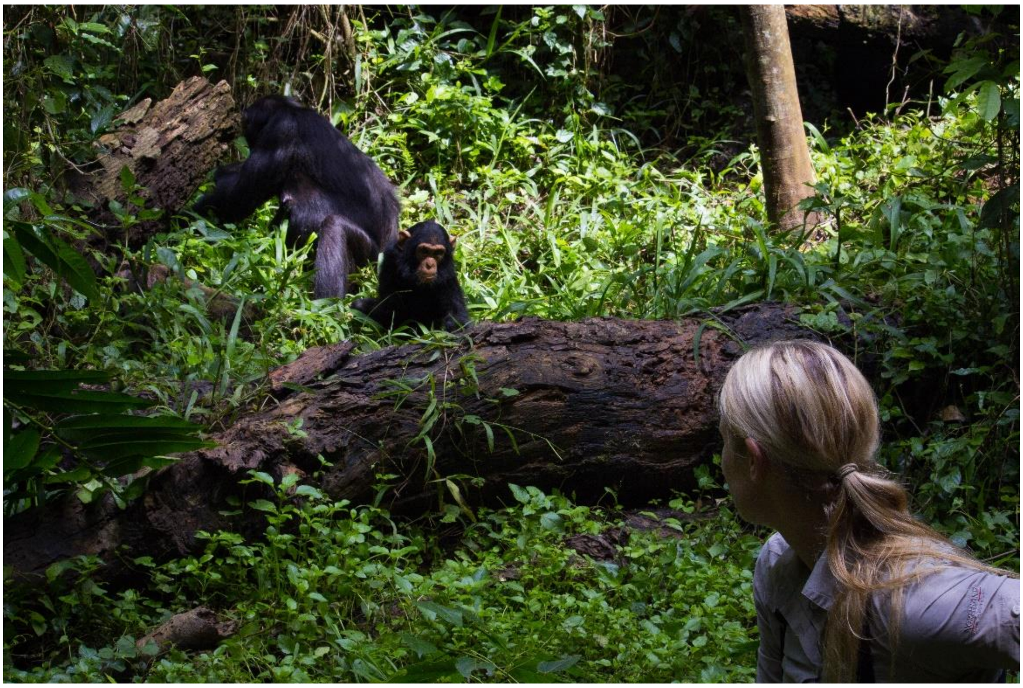
DAVIS EXPEDITION FUND

REPORT ON EXPEDITION / PROJECT

Expedition/Project Title:	Assessing Eastern chimpanzee (*Pan troglodytes schweinfurthii*) food availability and diet in two Ugandan Forests
Travel Dates:	25.05.2017 – 28.08.2017
Location:	Budongo and Bugoma Forest, Uganda
Group Members:	Iris Berger
Aims:	To compare the chimpanzee food availability of Budongo and Bugoma Forest, to contrast the diet of the chimpanzee communities in the two forests using faecal samples, and to assess how representative faecal samples are using behavioural observations.

Outcome (not less than 300 words):-

Assessing Eastern chimpanzee (Pan troglodytes schweinfurthii) food availability in Budongo and Bugoma Forest, and estimating the diet of the Kisindi chimpanzee community based on the feeding behaviour of the Sonso community



Background

<u>Taxonomy and behavioural diversity:</u>
Two different species of the genus Pan are recognized, namely bonobos (P. paniscus), and common chimpanzees (P. troglodytes) which are further subdivided into western (P. troglodytes verus), central (P. t. troglodytes), and eastern chimpanzees (P. t. schweinfurthii) and the Nigerian-Cameroon chimpanzees (P. t. vellorosus) (Groves, 2001). The majority of Eastern chimpanzees are found in the Democratic Republic of Congo (173000- 248000 individuals; Plumptre et al., 2010), outside of which 8000 Eastern chimpanzees occur, with around 5000 of them living in western Uganda (Plumptre at al., 2003). Whilst chimpanzees can be found in various different habitats, but they do remain forest-dwelling animals (Pruetz, 2006). The different subspecies inhabit different regions across Africa and show astonishing behavioural flexibility with respect to nest-construction (Möbius et al., 2008), tool-use (Whiten et al., 2001), social group structure (Boesch and Boesch-Achermann, 2000), and vocalization (Mitani, 1992). Sources of behavioural diversity between subspecies and between populations include genetics, anatomy, demography, ecology, diffusion boundaries, tool use, feeding, communication, and social organization (Wrangham et al., 1994). Certain food items may be eaten at one site but not another despite being available at both. McGrew et al. (1988) explained this by variations in the overall food availability, implying that in areas with low food abundance foods of lower quality may be eaten. Interestingly, the diversity of the dietary repertories of different populations is greater than it would be expected by differences in the resources and biotic environment alone playing a role (Nishida et al., 1983).

