0.30	63.20	30.84	87.82	3.18	0.38	79.38	17.07
Stemonorus scorpiodes / secundiflorus	No	MR	9.14	4.43	6.53	5.19	47.14	36.71	90.86	4.03	5.93	4.72	42.83	42.49	87.20	7.49	5.95	54.06	32.50
Syzygium garcinfolia	No	MR	8.41	1.29	1.33	0.1	65.81	31.47	91.59	1.18	1.22	0.09	60.28	37.23	90.51	1.47	0.11	72.71	25.71
Syzygium havilandii	No	MR	8.79	10.72	1.42	0.61	50	37.25	91.21	9.78	1.30	0.56	45.61	42.77	82.29	1.73	0.74	60.76	36.77
Syzygium sp.3 or 4	No	MR	8.96	4.65	1.88	0.22	59.31	33.94	91.04	4.23	1.71	0.20	54.00	39.86	87.19	2.16	0.25	68.03	29.56
Xylopia fusca	No	MR	10.36	2.25	4.07	1.6	62.22	29.86	89.64	2.02	3.65	1.43	55.77	37.13	87.83	4.63	1.82	70.84	22.70
Campnosperma coriaceum	Yes	MR	10.02	10.14	10.07	0.31	38.88	40.6	89.98	9.12	9.06	0.28	34.98	46.55	81.77	12.31	0.38	47.55	39.76
Diospyros bantamensis	Yes	MEH	7.41	8	4.71	0.47	55.5	31.32	92.59	7.41	4.36	0.44	51.39	36.41	85.73	5.49	0.55	64.74	29.22
Diospyros siamang	Yes	MEH	7.12	13.31	6.98	1.5	39.33	38.88	92.88	12.4	6.48	1.39	36.53	43.23	81.40	8.58	1.84	48.32	41.26
Dyera lowii	Yes	MEH	6.89	5.68	3.65	14.12	38.22	38.33	93.11	5.29	3.40	13.15	35.59	42.58	88.19	4.14	16.01	43.34	36.51
Gymnacranthera farquhariana	Yes	MR	9.14	1.9	3.02	0.74	70.8	23.54	90.86	1.73	2.74	0.67	64.33	30.53	89.29	3.38	0.83	79.29	16.50
Horsfieldia crassifolia	Yes	MR	9.61	2.22	3.21	2.97	68.22	23.38	90.39	2.01	2.90	2.68	61.66	30.74	88.58	3.62	3.35	77.02	16
Koompassia malaccensis	Yes	MEH	8.38	5.52	11.02	0.59	50.79	32.08	91.62	5.06	10.10	0.54	46.53	37.77	86.99	12.67	0.68	58.39	28.26
Madhuca mottleyana	Yes	MEH	7.17	3.97	3.46	4.35	65.28	22.94	92.83	3.69	3.21	4.04	60.60	28.47	89.41	3.87	4.87	73.01	18.25
Myristica lowiana	Yes	MEH	6.17	2.9	4.54	0.6	53.83	38.13	93.83	2.72	4.26	0.56	50.51	41.95	91.28	4.97	0.66	58.97	35.39
Palaquium cochlearifolium	Yes	MR	8.76	5.2	7.04	6.88	50.19	30.69	91.24	4.74	6.42	6.28	45.79	36.76	86.91	8.10	7.92	57.75	26.23
Palaquium pseudorostratum	Yes	MR	10.39	5.81	6.84	0.66	38.83	47.86	89.61	5.21	6.13	0.59	34.80	53.28	84.94	8.05	0.78	45.71	45.46
Palaquium ridleyii / xanthochymum	Yes	MR	9.27	2.85	5.19	0.23	67.89	23.84	90.73	2.59	4.71	0.21	61.60	30.90	88.38	5.87	0.26	76.81	17.06
Quassia borneensis	Yes	MEH	8.22	3.63	6.79	0.53	70.89	18.16	91.78	3.33	6.23	0.49	65.06	24.89	88.72	7.65	0.60	79.90	11.85

Tetractomia tetrandra	Yes	MEH	8.81	10.33	5.89	2.3	43.56	37.92	91.19	9.42	5.37	2.10	39.72	43.39	82.60	7.13	2.78	52.74	37.35
unknown	Yes	MR	9.32	1.92	14.37	0.34	64.54	18.83	90.68	1.74	13.03	0.31	58.52	26.40	89.10	16.13	0.38	72.43	11.06

Table 5. Energy calculation data for eaten and not-eaten species including all three NDF digestion coefficients. MR = M. Rothwell, MEH = M. E. Harrison.

