Conservation Status and Ecology of the Nigeria – Cameroon Chimpanzee in Kom – Wum Forest Reserve, North – West Region, Cameroon

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Summary

Global biodiversity is decreasing rapidly due to human modification of natural habitats, and large terrestrial mammals in the order Primates (engl. primates) are strongly affected. Chimpanzee (*Pan troglodytes*) populations and suitable habitats for this species are declining across Africa due to poaching, habitat degradation or loss, and diseases. The reduction in the population of the Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti*) is projected to exceed 50% between 1985 and 2060, but knowledge of the species abundance and ecology is still lacking for major chimpanzee conservation sites in the North – West Region of Cameroon. This thesis aimed to better understand the conservation status, habitat requirements, and food utilization of the Nigeria – Cameroon chimpanzee in Kom – Wum Forest Reserve with the objectives to 1) provide population estimates and assess threats (Chapter 3), 2) investigate environmental and human factors affecting nest site selection and nesting behaviour (Chapter 4), 3) identify suitable habitats (Chapter 5), 4) determine the common feeding habits (Chapter 6) and 5) document the tools used for food acquisition (Chapter 7).

Research was conducted by surveying line transects and recces monthly during two seasons: wet (May–September 2018) and dry (November 2019–March 2020). The population size was determined using 1) direct observations, 2) camera trapping, 3) marked nest counts, 4) standing crop nest counts, and 5) distance sampling methods along line transects. Threats to chimpanzees were assessed by georeferencing signs of chimpanzees and human activity along line transects. Nesting behaviour was investigated by recording the characteristics of nesting trees along line transects and recces. The effect of environmental and human factors on chimpanzee nesting was investigated using the Euclidean distance modeling in ArcGIS and regression analyses. Suitable habitats were identified by relating chimpanzee occurrence signs to local environmental variables related to relief, vegetation, and human impact using the Maximum Entropy species distribution model (MaxEnt). Feeding habits were investigated through direct examination of chimpanzee faeces, and tool use was documented through observation and measurement of tools in situ. Chimpanzee population estimates ranged from 10 (direct observation) to 83 (distance sampling) individuals per 92 km^2 area depending on method and were among the lowest compared to other populations across its distribution range. The mean encounter rate of chimpanzee activity signs was significantly higher in mature forests (2.3 ± SD 3.38 signs km^{-1}) than in secondary forests (0.3± SD 0.80 signs km^{-1}) and above 1000 m elevation (4.0 signs km^{-1}) than below 1000 m (1.0 signs km^{-1}). The mean encounter rate of human activity signs was significantly higher in secondary (8.0 ± SD 13.55 signs km^{-1}) than in mature forests (0.9 ± SD 2.14 signs km^{-1}). Poaching (n= 142 signs) was the main threat to chimpanzee (52% explained variation, N = 271), and the

occurrence of chimpanzee signs decreased significantly with increasing human activities. Chimpanzees preferentially selected tall mature forest trees at higher elevations with slopes for nesting, and they avoided areas close to villages and bare lands. However, only 8% of the study area represent suitable chimpanzee habitats, and a high proportion of these habitats are located at high elevations in unprotected areas adjacent to the reserve. Fruits dominated chimpanzees diet (98%), but they also consumed leaves and fruit pith (2%), in particular during the dry season. Indirect evidence also revealed the consumption of driver ants (genus *Dorylus*) by chimpanzees using tools. These tools are on average the longest recorded insect dipping tools for chimpanzees so far (129.6 cm ± SD 38.7 cm). Seasonality significantly affected the sizes of tools used by chimpanzees for driver ant predation. They preferentially used thicker (10.7 mm ± SD 3.5 mm) and shorter (106.7 cm ± SD 55.9 cm) tools for driver ant predation in the wet season, whereas longer (138.8 cm ± SD 25.8 cm) and thinner tools were used during the dry season (8.5 mm ± SD 3.8 mm).

The results in this thesis emphasize the need to protect the Nigeria – Cameroon chimpanzee with highest priority. Protected area managers should focus on reducing poaching, forest conversion to farmland, and the sprawl of settlements into conservation areas to protect the remaining chimpanzee population and suitable habitats in the reserve and surrounding unprotected forest. Mature forests at high elevations are crucial for chimpanzee conservation and should therefore be protected with high priority. This thesis has enhanced our understanding of the conservation status and ecology of chimpanzees in general and closed the knowledge gap on what little was known about the abundance, habitat requirements, and food utilization of the Nigeria – Cameroon chimpanzees in particular. These results can inform future conservation decisions for the protection of the Nigeria – Cameroon chimpanzee and the remaining suitable habitats.

Keywords: Chimpanzee abundance, feeding ecology, human disturbance, Kom – Wum Forest Reserve, line transect distance sampling, nesting patterns, Nigeria – Cameroon chimpanzee, suitable habitats, tool use behaviour.

Zusammenfassung

Die weltweite biologische Vielfalt nimmt aufgrund der Veränderung natürlicher Lebensräume durch den Menschen rapide ab, und große Landsäugetiere aus der Ordnung der Primaten sind davon stark betroffen. Die Populationen von Schimpansen (*Pan troglodytes*) und geeignete Lebensräume für diese Art gehen in ganz Afrika aufgrund von Wilderei, Verschlechterung oder Verlust von Lebensräumen und Krankheiten zurück. Der nigerianisch-kamerunische Schimpanse wird als gefährdet eingestuft, da zwischen 1985 und 2060 ein Rückgang seiner Populationsgröße um mehr als 50 % prognostiziert wird. Jedoch mangelt es immer noch an Kenntnissen über den Artenreichtum und die Ökologie für wichtige Schimpansenschutzgebiete in der Nordwestregion Kameruns. Diese Dissertation zielte darauf ab, den Erhaltungszustand, die Lebensraumanforderungen und die Nahrungsnutzung der Schimpansen in Nigeria und Kamerun im Kom-Wum-Waldreservat besser zu verstehen, und zwar mit den Zielen, 1) Populationsschätzungen zu erstellen und Bedrohungen zu bewerten (Kapitel 3), 2) Umwelt- und menschliche Faktoren zu untersuchen, die sich auf Wahl des Netzplatzes und Nestverhalten auswirken (Kapitel 4), 3) geeignete Lebensräume zu identifizieren (Kapitel 5), 4) die Ernährungsgewohnheiten zu bestimmen (Kapitel 6) und 5) die Nutzung von Werkzeugen zur Nahrungsbeschaffung dokumentieren (Kapitel 7).

Die Forschung wurde durch monatliche Erhebungen von Linientransekten und Aufklärungsspaziergänge während zweier Jahreszeiten durchgeführt: feucht (Mai-September 2018) und trocken (November 2019-März 2020). Die Populationsgröße wurde mithilfe von 1) direkten Beobachtungen, 2) Kamerafallen, 3) Zählungen von markierten Nestern, 4) Zählungen von Nestern an stehenden Pflanzen und 5) Entfernungsstichproben entlang von Linientransekten ermittelt. Die Bedrohung der Schimpansen wurde durch Georeferenzierung Zeichen von Schimpansen und menschlichen Aktivitäten entlang der Transektlinien ermittelt. Das Nistverhalten wurde durch die Aufzeichnung der Merkmale von Nistbäumen entlang der Transektlinien und der Aufklärungsspaziergänge untersucht. Die Auswirkung von Umwelt- und menschlichen Faktoren auf das Nisten der Schimpansen wurde mit Hilfe der Modellierungstechnik der euklidischen Distanz in ArcGIS und Regressionsanalysen untersucht. Geeignete Lebensräume wurden identifiziert, indem die während der Linienbegehungen und Erkundungen aufgezeichneten Schimpansenvorkommen zeichen mit lokalen Umweltvariablen in Bezug auf Relief, Vegetation und menschliche Einflüsse in Beziehung gesetzt wurden, wobei das Maximum-Entropie-Artenverteilungsmodell (MaxEnt) verwendet wurde.

Die Ernährungsgewohnheiten wurden durch direkte Untersuchung von Schimpansenkot untersucht, und die Verwendung von Werkzeugen wurde durch Beobachtung von Werkzeugen in situ dokumentiert.

Die Schätzungen der Schimpansen Population lagen je nach Methode zwischen 10 (direkte Beobachtung) und 83 (Entfernungsprobenahme) Individuen pro 96 km² Fläche und gehörten im Vergleich zu anderen Populationen im gesamten Verbreitungsgebiet zu den niedrigsten. Die mittlere Begegnungsrate von Zeichen der Schimpansenaktivität war in reifen Wäldern (2.3 ± SD 3.38 Zeichen km^{-1}) signifikant höher als in Sekundärwäldern (0.3 ± SD 0.80 Zeichen km^{-1}) und über 1000 m Höhe (4.0 Zeichen km^{-1}) als unter 1000 m (1.0 Zeichen km^{-1}). Die mittlere Begegnungsrate menschlicher Aktivitätszeichen in Sekundärwäldern (8.0 ± SD 13.55 Zeichen km^{-1}) signifikant höher als in Wäldern ausgewachsenen (0.9 ± SD 2.14 Zeichen km^{-1}). Wilderei (N = 142 Zeichen) war die größte Bedrohung für Schimpansen (52 % erklärte Variation, N = 271), und das Auftreten von Schimpansenzeichen nahm mit zunehmenden menschlichen Aktivitäten deutlich ab. Die Schimpansen wählten zum Nisten bevorzugt hohe, ausgewachsenen Waldbäume in höheren Lagen mit Abhängen und mieden Gebiete in der Nähe von Dörfern und kahlem Land. Geeignete Lebensräume für Schimpansen machen jedoch nur 8 % der untersuchten Fläche aus, und ein großer Teil dieser Lebensräume befindet sich in hohen Lagen in ungeschützten Gebieten, die an das Reservat angrenzen. Früchte dominierten die Ernährung der Schimpansen (98 %), aber sie verzehrten auch Blätter und Mark (2 %), vor allem während der Trockenzeit. Indirekte Beweise zeigten auch den Verzehr von Treiberameisen durch Schimpansen, welche Werkzeuge benutzen. Bei diesen Werkzeugen handelt es sich im Durchschnitt um die längsten bisher nachgewiesenen Insekten-Tauchwerkzeuge der Schimpansen (129.6 cm ± SD 38.7 cm). Die Jahreszeit hatte einen erheblichen Einfluss auf die Größe des Werkzeugs, das die Schimpansen bei der Jagd auf Treiberameisen verwendeten. In der Regenzeit verwendeten sie bevorzugt dickere (10.7 mm ± SD 3.5 mm), und kürzere Werkzeuge (106.7 cm ± SD 55.9 cm), während in der Trockenzeit längere (138.8 cm ± SD 25.8 cm) und dünnere Werkzeuge zum Einsatz kamen (8.5 mm ± SD 3.8 mm). Die Schutzgebietsverwalter sollten sich darauf konzentrieren, die Wilderei, die Umwandlung von Wald in Ackerland und die Besiedlung einzudämmen, um die verbleibende Schimpansenpopulation und geeignete Lebensräume im Reservat und im umliegenden ungeschützten Wald zu schützen. Ausgewachsenen Wälder in hohen Lagen sind für die Erhaltung der Schimpansen von entscheidender Bedeutung und sollten daher mit hoher Priorität geschützt werden. Diese Dissertation hat unser Verständnis des Erhaltungszustands und der Ökologie der Schimpansen im Allgemeinen verbessert und die Wissenslücke geschlossen, die über die Häufigkeit, die Lebensraumanforderungen und die Nahrungsnutzung der Nigeria-Kamerun-Schimpansen im Besonderen besteht. Diese Ergebnisse

können Entscheidungen zum Schutz des Nigeria-Kamerun-Schimpansen und seiner verbleibenden geeigneten Lebensräume verbessern.

Schlüsselwörter: Schimpansenvorkommen, Fütterungsökologie, menschliche Störungen, Kom-Wum Waldreservat, Linien-Transekt-Abstandsproben, Nistmuster, Nigeria-Kamerun-Schimpanse, geeignete Lebensräume, Werkzeugnutzung.

List of abbreviations

AUC	Area Under the Curve
AZA	Association of Zoos & Aquariums
Congo R	Republic of Congo
CT	Camera trapping
DO	Direct observation
DFR	Dja Faunal Reserve
DR Congo	Democratic Republic of Congo
DBH	Diameter at Breast Height
EN	Endangered
FR	Forest Reserve
GGNP	Gashaka-Gumti National Park,
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
KWFR	Kom – Wum Forest Reserve
LC	Least Concern
MaxEnt	Maximum Entropy
MNC	Mark Nest Count
NDVI	Normalized Difference Vegetation Index
NNFR	Ngel Nyaki Forest Reserve
NUL	Northern Uele Landscape
NP	National Park
PNDP	National Participatory Development Program
RAI	Relative Abundance Index
ROC	Receiver Operating Characteristic
SE	Seringbara
SDMs	Species Distribution Models
SD	Standard Deviation
SCNC	Standing Crop Nest Count
Spathic	Spatial Thinning
VIF	Variance Inflation Factor

Chapter 1: General Introduction

1.1 The effects of human activity on primates and habitats

Global biodiversity is decreasing rapidly due to human modification of natural habitats, and projections indicate that we are in the midst of a sixth mass extinction (Barnosky *et al.,* 2011; Pimm *et al.,* 2014). Forest conversion into agricultural fields, urban development, pasture lands, and the illegal harvesting of timber and non-timber forest products are the primary causes of this decline (Newbold *et al.,* 2015; Di Marco *et al.,* 2018). Terrestrial vertebrates are the most affected species, with more than half of their distribution range exposed to human activities (O'Bryan *et al.,* 2020). Large mammals and birds are more vulnerable to human activities than smaller mammals (Ripple, 2016; Cardillo *et al.,* 2005, Fritz, 2009). The mammalian order Primates (engl. primates) is strongly affected by human activities since they depend on tropical forest ecosystems for their survival (Isaac & Cowlishaw, 2004). Tropical forest conversion into agroecosystems and road development cause fragmentation, loss, and degradation of primate habitats (Estrada & Coates-Estrada, 1996; Estrada *et al.,* 2017). The effects of forest fragmentation include decreasing patch sizes, increased edge effects and patch isolation of primate habitats (Fahrig, 2003; Arroyo-Rodríguez *et al.,* 2013; Arroyo-Rodríguez & Dias, 2010). The associated effects of forest loss and degradation are changes in the distribution, the decline in numbers, and local extinction (Chapman *et al.,* 2006; Mittermeier *et al.,* 2009). About 75% of the world's primate species have declined due to habitat loss and degradation, and 60% of those are endangered (Estrada *et al.,* 2017, 2019). Like other primate species, great apes, including, chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), Eastern gorillas (*Gorilla beringei*), Western gorillas (*Gorilla gorilla*), Sumatran orangutans (*Pongo abelii*), and Bornean orangutans (*Pongo pygmaeus*) are endangered, and their populations and habitats are declining (Strindberg *et al.,* 2018; Voigt *et al.,* 2018; Wich *et al.,*2016; Oates, 1996).

Industrial and small-scale agriculture, resource extraction like mining and logging, infrastructure development, fire, several types of poaching (bushmeat, conflict, and live capture), and diseases like the Ebola virus are the main threats to great apes (Fruth *et al.,* 2016; Maisels *et al.,* 2016; Nowak *et al.,* 2019; Plumptre *et al.,* 2016; Singleton *et al.,* 2017; Strindberg *et al.,* 2018; Wich *et al.,* 2016; Walsh *et al.,* 2003). Most African great apes live outside protected areas, and a large percentage of their habitat coincides with areas suitable for oil palm plantations (Strindberg *et al.,* 2018; Wich *et al.,* 2014). Forest conversion to farmlands and illegal logging have reduced the availability of their habitats and negatively affected their densities (Morgan *et al.,* 2018; Kormos *et al.,* 2003). The suitable environmental conditions required for their survival have declined in the past 20 years (Junker *et al.,* 2012). Additionally, African great apes are illegally hunted for meat, their infants are occasionally kept as pets, and some are trafficked (Hicks *et al.,* 2010; Fruth *et al.,* 2016; Maisels *et al.,* 2016). Determining the population status of great apes is essential in measuring the impacts of a specific threat and the effectiveness of conservation strategies (Kühl, 2008).

1.2 Methods for estimating the density of great apes

Primatologists use a variety of methods to evaluate their status. Each method has advantages and disadvantages and can be used in specific situations (Vink et *al.,* 2020). Several techniques have been used to estimate ape abundance, including distance sampling (Buckland *et al.,* 1993), reconnaissance method (Walsh & White, 1999; White & Edwards, 2000), and camera trapping (Head *et al.,* 2013). Distance sampling is a widely used set of related methods for estimating the density and numbers of biological populations (Buckland *et al.*, 2001). There are several distance sampling techniques including the line transect, standing crop nest count (SCNC) and mark nest count (MNC). The line transect method is the most common distance sampling method used for the survey of large mammals where the observer conducts a consistent survey along a sequence of straight lines to count animals or groups of animals (Buckland *et al.*, 2001). The line-transect technique makes it easy to estimate animal densities through direct observations or indirect methods that involve counting signs of their presence like dung piles and ape nests (Mathot & Doucet, 2005; Plumptre & Cox, 2006). Ape nests are usually used as an indirect indicator of their presence because they are difficult to find in the wild (Basabose & Yamagiwa, 2002, Morgan *et al.,* 2006). Nest counts along line transects have been successfully used to derive relative estimates of population densities of chimpanzees which can be compared between locations, subspecies population estimates, or over time (Blom *et al.,* 2001). An evaluation and comparison of the two most common nest count approaches (standing crop nest counts and marked nest counts) with known chimpanzee population sizes documented the suitability of these methods to estimate the density of chimpanzees (Kouakou *et al.*, 2009). The SCNC is one of the most commonly used nest count techniques that consist of measuring the perpendicular distance of ape nests to the line transect to estimate chimpanzee densities (Kouakou *et al.,* 2009). This approach requires just one passage on a line transect. Estimating chimpanzee abundance using the SCNC requires calculating the site-specific nest production and decay rates (Kühl *et al.,* 2008). This is usually problematic because it requires studying habituated chimpanzee populations for a long time and accounting for spatial and spatial-temporal variation in decay rates. For this reason, researchers usually adopt the nest production rate from other studies, which often results in unreliable abundance estimates (Plumptre, 2000). The MNC method was proposed to overcome the problems associated with the estimation of nest decay studies (Hashimoto, 1995; Plumptre & Reynolds, 1996). In the MNC method, several visits are made to the line transect, and only the perpendicular distance of fresh nests to the line transect are used to estimate ape densities (Hashimoto, 1995; Plumptre & Reynolds, 1996). Although nest counts along transects have been effectively used to monitor the population status of great apes (Buckland *et al.,* 2001), they can be problematic in mountainous terrains where transects cannot be cut (White & Edwards, 2000). In such cases, other methods like reconnaissance (recce) surveys (Walsh & White, 1999) and camera trapping (Tobler *et al.,* 2008) are used. The recce method involves following a path of least resistance (e.g., human trails) through an area in a predetermined bearing and avoiding dense vegetation (Walsh & White, 1999). Camera trapping is using remote cameras to take photographs and videos of passing

animals or other objects that trigger them (Rovero & De Luca, 2007; Boitani, 2016). These wildlife cameras have been used to produce checklists of local fauna, population sizes, community composition, and the distribution of medium to large bodied mammals (Rovero & De Luca, 2007, Rovero *et al.,* 2017).

1.3 Species distribution models

Determining the suitable environmental conditions for species using Species Distribution Models (SDM) is vital for developing future conservation management plans (Guisan & Thuiller, 2005). Several SDM's like MaxEnt (Phillips *et al.,* 2006), Wallace (Kass *et al.,* 2018), GARP (Stockwell, 1999), and BIOMOD (Thuiller, 2003) have been used to predict the effects of human activities on patterns of biodiversity at different spatial levels (Guisan & Thuiller, 2005). MaxEnt is one of the most frequently used SDM's and has a generally high level of accuracy in predicting the distribution of species (Phillips *et al.,* 2006). MaxEnt uses only presence data of a species and produces accurate predictions even with an incomplete dataset and small sample size (Phillips *et al.,* 2006). It uses environmental data from the whole study area rather than only from parts of the area (Phillips & Elith, 2013). MaxEnt uses presence data plus background data (pseudo-absence data) from the study region because true absences are very difficult to obtain, especially for mobile species, and require higher levels of sampling effort to ensure their reliability compared with presence data (Mackenzie & Royle, 2005). MaxEnt has been used to predict the suitable environmental conditions for African great apes (Junker *et al.,* 2012), including gorillas at Mawambi Hills in Cameroon (Etiendem *et al.,* 2013), gorillas and chimpanzees at Dja Faunal Reserve (Tédonzong *et al.,* 2020) and Lobéké National Park in Cameroon (Ginath *et al.,* 2020), and chimpanzees at Greater Nimba Landscape in Guinea (Fitzgerald *et al.,* 2018), Nyungwe and Gishwati-Mukura National Parks in Rwanda (Tuyishimire *et al.,* 2020), Afi-Mbe-Okwangwo Forest Landscape in Nigeria (Onojeghuo *et al.,* 2015), in Forest Management Units of Mindourou, Lomié in Cameroon (Kehou *et al.,* 2021) and Mount Cameroon National Park (Mwambo, 2010).

1.4 Assessing primate diet

The diets of wild primates are frequently determined using indirect (macroscopic analyses of faeces) and direct methods like observations (Altmann, 1974). Direct observation methods involve locating chimpanzee groups and recording feeding activities like selecting, identifying, ingesting, and chewing food items per unit time (McLennan *et al.,* 2017, Matthews *et al.,* 2019). This method requires habituation and can expose the animals to hunting and disease (Morgan & Abwe, 2006; Deblauwe & Janssens, 2008). Macroscopic analysis of faeces has been used to assess the diet of great apes (Abwe *et al.,* 2020; Doran *et al.,* 2002; Tutin & Fernandez, 1993; Phillips & McGrew, 2014). Using macroscopic analysis of faeces may underestimate the diet composition because some smaller food items (<1mm in size) are difficult to see. Combining the direct observations and indirect methods wherever possible is

effective in monitoring dietary patterns, especially for species with significant seasonal variations in their diet (Matthews *et al.,* 2019, 2020).