<u>Communities:</u>
A chimpanzee community describes the collection of individuals that share a single range or territory. Moreover, sharing of information about food sources, fruit and meat, culture, and social and sexual aspects of life occurs (Reynolds, 2005). Furthermore, their social structure can be categorized as “fission-fusion” which involves a change in group size through the fission and fusion of subunits, called parties, in relation to their activity and the availability and distribution of resources (Bernstein, 1976).

<u>Cultures and tool use:</u>
Goodall (1973) first proposed the concept of chimpanzee cultures after observing differences in tool use and social behaviour in different chimpanzee populations. To qualify as a cultural trait it has to be something that can be learned by observing the established skills of others and passed on to future generations, albeit not through their genes (McGrew, 1992). Whiten et al. (1999) showed that 39 behavioural patterns, mainly in the domain of tool use, are customary in some communities, but not in others and due to ecological explanations being discounted in these cases they may be described as cultural traits.
Ugandan chimpanzees exhibit comparatively limited tool use behaviour (McGrew, 2010) with the Ngogo and Kanyawara communities in Kibale Forest and the Sonso community in Budongo Forest showing four, two and one tool use behaviour in the relation to food acquisition respectively (Gruber et al., 2012). Notably, the Sonso

community does not make use of sticks in their daily life which is in stark contrast to other chimpanzee communities in
Africa (Whiten et al., 1999). Furthermore, field experiments involving a hole filled with honey drilled in a log showed that Sonso chimpanzees do not make use of sticks even when put directly into the hole (Gruber et al., 2011).Genetic factors cannot provide an explanation considering the low genetic variation of Eastern chimpanzees (Goldberg and Ruvolo, 1997).
Notably, the appearance and maintenance of tool use is impacted by ecological variation (Gruber, 2016). Three hypotheses, namely the "invention", "necessity", and "opportunity" hypotheses, relating ecological factors to the emergence of tool use have been proposed (Fox et al., 1999). Whilst the invention hypothesis holds that new forms of tool use arise through chance events (Fox et al., 2004), the necessity hypothesis predicts the emergence of tool use in response to food scarcity and the opportunity hypothesis involves the encounter with the material required to make tools or the food source that is to be extracted with tools (Koops et al., 2013). Gruber et al. (2016) showed that low fruit availability, implying further travel between food patches, leads to Sonso chimpanzees engaging for longer with a log filled with honey, albeit merely the time travelled turned out to be significant for the use of tools. Nevertheless, the diversity, distribution, and abundance of chimpanzee food sources is likely to greatly impact the innovation and maintenance of tool use.

Budongo Forest:
The Budongo Forest is 435km2 of continuous moist semideciduous tropical rain forest (Plumptre, 1996), located at the top of the Albertine Rift in western Uganda between 1°37'N- 2°03'N and 31°22'-31°46'E (Reynolds, 2005). The mean altitude is 1100m and a mild slope in a southeast-northwest direction towards the Albertine Rift characterizes the forest. Four rivers run through the area, including the Sonso river which runs past the research station of the Budongo Forest Project (BFP). A map of western Uganda is shown in Figure 1 and a map of Budongo Forest in detail is depicted in Figure 2. The main annual rainfall is 1600 mm with its distribution over the year exhibiting a bimodal pattern where most rain falls between March and May, and between September and November (Tweheyo et al., 2003).