Latin Name	**Real OU food?**	**Collected by**	**Available energy Kcal/100 g (high NDF)**	**Available energy Kcal/100 g (exc. NDF)**	**Available energy kcal/100g (low NDF)**	**Available energy Kcal/g (high NDF)**	**Total protein + lipid+ NDF+ TNC (OM)**	**Energy from protein /item**	**Energy from lipid /item**	**Energy from NDF /item (high NDF)**	**Energy from TNC /item**	**Energy from NDF /item (low NDF)**	**% energy from protein (high NDF)**	**% energy from lipid (high NDF)**	**% energy from NDF (high NDF)**	**% energy from TNC (high NDF)**
Blumeodendron elateriospermum / kurzii	No	MR	198.10	58.31	104.91	1.98	100	0	0	0.03	0.01	0.01	11.18	1.41	70.56	16.85
Callophyllum hosei	No	MR	345.21	270.78	295.59	3.45	100	0	0.02	0.01	0.03	0	4.87	27.91	21.56	45.66
Combretocarpus rotundus	No	MR	191.27	47.36	95.33	1.91	100	0	0	0.04	0.01	0.01	4.01	0.69	75.24	20.07
Cratoxylon glaucum	No	MR	358.80	318.40	331.86	3.59	100	0.01	0.01	0.02	0.11	0.01	6.24	8.83	11.26	73.66
Garcinia bancana	No	MR	275.29	161.67	199.54	2.75	100	0	0.01	0.01	0.01	0	3.79	26.58	41.27	28.36
Lithocarpus sp. 1 cf. dasystachys	No	MR	250.07	146.40	180.96	2.50	100	0	0	0.01	0.02	0	10.97	0.69	41.46	46.88
Litsea sp. 1 cf. resinosa	No	MR	285.01	188.64	220.76	2.85	100	0	0.01	0.02	0.02	0.01	6.82	15.95	33.81	43.41
Magnolia bintulensis	No	MR	227.70	107.30	147.44	2.28	100	0.01	0	0.03	0.01	0.01	15.82	2.33	52.88	28.97
Mesua sp. 1	No	MR	339.56	292.75	308.35	3.40	100	0	0	0.01	0.05	0	6.25	4.08	13.79	75.89
Mezzettia leptopoda / parviflora	No	MR	268.49	162.54	197.85	2.68	100	0.01	0.01	0.03	0.02	0.01	8.37	15.21	39.46	36.96
Mezzettia umbellata	No	MR	229.27	111.13	150.51	2.29	100	0	0	0.02	0.01	0.01	12.85	0.97	51.53	34.65
Neoschortechinia kingii	No	MR	249.06	142.04	177.71	2.49	100	0	0	0	0	0	18.95	3.48	42.97	34.60
Palaquium leiocarpum	No	MR	321.82	253.98	276.59	3.22	100	0.01	0.01	0.01	0.03	0	10.22	11.50	21.08	57.19
Parartocarpus venenosus	No	MR	305.10	218.61	247.44	3.05	100	0.03	0.02	0.03	0.03	0.01	28.25	18.27	28.35	25.13
Sandoricum beccanarium	No	MR	313.37	227.89	256.38	3.13	100	0.01	0.02	0.03	0.03	0.01	15.04	21.70	27.28	35.98
Shorea teysmanniana	No	MR	213.66	84.35	127.46	2.14	100	0	0	0.02	0.01	0.01	5.95	1.58	60.52	31.95
Stemonorus scorpiodes / secundiflorus	No	MR	301.59	213.53	242.88	3.02	100	0	0.01	0.01	0.02	0	9.93	17.76	29.20	43.11
Syzygium garcinfolia	No	MR	228.15	109.70	149.19	2.28	100	0	0	0.05	0.04	0.02	2.58	0.44	51.92	45.07
Syzygium havilandii	No	MR	259.65	160.67	193.66	2.60	100	0	0	0.04	0.05	0.01	2.66	2.57	38.12	56.65
Syzygium sp.3 or 4	No	MR	239.97	129.15	166.09	2.40	100	0	0	0.04	0.04	0.01	3.59	0.95	46.18	49.28
Xylopia fusca	No	MR	241.15	125.75	164.22	2.41	100	0	0	0.02	0.01	0.01	7.69	6.80	47.85	37.66
Campnosperma coriaceum	Yes	MR	289.16	211.70	237.52	2.89	100	0.01	0	0.01	0.03	0	17.04	1.18	26.79	55.00
Diospyros bantamensis	Yes	MEH	249.25	143.79	178.95	2.49	100	0	0	0.01	0.01	0	8.82	1.98	42.31	46.89
Diospyros siamang	Yes	MEH	294.65	215.94	242.18	2.95	100	0.01	0	0.01	0.02	0	11.64	5.63	26.71	56.02
Dyera lowii	Yes	MEH	377.30	306.70	330.23	3.77	100	0	0.01	0.01	0.01	0	4.39	38.19	18.71	38.71
Gymnacranthera farquhariana	Yes	MR	216.14	86.98	130.04	2.16	100	0	0	0.02	0.01	0.01	6.26	3.45	59.76	30.53