1.5 Taxonomy and conservation status of the chimpanzee (*Pan troglodytes*)

The genus pan consists of the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) (Groves, 2001; Schwarz, 1934; Stone *et al.,* 2002). Chimpanzees are large mammals with black or brownish-black hair and pink to black skin on their bare faces (AZA*,* 2010). They are tailless, and their opposable thumbs and toes help them to hold objects easily. They walk bipedally, measure about 0.9 - 1.5m when standing, and weighs about 27.2–68kg. There is little difference in appearance between males and females, but males may be slightly larger (AZA, 2010). There are four subspecies of chimpanzee in the world and they are only found in Africa (Figure 2.1): the West African chimpanzee (*Pan troglodytes verus*), the central African chimpanzee (*Pan troglodytes troglodytes*), the East African chimpanzee (*Pan troglodytes schweinfurthii*), and the Nigerian – Cameroon chimpanzee (*Pan troglodytes ellioti*). They occur in different forest types from savanna woodlands, grassland-forest mosaics to tropical moist forests and montane forests (Goodall, 1968; Teleki, 1989; Nowak &Walker, 1999). The west African chimpanzees are restricted to forested areas in West Africa (Heinicke *et al.,* 2019), the central African chimpanzees occupies forested areas within central Africa (Maisels *et al.,* 2016), the Nigeria – Cameroon chimpanzee occurs in Nigeria, and Cameroon (Morgan *et al.,* 2011) and the east African chimpanzee are found in forested areas of east Africa (Plumptre *et al.,* 2016).
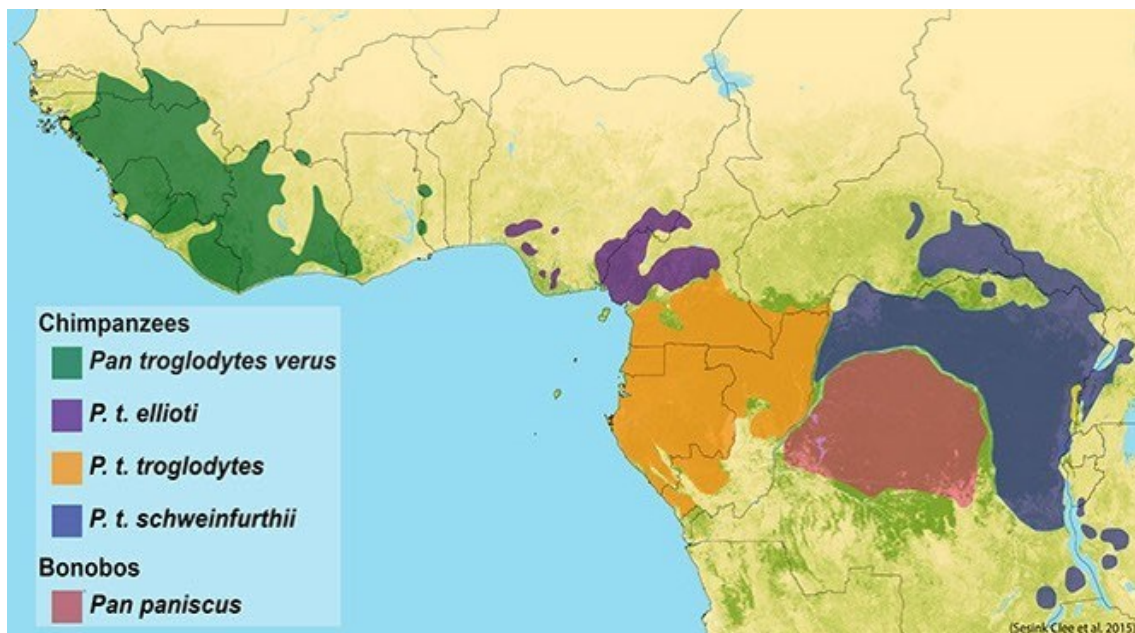
Figure 1.1 Distribution of chimpanzees in Africa (Sesink-Clee *et al.,* 2015)

The population of unhabituated chimpanzees in tropical Africa have declined by more than 66 percent in the last three decades (Butynski, 2001). The principal causes of chimpanzee decline are poaching (Humle *et al.,* 2016), habitat loss and degradation resulting from subsistence agriculture (Kormos *et al.,*

2003), and diseases (Walsh *et al.,* 2003). The threats worsen as about 80% of chimpanzees live outside protected areas (Strindberg *et al.,* 2018). The west African chimpanzee is critically endangered, with a population of about 52,800 individuals (Heinicke *et al.,* 2019). Their numbers have declined to more than 80% in the last 25 years (Kühl *et al.,* 2017; Kormos *et al.,* 2003). The Nigeria – Cameroon chimpanzee is endangered with a population size of about 6,000 to 9,000 individuals (Morgan *et al.,* 2011). A population reduction of between 50 and 80 percent is projected over three generations, from the middle of the 1980s to 2060 (Oates *et al.,* 2016). The central chimpanzee is endangered with a population size of about 128,760 individuals (Maisels *et al.,* 2016). Their population declined significantly since the 1970 across their entire, but no statistically significant decline was detected between 2003 and 2013 (Strindberg *et al.,* 2018). The east African chimpanzee is endangered and the most numerous with about 181,000–256,000 individuals (Plumptre *et al.,* 2016). Recent surveys show reductions of 80–98% of the east African chimpanzee at some important sites in the last 20 years.

1.6 Ecology of chimpanzees

All great apes construct nests, and nest construction in apes is similar despite the differences in their habitats and socioecology (Fruth & Hohmann, 1996). Nests are built by modifying plant parts into a circular structure to which leaves are added to make them comfortable for sleeping (Goodall, 1962). Like all other great ape species, chimpanzees make nests for resting and or sleeping almost daily (Koops et *al.,* 2007). Nests are the best indicators of chimpanzee presence in an area, and they have been widely used to assess their abundance and distribution (Kouakou *et al.,* 2009; Plumptre & Reynolds, 1996; Plumptre & Reynolds, 1997). Several studies have revealed that chimpanzees do not randomly select nesting sites and nesting trees (Hernandez-Aguilar *et al.,* 2020; Baldwin *et al.,* 1981). The decision to choose a site for nesting depends on several environmental factors (Baldwin *et al.,* 1981), including vegetation type (Koops *et al.,* 2012), relief (Abwe, 2018; Kamgang *et al.,* 2018), climatic conditions (Takemoto, 2004) and, the availability of fruits and habitat heterogeneity (Abwe *et al.,* 2019). Beyond the selection of nesting sites, other specific tree traits like species, tree height, tree diameter, the height of the lowest branch, nest height and the total basal area of chimpanzee feeding tree may affect the nesting behaviour of chimpanzees (Hernandez-Aguilar *et al.,* 2013; Chitayat *et al.,* 2021). Fruit phenology may affect the selection of a tree for nesting. For example, Basabose & Yamagiwa (2002) reported that chimpanzees preferred nesting on trees bearing fruits that they consume. Predation and human activities also affect the location of nests in trees (Anderson, 1984). According to Stewart *et al.* (2013), chimpanzees select nesting positions in trees that are not easily accessible by predators such as leopards. Also, chimpanzees tend to nest at relatively higher heights in trees in areas with high human activities (Hicks *et al.,* 2010; Last & Muh, 2013).

Chimpanzees are omnivorous, and their diet is dominated by wild ripe fruits of high nutritional quality (Tutin *et al.,* 1997; Morgan & Sanz, 2006). The components of their diet may also include animals (McGrew, 1983; Stanford, 2003) and non-fruit plant parts like leaves, pith and bark (Morgan & Sanz, 2006; Yamagiwa & Basabose, 2009). Some studies suggest that chimpanzees consume fruits based on their availability (Head *et al.,* 2011; Watts *et al.,* 2012). Other studies reveal that chimpanzees do not entirely consume fruit on their availability but also on preference (Dutton & Chapman, 2015). At some sites, fruit availability peaks during the wet season (Abwe *et al.,* 2019). At other sites, fruit availability is high during the dry season (Basabose, 2004; Yamagiwa & Basabose, 2006) but may also vary within seasons (Watts *et al.,* 2012). During seasons of wild fruit scarcity, chimpanzees rely on alternative food resources like fruit pith and leaves, called "fallback food" (Basabose, 2002, Chancellor, 2012). The term "fallback food" refers to food with poor nutritional quality which is consumed when preferred food is scarce (Doran *et al.,* 2002; Marshall & Wrangham, 2007). Figs (*Ficus* sp.) for example have previously been classified as fallback food for some populations (Abwe *et al.,* 2020), but were recorded as preferred food in other populations (Carvalho *et al.,* 2015, Dutton & Chapman, 2015; Newton-Fisher,1999; Yamagiwa & Basabose, 2009). Insects like termites, ants, and honeybees have also been proposed as fallback food (Yamagiwa & Basabose, 2009). In some habitats, chimpanzees include agricultural fruits in their diets during periods of wild fruit scarcity. For example, Hockings *et al.* (2009) found that chimpanzees at Bossou, Republic of Guinea consume cultivated fruit plants like sugar cane as fallback food. Chimpanzees may also include non-fruit agricultural crops like maize and okra in their diets (McLennan *et al.*, 2014). McLennan *et al.* (2013) showed that chimpanzees at Bulindi landscape, Uganda increased the consumption of fibre and energy-rich cultivars (cocoa, guava) during periods of fruit scarcity.

Chimpanzees use different habitat types for foraging depending on the spatial and temporal availability of their preferred food resources (Bryson-Morrison *et al.,* 2017; Basabose & Yamagiwa, 2002). Chimpanzees tend to prefer mature forests with large trees that produce abundant wild fruits for foraging , especially during the high fruiting season (Furuichi *et al.,* 2001; Bryson-Morrison *et al.,* 2017). Although chimpanzees generally avoid young secondary forest and cultivated areas, they provide a significant amount of important chimpanzee food during the low fruiting seasons (Bryson-Morrison *et al.,* 2016; Basabose, 2005). For example, at Kalinzu Forest, Uganda, the plant species *Musanga leo-errerae* provided important fallback food for chimpanzees during seasons of fruit scarcity (Furuichi *et al.,* 2001). At Bossou, Guinea, chimpanzees visited crop fields to supplement their diets with cultivars during periods of scarcity of wild fruits (Bryson-Morrison *et al.,* 2017).

Tool use has been observed in chimpanzees and other non-human primates. Besides humans, chimpanzees show an exceptional behavioural diversity compared to other primates. One of these behaviours is making and using tools in the wild (Goodall, 1964; Boesch & Boesch, 1990). Tool use plays a significant role in the daily life of chimpanzees in the wild and permits them to exploit a wide range of food resources (Boesch & Boesch, 1990). These food resources are usually insects like driver ants (Schöning *et al.,* 2007; Koops *et al.,* 2013), termites (Fowler & sommer, 2007), stingless bees (Dutton & Chapman, 2015), honey bees (Bessa *et al.,* 2021; Hicks *et al.,* 2019), and nuts (Boesch *et al.,* 1994; Morgan & Abwe, 2006). Based on the food resources exploited and functions, tools have been classified into, ant dip, ant dig, termite fish, leaf napkin, honey dip, stone hammers and anvils, and leaf sponge (McGrew &McGrew, 1992). Tools can further be grouped based on their form and functions (Sanz *et al.,* 2010). For example, Koops *et al.* (2015b) found that ant-digging tools were markedly wider than dipping tools at Seringbara, Guinea. At Goaulougo Triangle, Republic of Congo, Sanz *et al.* (2010) reported that tools used as part of a set to perforate driver ant mounds were significantly thicker than the accompanying dipping tools used to collect the ants. At Comoé National Park, Ivory Coast, Lapuente *et al.* (2017) showed that water dipping sticks tend to have longer and thicker brush-tips than honey dipping tools. At Goualougo, Sanz *et al.* (2004) reported that chimpanzees used stout woody sticks to puncture underground termite nests and fishing probes made from flexible herbaceous materials as part of a tool set to collect termites clinging to the end of the tools.

Seasonality may influence foraging tool use in wild chimpanzees (Fowler & Sommer, 2007; Schöning *et al.,* 2007). For example, Sanz & Morgan (2013), showed that driver ant predation was highly correlated with local rainfall at Goualougo. Also, Fowler & Sommer (2007) demonstrated that chimpanzees used longer tools more frequently in the dry season to collect ants that retreat deeper into their nests to avoid desiccation and shorter tools in the wet season to prey on driver ants that tend to spend more time outside their nest in the wet season (Schöning *et al.,* 2007). Tool use in insect exploitation in chimpanzees can be explained by two hypotheses. The necessity hypothesis states that tool-use in insect exploitation is triggered by scarcity of their preferred food (in particular fruits), while the opportunity hypothesis suggests that high encounter rates with insects or required material may trigger this behaviour (Fox *et al.,* 1999). For example, chimpanzees increased ant and honey bee consumption at times when their preferred fruits were scarce at Kahuzi-Biega, Democratic Republic of Congo (Yamagiwa & Basabose, 2009). Also, ant consumption increased when preferred fruits were scarce at La Belgique, Cameroon (Deblauwe, 2009). In contrast to this hypothesis, however, fruit scarcity did not correlate with tool-use for predation on driver ants at Seringbara or Gashaka (Koops *et al.,* 2013; Sommer *et al.,* 2017).

Tool use in chimpanzees has been described as cultural because it differs across different populations and appears to be socially acquired (Whiten *et al.,* 1999, Boesch & Boesch-Achermann, 2000). For instance, Pascual-Garrido (2019) reported that chimpanzees at Kasekela use longer, and wider termite fishing tools compared to chimpanzees at Mitumba, an area with similar vegetation composition

suggesting a cultural variation between the two neighbouring populations of chimpanzees. Boesch & Boesch (1990) reported that the chimpanzees of Taï National Park, Ivory Coast, and Gombe,Tanzania exploit driver ants while those of Mahale mountains,Tanzania do not utilise this resource, even if available. They further showed that chimpanzees at Taï National Park only take ants directly into their mouths while those at Gombe mostly pull through the tools with their fingers to gather ants into their mouth suggesting a cultural variation in tool use between Gombe and Taï (McGrew, McGrew, 1992,1974). At Budongo Forest Reserve, Uganda, Lamon *et al.* (2017) showed that moss-sponging spread from eight founder chimpanzee to 17 more group member three years after the behaviour was first observed, suggesting this behaviour is transmitted socially and is a subculture within the Sonso chimpanzee population.

1.7 The Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti* (Matschie,1914))

The Nigeria – Cameroon chimpanzees is endangered (Figure 1.2). It has the lowest estimated population size (6000 to 9000 individuals) and the smallest distribution range of all chimpanzee subspecies (Morgan *et al.,* 2011). Its distribution is restricted to defined areas in Cameroon (west of the Sanaga River) and southern Nigeria (Gonder *et al.,* 2006; Oates *et al.*, 2009). It can be found in a variety of habitats, including savanna woodland, farmland, mature and secondary moist lowland forest, montane and submontane forest, dry forest, forest galleries, and altitudes ranging up to 2000 m above sea level (Abwe *et al.,* 2019; Sesink- Clee *et al.,* 2015). Habitat conversion to farmland, habitat degradation, and poaching (for bushmeat, traditional medicine, and the pet trade) are major threats to its survival (Morgan *et al.,* 2011; Oates *et al.,* 2016). Climate change is anticipated to substantially reduce its habitats in mosaic forests, woodlands, and savanna within the next century (Sesink-Clee *et al.,* 2015). These chimpanzees face the greatest threats in two of its range subregions (North – West Cameroon and southwest Nigeria) with probably less than 250 chimpanzees per subregion justifying classification as critically endangered at a subregional level (Oates *et al.,* 2016).

Figure 1. 2 The Nigeria – Cameroon chimpanzee in Kom – Wum Forest Reserve (Fotang, 2018)

Until 2011, very little information was available about the abundance and ecology of the Nigeria – Cameroon chimpanzee (Morgen et al., 2011). The IUCN endorsed a regional conservation action plan for the Nigeria – Cameroon chimpanzee and outlined measures and strategies to prevent further population decline with recommendations to estimate their abundance and study their ecology (Morgan *et al.,* 2011). In response to this plan, several studies were conducted across its distribution range. For example, Abwe *et al.* (2020) showed that fruits were major components of chimpanzee diet in rainforest habitats (Ebo Forest Reserve) while non-fruit plant material (leaves, pith, and bark) were major components in the ecotone habitats (Mbam and Djerem National Park) of Cameroon. At Ngel Nyaki Forest Reserve, Nigeria, Dutton & Chapman (2015) showed that fruits (*Ficus* sp. in particular) were preferred chimpanzee food, but leaves, and animals were also consumed during periods of fruit scarcity. Dutton & Chapman (2015) also reported that chimpanzees build arboreal nests and preferentially select steeper areas for nesting. At Mbam-Djerem National Park, Cameroon Kamgang *et al.* (2018) reported that dense forest and steep slopes are preferred nesting areas for chimpanzees. At Tofala Hill Wildlife Sanctuary, Cameroon, Njukang *et al.* (2019) showed that chimpanzees preferentially choose areas of high altitudes with low encounter rates of logging and farming activities for nesting. Wade (2020) showed that chimpanzees preferred matured forests with closed canopy and elevations between 550 – 700m for nesting in Mone-Oku Forest, Cameroon. Last & Muh (2013) indicated that chimpanzees constructed more ground night nests in areas with low human activities and arboreal nests in areas with high human activities in Lebialem-Mone Forest Landscape, Cameroon.

1.8 Research goal, aim and objectives

The Kom – Wum Forest Reserve (KWFR) is considered a priority conservation area for the Nigeria – Cameroon chimpanzee, and recommendations were made to conduct surveys on their abundance and ecology (Morgan *et al.,* 2011). Initial chimpanzee surveys focused on confirming the presence of chimpanzees (Doumbé, 2015). A subsequent survey used the reconnaissance method to estimate chimpanzee abundance and anthropogenic activities and found 11.3 chimpanzee signs per km and 1.2 anthropogenic signs per km (Chuo *et al.,* 2017). Further surveys in this reserve revealed bushmeat hunting and exploitation of non-timber forest products like Mahogany (*Khaga ivorensis*), Iroko (*Meletia excels*) and Pygeum (*Prunus africana*) by the locals (Kah, 2015). Previous studies provided very little information about the 1) population size and threats to chimpanzee2) potential drivers of nesting in chimpanzees, 3) availability of suitable chimpanzee habitat, 4) diet composition of chimpanzees, and 5) tool use by chimpanzees in this high-priority conservation area.

   The goal of the research presented in this thesis was therefore to improve our knowledge on the conservation status and ecology of the Nigeria – Cameroon chimpanzee. It aims to better understand the population status, habitat requirements and food utilization of the Nigeria – Cameroon chimpanzee in KWFR in the North – West Region of Cameroon. Closing this knowledge gap will improve the conservation success for the subspecies and will help us to develop successful conservation plans in the future.

The objectives to achieve the goal are to:
1.   provide population estimates and information about major threats to chimpanzees
2.   investigate environmental and human factors affecting nesting in chimpanzees
3.   identify and predict suitable habitats of chimpanzees
4.   determine the feeding habits of chimpanzees and
5.   document tool use and discover tools used for driver ant predation.

I hypothesize that:
1.   human activities and forest degradation have reduced chimpanzee abundance. I predict that the encounter rate of chimpanzee signs is lower in secondary than in mature forests, that the encounter rate for chimpanzee signs is higher in the reserve than surrounding unprotected forests that are subject to more anthropogenic pressure, and that parts of the reserve with higher elevation have more chimpanzee signs compared to areas at lower elevation (Chapter 3).
2.   the selection of nesting trees by chimpanzees is driven by specific tree traits and that the selection of nesting areas further depends on the local vegetation composition and topography. I predict that chimpanzees i) construct more nests on tall primary trees (trees that provide the main support for nests), trees with larger diameters and high lowest branch height; ii) orientate their nests in direction of the slope and that iii) they frequently nest in mature forests, at higher elevations, and on steep slopes. We further hypothesize that predator presence and human

activity affects the nesting height, with the prediction that chimpanzees nest higher in trees if predators are present or when humans are active in the nesting location (Chapter 4).

3. the suitability of chimpanzee habitats and chimpanzee occurrence will vary with elevation, vegetation type and degree of human activities. We therefore predict that chimpanzee occurrence will increase with level of elevation, density of vegetation and decrease with density of human activities. So, chimpanzees will prefer habitats at higher elevation and dense forest habitats far away from human settlements to minimize contact with human activities and increase comfort (Chapter 5).

4. there will be inter-seasonal variation in the composition of chimpanzee diets and I predict that: i) chimpanzee diets will be fruit dominated and ii) the volume of fiber will be higher in the dry season than the wet season (Chapter 6).

5. chimpanzees use shorter tools in the wet season, and longer tools in the dry season (Chapter 7).

Chapter 2: General Methods

2.1 Study area

The KWFR was created in 1951 and spans two administrative units: Boyo and Menchum Divisions in the North – West Region of Cameroon (Figure 2.1a; Latitude 6° 9' 39.47"N and Longitude 10° 13' 9.16"E to Latitude 6° 19' 39.42"N and Longitude 10° 13' 3.93"). Extending to 565-1640 m above sea level in elevation (Figure 2.1c), the 80 km^2 KWFR is covered by sub-montane tropical forest that spreads over an undulating and picturesque landscape (Sunderland & Mannaseh, 2003). The temperature ranges from 15°C to 38°C with a mean yearly rainfall is 2,400 mm and humidity of 82% (PNDP, 2011). The area has two distinct seasons, a wet season (mid-March to mid-October) and a dry season (mid-October to mid-March). The KWFR is the richest in terms of primate diversity in the North – West Region of Cameroon (Doumbé, 2015). In addition to chimpanzees, KWFR harbours six diurnal and six nocturnal primate species (Chuo *et al.,* 2017; Doumbé, 2015; Fotang, 2018). Amongst these species, two are endangered (EN) and 11 are least concern (LC). The diurnal monkey species include: putty-nosed monkey (*Cercopithecus nictitans ludio,* LC), mona monkey (*Cercopithecus mona,* LC), olive baboon (*Papio anubis,* LC), tantalus monkey (*Chlorocebus tantalus,* LC), patas monkey (*Erythrocebus patas,* LC) and Preuss's monkey (*Allochrocebus preussi,* EN). The nocturnal primate species are: Thomas's dwarf galago (*Galagoides thomasi;* LC), Demidoff's dwarf galago (*Galagoides demidoff,* LC), Northern needleclawed galago (*Euoticus pallidus;* LC), Allen's galago (*Sciurocheirus alleni,* LC), Milne-Edward's potto (*Perodicticus edwardsi,* LC) and Calibar angwantibo (*Arctocebus calabarensis,* LC) which are protected entirely in Cameroon and restricted to west-Cameroon and east Nigeria (Doumbé, 2015). The presence of some mammals (red duiker (*Cephalophus dorsalis,* LC), bushbuck (*Tragelaphus scriptus,* LC), red river hogs (*Potamochoerus porcus,* LC), white-bellied pangolin (*Phataginus tricuspis,* EN) and birds (Bannerman's turaco (*Tauraco bannermani,* EN), blue turaco (*Corythaeola cristata,* LC) and blackcasqued wattled hornbill (*Ceratogymna atrata,* LC) have been verified (Fotang, 2018). The reserve encompasses the village communities of Mughom and Bueni in the south and borders the village communities of Bu, Mbengkas, Baiso and Mbongkissu (Figure 2.3b and c). These local communities rely on forest resources for their livelihood (Kah, 2015).
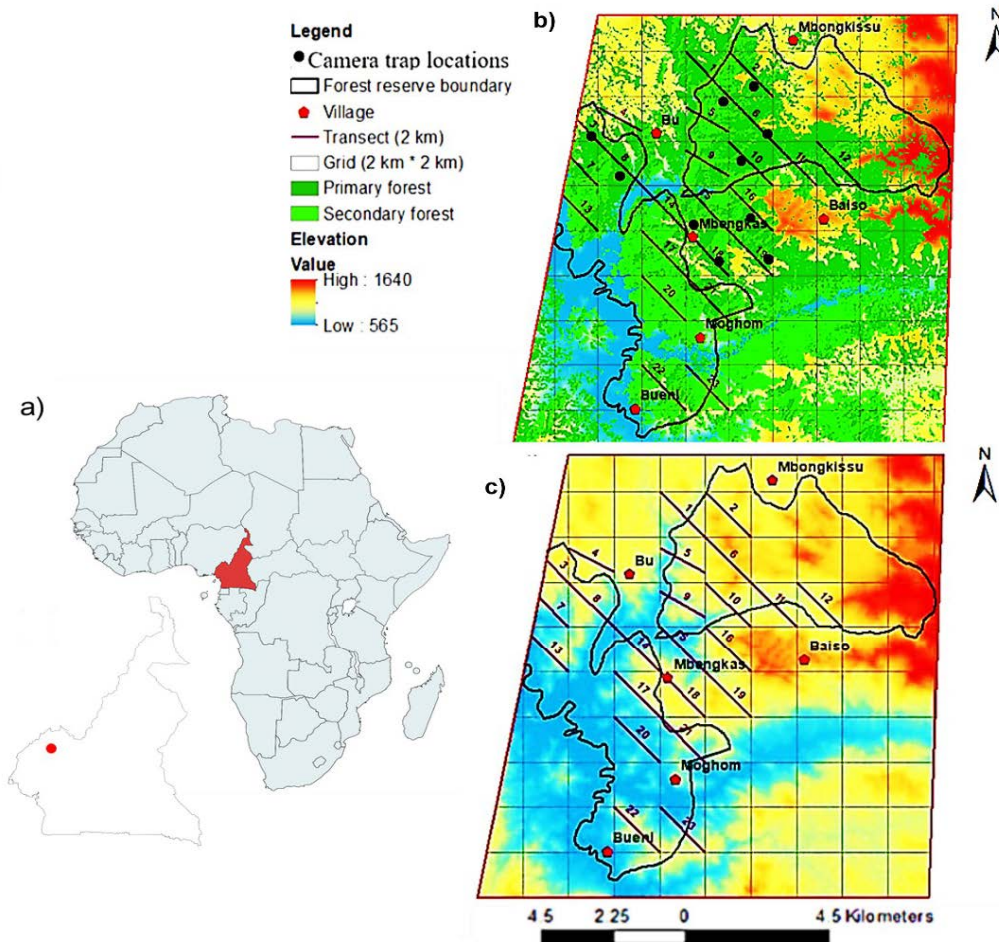
Figure 2. 1 Maps of a) Cameroon and the study location KWFR in North – West Cameroon (red point), b) KWFR including major villages with line transects for surveys (1 to 23) and location of camera traps and c) line transects and elevation (15 May to 23 September 2018).

2.2 Sampling

2.2.1 Satellite images and digital elevation models

A satellite image (Landsat 8, 30 m pixel) for February 9, 2017, was obtained from the United States Geological Survey to produce a land cover map of KWFR and surrounding unprotected forest. The elevation of the study zone was derived from a Shuttle Radar Topography Mission 30 m resolution Digital Elevation Model and superimposed on the land cover map (Figure 2.1c). Land cover was classified as mature forest, secondary forest, grassland, and water bodies using supervised classification and the maximum likelihood algorithm in ArcGIS version 10.6 (Ganasri & Dwarakish, 2015). Google Earth images were to digitize roads, rivers, and villages, and the distance to each feature as Euclidean distance.