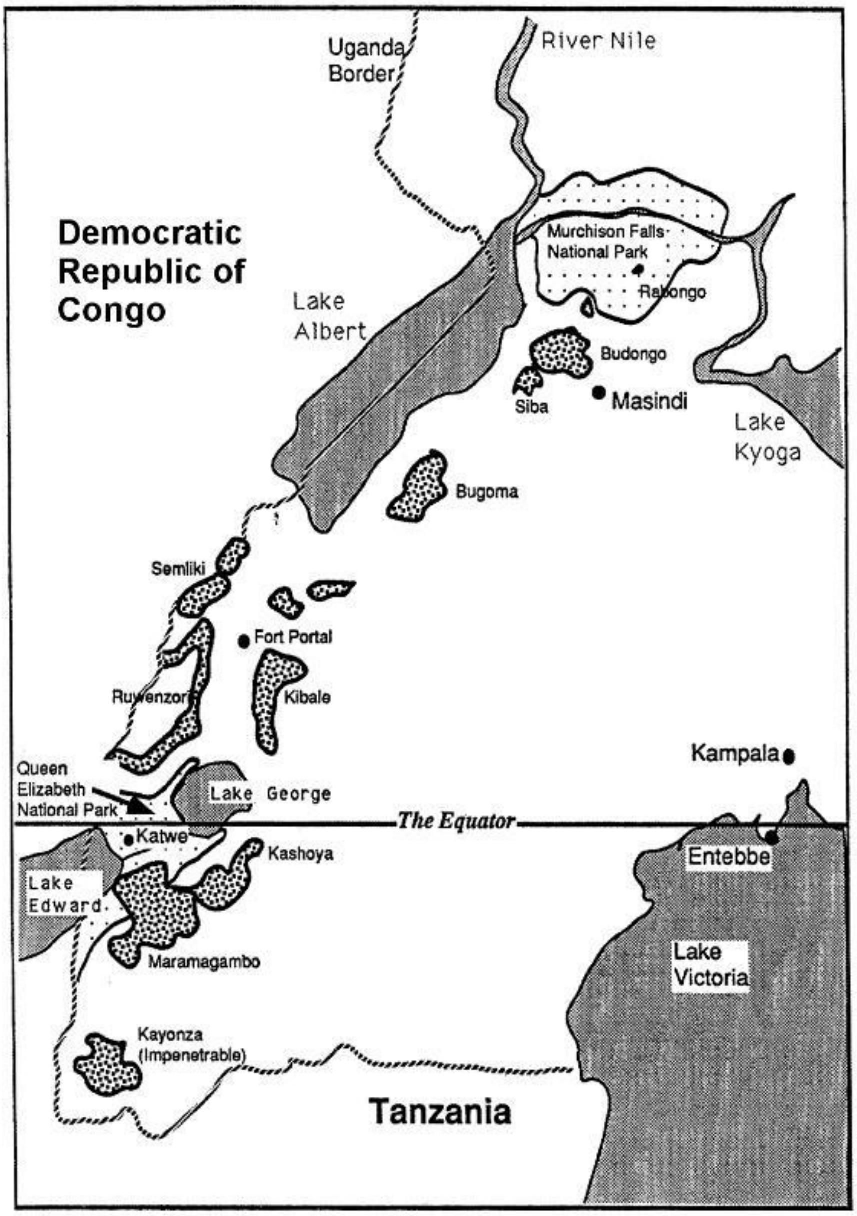


Figure 1: Map of western Uganda showing the location of Bugoma Forest and Budongo Forest in relation to each other (both encircled in red). Kibale Forest, another major site for research on chimpanzees, is also shown. Notably, Bugoma is geographically almost exactly in-between Budongo and Kibale (adapted from Paterson, 1991).