Horsfieldia crassifolia	Yes	MR	234.15	108.69	150.51	2.34	100	0	0.01	0.03	0.01	0.01	6.19	12.89	53.58	27.34
Koompassia malaccensis	Yes	MEH	264.95	169.84	201.54	2.65	100	0	0	0.01	0.01	0	19.13	2.30	35.90	42.67
Madhuca mottleyana	Yes	MEH	251.21	132.27	171.92	2.51	100	0	0	0.01	0.01	0	6.16	17.43	47.35	29.06
Myristica lowiana	Yes	MEH	263.46	167.39	199.41	2.63	100	0	0	0.01	0.01	0	7.55	2.25	36.46	53.74
Palaquium cochlearifolium	Yes	MR	302.66	208.59	239.94	3.03	100	0.01	0.01	0.02	0.02	0.01	10.71	23.54	31.08	34.67
Palaquium pseudorostratum	Yes	MR	295.50	221.04	245.86	2.96	100	0.01	0	0.02	0.04	0.01	10.90	2.37	25.20	61.53
Palaquium ridleyii / xanthochymum	Yes	MR	219.18	94.05	135.76	2.19	100	0.01	0	0.03	0.02	0.01	10.72	1.07	57.09	31.13
Quassia borneensis	Yes	MEH	213.54	83.38	126.77	2.14	100	0	0	0.01	0	0	14.34	2.52	60.95	22.19
Tetractomia tetrandra	Yes	MEH	288.89	202.98	231.61	2.89	100	0	0	0.01	0.01	0	9.87	8.67	29.74	51.71
unknown	Yes	MR	230.17	112.17	151.50	2.30	100	0.01	0	0.03	0.01	0.01	28.03	1.49	51.27	19.21

Original methods protocol developed for this project in collaboration with M. E. Harrison.

Protocol for Bark Project – 2007

Methods

Methods to be used follow those developed by , and currently in use in Sabangau and a number of other orang-utan research sites in Borneo and Sumatra.

In order to establish the reason/s for cambium species selection, preference indices (i.e. relative consumption/relative availability) will be defined for all food species, and food and abundant non-food species will be compared. Data on cambium species eaten have been collected from July 2003-present by H. Morrogh-Bernard and M.E. Harrison. Data on tree species abundance in phenology plots have been compiled by H. Morrogh-Bernard and S. Husson. These data will be made available for the analysis. Cambium species featuring prominently in orang-utan diets (n=7) have already been collected by M.E. Harrison and these data will be made available. Sample collection for minor (n=7) and non-food (n=20±) species will be carried out by M. Rothwell during the course of this project. A list of samples in need of collection will be provided.

Sample collection and processing:

- Collect bark samples from near the base of the tree, ensuring that the cambium layer is removed. Orang-utans typically eat bark from higher up on the trunk/on branches, but, although there may be significant within-species differences between bark/cambium properties at the base and in the canopy of the tree, between-species differences in properties at the base of the tree are highly likely to reflect between-species differences higher up, thus, in light of safety issues regarding tree climbing and bark collection high in the canopy, collection of samples at the base is preferred. This will require a local assistant to identify the species.

- Take the samples back to camp
- **Carry out any physical property tests – not possible due to equipment problems**
- Measure the area of each piece of bark collected
- Scrape off the cambium layer and measure its thickness using a thickness gauge
- Weigh the sample wet and put it in the oven
- Weigh samples in the oven every day until they obtain a constant weight, at which point they are dry and dry weight can be recorded
- Store the sample in silica gel and send it to the LIPI-Bogor lab for analysis (energy, protein, fat, fibre etc.), following methods used by Knott (1998).
- For each species calculate (list below), compare food and non-food species, and analyse in relation to preference index:
    - Physical properties
    - Average cambium thickness
    - Average dry weight of cambium/unit area bark
    - Potential intake rates (dry weight cambium/minute and energy/minute), assuming the species was eaten (using averaged feeding rate data that I will have collected for food species)