2.2.2 Survey design and methods

Georeferenced square grids of 2 km × 2 km cell size were generated in ArcGIS 10.6.1 and superimposed on satellite images of the reserve (80 km^2) and adjacent unprotected (20km^2) following a previous recce-

transect survey conducted in the area (Chuo *et al.,* 2017). Twenty-three grids were sampled with line transects (each 2 km long), equally spaced (1000 m), following Buckland *et al. (*2001). A recce survey of the whole area (100 km^2) was conducted to identify core areas of chimpanzee activity focusing on chimpanzee signs, including sightings, nests, faeces, feeding remains, tool-use sites, footprints, and vocalizations, and human-related activity signs including hunting, farming, logging, livestock grazing, and collection of non-timber forest products (Kühl, 2008). The recce method requires less effort, causes less damage to the forest, and more distance is covered within a short time compared to line transects (Plumptre &Cox, 2006). Based on the results from recce surveys, only 13 line transects (26 km) and recces (42.09 km) with at least one chimpanzee sign were sampled for data collection.

2.2.3 Data collection & analyses

Data were collected during the wet (May to September 2018) and dry seasons (November 2019 to March 2020). The population size of chimpanzee was estimated during the wet season using 1) direct observations, 2) camera trapping, 3) marked nest counts, 4) standing crop nest counts, and 5) distance sampling methods. An integrated method was used to overcome the known limitations of single methods (Howe *et al.,* 2017). The geographical location of direct observations along line transects and recces were marked using a GARMIN GPSMAP 64s device. LTL-5310A Acorn wildlife cameras were installed in 10 of the 13 sampled grids to photograph and capture the behaviour of chimpanzees because they are difficult to observe in the wild (Rovero & de Luca, 2007). The cameras were attached to trees at a height between 30 and 80 cm along frequently used chimpanzee routes leading to nesting and feeding sites to increase the probability of detecting them and their predators. They were set up cameras to function continuously for 24 hours at a resolution of 1080 pixels. The survey team checked cameras to change SD cards and batteries during transect visits (Rovero et al. 2010). The location, nest group size, perpendicular distance to the transect, and age class were recorded for all nests. Line transects were monitored once for the SCNC method and five times for MNC and distance sampling methods. The equation: Dind = Nall nests / 2Lw (prt), was applied for SCNC where: Dind is the number of individuals, Nallnests is the total number of nests observed on the transect, w is the effective strip width of the transect, L is the transect length (in kilometres), p is the proportion of nest builders in the population, r is the rate of nest production per individual per day, and t is the nest decay time (Ghiglieri, 1984). The equation Dind = Nnewnest / 2Lw (pri) was applied for MNC were Nnewnest represents new nests (fresh and recent nests) constructed during the intersurvey period, and i is the inter-survey period, and the other parameters remain the same as in the SCNC formula. The vegetation type was classified as mature forest, old secondary forest, or grassland during transect walks (White & Edwards, 2000). Threats to chimpanzees were assessed by georeferencing signs of chimpanzees and human activity along line transects and recces using the GPS.

Nesting data were collected for the two seasons of the survey by locating nesting sites opportunistically along line transects and recces because the chimpanzees are not habituated to human

observers. The characteristic of nesting trees and nests were determined following Baldwin *et al.* (1981). For each nesting site encountered, the GPS location, the number of nests per tree, the number of trees per nest, the tree height, the lowest branch height, the diameter at breast height (DBH), and the horizontal distance of the nest from the tree trunk was noted. Nest height, tree height, and lowest branch height were measured with a hypsometer (Nikon Forestry Pro 6x216x21\11-55YD), and tree diameter was measured with a 30 m tape. Nests were classified into "arboreal" or "ground" following (Furuichi & Hashimoto, 2000; Fruth & Hohmann, 1996; Koops *et al.,* 2007). The age of each nest was also classified as fresh, recent, old, and very old, following Tutin and Fernandez (1984). Nesting trees in the field were identified by a botanist, and unidentified plants were taken to the Cameroon National Herbarium for identification. To investigate environmental and human factors affecting nesting, vegetation types (White & Edwards, 2000), canopy cover (Koops *et al.,* 2012), slope (De Vere *et al.,* 2011), elevation, and human-related signs (Last & Muh, 2013; Tagg *et al.,* 2013) were recorded at nesting sites. The Euclidean distances modelling technique was then used to assess whether nests were distributed randomly with respect to elevation, slope, primary forest, secondary forest, bare land, villages, aspects, rivers, and signs of human activities following Enoguanbhor *et al.* (2020).

The Maximum Entropy Distribution Model (MaxEnt) version 3.1.4 was used to identify and predict suitable chimpanzee habitats in the study area (Phillips *et al*., 2006). MaxEnt requires occurrence points for the species in question and environmental data from the whole study area (Phillips & Elith, 2013). In total, 198 chimpanzee occurrence points (nests, dung, footprints, direct observations, feeding locations, tool use sites, and tracks) were recorded during line transect and recce surveys for the two seasons of the survey in KWFR. Of those, 178 points were used for training and 20 for testing. The chimpanzee occurrence data were related to nine environmental variables, including aspect, density of bare land, density of primary forest, density of secondary forest, elevation, distance to roads, distance to villages, distance to roads and rivers, and slope obtained from satellite images, digital elevation models and google earth images. One thousand generated background points representing all environmental variables were added to the 198 occurrence points resulting in 1198 points in the final model. The performance of the model was evaluated using the area under the curve of the receiver operating characteristic (Yackulic *et al.,* 2013). Suitable chimpanzee habitat was classified into four habitat suitability categories: highly suitable (>0.6–1.0); moderately suitable (>0.4–0.6); low suitable (>0.2–0.4); unsuitable habitat (>0–0.2) following Yang et al. (2013). The jackknife test was used to measure the percentage contribution for each environmental variable to chimpanzee habitat suitability (Phillips *et al.,* 2006) and a logistic output to measure the probability of chimpanzee occurrence with respect to the nine environmental variables (Phillips & Dudık, 2008).

To determine the feeding habits of chimpanzees, fresh chimpanzee faeces (not older than two days) were searched at feeding sites and beneath fresh nests during monthly transect and recce walks for the two periods of the survey. For each faeces encounter, the GPS location was taken, and genetic samples were collected using a Copan culture swap transport package. The remaining faeces were collected in

plastic bags, labelled with the date, and taken to the research camp. All samples were later placed in a 1mm meshed sieve, rinsed gently with water to avoid the loss of dietary components, and then dried in sunlight (Basabose, 2002). The content of the samples was separated into fruits (seeds, fruit skin, and tegument) and plant fibre (leaves and pith). The diversity of species consumed was identified through direct counting of the seeds of fruits in the faecal samples (macroscopic analyses of faeces). The percentage volume of each diet component in faeces sample per month was calculated following McLennan (2013).

Tool use behaviour was investigated by searching for tool use sites along line transects and recces for the two periods of the survey. At potential tool-use sites, it was first verified if tools were 1) associated with an insect mound, 2) projecting from an insect mound, 3) signs of modification (stripping of leaves, bark), 4) sources of tools found nearby, 5) signs of excavation of soil, and 6) associated with chimpanzee evidence following Hicks *et al.* (2019). The targeted food source (driver ants, termites, stingless bees, or honeybees) was then verified by inspecting the insect mounds and identifying them. Once the targeted food source was confirmed, the geographic location, the number of tools per site, types of modification made on each potential tool (cut at one or two ends, remove side twigs, stripped of bark), and tool age was estimated following Hicks *et al.* (2019). Tool lengths was measured with a meter tape and their respective diameters with a digital vernier calliper from the proximal (the end which was near to the stem, branch, or root of the plant from which the tool was removed) to the distal ends (the end furthest from the stem, branch or root of the plant) following Fowler & Sommer (2007). Additionally, the wear types on the tool ends were classified as sliced, blunt, frayed, pointed, and split (Fowler & Sommer, 2007). Tools were classified into trees or herbs and identified to the family level whenever it was possible, and nut cracking behaviour was checked beneath nut-producing trees. Ant feeding tools were classified into two classes following Koops *et al.* (2015a): those with blunted and dirty ends, with excavation of soil (potential digging or probing tools), and those without (potential dipping tools).

2.3 Chapter synthesis

This thesis is cumulative research with eight chapters. The introductory chapter (Chapters 1&2) is followed by five main chapters (Chapter 3, 4, 5, 6&7) and a general discussion and conclusion (Chapter 8). In chapter 1, I present a general introduction with a brief background on the effects of human activity on the population of primates, provide an overview of available methods to estimate the density of great apes, and introduce literature on the conservation status and the ecology of chimpanzees in general and the Nigeria – Cameroon chimpanzee in particular. This chapter ends with the goals, aims, and objectives of the study. In the general methods chapter, I describe the study area and explain the sampling design and applied methods (Chapter 2). In Chapter 3, I estimated the population size of the Nigeria – Cameroon chimpanzees in KWFR, determined which habitats (mature versus secondary forest) and elevation (high versus low) are preferred by chimpanzees, and evaluated the effects of human activities and forest degradation on their relative abundance, The aim of Chapter 4 was to investigate the effects

of environmental and human factors on the nesting behaviour of chimpanzees. Here, I investigated which traits of tree species (tree height, tree diameter) are preferred for nesting, the effects of environmental factors (vegetation, topography, seasonality) on nesting site selection, and verified the effect of predator presence and human activity on the selection of nest sites by chimpanzees. In Chapter 5, I identified and predicted suitable habitats for chimpanzees and determined the contribution of eight environmental variables to their occurrence. In Chapter 6, I determined the feeding habits of chimpanzees focusing on seasonal changes in diet and dietary preference. Chapter 7 examined the characteristics of tools used by chimpanzees in driver ant predation, looking for possible seasonal patterns and comparing results to those from other study sites. In Chapter 8, I discuss the main findings of chapters 3 to 7 in the context of the existing knowledge.

Chapter 3: Human Activity and Forest Degradation Threaten Populations of the Nigeria – Cameroon Chimpanzee (*Pan troglodytes ellioti*) in Western Cameroon

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Human Activity and Forest Degradation Threaten Populations of the Nigeria–Cameroon Chimpanzee (*Pan troglodytes ellioti*) in Western Cameroon

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Abstract

Increased human activities such as commodity-led deforestation, extension of agriculture, urbanization and wildfires are major drivers of forest loss worldwide. In Cameroon, these activities cause a loss of suitable primate habitat and could ultimately threaten the survival of chimpanzees (*Pan troglodytes*). We derived independent estimates of the population size of the Endangered Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti*) in Kom – Wum Forest Reserve, Cameroon, and surrounding unprotected forest areas through (i) direct observations, (ii) camera trapping, (iii) distance sampling, (iv) marked nest counts and (v) standing crop nest counts. In addition, we georeferenced signs of chimpanzee and human activity along line transects. We used a generalized linear mixed model to predict the occurrence of chimpanzee in response to edge length (measured as the perimeter of core forest patches), core area of forest patches (measured as area of forest patches beyond an edge width of100 m), habitat perforation (measured as the perimeter of non-forested landscape within core forest patches), patch size(measured as area of forest patches) and forest cover. Chimpanzee density estimates ranged from 0.1 (direct observation) to 0.9 (distance sampling) individuals km^{-2} depending on estimation method with a mean nest group size of 7 ± 5.4 (SD). The mean encounter rate for signs of chimpanzee activity was significantly higher in mature forests (2.3 signs km^{-1}) than in secondary forests (0.3 signs km^{-1}) and above 1000 m elevation (4.0 signs km^{-1}) than below 1000 m (1.0 signs km^{-1}). The mean encounter rate for signs of human activity was significantly higher in secondary (8.0 signs km^{-1}) than in mature forests (0.9 signs km^{-1}). Secondary forests, habitat perforation and edge length had a significant negative effect on the occurrence of chimpanzee signs. Overall, human activity and forest degradation affected the number of observed chimpanzee signs negatively. Regular anti-poaching patrols and reforestation programs in degraded areas could potentially reduce threats to populations of endangered species and may increase suitable habitat area.

Keywords: Bushmeat hunting, Core areas, Edge length, Forest fragmentation, Forest perforation, Nest counts, Mature forest, *Pan troglodytes ellioti,* Secondary forest

3.1 Introduction

Increasing human activities such as commodity-led deforestation, extension of agriculture, urbanization and wildfires are major drivers of forest loss worldwide (Curtis *et al.,* 2018). These activities cause habitat loss, fragmentation and destruction of natural ecosystems (Estrada *et al.,* 2017; Haddad *et al.,* 2015). The effects of forest fragmentation include decreasing patch sizes (larger number of smaller patches), increased edge effects (more fragmented landscapes contain more edge for a given amount of habitat) and patch isolation (distance from a patch to its neighbouring habitats, Fahrig, 2003). The loss of forest area and isolation of forest fragments can lead to a decrease in the abundance of animal and

plant species (Estrada *et al.,* 1999; Arroyo-Rodríguez & Mandujano, 2006). Forest mammals and primates in particular are vulnerable to the effects of forest fragmentation (Chapman & Peres 2001; Arroyo-Rodríguez & Mandujano 2006). While some studies have reported a negative effect of habitat fragmentation on primates (Estrada, 1996; Estrada *et al.,* 1999; Arroyo-Rodríguez & Dias, 2010), others have reported higher densities of primates in small forest fragments (González-Solís *et al.,* 2001), and some have indicated no changes in primate density between forest edge and interior (Bolt *et al.,* 2018). Although some primates show flexibility in human dominated landscapes (McLennan *et al.,* 2017), habitat loss and degradation have resulted in a decline of about 75% of the world's primate species, of which 60% are endangered (Estrada *et al.,* 2017, 2019). This situation makes it crucial to measure threats to primate populations by determining the population status and trends in density and distribution (Kühl , 2008).

Like populations of many other primate species, chimpanzee (*Pan troglodytes*) populations throughout Africa have declined due to habitat loss, habitat degradation, poaching and disease (Humle *et al.,* 2016; Walsh *et al.,* 2003). These activities are major threats to the rarest and least studied chimpanzee subspecies (Morgan *et al.,* 2011), the Nigeria – Cameroon chimpanzee of which about 3,500 individuals remain in the wild (Morgan *et al.,* 2011). In south-western Nigeria, agricultural activity, timber extraction and hunting are major threats to populations of chimpanzee (Ogunjemite & Dansu, 2014). In the Littoral and Southwest regions of Cameroon, the expansion of oil palm plantation and human population density is associated with permanent destruction of chimpanzee habitat (Morgan *et al.,* 2011). The loss of chimpanzee habitat in central Cameroon is driven by uncontrolled burning by cattle grazing herdsmen (Morgan *et al.,* 2011). Illegal timber exploitation, farming, hunting, bush fires and advancing pastures are major threats to chimpanzee survival in North – West Cameroon (Doumbé 2014; Morgan *et al.,* 2011). Unlike the Congo Basin south of the Sanaga River, that is characterized by lowland rainforests, the range of chimpanzee in the Gulf of Guinea is characterized by mountainous rainforest habitat (Abwe *et al.,* 2019, Sesink-Clee *et al.,* 2015). Forest type and anthropogenic disturbance influence nest site location (Koops *et al.,* 2012; Last & Muh 2013). Chimpanzee tend to build their nests in mature forest vegetation (Kamgang *et al.,* 2018), in areas with a low degree of human pressure (Last & Muh 2013; Njukang *et al.,* 2019) and at high elevations (Njukang *et al.,* 2019).

The current population estimates for the Nigeria – Cameroon chimpanzee are problematic (Hughes *et al.,* 2011), but suggest 1,500 chimpanzees survive in Nigeria (Hughes *et al.,* 2011), with the largest population of 900-1,000 individuals found in Gashaka-Gumti National Park, Nigeria (Sommer *et al.,* 2004). Ngel Nyaki Forest Reserve is home to 12-16 chimpanzees (Beck & Chapman 2008; Beck & Chapman 2008; Dutton, 2012) and about 400 chimpanzees may survive in Okwango Division of Cross River National Park (McManus, 2005). 3,000-4,000 individuals remain in Cameroon (Morgan *et al.,* 2011), split into two distinct genetic pools that occupy ecologically and environmentally distinct habitats in mountainous rainforest in western Cameroon and forest-woodland-savanna mosaic in central Cameroon (Abwe *et al.,* 2019; Sesink Clee *et al.,* 2015; Mitchell *et al.,* 2015). Strongholds for

chimpanzee in Cameroon include Ebo forest, with 626-1480 individuals (Ndimbe *et al.,* 2016), Mbam and Djerem National Park with more than 500 individuals (Greengrass & Maisels 2007; Kamgang *et al.,* 2018; Maisels *et al.,* 2009), and Banyang-Mbo Wildlife Sanctuary with 800-1,450 individuals (Greengrass & Maisels 2007). Tubah-Awing Forest and Kom – Wum Forest Reserve in the North – West region also harbor chimpanzee, and have been proposed as a multi-site protected area, affording appropriate legal status for the remaining wildlife and forest resources (Morgan *et al.,* 2011). As indicated by the publication dates, several of these estimates may be outdated.

In the last two decades, research and conservation efforts for chimpanzee have focused on populations in continuous forests such as Gashaka Gumti National Park (Fowler & Sommer 2007; Sommer *et al.,* 2004), Ebo forest (Abwe *et al.,* 2019, 2020; Abwe & Morgan, 2008), Lebialem complex-Banyang Mbo (Greengrass & Maisels 2007), Mbam & Djerem National Park (Abwe *et al.,* 2019, 2020; Kamgang *et al.,* 2018), and forests North – West of the Sanaga River and Takamanda-Mone-Mbulu (Funwi-Gabga *et al.,* 2014). Only recently have some populations in fragmented habitats received attention in Ngel Nyaki Forest Reserve in Nigeria (Beck & Chapman, 2008; Dutton & Chapman, 2015a, 2015b; Dutton *et al.,* 2016; Dutton, 2012; Knight *et al.,* 2016), Babanki-Finge Forest (Doumbé ,2014), Fungom Forest Reserve and Kom – Wum Forest Reserve in Cameroon (Chuo *et al.,* 2017; Doumbé, 2015; Fotang, 2018).

The IUCN-endorsed regional conservation action plan for chimpanzee outlined measures and strategies to prevent further population decline (Morgan *et al.,* 2011). Kom – Wum Forest Reserve is described as a priority conservation site in the plan with a focus on surveys to confirm chimpanzee presence and estimate population size (Morgan *et al.,* 2011). An initial survey in Kom – Wum Forest Reserve used trails made by local people to access the reserve and found 458 chimpanzee nests (Doumbé, 2015). A subsequent survey used the reconnaissance method to estimate chimpanzee abundance and anthropogenic activities and found 11.3 chimpanzee signs per km and 1.19 anthropogenic signs per km (Chuo *et al.,* 2017). The main objectives of our study were to: 1) determine the population size of chimpanzee in Kom – Wum Forest Reserve and surrounding forests using five independent methods, 2) understand habitat preferences in relation to forest type (mature versus secondary forest) and elevation (above and below 1,000 m - following Koops *et al.,* 2012 and close to midpoint for the study area) in the study area, and 3) investigate the effect of human activity on the relative density of chimpanzee in the study area. We hypothesized that human activities and forest degradation reduce chimpanzee abundance (Bryson-Morrison *et al.,* 2017; Morgan *et al.,* 2018). Thus, we predicted that the encounter rate of chimpanzee signs is lower in secondary than in mature forests, that the encounter rate for chimpanzee signs is higher in the reserve than surrounding forest that are subject to more anthropogenic pressure, and that parts of the reserve with higher elevation would have more chimpanzee signs compared to lower elevation.

3.2. Materials & methods

3.2.1 Sampling

3.2.1.1 Satellite images and digital elevation models

We obtained a satellite image (Landsat 8, 30 m pixel) for February 9, 2017 from the United States Geological Survey to produce a land cover map of the study area. We derived the elevation of the study zone from a Shuttle Radar Topography Mission 30 m resolution Digital Elevation Model and superimposed this on the land cover map (Figure 2.1c). We classified land cover as mature forest, secondary forest, grassland and water bodies using supervised classification and the maximum likelihood algorithm in ArcGIS version 10.6 (Ganasri & Dwarakish, 2015) as recommended in Enoguanbhor *et al.* (2019). We imported the land cover types to the Landscape Fragmentation Tool in ArcGis (Vogt *et al.,* 2007). We included mature and secondary forests in the forest class and grassland and water bodies in the non-forest class (Vogt *et al.,* 2007). We used an edge-width of 100 m to further classify forest into edge, core, perforated, and patch (Vogt *et al.,* 2007). We generated georeferenced square plots 2 km × 2 km in ArcGIS 10.6.1 and superimposed them on satellite images of the study zone (Figure 2.1 b). For each square we calculated percentage forest cover, edge length, core area of forest patches, patch size, and forest perforation using the geometric landscape tool in ArcGIS. We measured edge length as the perimeter of core forest patches, core area of forest patches as forest area beyond the edge width of 100 m, perforated as the perimeter of non-forested landscape within core forest patches and patch size as area of forest patches. We used data collected during the survey (May to September 2018) to confirm the Geographical Information System Classification as recommended by Congalton (1991).

3.2.1.2 Survey techniques and design

We conducted fieldwork between 15 May and 23 September 2018 using (i) direct observation, (ii) camera trapping, (iii) distance sampling, (iv) marked nest count and (v) standing crop nest count. We chose this integrated approach to overcome the known limitations of single methods (Howe *et al.,* 2017). We selected the nest count method based on the fact that chimpanzee in Kom – Wum Forest Reserve were not habituated and thus were extremely difficult to observe in the wild (Plumptre & Reynolds, 1996). We used camera trapping to increase the probability of detecting chimpanzee (Rovero & Luca 2007; Rovero *et al.,* 2010). We established line transects following a recce-transect survey conducted in this area (Chuo *et al.,* 2017). We sampled the georeferenced square grids of 2 km × 2 km with transects. In total, we superimposed 23 systematic, equally-spaced (1000 m) line transects (each 2 km long with a random start) across 23 grids (92 km^2) in the study zone (Buckland *et al.,* 2001). We generated the starting point of each transect using a random number table. We oriented line transects in the northwest-southeast direction perpendicular to three rivers which flow through the reserve. We considered transects in grids at the border as inside the reserve if the surface area of the grid within the reserve boundaries was ≥50% of the surface area of a full grid cell. We surveyed all transects assuming that we

detected chimpanzee nests on the transect line with certainty, and that we measured distances from the center of the nest to the line transect correctly (Buckland *et al.,* 2001).

In the field, we identified the starting point of each predetermined line transect from the land cover map and the position of wildlife cameras using a GARMIN GPSMAP 64s device. We installed one LTL-5310A Acorn wildlife camera in each of 10 grids which contained at least one chimpanzee nest group along frequently used chimpanzee paths and feeding or tool use sites (Figure 2.1a). We programmed cameras to operate 24 h a day and to take one photograph and then continue taking a video for 60 s at a resolution of 1080 p at a height 30-80 cm above the ground. The survey team checked camera traps to replace SD cards and batteries during transect visits. We left camera traps at their locations if a chimpanzee was photographed and moved them to a new position if no images of chimpanzee were obtained (Rovero *et al.,* 2010). We replaced defective cameras which contained pictures of chimpanzee in two grids with functional cameras from two grids which did not photograph chimpanzee.