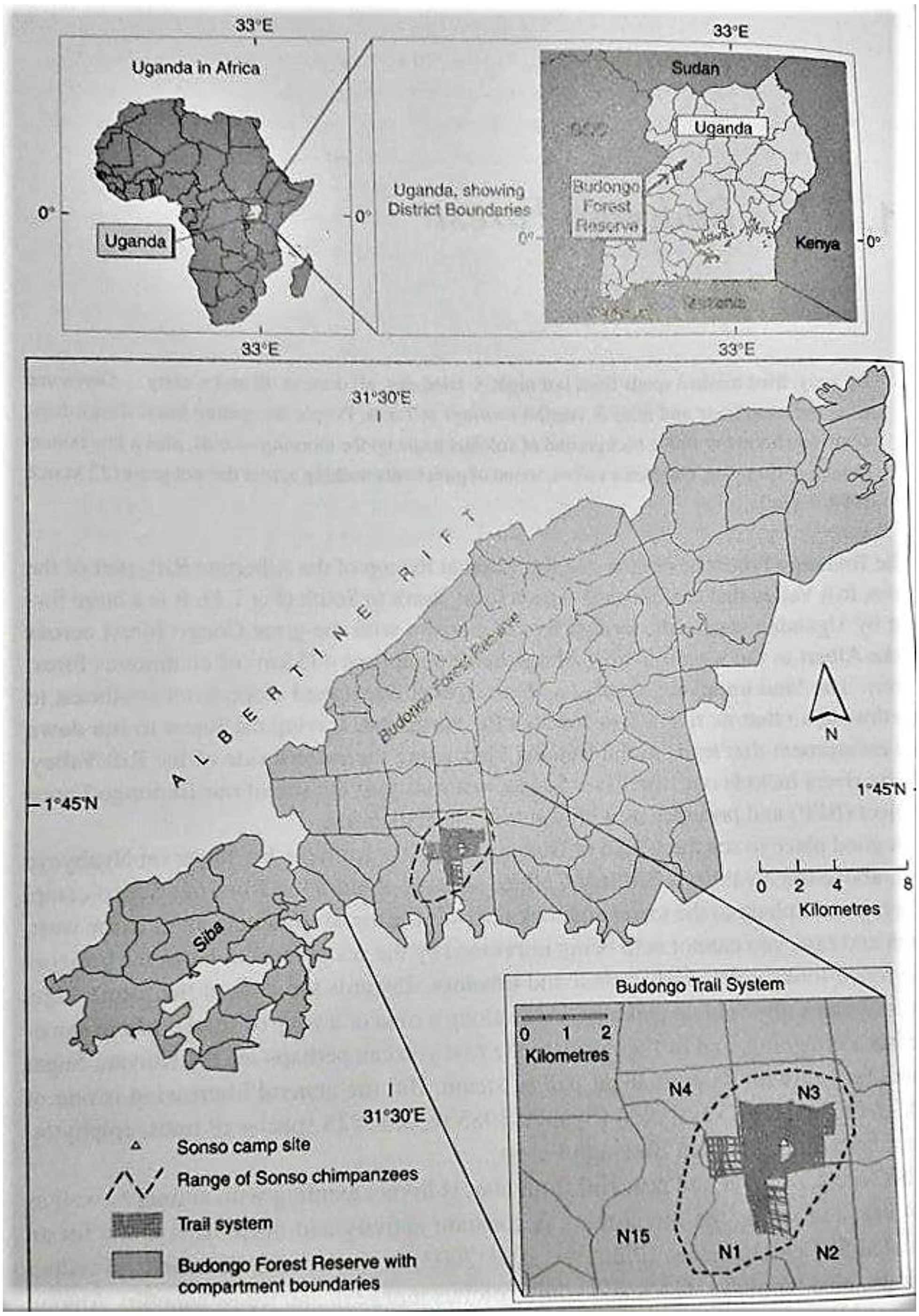


Figure 2: Map of the Budongo Forest. The figure on the top left depicts the location of Uganda in Africa, the top right figure illustrates where the Budongo Forest can be found in Uganda, and the bottom figure shows the outline of the forest and the relative location of the BFP research station and the range of Sonso chimpanzees. The Budongo trail system is shown in the bottom right corner (Reynolds, 2005).

Plumptre et al. (2003) estimated that 584 chimpanzees live in the forest alongside redtail monkeys, blue monkeys, black and white colobus monkeys, and forest baboons. Additionally, 226 bird species have been recorded (Plumptre et al., 2003). In Budongo Forest 725 species of trees, epiphytes, herbs, lianas, and shrubs are thought to be present (Synnott, 1985). Brasnett (1946) described Budongo to be 300-500 years old and suggested the occurrence of three successional stages in the Budongo Forest, namely Colonizing, Intermediate, and Climax. Plumtre (1996) showed that Budongo Forest exhibits a gradual change of tree species composition from the southwest to the northeast, with the southwest having more species associated with Colonizing and Mixed Forest and many Cynometra forests are present in the northeast. Notably, humans have played an enormous role in forest dynamics and the current species composition (Reynolds, 2005). During the British Protectorate four sawmills were established in Budongo (Synott 1972). Mahoganies were the main species cut, albeit Milicia excels and other timber trees were selectively logged as well (Plumptre, 1996). This and the use of arboricide on Cynometra alexandriiand other “weed” species caused the predominance of Cynometra forests to be replaced by Mixed Forest 40 years later (Plumptre, 1996).The overall result was the increase of a variety of fruiting trees, such as figs, which consequently benefited fruit eating animals including chimpanzees (Tweheyo, 2003). Notably, nowadays the Budongo Forest has greater densities of trees producing fleshy fruits and consequently fruit-eating primates in its logged and arboricide-treated forests than it does in its Nature Reserves (Reynolds, 2005). Some of the foods found in each of the four forest types are as follows: The Colonizing Forest contains many Broussonetia papyrifera and Maesopsis eminii, the Mixed Forest has the most food species including Celtis gomphophylla and Celtis mildbraediias well as many Ficus species, the Cynometra Forest is characterized by the climax species Cynometra alexandri, and the Swamp Forest provides the fruits of Pseudospondias microcarpa, the pith of Calamus deerata and the woody inside of the stems of Raphia farinifera (Reynolds, 2005).

Budongo Forest Project:

The project was founded by Prof. Vernon Reynolds in 1990 after he had first studied the chimpanzees of the Sonso community in Budongo in 1962 (Reynolds, 2005). Today, the institution is more commonly referred to as the Budongo Conservation Field Station (BCFS) and has achieved an international reputation of conducting excellent research and conservation in Uganda (BCFS, 2016).

Sonso community:

The Sonso community has been habituated since 1995, where the process of habitation took five years without the use of provisioning. This means that their natural foraging methods were not disrupted, albeit it made habituation more difficult (Reynolds, 2005). Since then data has been continuously collected, implying the availability of large data files on various aspects of their behaviour, ecology, and demography (Reynolds, 2005). Newton-Fisher (2003) estimated the home range of the Sonso community to be between 6.78 and 14.51 km2 and he estimated their density to be between 6.8 and 3.2 chimpanzees/km2. The calculations are based on 46 individuals that were present at that time and it is mildly higher than previous estimates (Reynolds, 2005). He attributed this high density to the area being particularly rich in chimpanzee foods and to comparatively low levels of timber exploitation taking place at that time (Newton-Fisher, 2003). The current Sonso community size is about 70 individuals (Gruber, person. comm).