We recorded signs of chimpanzee presence during transect surveys, including nests, sightings, vocalizations, feeding signs, footprints, faeces and tool use sites (Figure 3.2a). We recorded signs of human-related activity including hunting, farming, logging, livestock grazing and collection of non-timber forest products (Figure 3.2b). In the survey, we defined a nest as a structure with visible twigs which appear to be broken or bent inwards by chimpanzees (Tutin & Fernandez, 1984). We distinguished arboreal (night or day) and ground (night or day) nests (Figure 3.3). We considered a nest as "arboreal night" if it was elaborately constructed, with a circular thick cushion-like support, and sometimes with faeces beneath and as "arboreal day" if it was poorly constructed, with weak-cushioning support (Fruth & Hohmann,1996). We considered nests as "ground night" if they were well constructed, contained chimpanzee hair and were in the vicinity of other arboreal nests (Furuichi & Hashimoto, 2000; Koops *et al.,* 2007). Ground day nests were simple weak cushion-like constructions made up of an assemblage of leaves that contained chimpanzee hair (Boesch, 1995). We assumed all nests we encountered during the survey were constructed by chimpanzee because gorillas do not occur in this forest (Chou *et al.,* 2017; Doumbé, 2015).
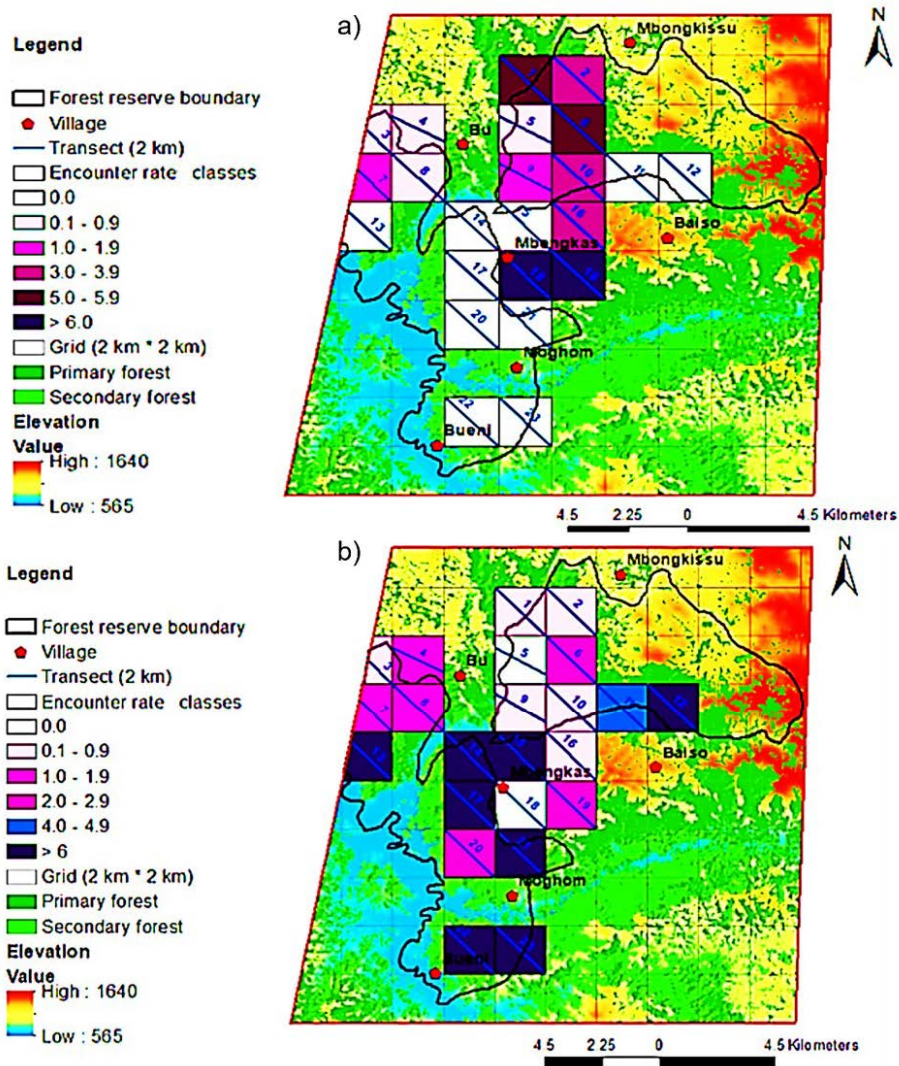
Figure 3. 1 Encounter rate classes for signs of a) chimpanzee and b) human activity during a survey in Kom – Wum Forest Reserve, Cameroon (15 May to 23 September 2018).
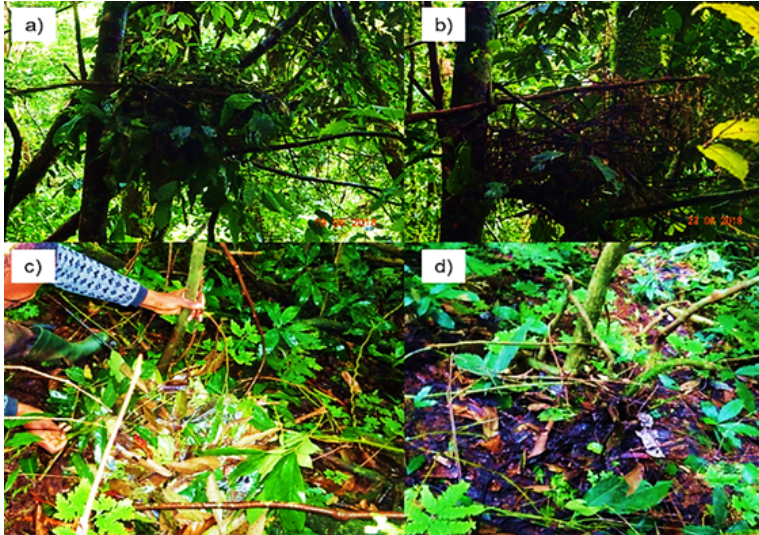
Figure 3. 2 Stages of deterioration in nests made by chimpanzees: a) new arboreal nest (0-16 days), b) old arboreal nest (83-91 days), c) new ground nest (0-3 days), and d) old ground nest (30-75 days) in Kom – Wum Forest Reserve, Cameroon (15 May to 23 September 2018).

We defined nest age following Tutin & Fernandez (1984). We considered nests of the same age class within a radius of 50 m of each other as belonging to the same group (White & Edwards, 2000). We recorded the GPS location, nest group size, perpendicular distance to the transect and age class of nest for all nests. We classified vegetation type as mature forest, old secondary forest or grassland (White & Edwards, 2000). Mature forest consisted of mixed forest with many large trees, high canopy cover and sparse vegetation cover on the ground, consisting of mostly shrubs and mixed forest, with understory dominated by lianas and Marantaceae. Old secondary forest included areas with large trees but showing evidence of disturbance by humans, absence of food crops, with occasional oil palm or mango trees. Grassland was grazing land characterized by short-grass mixed with arable fields and cattle paths. We assessed the area covered by each vegetation type along line transects using a hip chain distance measurer.

3.2.1.3 Monitoring nests and deterioration rates

Based on the results of the first survey, we revisited 13 transects with at least one chimpanzee nest group. We revisited transects approximately every 16 days to establish nest decay rate. We considered new nests encountered during re-visits as constructed between transect walks (Plumptre & Reynolds, 1996). We tagged and revisited all observed nests in the first survey of line transects to evaluate their deterioration. We considered nests as fully decayed when the nest frame had completely disappeared, the branches could no longer be recognized and branches did not appear to be broken or bent by chimpanzees (Kouakou *et al.,* 2009; Tutin & Fernandez 1984). Overall, we surveyed 13 transects five times (130 km) and 10 transects once (20 km), giving an effective effort of 150 km (Table A 2.1).

3.2.2 Statistical analysis

We used Distance 7.0 (Thomas *et al.,* 2010) and R studio version 3.5.1 for statistical analysis (Venables *et al.,* 2008). We checked the normality of residuals with the Shapiro-Wilk normality test and homogeneity of variances using the Levene test. We compared encounter rates of chimpanzee and human activity signs between forest type (mature versus secondary forest), elevation (above versus below 1000 m) and location of transects (inside versus outside reserve boundaries) based on Cohen's d as a measure of effect size and the Wilcoxon rank-sum test (Ho *et al.,* 2019). We used multiple regression (Kim, 2019) to test the effect of human activity (logging, farming, grazing and harvesting of non-timber forest products) on the encounter rate of chimpanzee signs in the reserve. We used a generalized linear mixed-effect regression model (Baayen *et al.,* 2008), with binomial family to predict the effect of edge length, habitat perforation, patch size and forest covers (mature and secondary forests) on the probability of chimpanzee occurrence. We used locations with signs of chimpanzee presence (direct sightings, nests, dung or tool use sites) to extract presence pixel values. We produced chimpanzee absence points (background pixel values) using 100 randomly generated points from each grid containing a chimpanzee point. We used Pearson correlation to test the correlation between predictors in regression analyses.

3.2.2.1 Direct observations and camera trapping

We based direct observation of chimpanzee on groups not individuals (Kühl , 2008). We estimated the relative abundance index (RAI, equation 1) from camera trap data as the number of photographs per 100 trap days (O'Brien *et al.,* 2003). We considered photographs of chimpanzee as independent if the time between two consecutive photographs was longer than 30 mins (O'Brien *et al.,* 2003). We considered photographs with one or more chimpanzee individuals as single independent photographs (Jenks *et al.,* 2011). We defined a trap day as a camera trap installed at a single location for 24 h and the total number of trap days as the sum of trap days for all camera traps minus the days that cameras were defective or ran out of batteries. We noted the date, time and number of individuals for each camera event.

Equation 1 Relative Abundance Index (RAI)

$$\text{RAI} = \left(\frac{\sum of\, all\, independent\, photographs\, of\, chimpanzee\, for\, all\, cameras\, x\, 100}{Total\, number\, of\, camera\, trap\, days\, (Number\, of\, cameras\, x\, number\, of\, days\, cameras\, are\, operational)} \right)$$

$$\text{RAI} = \left(\frac{9x100}{(5*126)} \right) = 1.4 \text{ per 100 days of camera trapping}$$

Density, distance sampling, standing crop nest count and marked nest count

We considered all nests (N = 271) in standing crop nest count (SCNC) analysis as it identifies nest decay rate (Plumptre & Reynolds, 1996) but only nests encountered during the first transect survey (N = 158) for distance sampling analysis. We selected this approach to allow comparison of distance sampling

results to previous studies that used the same approach. We used only new nests encountered during the inter-survey period (N = 113) for marked nest count (MNC) analysis (Plumptre & Reynolds, 1996). We tested several models in distance analyses, and considered the model with the lowest Akaike Information Criterion (AIC) as the best model (Buckland *et al.,* 2001). We based the analysis on single nest observations because we encountered fewer nest groups (N = 59) than required to provide a reliable estimate in Distance (N = 60). We used the effective strip width of all transects (as calculated in distance sampling) to estimate nest density in the SCNC and MNC methods. We converted nest density estimates to density of chimpanzee by applying the formula: $D_{ind} = N_{all\ nests} / 2Lw\ (prt)$, for SCNC where: D_{ind} is the number of individual, N is the number of nests observed along transect, w is effective strip width of transect, L is the transect length (in km), p is the proportion of nest builders in the population, r is the rate of nest production per individual per day, and t is the nest decay time (Ghiglieri, 1984). When using the marked nest count method, the formula becomes: $D_{ind} = N_{newnest} / 2Lw\ (pri)$ where $N_{newnest}$ is the number of new nests (fresh and recent nests) constructed during the inter-survey period, i is the inter-survey period and the other parameters remain the same as in the SCNC formula (Buckland *et al.,* 2001; Hashimoto, 1995; Plumptre & Reynolds, 1996). We obtained densities by correcting for factors such as nest decay rate (estimated in this study) for distance sampling and SCNC, the proportion of nest builders in the population (0.83) following Plumptre & Cox (2006) and the nest production rate per individual per day (1.09) following Morgan *et al.* (2006) and Plumptre & Reynolds (1996). We obtained population sizes by extrapolating chimpanzee density estimates to the total forest area of 92 km^2.

3.2.2.2 Chimpanzee and human activity signs

We calculated encounter rates (number of observations/km) as the total number of signs encountered (N) divided by the total length of the transect (L) in km (Mathot & Doucet, 2005). We calculated encounter rates for signs of chimpanzee and human activity. We defined encounter rate classes and assigned values for each transect. We imported the encounter rate classes into ArcGIS software (ArcMap 10.6.1, ESRI) and assigned different colour bands to different encounter rate classes (no observation = 0.0; few observations = 0.1 - 2.9; many observations >3). Finally, we created spatial distribution maps with different colour bands representing the relative density of chimpanzee and human activity.

3.3. Ethical Note

This research respected the principles for research on nonhuman primates outlined in the American Society of Primatologists manual for the ethical handling of primates. The research permits to conduct this research were obtained from the Ministry of Scientific Research and Innovation in Cameroon.

3.3 Results

3.3.1 Density, direct observations and camera trapping

In total, we counted 271 nests along 23 transects which we surveyed repeatedly over 131 days, for a total survey effort of 150 km. The mean nest group size was 7.0 ± 5.4 (SD, range 2-22). We found 22 fresh nests and fresh chimpanzee faeces at a single location, suggesting that the chimpanzee group left the site a few minutes prior to the visit and slept in the nests overnight. We sighted chimpanzee five times (5 groups, 0.03 groups km^{-1}) during the survey and the maximum group size we observed directly was at least 10 individuals. We estimated chimpanzee density at 0.1 individuals km^{-2} through direct observation, with a maximum group size of 10 chimpanzees in 92 km^2 of the forested area. Camera traps obtained nine independent photographs of chimpanzee (Figure 3.4). The number of individuals in independent photographs or videos ranged 2-9. The relative abundance index of chimpanzee was 1.4 individuals for 100 days of camera trapping (equation 1). The largest photographed group of nine chimpanzees was two adult females each carrying offspring, two weaned juveniles, one adult male, and two adults whose sex we could not determine.

Figure 3. 3 Chimpanzee in Kom – Wum Forest Reserve, Cameroon, photographed by wildlife cameras with a) a juvenile leading a group and b) a juvenile and a nursing adult female (15 May to 23 September 2018).

3.3.2 Nest decay rates

We obtained a mean decay time of 101.0 ± 25.5 (SD) days and an inter-survey period of 64 days by monitoring seven ground nests and 28 arboreal nests from the beginning of the study until all nests decayed completely. All seven ground nests had decayed completely within 75 days while the 28 arboreal nests decayed completely after 126 days (Figure 3.3c and d).

3.3.3 Density, Distance sampling, SCNC and MNC

The half-normal + cosine adjustment model gave the best fit in distance sampling with the lowest AIC value. Chimpanzee densities were 0.9 individuals km^{-2} using distance sampling (Table 3.1). Mean nest densities were 21.1 km^{-2} for MNC and 44.0 km^{-2} SCNC analysis. When corrected for an inter-survey period of 64 days and nest decay rate of 101 days, chimpanzee densities were 0.4 km^{-2} for MNC and 0.5 individuals km^{-2} for SCNC methods (equations 2 and 3). Distance sampling produced the largest nest density per km^{-2} while MNC produced the lowest, resulting in large variability in estimated population sizes in Kom – Wum Forest Reserve (Table 3.1).

Table 3. 1 Density estimates for chimpanzees in Kom – Wum Forest Reserve, Cameroon, using three methods (15 May to 23 September 2018)

Parameters	Distance sampling	Marked nest count	Standing crop nest count
Number of nests	158	113	271
Distance (km)	46	130	150
Strip width (km)	0.02	0.02	0.02
Decay time/Inter-Survey period (days)*	101	64	101
Proportion of nest builders*	NA	0.83	0.83
Nest density (km^{-2})	80.4	24.9	43.9
Chimpanzee density (km^{-2})	0.94	0.37	0.48
Number of chimpanzees	83	37	46

* Proportion of nest builders in the population from Plumptre & Cox (2006) and nest construction rate per day from Plumptre & Reynolds (1996)

Equation 2 MNC equation for transects 1,2,3, 5, 6,9,10,16,18 and 19

$$\left(\frac{Nnewnest(113)}{(2 * w(0.02056) * L(130))/(p(0.83) * r(1.09) * i(64))} \right)$$

Dind. = 113/309.5 = 0.37 weaned chimpanzee km^{-2}

Equation 3 SCNC for all transects

$$Dind = \left(\frac{N(271)}{\left(2 * w(0.02056) * L(150)\right)\left(p(0.83) * r(1.09) * t(101)\right)} \right)$$

Dind. = 271/563.6 = 0.48 weaned chimpanzee km^{-2}

3.3.4 Chimpanzee activity signs

In total, we encountered 405 signs of chimpanzee activity along the 23 transects resulting in 2.7 signs km^{-1}. Nests (N =271) were the most common signs followed by food remains (N = 68), faeces (N = 35), vocalizations (N = 26) and tool use sites (N = 5). The mean encounter rate of chimpanzee signs was significantly higher in mature (2.27 ± SD 3.38 sign km^{-1}) than in secondary forest (0.31 ± SD 0.8 sign km^{-1}, Figure 3.4a, N = 23, W = 364.5, d = 0.9 (95.0%CI 0.0, 1.86), P = 0.016) and significantly lower below 1000 m (0.98 ± SD 1.8 sign km^{-1}) than above 1000 m elevation (3.96 ± SD 2.9 sign km^{-1}, Figure 3.4b, Wilcoxon rank-sum test: N = 23, W = 18.5, d = 1.4 (95.0%CI 0.14, 3.01), P = 0.025). The mean encounter rate of chimpanzee signs did not differ significantly between areas outside (3.31 ± SD 3.0 sign km^{-1}) and inside the reserve boundaries (1.08 ± SD 1.8 sign km^{-1}, Figure 3.4c, Wilcoxon rank-sum test: N = 23, W = 28.5, d = -0.97 (95.0%CI -2.37, 0.13), P = 0.060).
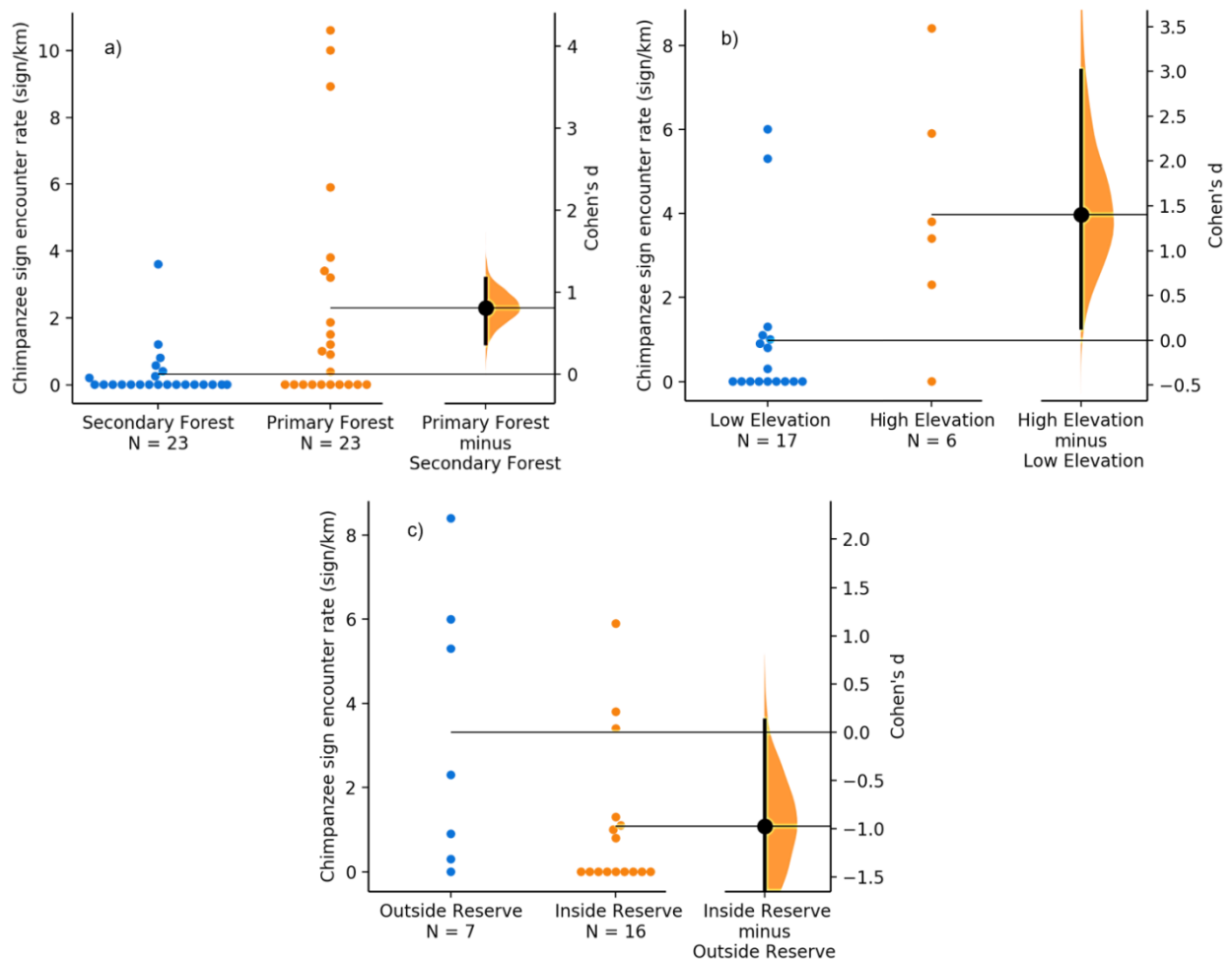
Figure 3. 4 Gardner-Altman estimation plots for mean encounter rates of chimpanzee signs in a) secondary and mature forest, b) low and high elevation and c) outside and inside Kom – Wum Forest Reserve, Cameroon, (15 May to 23 September 2018). In each panel, empirical data for both groups are plotted on the left axis; mean Cohen's d is represented as a dot and horizontal line on the right axis; vertical error bars represent bootstrap 95% confidence interval together with the resampling distribution from 5000 resamples.

3.3.5 Encounter rates of human signs

Overall, we encountered 271 human signs along the 23 transects. Hunting (N =142) was the most common sign, followed by farming (N = 52), logging (N = 41), grazing (N = 22) and collection of non-timber forest products (N = 14). The encounter rate of human activities was 1.9 signs km^{-1}. Common signs of hunting included snares, cartridge cases, hunting camps and traps. The mean encounter rate of human signs was significantly lower in mature ($0.94 \pm$ SD 2.14 sign km^{-1}) than in secondary forest ($8.02 \pm$ SD 13.55 sign km^{-1}, Figure 3.5a, Wilcoxon rank-sum test: N = 23, W = 358, d = -7.09 (95.0%CI -15.3, -3.2), P = 0.029). The mean encounter rates of human signs did not differ significantly between elevations (above 1000 m: $1.4 \pm$ SD 1.61 signs km^{-1}; below 1000 m: $5.58 \pm$ SD 5.39 signs km^{-1}, Figure 3.5b, Wilcoxon rank-sum test: N = 23, W = 27.5, d = -0.901 (95.0%CI -1.53, -0.364), P = 0.204) or

between areas outside (1.54 ± SD 2.5 sign km^{-1}) and inside the reserve (5.28 ± SD 5.4 sign km^{-1}, Figure 3.5c, Wilcoxon rank-sum test: N = 23, W = 80, d = 0.79 (95.0%CI 0.0732, 1.38), P = 0.057).

Human activity significantly affected the encounter rate of chimpanzee signs (N = 23, R^2 = 0.21, df = 20, d = -0.65 (95.0%CI -1.15, -0.07), P = 0.036). Hunting had a significant negative effect on the encounter rate for signs of chimpanzee, while harvesting of non-timber forest products had no significant effect (Table 3.2). The occurrence of chimpanzee signs was negatively related to secondary forest (P < 0.001), habitat perforation (P < 0.001), and the edge length (P < 0.001) and positively related to core areas (P < 0.001).

Table 3. 2 Estimated coefficients and standard errors for a general linear model using human activity signs to predict chimpanzee activity in Kom – Wum Forest Reserve, Cameroon (15 May to 23 September 2018).