Chimpanzees have been observed to eat the following kinds of plants: trees, shrubs, herbs, climbers, and epiphytes (Reynolds, 2005). The plant parts consumed include fruits, leaves, flowers, bark, seeds, stem/pith, gum, and wood, where ripe fruit and young leaves make up the majority of the diet (Reynolds, 2005). Young leaves have a high sugar and protein content and young leaves of many species are thus eaten by chimpanzees, including figs (Tweheyo and Lye, 2003). Khaya anthotheca

(“Budongo mahogany) provides bark and gum, albeit bark is also eaten from other species including Ficus exasperata and Cynometra alexandri (Reynolds, 2005).
Four independent studies have been conducted analysing the food preferences of Sonso chimpanzees. Plumptre and Reynolds (1994) recorded the species and plant parts eaten during a series of half-hour scans over a two year study period. Their results and the other three studies (Newton-Fisher, 1999; Fawcett, 2000; Tweheyo et al., 2004) show that the preferred foods are Broussonetia papyrifera (paper mulberry tree), Ficus spp. and Celtis mildbraedii. Notably, these results are likely to be very specific to the Sonso community, considering that the paper mulberry tree was introduced in that particular area in the 1950s around the Sonso Sawmill, implying that even other communities within Budongo are likely to exhibit different dietary preferences (Reynolds, 2005). Ficus sur is the most frequently eaten fig species and its fruits non-seasonally, where its great abundance implies that in most months a fruiting tree can be found (Reynolds, 2005). In contrast, the paper mulberry tree has two distinct fruiting seasons occurring in the two dry seasons (Fawcett, 2000).
Reynolds et al. (1998) found that Sonso chimpanzees preferred to eat foods with a higher sugar content over fruits with a lower sugar content and that they chose foods irrespective of the levels of condensed tannins. The latter is surprising and may suggest that chimpanzees have a much higher tolerance of condensed tannins compared to humans (Reynolds et al., 1998).
Food availability is dependent on its abundance and dispersion. A list of the chimpanzee food species recorded in the Sonso community between 1990- 2004 can be found in the Appendix. Important seasonally fruiting trees in Budongo include Cynometra alexandri, Celtis spp., Pseudospondias microcarpa and Maesopsis eminii (Reynolds, 2005). Plumptre et al. (1997) examined the diet of Sonso chimpanzees based on transect walks and phonological data over two years and showed that severe fluctuations in food availability occurred. In Kibale forest, Uganda, Chapman et al. (1994) showed that the diameter at breast height (DBH) is a good predictor of a tree’s food abundance. This was subsequently confirmed for Budongo (Newton-Fisher et al., 2000). Further studies on food availability were conducted by Newton-Fisher (1999) and Reynolds (2005). The former was based on a 15-month study during which the time spent feeding and the food item eaten were recorded. The latter involved a study of the number of chimpanzee food trees in blocks near the trail system around Sonso camp regardless of phenological state. An estimate of potential food availability was obtained by multiplying the number of stems of each species by their DBH.
Sonso chimpanzees rarely feed on Cubitermes termites and they break open the mounds using hands or teeth. Notably, they have never been observed to use sticks or other tools for termite or ant eating (Reynolds, 2005; Gruber, person. comm.), whereas this behaviour is common in other areas including Bossou, Gombe, Tai and Assirik (McGrew, 1992). Leafsponging, which involves drinking water and using a crumpled leaf to soak it up and squeeze it into the mouth, is the commonest form of tool use in Sonso (Quiatt and Kiwede, 1994). Other examples include the use of sticks as an invitation to play and the manipulation of branches and leaves for nest-building (Reynolds, 2005). A new technique, moss sponging to access mineral-rich suspensions from a clay pit, has been learned by some Sonso chimpanzees very recently (Hobaiter et al., 2014). Compared to other communities studied the Sonso chimpanzees show less technological sophistication (Reynolds, 2005; Gruber person. comm.). Reynolds (2005) suggests that this is due to their habitat being rich

in preferred foods (ripe fruits) and the apparent lack of times of severe food-shortage. Furthermore, the fact that Western chimpanzees use more sophisticated stone tools than Eastern chimpanzees and that Eastern chimpanzees in the south appear to be more skilled in termite fishing than in the north suggests that tool use may be seen as a cultural factor that has not reached Budongo (Reynolds, 2005).