Coefficients	Estimate	Standard Error	t	P
(Intercept)	3.00	0.64	4.69	<0.001
Hunting	-0.56	0.24	-2.29	0.033
Non-timber forest product collection	-0.65	0.80	-0.81	0.425
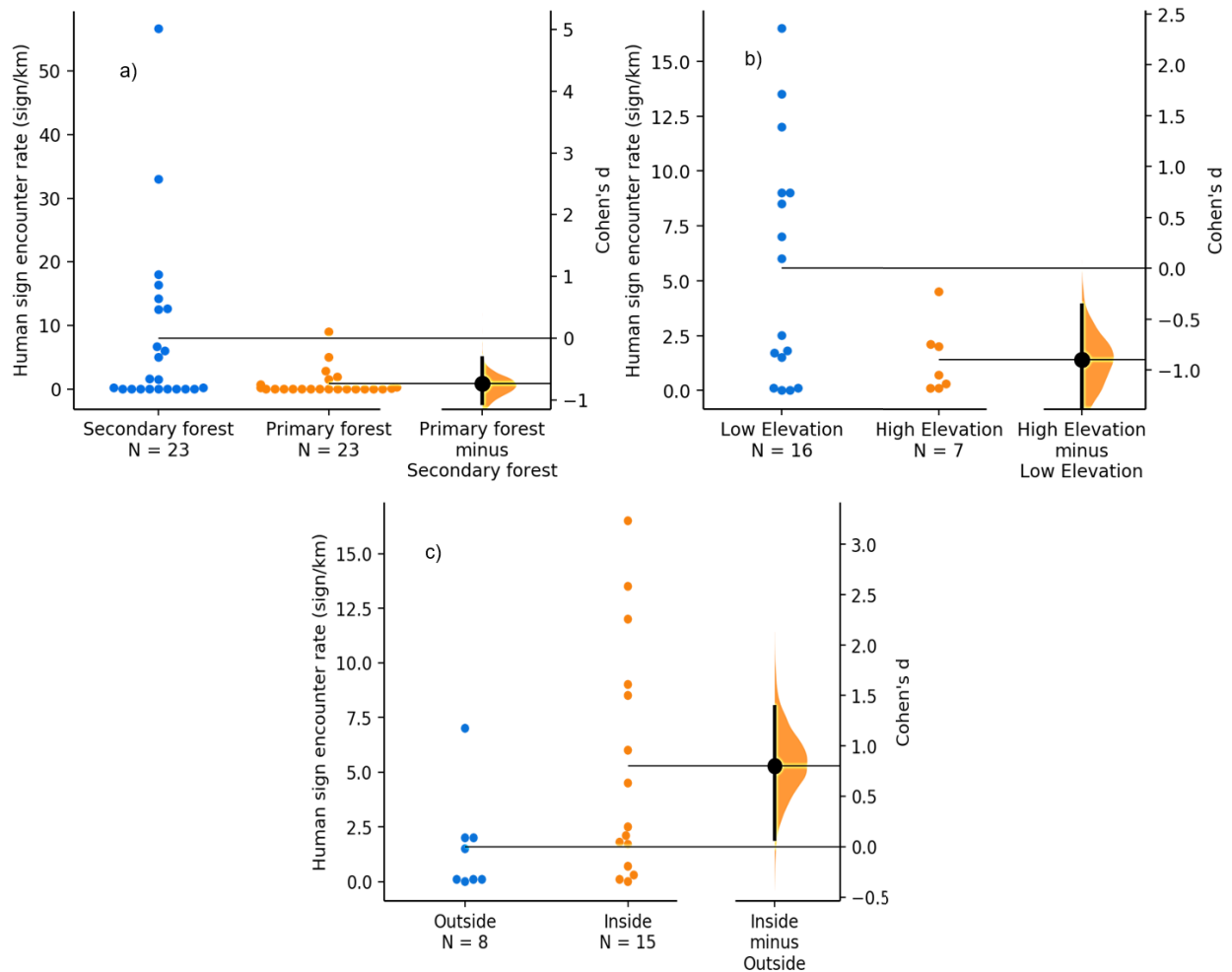
Figure 3. 5 Gardner-Altman estimation plots of mean encounter rates of human signs in a) secondary and mature forest, b) low and high elevation and c) outside and inside Kom – Wum Forest Reserve, Cameroon, (15 May to 23 September 2018). In each panel, empirical data for both groups are plotted on the left axis; mean Cohen's d is represented as a dot and horizontal line on the right axis; vertical error bars represent bootstrap 95% confidence interval together with the resampling distribution from 5000 resamples.

3.4 Discussion

We estimated 10 (direct observation) to 83 (distance sampling) chimpanzees in the study area using the different methods. Signs of chimpanzee activity were significantly more common in mature forests than in secondary forest and at an elevation over 1000 m than at less than 1000 m. The frequency of chimpanzee signs decreased with increasing human activity, particularly hunting. Secondary forest cover, habitat perforation and edge length negatively affected the occurrence of chimpanzee signs while core area had a positive effect. Using several methods to estimate chimpanzee density facilitated the assessment of the state of chimpanzee populations. The results are alarming, as most density estimates from this study are the lowest in the published literature (Table 3.3; with the exception of distance sampling). This estimate of the population size of the chimpanzee in Kom – Wum Forest Reserve,

coupled with previous integrated assessments in Ngel Nyaki Forest Reserve in Nigeria (Dutton, 2012), highlight the urgent need to take action to conserve this subspecies in fragmented habitats.

Table 3. 3 Densities of chimpanzee across study sites (15 May to 23 September 2018, for this study only).

Study site	Country	Decay rates (days)	Method	Density (km^{-2}, RAI) ± 95% CI	Reference
KWFR	Cameroon	-	CT	1.43	This study
DFR	Cameroon	-	CT	1.61(0.77–2.9)	(Bruce *et al.,* 2018)
KWFR	Cameroon	-	DO	0.12	This study
GGNP	Nigeria	-	DO	1.3	(Sommer *et al.,* 2004)
NNFR	Nigeria	-	DO	1.5	(Dutton, 2012)
KWFR	Cameroon	101	DS	0.94 (0.50-1.77)	This study
NNFR	Nigeria	168.48	DS	0.33	(Dutton, 2012)
KWFR	Cameroon	-	MNC	0.37	This study
NNFR	Nigeria	-	MNC	1.67	(Beck & Chapman, 2008)
NNFR	Nigeria	-	MNC	0.69	(Dutton, 2012)
KWFR	Cameroon	101	SCNC	0.48	This study
MDNP	Cameroon	88	SCNC	0.88 (0.55–1.41)	(Kamgang *et al.,* 2018)
NNFR	Nigeria	168.48	SCNC	1.5	(Dutton, 2012)

Camera trapping, Direct observation, Distance sampling, Dja Faunal Reserve, Kom – Wum Forest Reserve, Gashaka-Gumti National Park, Mbam Djerem National Park, Ngel Nyaki Forest Reserve

3.4.1Chimpanzee density

In contrast to the five chimpanzee groups seen during the present study, previous surveys encountered one or two groups in Kom – Wum Forest Reserve (Chuo *et al.,* 2017; Doumbé, 2015). Our sampling effort (150 km) was higher than in previous surveys (46 km), but our encounter rate of chimpanzee groups (0.03 groups km^{-1}) was similar to that in previous studies (0.02 groups km^{-1}). This suggests that the group sizes of chimpanzee observed directly are similar across studies and that the population may be stable since the first survey in 2015. Sampling effort could therefore be reduced in future studies. The number of independent photographs captured by camera traps (N = 9) was higher than the number of direct observations of chimpanzee (N = 5). We could also identify the sex of a few chimpanzee individuals from camera trap footage. The relative abundance of chimpanzee estimated in our study was close to estimates for the central chimpanzee (*Pan troglodytes troglodytes*) in the northern sector of Dja Faunal Reserve in Cameroon (Bruce *et al.,* 2018). A similarity in the habitat of both reserves (rainforest) can explain the closeness of these results: lowland montane rainforest for Kom – Wum Forest Reserve

(Sunderland & Mannaseh, 2003) and lowland rainforest for Dja Faunal Reserve (Abwe *et al.,* 2019, Sesink- Clee *et al.,* 2015).

Estimates of nest decay time needed for additional density methods indicated 101 days for total decay, which is lower than estimates from Ngel Nyaki Forest Reserve in Nigeria (Dutton, 2012). Ground nests decayed considerably faster than arboreal nests. Ground nests are often poorly constructed, since they are usually used temporarily during the day for resting (Brownlow *et al.,* 2001; Koops *et al.,* 2007). Site-specific differences are not surprising given that nest decay times vary over space and time and with sample period, tree species, forest type, nest height and position, soil pH and average rainfall (Ancrenaz *et al.,* 2005; Buij *et al.,* 2003; Johnson *et al.,* 2005; Kouakou *et al.,* 2009; Marshall *et al.,* 2007; Mathewson *et al.,* 2008; van Schaik *et al.,* 1995; Walsh & White, 2005).

The density estimate for chimpanzee based on distance sampling was the only estimate that was higher than previously derived densities for chimpanzee (Kamgang *et al.,* 2018). Density estimates based on the SCNC and MNC methods were lower than all previously published results. The higher densities of chimpanzee in Ngel Nyaki Forest Reserve could be a result of the reserve's small size (7 km^2) (Beck & Chapman, 2008; Dutton, 2012) compared to Kom – Wum Forest Reserve (80 km^2). The higher estimated densities for the Western chimpanzee (*Pan troglodytes verus*) in Taï National Park is probably due to the presence of large undisturbed remnants of mature tropical forest (Boesch & Boesch-Achermann, 2000; Kouakou *et al.,* 2009). Generally, density estimates of 0.1-0.9 chimpanzees km^{-2} in this study fall within the ranges for sites of central chimpanzees in Cameroon (0.1-1.2 km^{-2}) (Ngalla *et al.,* 2005) and of other populations of chimpanzees across West Africa (0.2-2.0 km^{-2}) (Kormos *et al.,* 2003).

Nest decay time and season may have influenced the results of the SCNC (0.5 chimpanzee km^{-2}, 43 individuals) and distance sampling approaches (0.9 chimpanzee km^{-2}, 83 individuals) as both rely on nest decay time to estimate chimpanzee density (Mathewson *et al.,* 2008; Tutin *et al.,* 1995). The result of the MNC technique (0.4 Chimpanzee km^{-2}, 37 individuals) was comparable to the ten chimpanzee directly observed and the largest nest group size (22 nests) encountered during our survey. Subsequent surveys in Kom – Wum Forest Reserve should consider using the MNC technique, since it is not biased by estimated nest decay rates and is sensitive in detecting changes in density, movement and seasonal habitat use (Buij *et al.,* 2003; Devos *et al.,* 2008). The survey period should include data from the dry season for SCNC and distance sampling methods to accurately estimate average nest decay times in the dry season. The SCNC method is cheaper, requires less labour and will produce accurate estimates if the nest decay time is properly calculated (Kouakou *et al.,* 2009). However, other parameters such as elevation, wood density and soil pH should be considered when employing the SCNC method (Buij *et al.,* 2003; van Schaik *et al.,* 1995). Each method has strengths and weaknesses and is applicable under certain conditions (Vink *et al.,* 2020). Overall, 10-83 chimpanzee live in the study area depending on the estimation method.

3.4.2 Chimpanzee activity

The observed encounter rate for chimpanzee signs (2.7 signs km^{-1}) was considerably lower than rates previously reported for this study area (Chuo *et al.,* 2017), but there were differences in activity signs between habitat types. We found higher encounter rates in mature forest at higher elevation. At Tofala Hill Wildlife Sanctuary, chimpanzee also nests more frequently in mature vegetation at higher elevations (800-1,000m; Njukang *et al.,* 2019). At Babanki-Finge forest in Cameroon, a majority of nests were recorded in dense vegetation at 500-2,300m (Doumbé, 2014). At Mbam and Djerem National Park in Cameroon, chimpanzee preferred dense habitats at higher elevation (Kamgang *et al.,* 2018). Similar results were recorded from Seringbara, Nimba Mountains in the Republic of Guinea, where chimpanzee *n*ests were more abundant in mature forest and above 1,000 m than in secondary forest and below 1000 m (Koops *et al.,* 2012). More recent research in the Nimba Mountains revealed that chimpanzee preferred old-growth over secondary forest for nesting (Granier *et al.,* 2014). Higher encounter rates of human activity in the secondary forests in Kom – Wum Forest Reserve may be linked to the low encounter rates for chimpanzee *s*igns compared to mature forest areas. Higher encounter rates for chimpanzee signs in mature forests in Tofala Hill Wildlife Sanctuary and Babanki-Finge forest in Cameroon were also associated with lower encounter rates for hunting, logging and farming. A review of 52 chimpanzee nest surveys across West Africa showed that chimpanzee prefer rainforests with a low degree of human impact (Heinicke *et al.,* 2019). In the southeastern forest region of Bossou, Guinea, chimpanzee preferred mature forest with abundant supply of wild fruits over disturbed habitats for travelling and resting (Bryson-Morrison *et al.,* 2017). Similarly to other chimpanzee subspecies, the chimpanzee of Kom – Wum prefer mature forest compared to secondary forest. Mature forest tend to provide suitable conditions (habitat with enough food and shelter) for the Nigeria – Cameroon chimpanzee (Carvalho *et al.,* 2021) and other great apes species (Junker *et al.,* 2012).

After controlling for the effect of forest cover, habitat perforation, edge length and secondary forest had a significant negative effect on chimpanzee occurrence in Kom – Wum Forest Reserve. In contrast, core areas had a significant positive effect. The low occurrence of chimpanzee in perforated forest, at forest edges and secondary forest is probably best explained by higher human activity in these areas, as previously reported (Morgan *et al.,* 2011). This interpretation is supported by results from Guinea where chimpanzee was more likely to feed away from cultivated areas than away from mature forest (Bryson-Morrison *et al.,* 2017). Other primates respond negatively to habitat degradation (Arroyo-Rodríguez & Dias 2010). For example, in LosTuxtlas and the lowlands of Tabasco, Mexico, the mantled howler (*Alouatta palliata*) preferred interior forest with high quality habitat (feeding trees with larger Diameter at Breast Height) to edge forest (Arroyo-Rodríguez and Mandujano 2006; Muñoz *et al.,* 2006). Although we did not assess food availability of chimpanzee in forest edges and interior forest in this study, the positive relationship between chimpanzee occurrence and core areas in Kom – Wum Forest Reserve could be explained by resource availability (e.g. food and nest sites). At Goualougo Triangle in the

Republic of Congo, transects that traversed the core area of the community range had higher encounter rates of chimpanzee nests and nests sites compared to more peripheral areas (Morgan *et al.,* 2006).

The results we obtained for Kom – Wum Forest Reserve contrast with those from Nyungwe National Park, Rwanda, where chimpanzee used forest edges for feeding, nesting and travelling (Hasabwamariya, 2018). This difference may be a consequence of the behavioural flexibility of primates living in human-dominated landscape (McCarthy *et al.,* 2017). The persistence of primates in human disturbed landscapes can be related to their flexibility in diet selection (Marsh *et al.,* 2016). For example, in Magdalena Valley, Colombia, white-fronted capuchin (*Cebus albifrons)* (a more diet generalist species) was encountered in a majority of fragments irrespective of high human disturbance. In contrast, the brown spider monkey (*Ateles hybridus)* (a species with a more selective diet) was absent or less abundant in highly disturbed forest fragments. At La Suerte Biological Research Station, Costa Rica, there was no difference in the encounter rates of mantled howler(*Alouatta palliata*), white-faced capuchins (*Cebus capucinus*) and Central American spider monkeys (*Ateles geoffroyi*) in forest edges with high human disturbance and interior forest (Bolt *et al.,* 2018).

3.5 Conclusion

This study shows that forest degradation resulting from human activity had a significant negative impact on the encounter rate of chimpanzee signs in Kom – Wum Forest Reserve, Cameroon. Chimpanzee signs were mostly found in mature forest compared to secondary forest, at higher elevation than lower elevation, and their signs less frequently observed with increasing human activities. This study supports previous work showing that sampling effort and methodological approach can yield variable estimates of population size (Vink *et al.,* 2020). The MNC technique is sensitive in detecting changes in density(Buij *et al.,* 2003; Devos *et al.,* 2008) and is therefore recommended in combination with camera trapping to monitor the population status of chimpanzees. Our results reveal the importance of undisturbed mature forests as core habitats for chimpanzee populations in Kom – Wum Forest Reserve and surrounding forests. Secondary forests may provide essential habitats for chimpanzees (Basabose, 2005), but chimpanzee in this study tended to avoid secondary forest, most likely due to high human activity. Future effort focusing on the conservation of chimpanzees in Kom – Wum Forest Reserve should be directed towards reducing human activities and reforestating degraded areas. Local human communities need to be actively involved in monitoring programs and law enforcement activities, such as regular anti-poaching patrols within and around the reserve, to prevent hunting. Providing incentives to local community members to generate alternative livelihood activities such as piggeries and poultry farms have potential to reduce the pressure on forest resources (Van Vliet, 2011). The promotion of conservation education is essential to discourage bushmeat hunting and to maintain continuous forest through the reforestation of degraded areas.

Chapter 4: Environmental and Anthropogenic Effects on the Nesting Patterns of Nigeria – Cameroon Chimpanzees in North – West Cameroon

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Environmental and anthropogenic effects on the nesting patterns of Nigeria–Cameroon chimpanzees in North-West Cameroon

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Abstract

Environmental conditions and human activity influence the selection of nest sites by chimpanzees and may have serious conservation implications. We examined the characteristics of nesting trees preferred by chimpanzees, investigated the effect of vegetation composition and topography on nest site locations and seasonality on nesting heights of chimpanzees, and verified the effect of predator occurrence and human activity on the nesting behavior of the Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti*) in Kom – Wum Forest Reserve (KWFR) and surrounding unprotected forest in Cameroon. We recorded 923 nests, 502 signs of human activity, and 646 nesting trees along line transects and recces (reconnaissance) for two seasons. We found that chimpanzees constructed more arboreal nests on tall primary trees with high lowest branch height and large diameter at breast height. Moreover, they oriented their nests within trees in the slope direction when the nesting trees were located on slopes. Additionally, the occurrence of chimpanzee nests was positively related to increasing elevation and slope and decreased with distance to mature forest. In contrast, the number of nests increased with distance to secondary forest, open land, and villages, and nesting height was not influenced by seasons. While we recorded no signs of large nocturnal chimpanzee predators at nesting trees, we found signs of hunting activity at nesting locations. Nesting high in trees is likely a way of avoiding hunting, while nest orientation within trees in slope direction shortens escape routes from human hunters. Our findings suggest that chimpanzees select safe trees (tall trees with high lowest branch height) located in nesting areas (mature forest, high elevation, and steep slopes) that are not easily accessible by humans. Therefore, conservation efforts should focus on protecting mature forests at high elevation and steep slopes and reducing human impact.

Keywords: Ecological factors, Human activity, Nesting behavior, Nigeria – Cameroon chimpanzee, Predation

4.1 Introduction

All weaned non-human great apes construct sleeping or resting platforms (hereafter "nests") by modifying branches and leaves of trees (Tutin & Fernandez, 1984; Goodall, 1962). This behavior is common for chimpanzees, bonobos, orangutans (Fruth & Hohmann, 1996), and gorillas (Iwata & Ando, 2007). Like other great apes, chimpanzees build a new nest every night or may re-use old nests after adding new material to reinforce them (Hernandez-Aguilar, 2006; Hernandez-Aguilar, 2009). Generally, their nests can be arboreal (Poulsen & Clark, 2004) or can be built on the ground (Furuichi & Hashimoto, 2000; Abwe & Morgan, 2008; Tagg *et al.,* 2013). They can further be categorized as night or day nests (Brownlow *et al.,* 2001; Koops *et al.,* 2012). Usually, night nests are arboreal and more elaborate constructions (Fruth & Hohmann, 1996; Reynolds, 2005), while day nests tend to be terrestrial and the structure is less sophisticated (Brownlow *et al.,* 2001; Koops *et al.,* 2012). Day nests on the ground are constructed with leaves or consist of ferns which are used for resting during the day,

whereas night nests on the ground consist of bent and broken branches (Furuichi & Hashimoto, 2000). Unlike day nests on the ground are mostly found without trees in their neighborhood, night nests on the ground usually occur in groups and are linked with arboreal nests in their surroundings (Koops *et al.,* 2007). Furthermore, day nests on the ground are used to protect chimpanzees from the cold soil surface (Boesch, 1995).

The selection of individual nesting trees by chimpanzees has been attributed to the morphological characteristics of trees, including the tree diameter, tree height, and lowest branch height (Hernandez-Aguilar *et al.,* 2013; Hakizimana *et al.,* 2015) as well as the species type (Brownlow *et al.,* 2001; Sanz *et al.,* 2007; Stanford & O'Malley, 2008). In addition to the selection of individual trees, chimpanzees also select nesting areas within forests, including a preference for mature forest cover (Koops *et al.,* 2012; Bryson-Morrison *et al.,* 2017), high elevation (Koops *et al.,* 2012; Barca *et al.,* 2018), steep slopes (Dutton *et al.,* 2016; Abwe; 2018; Kamgang *et al.,* 2018) and closed canopy (Abwe, 2018). Besides habitat and topographic factors, seasonality may affect nest construction in great apes. For example, Takemoto (2004) noted that chimpanzees tend to show arboreal behavior in the wet season to minimize the effect of heat loss and spend more time on the ground during the dry season due to an increase in surrounding temperatures. Similarly, Koops *et al.* (2012) demonstrated that nesting at elevated heights in the wet season is a strategy to avoid constructing nests in humid conditions closer to the ground.

Non-human primates select nesting sites in trees to reduce access or detection by predators (Anderson, 1984). For instance, Stewart *et al.* (2013) showed that chimpanzees nest at high and peripheral nesting positions within trees in areas with potential terrestrial predators such as leopard (*Panthera pardus*) and lion (*Panthera leo*). Furthermore, human activity may also affect the selection of nesting locations by chimpanzees (Tagg & Willie, 2013; Heinicke *et al.,* 2019). Particularly, the construction of night nests on the ground by chimpanzees is more frequently observed in areas with limited human activity (Hicks *et al.,* 2010; Last & Muh, 2013).

Agricultural activity, illegal timber exploitation, uncontrolled burning, and illegal hunting are major anthropogenic threats to the Nigeria – Cameroon chimpanzee (Morgan *et al.,* 2011). This chimpanzee subspecies has about 3,500 individuals remaining in the wild, is the most threatened subspecies, and relatively unstudied. Since the recognition of the Nigeria – Cameroon chimpanzee subspecies in 1997 (Gonder *et al.,* 1997), several studies have been conducted to improve our understanding of their nesting behavior at several sites, including the selection of nest trees and areas in relation to ecological conditions and human activity in Ngel Nyaki Forest Reserve (Dutton *et al.,* 2016) and Gashaka-Gumti National Park (Fowler, 2006) in Nigeria. In Cameroon, recent studies focused on the selection of nest locations in relation to the availability of fruits in Ebo Forest Reserve (Abwe, 2018), the effects of preference for a particular habitat type and topography in Mbam-Djerem National Park (Kamgang *et*

al., 2018), and in Ebo Forest Reserve (Abwe, 2018), the effect of human activity on arboreal and ground nest location in Lebialem-Mone Forest (Last & Muh, 2013), Tolafa Hill Wildlife Sanctuary (Njukang *et al.,* 2019), Mone-Oku Forest (Wade, 2020) and Babanki–Finge Forest (Doumbé, 2014). However, information on nesting behavior of the Nigeria – Cameroon chimpanzee is still missing from priority conservation areas as outlined in the IUCN-endorsed regional conservation action plan (Morgan *et al.,* 2011). The Kom – Wum Forest Reserve (KWFR) is considered a high priority conservation area for the Nigeria – Cameroon chimpanzee, and recommendations were made to conduct surveys on their abundance, behavior, and distribution (Morgan *et al.,* 2011). Initial chimpanzee surveys in KWFR focused on confirming the presence of chimpanzees (Doumbé, 2015), estimating the population size (Chuo *et al.,* 2017; Fotang *et al.,* 2021), and indicating habitat preferences (Fotang *et al.,* 2021). Doumbé (2015) and Chuo *et al. (*2017) further suggested that chimpanzee predators are absent from KWFR, potentially resulting in specific nesting behavior. However, previous studies provided very little information about potential drivers of nesting behavior in this high-priority conservation area.

To improve our understanding of factors affecting nest building in chimpanzees in general, and to add to previous knowledge on nesting ecology of the Nigeria – Cameroon chimpanzee in particular, our study aims to analyze: a) which traits of tree species are preferred for nesting (nesting tree selection); b) the effects of environmental factors (vegetation, topography, seasonality) on nesting behavior (nesting area selection) and c) if predator presence and human activity affect the selection of nest sites and nest distribution in trees (disturbance) in KWFR. We hypothesize that the selection of nesting trees by chimpanzees is driven by specific tree traits and that the selection of nesting areas further depends on the local vegetation composition, topography, and seasons (Koops *et al.,* 2012). We predict that chimpanzees i) construct more nests on tall primary trees (trees that provide the main support for nests), trees with larger diameter and high lowest branch height; ii) orientate their nests in the direction of the decreasing slope, iii) frequently nest in mature forests, at higher elevations, on steep slopes and that iv) nest higher in the wet season than the dry season. We further hypothesize that chimpanzees nest higher in trees if predators are present or when humans are active in the nesting location. We recommend conservation actions required to ensure the long-term survival of chimpanzees in the reserve.

4.2 Material & methods

4.2.1 Ethics statement

We conducted this research respecting the principles for research on non-human primates outlined in the American Society of Primatologists manual for primates' ethical handling. We obtained authorization from the Ministry of Scientific Research and Innovation in Cameroon and respected the protocols of the 1994 forestry and wildlife law governing research on chimpanzees.

4.2.2 Chimpanzee nest surveys and description of nesting trees

We generated a 2 x 2 km grid across the study area (100 km^2) to place line transects (each 2 km in length) equally spaced (1000 m) following a systematic design (Buckland *et al.,* 2001). Additionally, we considered the reconnaissance (recce) method to identify hotspots of chimpanzee activity since they are unhabituated (Kühl*,* 2008). Based on the results from recce surveys, we monthly surveyed 13 line transects (26 km) and 42.09 km recce with at least one chimpanzee nest during two seasons: wet (May to September 2018) and dry (November 2019 to March 2020). For every nesting site encountered, we recorded the characteristics of nesting trees following Baldwin *et al.* (1981). We also marked nesting tree locations using a GARMIN GPSMAP 64s device and recorded the nest height, tree height, and lowest branch height using a hypsometer (Nikon Forestry Pro 6x216x21\11-55YD). Furthermore, we noted the number of nests per tree and the number of trees per nest (integrated nest), and measured the diameter at breast height (DBH) and the horizontal distance of the nest from the tree trunk using a 30-meter tape. For each nest, we recorded the nest type following Furuichi & Hashimoto (2000). Additionally, we defined the nest age classes per tree as fresh - when all leaves in the nest were green; recent - drying leaves of distinct colors; old - nest structure is unbroken with most of the leaves being brown; and very old - nest with holes displaying little or no leaves, but still be distinguished by bent twigs following Tutin & Fernandez (1984). Simultaneously, we calculated the vertical position of a nest within the crown following Hernandez-Aguilar *et al.* (2013). We recorded the slope direction for nests and the nest orientation within a tree using a Gearmax® Professional military clinometer following Hernandez-Aguilar *et al.* (2013). For nesting trees located on slopes, we classified nests as oriented to the east (>22.5° and ≤ 167.5°), west (>202.5° and ≤ 337.5°), north (>337.5° and ≤ 22.5°), and south (between >167.5° and ≤ 202.5°). Nesting trees in the field were identified by a Ph.D. botanist student (Nkemnkeng Francoline, Jong) from the University of Dschang, Cameroon. Samples and pictures of unidentified plants were taken to the Cameroon National Herbarium for identification by experts. We conducted a Bivariate Spearman's rank correlation analyses to test the relationship between tree height and nest height, DBH, and lowest branch height. The Chi-squared tests were used to analyze whether chimpanzee nest orientation depended on slope direction and the Wilcoxon rank-sum tests to compare mean nest heights between wet and dry seasons.

4.2.3 Environmental determinants of nesting sites

We described vegetation at nesting sites following White & Edwards(2000): mature forests - mixed forest with many large trees, unbroken canopy, and scanty vegetation cover on the ground, and mixed forest with dense vegetation cover on the ground dominated by lianas and Marantaceae; old secondary forest included - sections of forest with large trees, but showing indicators of previous disturbance by humans, with no grown crops, but occasionally with old palm or mango trees still present; and grassland - grazing land depicted by short-grass mixed with arable fields and cattle paths. Following Koops *et al.* (2012)*,* we classified canopy cover as: no cover (0%) - nests with no branches with leaves over a nest;

little cover - when 1-25% of nests were covered by branches with leaves; light cover - when 26–50% of nests were covered; moderate cover - when 51–75% of nests were covered; and complete cover - when 76–100% of nests were covered. The slope for each nest was classified as flat ground (0°), gentle (1-5.7°), steep (5.7°-26.6°) or precipitous (>26.6°) following De Vere (2011).

In addition to field surveys, we acquired land cover from remote sensing data (Landsat 8, 30 m pixel, on September 02, 2017). The imagery was classified into mature forest, secondary forest, bare lands, and water bodies using supervised image classification and the maximum likelihood algorithm (Ganasri & Dwarakish, 2015). We obtained the elevation from a Shuttle Radar Topography Mission 30 m resolution Digital Elevation Model (Jarvis, 2008).

To assess whether nests are distributed randomly regarding the environmental variables or not, we created 2000 random points for each variable; that is, 2000 points for elevation, slope, mature forest, secondary forest, bare land, villages, aspects, rivers, and signs of human activities (Figure 4.1). We used the whole KWFR Reserve and surrounding forest with chimpanzee nests to define the limits of the random points. We then created layers representing distances to the random points generated to each environmental variable by calculating Euclidean distances and extracted these distances to nest locations following Enoguanbhor *et al.* (2020).

We first checked collinearity among environmental variables by calculating the variance inflation factor (VIF) using the package usdm (Naimi *et al.,* 2014). We excluded all environmental variables with a VIF > 5 (Table 4.3). We then performed a Pearson correlation test to calculate the collinearity among pairs of environmental variables. For each pair of significantly correlated environmental variables (slope versus aspect and elevation versus rivers), we eliminated one of the environmental variables (i.e., aspect and rivers). Our final model considered seven environmental variables, including elevation, slope, distance to mature forest, distance to secondary forest, distance to bare land, distance to villages, and distance to signs of human activities (Table 4.3). We used the package car (Fox &Weisberg, 2018) and a linear model function to perform a multiple regression analysis of the relationship between the dependent variable (chimpanzee nest locations) and independent variable, including ecological (distance to mature forest, distance to secondary forest, elevation, slope, aspect, distance to rivers) and human factors (distance to villages, distance to bare land, distance to signs of human activity). All spatial analyses were conducted in ArcGIS 10.6.1 (ESRI, 2018) and hypothesis testing in R (R core team, 2016) version 3.5.1 (Venables *et al.,* 2009).

4.2.4 Antipredator/human avoidance

To investigate the effect of predator or human activity on the nesting behavior, we searched for signs of chimpanzee predators or human activity along transects and recces. We further attached ten camera traps to trees at a height between 30 and 80 cm along frequently used chimpanzee routes leading to nesting

sites to increase the probability of detecting chimpanzee predators (Fotang *et al.,* 2021). We recorded human signs (farms, spent cartridges, snares, non-timber forest product collection, timber extraction, grazing activities) within a 50 m radius of each nesting site following White & Edwards (2000).

We calculated the Kilometric Count Index for human signs (encounter rates of human signs) as the total number of human signs encountered (N) during the survey divided by the total length of the transect (L) in km (Mathot & Doucet, 2005).

4.3 Results

4.3.1 Physical characteristics of nesting trees

We found arboreal, ground, and liana nests in descending order during our survey (Table 4.1). Most nests were recorded in the wet season. Consequently, more trees were used for nesting in the wet season (Table 4.1). Most nests were built in a single tree, and the rest (integrated nests) were built by integrating the branches from other trees (non-single trees). The majority of trees provided the main support for nests (primary trees), and the rest provided minor support (secondary trees). The mean height and DBH of primary trees were greater than those of secondary trees (Table 4.2). The height of nesting trees and nest height (r = 0.91, N = 625), the tree DBH (r = 0.59, N = 625) and the lowest branch height (r =0.62, N = 221) were positively correlated.

Table 4. 1 Number of nests and trees recorded per season (wet and dry), in total and percentage of each nest category.

Season	N wet	N dry	N total	Percentage
Nests				
All nests	552	371	923	100
Arboreal nests	541	307	848	92
Ground nests	11	61	72	8
Nests built in liana	0	3	3	<1
Nests built in single trees	531	300	831	-
Integrated nests	10	7	17	-
Nesting trees				
All trees	425	221	646	100
Praimary trees	404	221	625	97
Secondary trees	10	11	21	-
Single trees	392	216	608	-
Non-single trees	24	14	38	3

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Table 4. 2 Physical characteristics of nesting trees and nests

	Mean	Median	SD	Range	N
Nesting trees					
DBH of primary trees (cm)	42.0	37.0	23.8	3.8–155.3	625
Height of primary trees (m)	17.0	17.0	5.8	1.0–37.9	625
Number of nests per tree (N)	1.4	1.0	5.3	1.0–6.0	625
Lowest branch height (m)	10.0	9.8	4.9	0.8–30.4	221
Crown height (m)	6.3	5.3	4.2	0.4–20.8	221
DBH of secondary trees (cm)	15.3	5.8	25	1.0–105.1	21
Height of secondary trees (m)	8.6	10.4	6.0	1.0–24.5	21
Nests					
Nest height (m)	15.5	15.6	5.4	1.0–33.4	851
Distance from tree trunk (m)	1.4	0.9	2.0	0.0–13.8	307
Number of trees per nest (N)	2.2	2.0	0.8	1.0–5.0	38

Of the 923 nests, 20 nests had no vegetation above the nest (0% cover), 223 had little vegetation above the nest (1 – 25% of the nest was cover by branches with leaves), 250 (26%) had light vegetation above the nest (25 – 50% of the nest was covered by branches with leaves), 271 moderately covered (51 – 75% of a nest was covered by branches with leaves) and 159 of the nest was completely covered by vegetation (branches with leaves covered 100 % of the nest). Of 307 arboreal nests recorded in the dry season, 213 were constructed on western slopes, 49 on eastern slopes, and 45 on north or south-facing slopes. Of the nest constructed on the eastern slopes, 25 were oriented east of the tree trunk, 19 were found exactly on the top of the base of the tree trunk (no orientation), three were oriented north of the tree trunk, one was oriented west of the tree trunk, and one was oriented south of the tree trunk. Of the 213 nests constructed on western slopes, 90 were oriented west from the tree trunk, 77 had no orientation within the tree since they were found exactly on the top of the trunk, 28 north, 17 east, and one south. Of 307 nests, 106 were oriented west within the tree (>202.5° and <337.5°), 107 directly on the trunk, 50 were oriented east within the tree (>22.5° and <167.5°), 22 north within the tree and 22 south within the tree.

There was a significant relationship between nest orientation within the tree and slope direction (Chi-squared test = 40.675, P < 0.010). Most nests located on the west slope were oriented in western direction (Chi-squared test = 79.752, P < 0.001). Of the 72 ground nests recorded, 57 were night nests and 15 day nests. All ground nests were located on precipitous slopes (> 26.6°) and were found under high canopy cover (75 – 100%). A majority of the ground nests were further supported either by a tree trunk, tree roots, fallen wood, a stone, or liana from different plants.

4.3.2 The environmental determinants of the selection of nesting locations

The multiple linear regression model indicates that the locations of chimpanzee nests decreased with distance to mature forest and increases with slope and elevation (Table 4.3; df=1992, R²=0.69, F=628.8, P<0.001; Figure 4.1b f and c). In contrast, the number of chimpanzee nests increased with distance to secondary forests, bare land, and villages (Table 4.3; Figure 4.1 a,d and e). Of 923 chimpanzee nests, we found 532 (58%) in mature forest and 391 (42%) in secondary forest. Chimpanzees built nests at elevations between 836 and 1279 m above sea level (Figure 4.1c) with increasing nest locations at higher elevation (Table 4.3). We found 290 nests below 1000 m and more 633 above 1000 m (N=923). Of the 923 nests, we found 17 on flat ground, one on a gentle slope (0 – 5.7°), 30 on a steep slope (5.7°– 26.6°), and 875 on a very steep slope (>26.6°). The mean nest height of chimpanzees nest did not differ between the wet season (15.9 m SD ±3.3, N=541) and the dry season (14.8 m ± SD 2.8; Wilcoxon rank-sum test: W=41, P = 0.460, N=307).

Table 4. 3 Multiple linear regression model showing environmental variables, of chimpanzee nest site selection and the variance inflation factor.

Environmental variable	Parameter estimates	Standard Errors	P	Variance Inflation Factor
Intercept	544.41	145.38	<0.001	
Elevation	0.49	0.14	<0.001	1.40
Slope	0.22	0.09	<0.05	1.01
Distance to mature forest	2.98	0.55	<0.001	1.54
Distance to secondary forest	-1.71	0.15	<0.001	1.72
Distance to bare land	-0.41	0.12	<0.001	1.51
Distance to villages	-0.22	0.03	<0.001	1.41
Distance to signs of human activity	1.09	0.02	<0.001	1.65
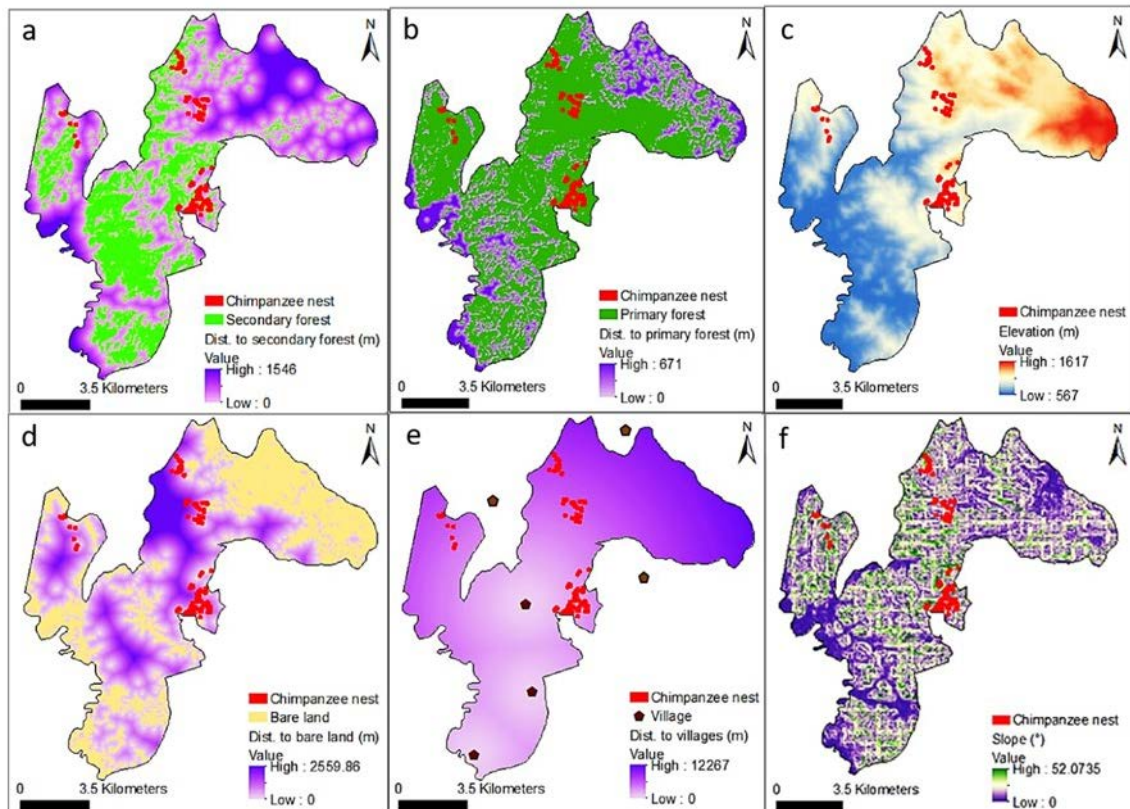
Figure 4. 1 The distribution of chimpanzee nests with a) distance to mature forest, b) distance to secondary forest, c) elevation, d) distance to bare land, e) distance to villages, and f) slopes.

4.3.3 Antipredator/human avoidance hypothesis

We found no signs of chimpanzee predators (vocalizations, faeces or footprints) during the line transect and recce surveys, and the cameras recorded no pictures of large nocturnal chimpanzee predators (leopards). In total, we recorded 502 signs of human activity over a survey effort of 700.9 km for the two survey periods. These included 325 signs of hunting (spent cartridges, active wire snares, hunter huts, carcass of a killed chimpanzee in a hunter's hut), 80 farms, 34 signs of grazing activity, 46 cases of illegal timber harvesting, and 17 signs of non-timber forest products collection. Of the 502 signs recorded, we found 34 (all hunting signs) within a 50 m radius of the nesting sites. The encounter rate of human activities within a 50 m radius of the nesting sites was 0.05 signs km^{-1}. The overall encounter rate of signs of human activity recorded for the two survey period was 0.72 signs km^{-1}.

4.3.4 Nesting tree species

Chimpanzees used at least 17 plant species for constructing their nests. The four most frequently used tree species were strombosia (*Strombosia* sp.) (22%), *pseudospondias (Pseudospondias macrocarpa)* (20%), umbrella tree (*Musanga cercropioides*) (16%) and calabash nutmeg (*Monodonra myristica*) (10%, for a list of all species see supplementary materials (A 3.1)).

4.4 Discussion

Our data support previous work that chimpanzees select safe trees for nesting and locate nests in areas with relatively low human disturbance. As predicted, chimpanzees prefer taller trees with high branches and large diameters for nesting. They preferentially located nests in mature forest vegetation at a higher elevation and on steep slopes where nests were oriented in the slope direction. On the contrary, nesting tree heights were not influenced by seasons. Furthermore, we found human signs within nesting at locations, but chimpanzees avoided human activity by nesting high in trees, preferably located on steep slopes, and by constructing ground nests only on very steep slopes. While we recorded no signs of large nocturnal chimpanzee predators, we found remains of a killed chimpanzee in a hunter's hut, suggesting that humans still eat chimpanzee meat in the area.

4.4.1 Physical characteristics of nesting trees

Our results support previous work showing that tree height is the most preferred tree trait by chimpanzee for nesting than the lowest branch height and tree diameter (Hernandez-Aguilar *et al.,* 2020). Most tall trees had a high lowest branch height and large diameters confirming that nesting tree selection primarily depends on tree height. These results further support previous work that chimpanzees prefer tall trees with high lowest branch height for nesting (Hernandez-Aguilar *et al.,* 2013; Hakizimana *et al.,* 2015). At Mon-Oku Forest in Cameroon, tall and large trees were also selected trees to build multiple nests (Wade, 2020). Fowler (2006) reported that nesting trees' mean height and diameter were higher than those of surrounding non-nesting trees at Gashaka-Gumti-National Park in Nigeria. Our results also support previous work that chimpanzees prefer some tree species for nesting over others (Brownlow *et al.,* 2001; Furuichi and Hashimoto, 2004; Sanz *et al.,* 2007; Stanford & O'Malley 2008; Hakizimana *et al.,* 2015). Overall, four species (*Strombosia* sp., *Pseudospondias macrocarpa, Musanga cercropioides,* and *Monodonra myristica*) contributed 68% of all plant species used for nesting by chimpanzees in KWFR. Similarly, 84% of all chimpanzee nests were built in five plant species at Njuma in Cameroon (Abwe, 2018), and 52.7% of all chimpanzee nests were built in *Dialium guineense* at Lagoas de Cufada Natural Park, in Guinea, (Carvalho *et al.,* 2015). Furthermore, *Strombosia* sp. was among the most used tree species by chimpanzees for nest building in Ebo forest and Mbam and Djerem (Abwe, 2018), Babanki-Finge (Doumbé, 2014), Mone-Oku Forest Reserve (Wade, 2020), and Ngel Nyaki Forest Reserve (Dutton *et al.,* 2016). At Albert Lake escarpment, in the Democratic Republic of the Congo, *Monodonra myristica*, followed by *Strombosia* sp. were the most used tree species for nesting by chimpanzees (Laudisoit *et al.,* 2021). Although two of the most important nesting trees *Pseudospondias macrocarpa and Monodonra myristica*, are also important fruit species in the chimpanzees' diet in KWFR (Fotang, 2018), further studies on tree phenology are required to fully understand if the observed preferences for nesting by chimpanzees is based on fruit availability. Our results suggest that preferences for some tree species are related to physical tree characteristics.

The average nest height of chimpanzees at most previous study sites was between 10 to 20 m, and the average nest height of chimpanzees in KWFR was at the upper end of this range (Table 4.4). The higher arboreal nesting height of the Nigeria – Cameroon chimpanzees in KWFR and some sites across its distribution range (For example, Mone-Oku (Cameroon), Lebialem–Mone (Cameroon), and Ngel Nyaki (Nigeria) can be explained by the more common human disturbance compared to other sites (Gashaka Gumti National Park (Nigeria)) (Table 4.4). However, other factors like the availability of tall nesting trees and altitudinal differences may further affect nesting tree heights of the Nigeria – Cameroon chimpanzees. For example, the relatively low nesting heights of this chimpanzee species at the highly fragmented Babanki-Finge Forest (1500–2300 m) compared to KWFR (565–1640 m) in Cameroon have been previously explained by the absence of tall trees and altitudinal difference (Doumbé, 2014). The observed orientation of nests towards the slope direction could reduce the escape route through neighboring trees or increase the functional nest height and thereby minimize contact with predators (Goodall, 1968; Koops *et al.,* 2012). Hernandez-Aguilar *et al.* (2013) reported that chimpanzees orientate nests in the slope direction to maximize exposure to sunlight during sunrise for nests orientated eastwards and during sunset for nests oriented westwards

Table 4. 4 Physical characteristics of nesting trees of different chimpanzee subspecies across Africa.

Subspecies and species	Country	Study site	Nest height(m)			DBH (cm)			
			N	Mean	SD	N	Mean	SD	
P.t. ellioti	Cameroon	Kom–Wum	851	15.53	5.44	625	42.08	23.8	This study
P.t. ellioti	Cameroon	Mone–Oku		18	8.7		36	20.3	(Wade, 2020)
P.t. ellioti	Cameroon	Bekob	397	10.8	5.2	383	23.46	15.52	(Abwe, 2018)
P.t. ellioti	Cameroon	Ganga	2014	13.27	5.9	1910	23.11	16.4	(Abwe, 2018)
P.t. ellioti	Cameroon	Njuma	639	13.18	5.85	623	22.71	17.89	(Abwe, 2018)
P.t. ellioti	Cameroon	Tofala Sanctuary	87	15.81	7.07				(Njukang *et al.,* 2019)
P.t. ellioti	Cameroon	Babanki–Finge	40	9.12	3.08				(Doumbé 2014)
P.t. ellioti	Nigeria	Ngel Nyaki	311	20.5	7.18		37.6	23	(Dutton *et al.,* 2016)
P.t. ellioti	Nigeria	Gashaka Gumti		8			61.8	41.5	(Fowler, 2006)
P.t. ellioti	Cameroon	Lebialem–Mone		21.9	8.3				(Last & Muh, 2013)
P. t. troglodytes	Congo R	Goualougo	247	17.3	7.4				(Sanz *et al.,* 2007)
P. t. verus	Cote d'Ivoire	Nimba Mts	764	8.02	4.57	764	27.9	24.01	(Granier *et al.,*2014)
P. t. verus	Guinea	Seringbara	1376	11.3	6.3		24.5	19.5	(Koops *et al.,* 2007)
P. t. verus	Senegal	Fongoli	1665	8.3	4.1				(Pruetz *et al.,* 2008)
P. t. verus	Senegal	Assirik	694	13.55	4.2				(Pruetz *et al.,* 2008)
P. t. verus	Senegal	Bagnomba	550	7.9	3.62				(Badji *et al.,* 2018)
P. t. verus	Sierra Leone	Gola National Park	96	21.3	5.6		32.6	10.2	(Barca *et al.,* 2018)
P. t. verus	Senegal	Diaguiri	871	10.9	1.7				(Ndiaye *et al.,* 2018)
P. t. verus	Guinea-Bissau	Lagoas de Cafada	459	14.6	2.14				(Carvalho *et al.,* 2015)
P. t. schweinfurthii	DR Congo	Kahuzi–Biega	104	9.4	4.8				(Basabose & Yamagiwa, 2002)
P. t. schweinfurthii	Burundi	Kibira Natioan Park		12.1	5.8		36.3	16.2	(Hakizimana *et al.,*2015)
P. t. schweinfurthii	Tanzania	Ugalla		13.4	5.1		39.6	19.3	(Ogawa *et al.,* 2007)
P. t. schweinfurthii	Tanzania	Issa		12.2	4.19		35.6	15.8	(Hernandez-Aguilar *et al.,* 2013)
P. t. schweinfurthii	Uganda	Bwindi	3414	16.06	6.2				(Stanford & O'Malley 2008)
P. t. schweinfurthii	Uganda	Semliki	324	11	5.81	405			(Hunt & McGrew, 2002)

3.4.2 Environmental determinants of the selection of nesting locations

Our results suggest that distance to mature forest, distance to secondary forest, and human activities are the most important determinants for selecting nesting sites by the chimpanzees. Additional local nest site conditions like elevation and slope are important too (Table 4.3). Most mature forest patches remaining in the study area are found at a higher elevation and on steep slopes that are rarely used by humans and harbor tall and primary trees that are important for nesting. Our results support previous findings that mature forest vegetation and high elevation areas are preferred for nesting over secondary forest and lowland areas (Koop *et al.,* 2012; Granier *et al.,* 2014; Njukang *et al.,* 2019; Carvalho *et al.,* 2021). The positive association between mature forest and nest locations reported in this and previous studies may also be due to the presence of a high density of large fleshy fruits trees (Balcomb *et al.,* 2000; Potts *et al.,* 2011, Chitayat *et al.,* 2021), and low impact of human activities (Strindberg *et al*., 2018). Although secondary forests may provide important food resources for chimpanzees (Basabose, 2005), our results strongly suggest that chimpanzees rarely nest in this vegetation type because of poaching and harvesting of timber and non-timber plant products (Fotang *et al.,* 2021b). Chimpanzees avoided low elevations areas in this study because these habitats are made up of rich soils suitable for farming, especially along the banks of three rivers that flow through the reserve (Kah, 2015; Chou *et al.,* 2017; Fotang *et al.,* 2021b). While riparian forest provides suitable nesting habitat for chimpanzee in the Greater Mahale Ecosystem in Tanzania (Dickson *et al.,* 2020; Chitayat *et al.,* 2021), this forest type is not suitable for chimpanzees nesting in KWFR because they are frequently cultivated. The avoidance of bare land by chimpanzees is due to the absence of nesting trees and the exposure to extensive cattle and subsistence agriculture by small-scale farmers. Similarly, chimpanzee nest sites were located far away (4 km) from the nearest settlement in Mone-Oku Forest in Cameroon (Wade, 2020). The positive statistical relationship between hunting signs and nesting locations suggests that hunters and chimpanzees frequently utilize transects and recces. However, the construction of nests on very steep slopes in this study could be a way of escaping human activities, as for example reported from Ebo Forest Reserve in Cameroon (Abwe & Morgan, 2008), in Mahale Mountains National Park in Tanzania (Chitayat *et al.,* 2021) and Kibira National Park in Burundi (Hakizimana *et al.,* 2015).