Bugoma Forest:
Bugoma Forest is separated from Budongo by 40km, thus representing the closest forest to Budongo (Figure 2) (Reynolds, 2005). Other western forests beyond Bugoma include Kibale, Ruwenzori, Maramagambo, Kasyoka-Kitomi, Semliki, Kalinzu, Itwara, and Bwindi (Reynolds, 2005). These forests were once part of a continuous forest, however, cooler and drier climatic conditions caused the division of the forests seen today. Hence, ample possibilities for migration were once established, but the movement of chimpanzees between forests is probably prevented today (Gruber, person. comm.). A high degree of relatedness between all the chimpanzees of western Uganda is suggested by genetic data (Wrangham and Goldberg, 1997).
Much less is known about the history and forest composition in Bugoma compared to Budongo. A biodiversity survey conducted by Plumptre et al. (2010) yielded the following results: the Uganda mangabey is relatively common, elephants can be found in the area, and density of chimpanzees is 1.24 km-2(both group and individual density). This is lower than the density recorded in 1999 by Plumptre et al. where group density was 1.87km-2 and individual density 1.90km-2. However, the current chimpanzee density is unknown and since the Kisindi community in Bugoma is only now in the process of becoming habituated, practically no research has been done on this community.

Kisindi community:
Their dietary preferences and their degree of tool use is unknown, albeit Gruber suggests that they do use tools based on the ecology of Bugoma being more similar to Kibale (where tool use has been recorded) than to Budongo (Gruber, person. comm.). Additionally, several riverine communities in the vicinity, e.g. Bulindi or Kasokwa, are believed or have been documented to use sticks during foraging (McLennan, 2011), strengthening the likelihood that the Bugoma chimpanzees may also use these tools, in addition to near universal behaviour among chimpanzees such as leaf-sponging.

Scientific rationale and aims:

Given the great influence food availability can have on the ecology and evolution of chimpanzees this study aimed to ascertain the abundance and diversity of chimpanzee foods in Bugoma Forest, where the Kisindi community was studied. This was conducted in comparison to the chimpanzee food availability in Budongo Forest, where the Sonso community was investigated. Furthermore, another aim of this study is to determine the present food preferences of the Sonso community through observations. Whilst detailed studies analysing this for the Sonso community have previously been conducted, the last one was 17 years ago. Notably, the forest is under constant change due to natural and anthropogenic factors and analysing the feeding preferences of chimpanzees by conducting feeding scans was therefore justified.

Notably, elaborate studies analysing the forest dynamics and composition of Budongo Forest and their impact on the feeding behaviour of Sonso chimpanzees have shown the habitat of the Sonso community to be remarkably rich in chimpanzee foods, particularly ripe fruit. This may at least partly explain the very limited tool use of the chimpanzees of Budongo Forest. The tree species composition in Bugoma Forest has not been changed by humans in the same manner as Budongo Forest has, were silvicultural work has led to an increase in fruiting trees. Thus, chimpanzee food availability was expected to be lower in Bugoma. This, and the fact that Bugoma is closer to Kibale Forest and other Eastern chimpanzee communities which facilitates greater cultural transmission, suggests that Kisindi chimpanzees may use tools more readily than the chimpanzees of Budongo. Hence this study aimed to determine whether there is evidence of tool use in the Kisindi community.

Faecal samples were used to gain an insight into the diet of the Kisindi chimpanzees, with a focus on identifying seeds and nuts. An estimate of how reliable faecal samples are as an indicator of chimpanzee diet was needed; as the Kisindi chimpanzees are not fully habituated (and so observational data could not be reliably collected) the study relied on observational data and faecal samples from the Sonso chimpanzee community to determine the reliability of faecal sample analysis as an indicator of chimpanzee diet.

Methods:

For each forest, 12 500-metre-long, 6-m-wide transects were conducted. The location of the transects in Budongo were determined based on a previous study (de Moor, unpublished data) where the transects were chosen in consideration of chimpanzee range data and forest composition. Here, the transects were shifted 50m north for N-S transects, and east for E-W transects, so that all transects ran through “forest blocks” and not followed the trails of the pre-existing grid system (Figure 3). The arrangement of the transects to each other was transposed to Bugoma, where the exact location was chosen based on chimpanzee range data from 2016 (Figure 4). For N-S transects, the transect was always started in the north, for E-W transects, the transect was always started in the east. Additionally, every 50m a circle with a radius of 7m was constructed and marked using a GPS. Within the circle and along the transect all trees (DBH>10cm) were identified, determined if they are a chimpanzee-feeding tree, their circumference measured, and their phenological stage noted. Additionally, the presence, height and activity of any termite or ant mounds was noted, and the tool availability, i.e. the number of vines, twigs and terrestrial herbaceous vegetation within the north-facing quarter of a 5-m-radius circle, determined.