4.4.3 Antipredator/human avoidance hypothesis

Although the selection of tall trees for nesting by chimpanzees is related to the presence of chimpanzee predators such as leopard at some study sites (Pruetz *et al.,* 2008; Hernandez-Aguilar *et al.,* 2013; Stewart & Pruetz, 2013), the preference for tall trees for nesting in KWFR may be also related to human activities such as poaching and harvesting of timber and non-timber forest

products (Fotang *et al.,* 2021). In fact, chimpanzee predators such as leopard were not found in KWFR in the current and past surveys (Doumbé, 2015; Chuo *et al.,* 2017). A low encounter rate of human activity signs within 50 m around nesting sites in this study further suggests that chimpanzees selected nesting areas that were difficult for humans to access. In Bili-Uéré, northern DR Congo, chimpanzees constructed nests higher up in the trees when faced with high levels of human hunting activity and presence (Hicks *et al.,* 2010). Dutton *et al.* (2016) reported that the high nesting of chimpanzees in trees at Ngel Nyaki could be explained by the increasing presence of research in the forest since 2006. The construction of arboreal nests by chimpanzees in the Tofala Hill Wildlife Sanctuary in southwest Cameroon was also attributed to a strategy that focuses on avoiding predation by humans (Njukang *et al.,* 2019). Overall, our findings support the human avoidance hypothesis that arboreal nesting increases with increasing human disturbance (Stewart *et al,* 2011; Last & Muh, 2013; Carvalho *et al.,* 2015; Hakizimana *et al.,* 2015).

4.5 Conclusion and conservation implications

We show that chimpanzees prefer locating nests in mature forest vegetation, at higher elevations with slopes and away from villages and bare land exposed to cattle grazing and farming activities. They further selected tall trees with a high lowest branch height and large DBH for nest construction and orientated their nests in the slope direction for security reasons. We recorded no large nocturnal predators, but observed signs of human activity within nesting locations and evidence of chimpanzee hunting. Chimpanzees may escape human activities by nesting high in trees and constructing ground nests exclusively on steeper slopes. Our results suggest that mature forests at higher elevations and steep slopes are crucial for the conservation of chimpanzees as they are preferred habitats for nesting. We recommend protecting such habitats because they contain preferred nesting trees and a topography that is anyway not ideal for human use (e.g., as agricultural production areas). We also recommend regular law enforcement patrols to curb poaching and the implementation of sustainable land-use practices to prevent forest conversion into agricultural fields in the reserve. We propose that chimpanzee nesting locations in the surrounding forests should be included in the reserve's management plan.

Chapter 5: Mapping Suitable Habitat for Nigeria – Cameroon Chimpanzees in Kom – Wum Forest Reserve, North – West Region, Cameroon

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Mapping suitable habitat for Nigeria–Cameroon chimpanzees in Kom-Wum Forest Reserve, North-Western Cameroon

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Abstract

Great apes lose suitable habitats required for their reproduction and survival due to human activities across their distribution range in Africa. Little is known about habitat suitability and status for the Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti* (Matschie,1914)), particularly for populations inhabiting forest reserves in the North – West Cameroon. To address this knowledge gap, we employed a common species distribution model (MaxEnt) to map and predict suitable habitats for chimpanzees in Kom – Wum Forest Reserve, North – West Cameroon based on environmental factors that potentially affect habitat suitability. We related these environmental factors to a dataset of chimpanzee occurrence points (nests, dung, footprints, direct observations, feeding locations, tool use sites and tracks) recorded during line transect and reconnaissance (recce) surveys in the forest reserve and surrounding unprotected forests. Up to 92% of the study area is unsuitable as habitat for chimpanzees. Suitable habitats only represented 8% of the study area, with a high proportion of very suitable habitats located in unprotected areas outside the forest reserve. Elevation, land cover with secondary forest and distance to villages and mature forests were the most important predictors of habitat suitability for the Nigeria – Cameroon chimpanzee. The probability of chimpanzee occurrence increased with elevation, density of secondary forest, distance from villages and density of mature forest. Our study provides evidence that suitable chimpanzee habitats in the reserve are already lost, suggesting that efforts to maintain these protected areas for chimpanzee conservation are insufficient. The reserve management plan needs to be adopted to conserve the remaining suitable habitat inside and adjacent to the protected areas and to avoid local extinction of this critically endangered chimpanzee subspecies.

5.1 Introduction

Human activities such as deforestation and forest degradation are causing continuous declines in the habitat suitability for terrestrial mammals worldwide (Pereira *et al.,* 2010; Hansen *et al.,* 2013; Newbold *et al.,* 2015). Junker *et al.* (2012) reported a dramatic decline in the amount of suitable habitat for great apes across Africa over the last two decades. This decline is due to forest conversion to farmlands, commercial logging, industrial agriculture, and road infrastructure development (Kormos *et al.,* 2003; Zimmerman & Kormos, 2012; Morgan *et al.,* 2013; Laurance *et al.,* 2014; Rainer *et al.,* 2015). The availability of suitable habitats for chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) has declined over time, especially outside protected areas (Strindberg *et al.,* 2018; Heinicke *et al.,* 2019). The related human activities resulted in a

decrease in chimpanzee densities as well as behavioral change of primates (Strindberg *et al.,* 2018; Kühl e*t al.,* 2019).

In addition to human impact, environmental factors such as climate, habitat types, and relief play an important role in shaping the occurrence and distribution of chimpanzees (Sesink–Clee *et al.,* 2015; Abwe *et al.,* 2019; Kalan *et al.,* 2020). For example, Lehmann *et al.* (2010) found that the survival of chimpanzees is strongly influenced by increasing temperatures, changes in rainfall patterns, and the minimum viable community size. Ginath *et al.* (2020) reported that dense forests are crucial determinants of suitable chimpanzee habitat within the Lobeke National Park in South-East Cameroon. In the Greater Nimba Landscape, Guinea, West Africa, Fitzgerald *et al.* (2018) showed that Normalized Difference Vegetation Index (NDVI), elevation, and hierarchical slope were important predictors of suitable chimpanzee habitats. By applying high-resolution Landsat mapping in parts of western Equatorial Africa, *Jantz et al.* (2016) demonstrated that elevation and canopy cover were important predictors for habitat suitability. In the northern periphery of the Dja Faunal Reserve in Cameroon, Tédonzong *et al.* (2020) showed that chimpanzee occurrence increases with increasing elevation and habitat availability. At Mawambi Hills in Cameroon, Etiendem *et al.* (2013) further supported previous observations suggesting that elevation, distance to villages, and slope steepness are important predictors of habitat suitability for cross river gorillas (*Gorilla gorilla diehli*). Integrating these factors in Species Distribution Models (SDMs) helps to identify areas of suitable and unsuitable habitat to aid conservation and provide recommendations for future efforts in habitat conservation (Sofaer *et al.,* 2019; Baker *et al.,* 2021).

Several SDMs have been used to map and predict the geographic range of mammal species (Elith & Leathwick, 2009). One of the most commonly used SDMs in this context is the Maximum Entropy (MaxEnt) species distribution model (Elith *et al.,* 2011; Phillips *et al.,* 2006). MaxEnt has been previously used to map and predict habitat suitability for great apes at a continental (Junker *et al.,* 2012) or regional scale (Sesink-Clee *et al.,* 2015), and at several study sites across Africa, including Greater Nimba Landscape in Guinea (Fitzgerald *et al.,* 2018), Nyungwe National Park and Gishwati-Mukura National Park in Rwanda (Tuyishimire *et al.,* 2020), Afi-Mbe-Okwangwo forest landscape in Nigeria (Onojeghuo *et al.,* 2015), Dja Faunal Reserve in Cameroon (Tédonzong *et al.,* 2020), Mawambi Hills in Cameroon (Etiendem *et al.,* 2013), Lobéké National Park in Cameroon (Ginath *et al.,* 2020), in Forest Management Units of Mindourou, Lomié, and Messok towns in the Eastern region of Cameroon (Kehou *et al.,* 2021) and Mount Cameroon National Park (Mwambo, 2010).

Despite these previous studies, information is still missing for some protected areas across the distribution range of the Nigeria – Cameroon chimpanzee (Morgan *et al.,* 2011). Junker *et al.* (2012) reported that the availability of suitable habitat for the Nigeria – Cameroon chimpanzee decreased slightly between the 1990s and 2000s. Sesink-Clee *et al.* (2015) conducted an additional assessment, and their results predicted that suitable habitat for this subspecies in the ecotone region of Cameroon would decline drastically by 2080, while habitat availability in the rainforest region in North – West Cameroon is predicted to remain stable. Onojeghuo *et al.* (2015) reported that suitable habitats of the Nigeria – Cameroon chimpanzee are facing severe threats from deforestation and forest fragmentation in Afi Mountain Wildlife Sanctuary, Afi River Forest Reserve, Mbe Mountains and Cross River National Park in the northern part of Cross River State in Nigeria. However, little is known about the actual habitat suitability and availability for the Nigeria – Cameroon chimpanzee, particularly for chimpanzee populations inhabiting forest reserves in North – West Cameroon.

In the North – West Region of Cameroon, Kom–Wum Forest Reserve (KWFR) is a priority conservation site for the Nigeria – Cameroon chimpanzee and in terms of primate diversity in general (Morgan *et al.,* 2011; Doumbé 2015; Chuo et al., 2017; Fotang *et al.,* 2021a). This chimpanzee sub-species is highly threatened by habitat loss and poaching, with approximately 6,000 individuals remaining in the wild (Morgan *et al.,* 2011). Previous surveys at this site focused on estimating chimpanzee abundance and habitat preference using the line transect method (Fotang *et al.,* 2021a). Habitat preferences were determined using linear regression techniques (e.g., generalised linear mixed model and multiple linear regression) without informing about any spatial arrangement (Fotang *et al.,* 2021a; Fotang *et al.,* 2021b). Modelling suitable habitat for the Nigeria – Cameroon chimpanzee in this reserve using spatial models like MaxEnt can improve our understanding of their habitat requirement and threats affecting their survival.

So far, data on the availability of suitable habitat for chimpanzees in and around the reserve has yet to be measured. Considering the limited information on suitable habitat for chimpanzees in this reserve, it is important to map and prioritize potential chimpanzee habitat to develop site-specific conservation plans for long-term monitoring of chimpanzee populations. This study, therefore, aims to better understand the habitat requirements of chimpanzees and specifically to 1) identify and predict suitable chimpanzee habitat, 2) evaluate the contribution of environmental variables to chimpanzee habitat suitability, and 3) determine the probability of chimpanzee occurrence with respect to environmental variables in KWFR using MaxEnt.

5.2 Materials & methods

4.2.1 Survey designs and occurrence data

We produced geo-referenced 2 km x 2 km square grids in ArgGis10.6 and superimposed them on a map of the study area (100km^2) following a systematic random design (Buckland *et al.,* 2001). We sampled 23 grids (92 km^2) with spatial line transects (each 2 km in length) linked by 42.09 km recces (Fotang *et al.,* 2021). In the field, the first author, two experienced forest guides, and two community eco-guards repeatedly surveyed recce-transects 16 days for every month from May to September 2018 and from and from November 2019 to March 2020 for signs of chimpanzee activity (chimpanzee occurrence points). We used the recces to access start-of-line transects and increase encounters with chimpanzee signs. We marked the locations of chimpanzee signs using a handheld GPS. At nesting sites, we searched for chimpanzee nests within a 50 m radius (White & Edwards, 2000). In total, we recorded 653 chimpanzee occurrence points including nesting locations, tool used sites, dung, feeding locations, direct observations, tracks and footprints over a survey effort of 700.9 km for the two survey periods. We re-used chimpanzee sign occurrence points (N=362) recorded during previous line transect surveys between May and September 2018 (Fotang *et al.,* 2021) and new chimpanzee occurrence points (N=291) recorded during recce and line transect between November 2019–March 2020 in KWFR. All nests detected during the survey were constructed by chimpanzee, as gorillas are not present in this forest (Doumbé, 2015; Chuo *et al.,* 2017; Fotang *et al.,* 2021). Spatial thinning was done using the thin function in the spThin R package (Aiello-Lammens *et al.,* 2015). The thinning reduced chimpanzee occurrence points to 198 that were used in the final model.

5.2.2 Environmental variables

To model the habitat suitability of chimpanzees within the study area, we used nine environmental variables, including aspect, the density of bare land, density of mature forest, density of secondary forest, elevation, distance to roads, distance to villages, distance to roads and rivers, and slope derived from a variety of sources. First, we obtained land cover data (mature forest, secondary forest, bare lands, and water bodies) for the study area from a land cover classification map generated by Fotang *et al.* (2021). Second, we obtained topographic data by calculating aspect and slope in ArcGIS using elevation data from a Shuttle Radar Topography Mission 30 m resolution Digital Elevation Model (Jarvis, 2008). Third, we re-scaled the raster layers of all environmental variables at 50 x 50 m grid cells (pixels). Lastly, we converted the rater layers to points (number of pixels) and used the Kernel Density interpolation method in ArcGIS to

calculate the densities of mature forest, secondary forest, and bare lands per km^2 (Figure 5.1; Tarjuelo *et al.,* 2017).

Additionally, we used Google Earth images to digitize roads, rivers, and villages and then measured the distance to each feature as Euclidean distance. To check for collinearity between variables, we used the package usdm in R (Naimi *et al.,* 2014). We set a correlation threshold of 0.7 and used the variance inflation factor (VIF) to choose which variable to remove. When the correlation between two variables was greater than a threshold value of 0.7, the variable with the greater VIF was removed, and the correlation matrix was calculated again until the threshold condition was satisfied (Naimi *et al.,* 2014). We only discarded distance to rivers after analyzing for collinearity. Our final models had eight environmental variables, including density of bare land, density of mature forest, density of secondary forest, elevation, distance to roads, distance to villages, aspect, and slope.
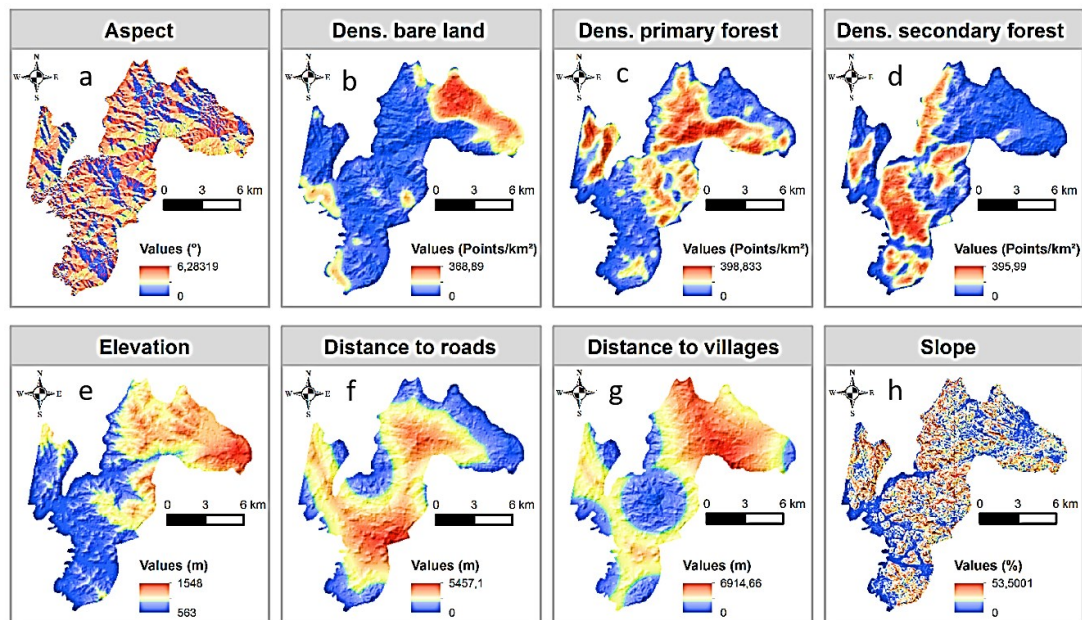
Figure 5. 1 Environmental variable with a) aspect, b) density of bare land, c) density of mature forest, d) density of secondary forest, f) elevation, e) distance to roads, g) distance to villages and h) slope.

5.2.3 Species distribution model

We employed the Maximum Entropy Distribution Model (MaxEnt) version 3.1.4 to predict suitable chimpanzee habitat in relation to eight environmental variables in the study area (Phillips *et al.,* 2006). MaxEnt has many advantages. First, it uses only presence data of a species and produces accurate prediction even with an incomplete dataset and small sample size (Phillips *et al.,* 2006). Second, it uses environmental data from the whole study area rather than only from

parts of the area (Phillips & Elith, 2013). Third, Maxent uses presence data plus background data (pseudo-absence data) from the study region because true absences are very difficult to obtain, especially for mobile species, and require higher levels of sampling effort to ensure their reliability compared with presence data (Mackenzie & Royle, 2005). Forth, MaxEnt can also be integrated inside other presence only species distribution models such as Wallace (Kass *et al.,* 2017). Lastly, MaxEnt employs regularization to prevent overfitting that is better than variable-selection methods oftern used for regression-based models such as generalized linear models (Phillips & Dudik, 2008).

We used 198 chimpanzee occurrence points for modelling (178 points for training and 20 for testing). We added 1000 generated background points to the 198 training points resulting in 1198 points in the final model. We evaluated the performance of the model using the area under the curve (AUC) of the receiver operating characteristic (ROC) (Yackulic *et al.,* 2013). To quantify the habitat suitability of chimpanzee in the reserve, we classified potential chimpanzee habitat into four habitat suitability index scores: highly suitable (>0.6–1.0); moderately suitable (>0.4–0.6); low suitable (>0.2–0.4); unsuitable habitat (>0–0.2) following Yang et al. (2013). We then used a jackknife test to measure each environmental variable percentage contribution to chimpanzee habitat suitability (Phillips *et al.,* 2006). We used a logistic output to measure the probability of chimpanzee occurrence with respect to the eight environmental variables (Phillips & Dudık, 2008).

5.3 Results

5.3.1 Suitable habitat area

The MaxEnt model fit was very good with an AUC value of 0.958 (SD ±0.009). We found that 91% of the study area is unsuitable for chimpanzees, 5% is of low suitability, 3% is moderately suitable, and 1% is highly suitable (Figure 5.2). In total, 65% of suitable chimpanzee habitat occurred outside the reserve boundary (Figure 5.2).
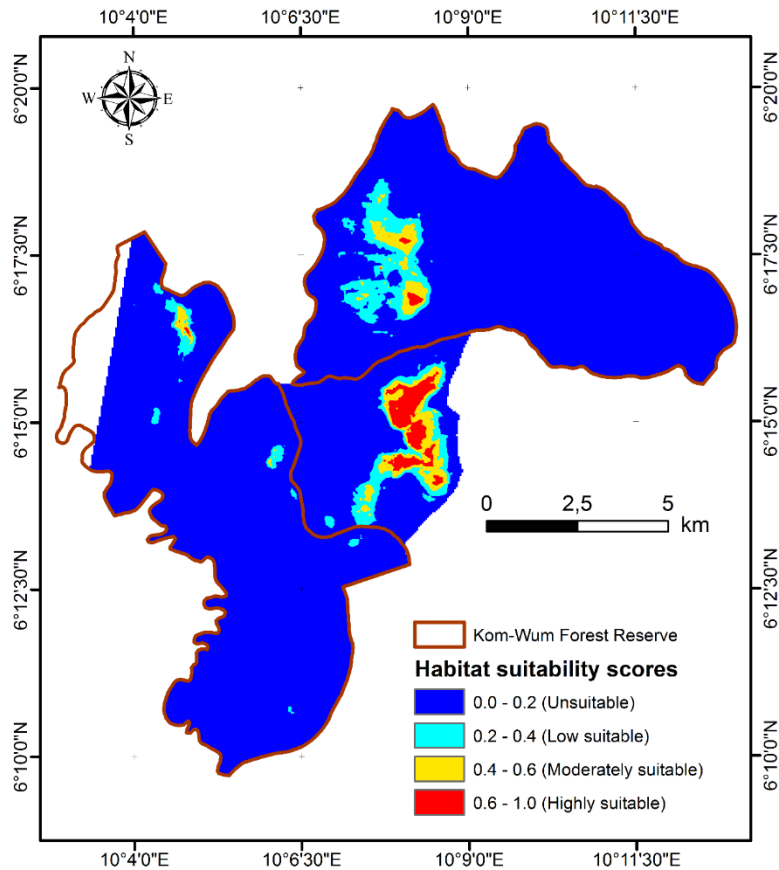
Figure 5. 2 Predicted habitat suitability map for chimpanzee in KWFR

5.3.2 Percent contribution of each environmental variable to the MaxEnt Model

Elevation (42.9%), secondary forest (18.6%), the distance to villages (14.5%) and mature forest (11%) were the highest contributors to chimpanzee habitat suitability in the reserve and the remaining five environmental variables only contributed 12.6%. If variables are considered alone, the Jackknife test supported elevation and density of secondary forests as the most significant contributors to chimpanzee habitat suitability (Figure 5.3). The overall contribution of the variables was reduced by 19.8 % if elevation was removed, by 11.7 % if distance to villages was removed, and by 3.9% if density of secondary forests was removed (Figure 5. 3).
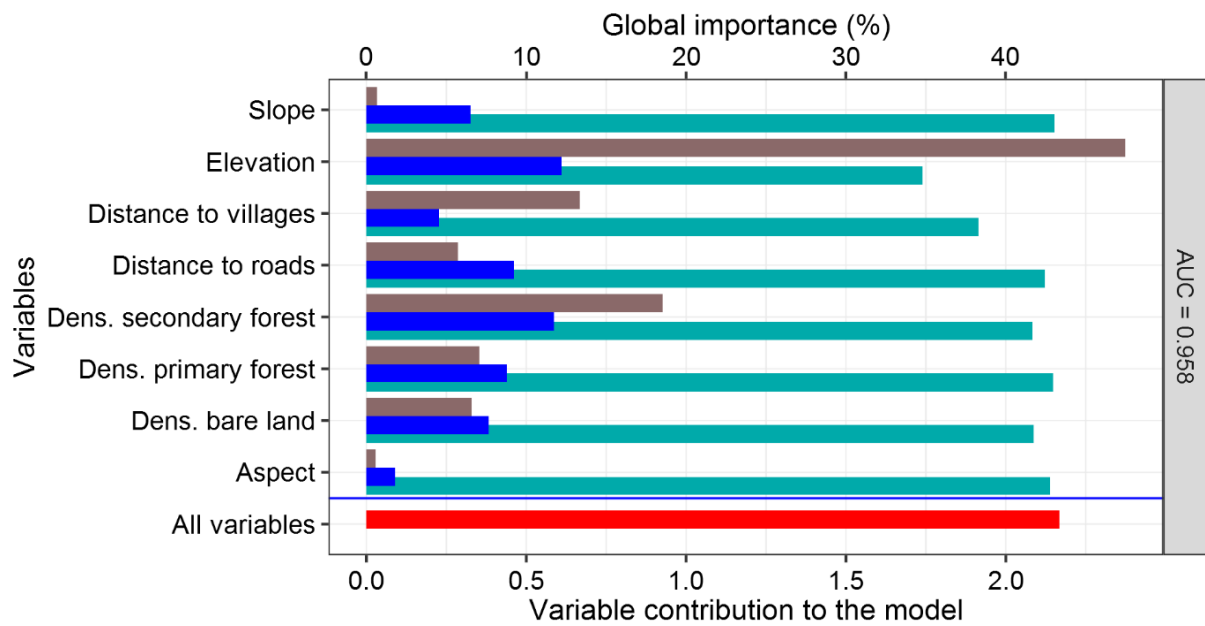
Figure 5. 3 Jackknife regularised training gain and variable contribution to the MaxEnt Model.
Blue columns show the model gain when variables are considered alone. Dark green bars show
the training gain without variable. Red bars show the training gain when all variables are used in
the model. Brown columns show the global importance.