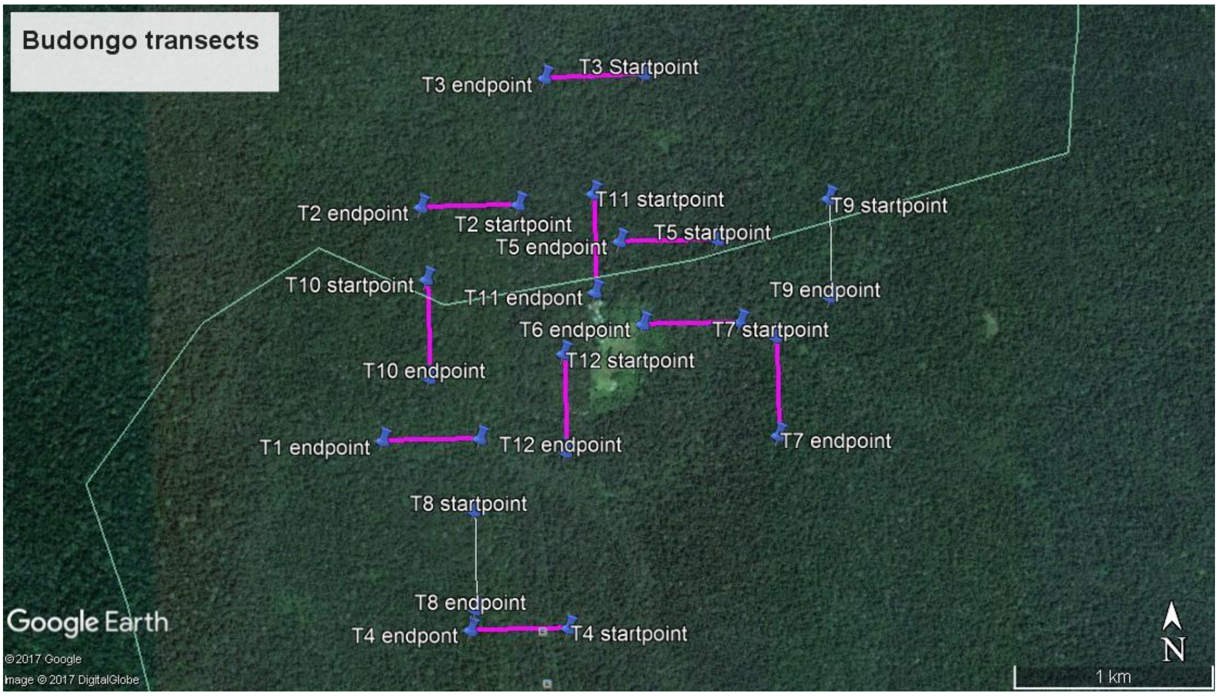


Figure 3: The arrangement of the transects in Budongo.

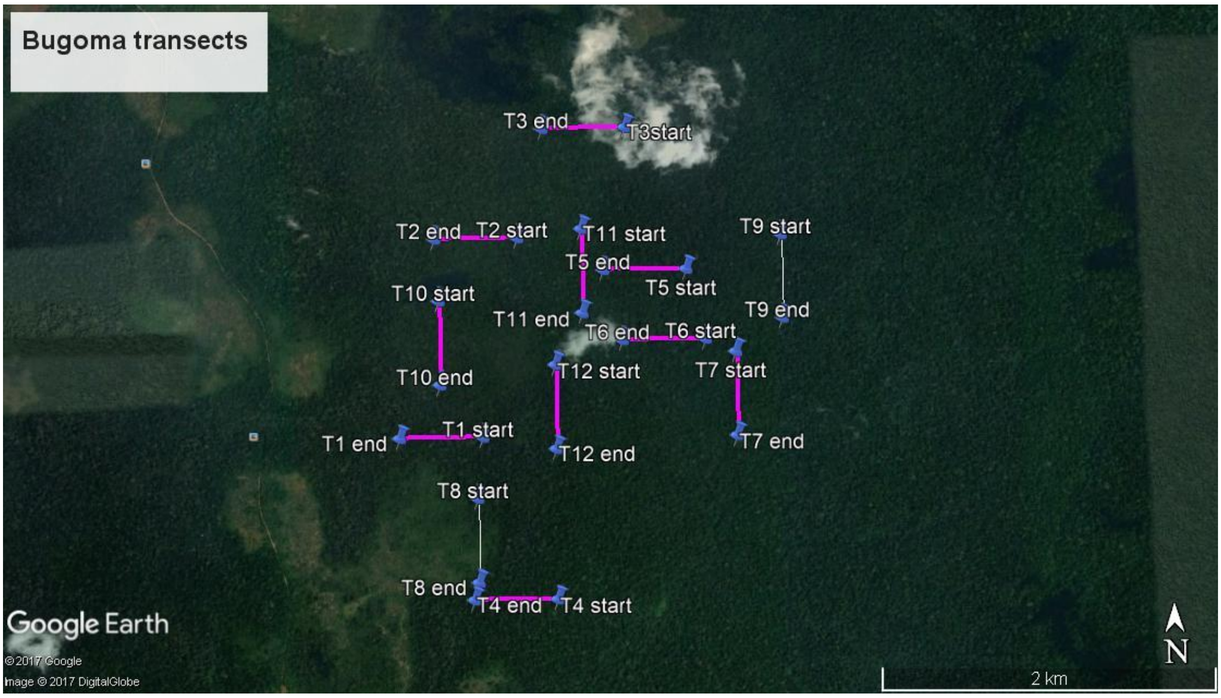


Figure 4: The arrangement of the transects in Bugoma.

Transect number	GPS starting location (UTM)	GPS finishing location (UTM)
T1	337507 190148	337007 190148
T2	337733 191332	337233 191332
T3	338389 191983	337889 191983
T4	337944 189182	337444 189182
T5	338746 191134	338246 191134
T6	338856 190714	338356 190714
T7	339036 190636	339036 190136
T8	337472 189785	337472 189285
T9	339319 191332	339319 190832
T10	337255 190963	337255 190463
T11	338116 191380	338116 190880
T12	337948 190573	337948 190073

Table 1: The GPS locations of the transects in Budongo.

Transect number	GPS starting location (UTM)	GPS finishing location (UTM)
T1	278357 145091	277857 145091
T2	278583 146275	278083 146275
T3	279239 146926	278739 146926
T4	278794 144125	278294 144125
T5	279596 146077	279096 146077
T6	279706 145657	279206 145657
T7	279886 145579	279886 145079
T8	278322 144728	278322 144228
T9	280169 146275	280169 145775
T10	278105 145906	278105 145406
T11	278966 146323	278966 145823
T12	278798 145516	278798 145016

Table 2: The GPS locations of the transects in Bugoma.

Feeding observations were conducted from 7 am to 5 pm to investigate what tree species and on what part of the tree the chimpanzees were feeding on. Binoculars were used when needed. A focal chimpanzee was followed for two or three consecutive days and the species of the feeding tree, the food item, and the duration and time of feeding was noted. The same data was collected for all other individuals present, giving a total number and identity of feeding individuals. Thus, chimpanzee diet was measured in terms of time spent feeding.

In Budongo, faecal samples were collected in zip lock bags when an individual was seen to defecate. The date, time, name of the individual, name of the focal individual, completeness (i.e. whether >95% of the sample were collected), was noted. In Bugoma, individuals were not seen to defecate, but faeces were collected when following chimpanzee parties in the forest, or when they were encountered on the path where their age was estimated (where only samples <5 days were collected). Following Plumptre (1997) faecal samples were weighted, washed, sieved, and all the seeds within identified and counted. Very abundant seeds, such as figs, were counted in a sector of the sieve and then multiplied by the number of possible sectors in the sieve. Furthermore, the areas of bark and leaves were recorded by counting the number of around 1 cm^2 pieces in the faecal sample. Additionally, the presence of flesh and bones, was noted.

Six camera traps were constructed at “strategic points” in Bugoma Forest and videos were automatically taken when the sensor was triggered. This included points overlooking termite moulds, ant nests, wasp nests, bee hives, nuts with hard shells, and areas where the chimpanzees are known to spend a lot of time.

Preliminary results (data collected)

All 24 transects were successfully completed and >90% of the trees were identified down to species. In Budongo, the ratio of feeding trees to non-feeding trees was 0.602059597, whereas it was 0.485996479 in Bugoma. This is in line with previous research which found a remarkably high-density of chimpanzee feeding trees in Budongo due to anthropogenic activities. Statistical analysis will be conducted in the next few months to ascertain whether the difference is significant and whether the forests differ in the amount of potentially available fleshy fruit which chimpanzees feed on.

Overall, there were fifteen focal-chimpanzee follows with seven males and six females (two individuals were followed twice), totalling 38 days of feeding observations. Twice the focal individual had to be changed as it was not possible to locate it on a subsequent day.

In Budongo, 106 faecal samples were collected, whereas 46 were collected in Bugoma. Over 90% of the seeds were identified, albeit not always down to species.

On an informal level, the observed feeding preferences of the Sonso chimpanzees are similar to previous dietary studies (Reynolds, 2005), where fig trees of various species and the paper mulberry tree represented a major part of the diet. The diet of the Sonso chimpanzees changed throughout the months in accordance with the phenological stage of the individual tree species. Notably, the food items and tree species differed in their representation in the faecal samples, for example fig seeds were always found in high abundance when the chimpanzees fed on it, whereas leaves of any tree species were almost never recorded in the faecal samples. Whilst a formal statistical analysis is absolutely essential to draw any conclusions, it seemed that there were less seeds of fewer species in the faecal samples from the chimpanzees of Bugoma.

Notably, this study forms the basis for Iris Berger’s Bachelor’s thesis which she will finalise in May 2018. Hence, all analyses will be conducted, and the results will be interpreted, in the next few months.

Acknowledgements

I am immensely grateful for the generous financial support I received from the Davis Expedition Fund and the National Geographic Society. Many thanks to Dr. Matt Bell, Dr. Thibaud Gruber, Dr. Catherine Hobaiter, and Dr. Matt McLennan for their academic support.