5.3.3 Variable response curves

The probability of chimpanzee occurrence increased with elevation, slope, and mature and
secondary forest density (Figure 5.4 c, f, d, & g). In contrast, chimpanzee occurrence decreased
closer to villages, roads, and bare land (Figure 5.5, h, e & b). The probability of chimpanzee
occurrence was higher for elevation above 1200m than 800-1200m (Figure 5.4c). As for the slope,
the probability was only slightly higher for the 20-40 degree than for the less than 20 degree
section of the curves and dropped significantly after 40 degrees (Figure 5.4 f). Chimpanzees were
less likely to be found in areas closer than 2000 m to roads and villages (Figure 5.4 h & e). The
probability of occurrence started to increase in areas with a density of less than 100 points (number
of pixels) per square kilometer in mature and secondary forests and peaked at 300 points (Figure
5.4 d and g)
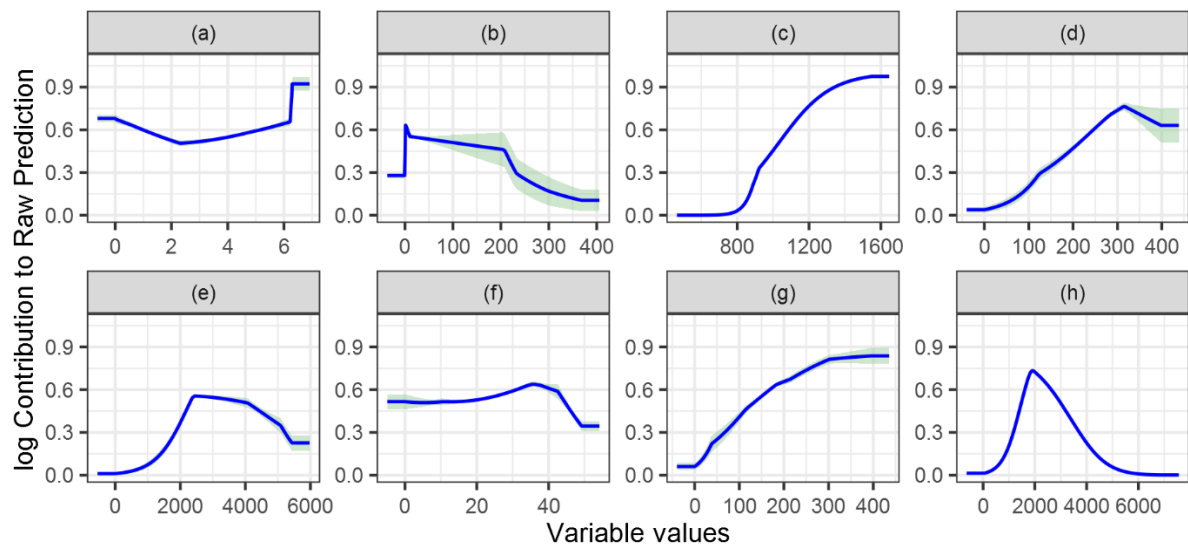
Figure 5. 4 Response curves of chimpanzees to different environment variables with a) aspect, b) density of bare land, c) elevation d) density of mature forest, e) distance to roads, f) slope, g) density of secondary forest, and h) distance to villages.

5.4 Discussion

Suitable chimpanzee habitat is degraded in the study area and this population could go extinct unless immediate action is taken. Elevation, secondary forest, and distance to villages and mature forests were the most important predictors for habitat suitability in the study area. These results are alarming, as the proportion of suitable habitat for this rare chimpanzee subspecies in KWFR is one of the lowest compared with values reported at other sites across its distribution range. Our results highlight the urgent need to improve the management of this protected area.

5.4.1 Suitable habitat area

The area of suitable chimpanzee habitat is small in the study region, and a large proportion of highly suitable chimpanzee habitat occurs outside the reserve. Although the natural vegetation cover is much larger, chimpanzees are confined to less than 10% of the area because of illegal gun hunting, trapping, and harvesting of timber and non-timber forest product within the reserve (Fotang *et al.,* 2021a). Also, extensive cattle grazing, and bushfires associated with cattle rearing especially at forest edges have forced chimpanzee to inhabit core habitats in the reserve (Fotang *et al.,* 2021b, Morgan *et al.,* 2011). Additionally, chimpanzees tend to avoid vegetation at low elevations areas as these habitats are frequently cultivated to grow maize, cocoa and banana due to rich soils, especially along the banks of three rivers (Meteh, Tschuh Akooghe, and Mughom)

that flows through the reserve (Chuo *et al.,* 2017; Fotang *et al.,* 2021b). Furthermore, suitable chimpanzee habitat had been destroyed by the inhabitants of Bu and Mbengkas for rice cultivation and for the creation of a new settlement inside the reserve called Nduneei (Kah, 2015). As a result, chimpanzees of KWFR occupy highly suitable core habitat even outside the protected area, which may expose them to further hunting and increased risk of local extinction (Heinicke *et al.,* 2019; Crooks *et al.,* 2017). The preference for habitat outside KWFR may result from high availability of preferred fruits and nesting sites in these areas (Basabose & Yamagiwa, 2002, Abwe *et al.,* 2019).

The proportion of suitable chimpanzee habitat in KWFR (9%) is among the lowest compared to those reported at other sites across this sub-species distributional range, including 1.9% in Afi River Forest Reserve, 14.3% in Mbe Mountains, 29.4% in Afi Mountain Wildlife Sanctuary, and 54.4% in Cross River National Park in Nigeria (Onojeghuo *et al.,* 2015). Similarly, suitable chimpanzee habitat in KWFR is lower than 61.0% reported in Forest Management Units of Mindourou, Lomié and Messok towns in the Eastern region of Cameroon (Kehou *et al.,* 2021), 67.4% in Mount Cameroon National Park (Mwambo*,* 2010), and 71.0% Lobéké National Park in South-East Cameroon (Ginath *et al.,* 2020).

5.4.2 Environmental variables in suitable areas

Elevation showed the highest contribution in predicting suitable chimpanzee habitat as chimpanzee occurrence increased with elevation. The increase in the probability of chimpanzee occurrence between 800 to 1200 m is best explained by the steep slopes. These areas are not suitable for farming and are very difficult to access by illegal timber exploiters and poachers; therefore, these areas are relatively safe for chimpanzees (Fotang *et al.,* 2021). The low land areas (< 800 m) are often cultivated with rice and maize and suffer from logging, fishing, and hunting along the banks of rivers Menchum, Tschuh Akooghe, and Mughom (Kah, 2015). Our results support previous work that elevation is the best predictor of suitable chimpanzee habitat (Jantz *et al.,* 2016). Elevation is also the best single predictor of chimpanzee habitat suitability in the northern periphery of Dja Faunal Reserve in Cameroon (Tédonzong *et al.,* 2020). At Seringbara, Nimba Mountains, chimpanzees occur in areas between 800 and 1000 m for feeding and areas above 1000 m for nesting (Koops *et al.,* 2012). Further surveys at Seringbaran revealed that the suitability of chimpanzee habitat increased above 700 m due to the absence of crop fields (Fitzgerald *et al.,* 2018). At Tofala Hill Wildlife Sanctuary in Cameroon, the selection of nesting sites at higher altitudes (800–1000 m) by chimpanzees was linked to the avoidance of high encounter rates with agricultural and logging activities at lower altitudes (Njukang *et al.,* 2019).

Etiendem *et al.* (2013) indicated that elevation contributed most to suitable habitat for the cross river gorillas at Mawambi Hills, South-West Cameroon and that suitable gorilla habitat and gorilla occurrence was optimal at higher mid-elevations (150 and 450 m) due to harvesting of non-timber products and poaching in low land areas. Regardless of the differences in preferred elevation values, both ape species preferred using higher elevation habitat. The difference in preferred elevation may result from the higher montane elevation range in KWFR (563–1546 m) compared to Mawambi (200–600 m).

Secondary forest density showed the second highest contribution to suitable chimpanzee habitat, and the probability of chimpanzee occurrence increased with the density of secondary forest. Similarly, Tédonzong *et al.* (2020) showed that the probability of chimpanzee occurrence increased with the density of their preferred nesting habitat at northern periphery of the Dja Faunal Reserve in Cameroon. In contrast, Fotang *et al.* (2021) showed that secondary forests cover has a significant negative effect on the occurrence of chimpanzee signs. The difference in the results may be due to the different methods applied, the addition of new survey data (2019-2020 survey) in this paper, or the different sets of explanatory variables considered in the two studies. For example, Fotang *et al.* (2021) considered "area of secondary forest" in contrast to "density of secondary forest" in this paper thus resulting in the opposite assessments of secondary forest type suitability for chimpanzees. Also, Fotang *et al.* (2021) used data from line transects (wet season survey) while data used in this paper was obtain from recce and line transect for two seasons (wet (May to September 2018) and dry (November 2019 to March 2020). Additional, Fotang *et al.* (2021) considered linear regression models (generalised linear mixed-effect model and multiple linear regression) versus spatial models (MaxEnt) in the current paper. Furthermore, (Fotang *et al.* (2021) did not consider "distance from the village" while this paper does not use data on traces of human activity). These findings suggest that different methodologies and sampling effort may yield variable results.

Distance to villages was the third most important contributor to suitable chimpanzee habitat, followed by distance to roads and density of bare lands. Our results revealed that chimpanzees avoided villages, roads and bare lands. The low occurrence of chimpanzees close to villages and roads (< 2000 m) could be explained by the conversion of dense forest vegetation into maize fields and bare lands for the establishment of new settlements. Similarly, at Cantanhez National Park Guinea-Bissau, chimpanzees forage frequently in forested areas far away from villages (Bersacola *et al.,* 2021). In non-protected areas of Tanzania, chimpanzee densities were low close to settlements due to the destruction of chimpanzee habitat through cultivation (Ogawa *et al.,* 2006, 2013). At Mawambi Hills, South-West Cameroon, suitable habitat for great apes was low

close to villages (Etiendem *et al.,* 2013). Chimpanzees avoided roads in KWFR because roads lead to rice fields and are usually surrounded by maize and bean fields. Pedestrians and motorcycles frequently use these roads to transport farm products to neighbouring villages. Our results support data from south-western Sierra Leone where chimpanzees avoid roads and use areas that are not cultivated by farmers (Garriga *et al.,* 2019). In contrast to our findings, chimpanzees did not avoid roads in Cantanhez National Park Guinea-Bissau because these roads are located in the centre of their home range (Bersacola *et al.,* 2021).

Mature forest vegetation was the fourth most important contributor to suitable chimpanzee habitat and slopes contributed little to overall suitability of chimpanzee habitat in the study area. However, we observed a positive correlation between chimpanzee occurrence and the density of mature forest and steep slopes. The preference for mature forest by Kom – Wum chimpanzee could be explained by the availability of their preferred nesting and feeding trees, while the selection of steep slope may be a way of avoiding human disturbance (Fotang *et al.,* 2021). In the northeastern part of the Nimba Mountains in Côte d'Ivoire and Guinea, the probability of finding chimpanzee nests increased in mature forests, especially on steep slopes (Granier *et al.,* 2014). Chimpanzee nesting habitat preference in Lagoas de Cufada Natural Park (LCNP) was associated with dense canopy forest (Sousa *et al.,* 2014). At the Greater Mahale Ecosystem in Tanzania, nesting on steep slopes was identified as a predator avoidance strategy (Chitayat *et al.,* 2021). Although suitable chimpanzee habitat in North – West Cameroon are predicted to remain intact in the next six decades (Sesink-Clee *et al.,* 2015), chimpanzee habitats in KWFR are already scarce, and may no longer be suitable in the near future (Fotang *et al.,* 2021b)

5.4.3 Limitation of the study

We did not include climatic variables in our model. We, therefore, recommend that future models should include additional environmental factors that may impact the habitat suitability of chimpanzees, such as temperatures and rainfall (Lehmann *et al.,* 2010).

5.5 Conclusion

The majority of areas in KWFR are unsuitable habitats for chimpanzees, and a high proportion of highly suitable habitat is located outside the protected area. Optimum chimpanzee habitat was found at high elevations (800–1200 m) more than 2000 m further from villages, roads, with no bare lands. In response, the likelihood of finding chimpanzees increased with elevation, forest density, and decreased with the density of bare land, distance to villages and roads. While elevation remains the strongest predictor of suitable chimpanzee habitat in the area, dense forests are crucial for expansion of the chimpanzee population if human activities are reduced. Our

findings suggest that dense forests at high elevation are potential habitats for chimpanzees and should be protected with high priority. Protected area managers have to focus on a reduction of forest conversion to farmland and settlements to protect the remaining suitable habitats in the reserve. In addition, the reserve boundary should be extended to include suitable chimpanzee habitat outside the reserve in future management plans.

Chapter 6: Feeding Habits of Chimpanzees in Kom – Wum Forest Reserve

Manuscript in preparation

Abstract

Fruits make up a high percentage of chimpanzee diet and their diet varies between seasons due to fruit availability. We examine diet preferences and the effects of seasons on the composition of chimpanzee diet through macroscopic inspection of 59 faecal samples collected between May 2018 and March 2020 in Kom – Wum Forest Reserve. Chimpanzee diet contained 23 food components, among which 15 were the seeds of different fruit species, and the rest was plant fibre (leaves and pith). Fruit made up 98% of faecal samples, fibre represented 2% and no animal diet components was recorded. The mean number of fruit species per faecal sample was 2.49 ± SD 1.2. The volume and diversity of fruits in faecal samples did not differ between seasons but the volume of fibre in dry season samples was significantly higher than the volume in wet season samples. *Landolphia* sp. *Pseudospondias macrocarpa, and Cyclomorpha solmsii* were preferred chimpanzee food, while Figs (*Ficus* sp.) and *Marantochloa filipes* were consumed as a fallback food.

Keywords: Seasonality, diet, chimpanzee, preferred food, fallback food, fruits

6.1 Introduction

Fruits make up a high percentage of chimpanzees, bonobos and gorillas diet and they spend a large amount of their foraging time eating fruits (Tutin & Fernandez, 1985). Their diet consists of about 78% fruits (Tutin & Fernandez, 1985). In seasons with clump fruit distribution and high fruit availability, chimpanzee party size tends to increase (Basabose, 2004) and they tend to increase fruit consumption (Carvalho *et al.,* 2015). During seasons of food scarcity, chimpanzees increase the consumption of fallback food (Furuichi *et al.,* 2001; Wrangham et *al.,* 1998). Fruit availability varies between seasons and different study sites: at some study sites, ripe fruits are abundant during the wet season (Abwe *et al.,* 2019; Tutin *et al.,* 1997), while at other study sites fruit abundance increases during the dry season (Basabose, 2005; Hockings *et al.,* 2009). Chimpanzees have been observed to move between forest types in their habitats depending on fruit availability (Basabose & Yamagiwa, 2002). Research on dietary ecology and fruit availability have been conducted for several chimpanzee populations including, *Pan troglodytes verus* at Lagoas de Cufada Natural Park, Guinea-Bissau (Carvalho *et al.,* 2015), *Pan troglodytes schweinfurthii* at Kahuzi, Democratic Republic of Congo (Basabose, 2002), *Pan troglodytes*

schweinfurthii at Kalinzu Forest, Uganda (Furuichi *et al.,* 2001), and *Pan troglodytes verus* at Bossou, Guinea (Yamakoshi, 1998). Previous research on the dietary ecology of Nigeria – Cameroon chimpanzee (*Pan troglodytes ellioti*) focused on tool-use at Gashaka-Gumti National Park, Nigeria (Fowler, 2006) and Ebo forest, Cameroon (Morgan & Abwe, 2006). Only recently have some studies been conducted on the dietary patterns and fruit availability of Nigeria – Cameroon chimpanzee in the Ngel Nyaki Forest Reserve, Nigeria (Dutton & Chapman, 2015), Ebo Forest Reserve and Mbam and Djerem National Park, Cameroon (Abwe *et al.,* 2020). However, knowledge of the dietary ecology of the Nigeria – Cameroon chimpanzee is still lacking in some priority conservation sites for the Nigeria – Cameroon chimpanzee in the North – West Region of Cameroon, like the KWFR (Morgan *et al.,* 2011). Therefore, this study aims to investigate the dietary composition, preference, and the effects of seasonal variation on the dietary ecology of the Nigeria – Cameroon chimpanzees in KWFR. Studying the composition of chimpanzee diets and identifying the factors that determines diet selection is crucial in understanding their habitat requirements and designing conservation plans to protect them better.

6.2 Materials & methods

6.2.1 Data collection

We searched for chimpanzee faeces along line transect and recces at feeding, nesting, and tool-use sites during the wet (May to September 2018) and dry seasons (November 2019 to March 2020). When fresh chimpanzee faeces droppings were encountered, we collected genetic samples using a Copan culture swap transport package (Figure 6.1 b). The remainder faeces was placed in a 1mm meshed sieve, rinsed gently with water to avoid the loss of dietary components, and then dried in sunlight (Basabose, 2002). We separated samples into fruits (seeds, fruit skin and tegument), and plant fibre (leaves and pith) and stored them in plastic bags. Fruit species were identified through direct examination of faecal samples, and the information was entered in a data collecting sheet. We gave codes for unidentified seeds in the field for future identification by experts at the National Herbarium in Yaoundé, Cameroon.

Figure 6. 1 Chimpanzee faecal samples with a) chimpanzee faeces in situ b) collecting genetic sample with a copan swap, c) sundried seeds after washing, and d) seeds place on a graph paper to determine the percentage volume of each fruit species in faeces.

6.2.2 Data analyses

We considered diet elements contributing ≥50% of the total faecal components in months that they were consumed or accounting for ≥50% of the total volume of feacal components in months that they were consumed as a preferred food. Fallback foods were faecal components whose consumption was high when preferred food was scarce (Doran *et al.,* 2002; Marshall & Wrangham, 2007). We used the nonparametric Wilcoxon rank sum test to compare the composition of chimpanzee diet between seasons (wet versus dry).

6.3 Results

6.3.1 Diet composition

We recorded 59 faecal samples between May 2018 and March 2020, averaging six samples per month (range 3 – 29). Of those, 35 were collected during the wet season and 24 samples during the dry season. The samples contained 23 components, including 13 identified seeds of fruits, five unidentified plant fibre, two unidentified seeds of fruits and three unidentified full leaves (Table 6.1). Fruits represented 98% of the total volume of faecal samples, while fibre represented 2%.

We found no animal parts in faecal samples. The mean number of fruit species per faecal sample was 2.49 ± SD 1.2 (range 1–5, N=59). *Landolphia* sp.was the most common fruit identified in the faecal samples, appearing in 69.5% of all samples. *Landolphia* sp. (48.3%), *Myrianthus arboreus*, (14.71%), *Monodora myristica* (13.7%) and *Marantochloa filipes* (8.4%) represent 85.1% of the total volume of faecal components.

6.3.2 Seasonality

We found no significant difference in the mean number of fruit species per faecal sample between the wet season (2.42 ± SD 1.1) and the dry season (2.58 ± SD 1.3; Wilcoxon rank sum test: W = 401, P = 0.767). There was no difference in the mean volume of fruits in faecal samples between the wet season (28.40 ± SD 20.2) and the dry season (26.28 ± SD 28.3; Wilcoxon rank sum: test: W = 488; P = 0.297). However, the volume of fibre in dry season faecal samples (17.5 ± SD 17.1, N = 4) was significantly higher than the volume in the wet season (1.25 ± SD 0.5; Wilcoxon rank sum: test: W = 28; P = 0.008, N=8). *Landolphia* sp*., Myrianthus arboreus, Pseudospondias macrocarpa and Monodora myristica* appeared in both the wet and dry season samples, *Ficus* sp*. and Marantochloa filipes* appeared only in the dry season samples, while *Pycnanthus angolensis, Canarium scheinfurthii, Vitex grandifolia, Antrocaryon klaineanum and Diospyros* sp*.* appeared only in the wet season samples (Table 6.1).

6.3.3 Preferred chimpanzee food and fallback food

Landolphia sp*., Marantochloa filipes, Cyclomorpha solmsii, Ficus* sp*.* and *Pseudospondias macrocarpa* met the criteria of preferred because they contributed ≥50% of the total faecal samples components in some months that they were consumed or accounted for ≥50% of the total volume of food components in some months that there were consumed. Figs (*Ficus* sp*.*) and *Marantochloa filipes* were considered as fallback because they appeared in faecal samples only in the dry season (probably period of fruit scarcity).

Table 6. 1 Total number of faecal samples and the abundance of each sample component per month in KWFR (Preferred food are bolded)

Months	1	2	3	4	5	6	7	8	9	10	11	12	≥50%
Total number of samples	8	7			3		3	29				9	0
Components of samples													
***Landolphia* sp.**	34	42			25		13	308				26	2
Marantochloa filipes	220	245										116	2
Monodora myristica	6	56					3	38				1	0
Strombosiopsis tetrandra Engl.	11												0
Pseudospondias microcarpa					6							207	0
Cyclomorpha solmsii							28	9					1
Myrianthus arboreus								243					0
Unidentified seeds		12											0
Unidentified seeds		1											0
Pycnanthus angolensis								3					0
Diospyros ssp.								1					0
Antrocaryon klaineanum								6					0
Canaium scheinfurthii								6					0
Vitex grandifolia								2					0
Ficus sp.												1085	1
Total	271	356			31		44	616				1435	6

Table 6. 2 Total number of faecal samples and the volume of each sample component per month in KWFR (Preferred food are bolded)

Months	1	2	3	4	5	6	7	8	9	10	11	12	≥50%
Number of samples	8	7			3		3	29				9	0
Components of samples													
Landolphia sp.	39.5	52.2			45.6		26	573				33	2
Marantochloa filipes	27.8	109										49	
Monodora myristica	6						4	50.5				1	
Strombosiopsis tetrandra Engl.	10												
Pseudospondias microcarpa		40			9		8					161.5	1
Cyclomorpha solmsii								3					0
Myrianthus arboreus								239					0
Unidentified seeds		6.5											0
Unidentified seeds		1											0
Pycnanthus angolensis								3					0
Diospyros sp.								1					0
Antrocaryon klaineanum								5					0
Canaium scheinfurthii								18					0
Vitex grandifolia								4					0
Ficus sp.												31	0
Unidentified fibre		32			1		1	2					0
Unidentified fibre	3												0
Unidentified fibre	2.5				1								0
Unidentified fibre	2						1						0
Unidentified fibre	16							3					0
Full leaves	51											14	0
Unidentified fibre	35											14	0
Total	192.8	240.7			56.6		40	901.5				303.5	3

6.4 Discussion

Our study has improved our understanding of what little is known about the dietary ecology of the Nigeria – Cameroon chimpanzees. Fruits dominated the diet of chimpanzees, and the diversity of fruits in their diet was lower than those of other chimpanzee populations. *Landolphia* sp. *Cyclomorpha solmsii and Pseudospondias macrocarpa* were preferred food. *Figs* (*Ficus* sp.*),*

Marantochloa filipes and fibre were important components of faecal samples during the dry season, suggesting that they were consumed as fallback food. The proportion and diversity of fruits consumed did not differ between seasons, but the volume of fibre significantly increased in feaces samples during the dry season. We found no remains of animal prey in faecal samples, but indirect evidence indicated that chimpanzees use tools to exploit driver ants (see chapter 7).

6.4.1 Diet composition and site comparison

Like other chimpanzee populations across Africa, the chimpanzee diet in KWFR was dominated by fruits (Tutin *et al.,* 1997; Morgan & Sanz, 2006). The number of fruit species in the diet of chimpanzee was similar to those at Gishwati Forest Reserve, Rwanda and Bwindi Impenetrable National Park,Uganda, but two times lower than those recorded at Ebo Forest Reserve and Mbam and Djerem National Park, Cameroon, Ngel Nyaki Forest Reserve, Nigeria, at Kahuzi, Democratic Republic of Congo (Table 6.3). Lowland rainforest ecosystems typically exhibit greater plant species diversity and fruiting phenology than drier savanna-ecotone (Stumpf, 2011) and montane habitats (Nkurunungi *et al.,* 2004). The low diversity of fruits in the diet of chimpanzees in KWFR compared to Ebo Forest Reserve can be explained by the difference in habitat types and altitudes: submontane rainforest at higher elevation for KWFR compared to lowland rainforest at lower elevation for Ebo Forest Reserve (Abwe *et al.,* 2019, 2020; Sesink-Clee *et al.,* 2015). The difference in the number of fruits in the diet of chimpanzees in KWFR and Ngel Nyaki with similar habitats (submontane forest) and altitudes can be explained by the difference in the fruiting cycles of plants in the two reserves (Marshall *et al.,* 2009).

Table 6. 3 Comparison of the diversity of fruits in chimpanzee diet in different habitat types and elevation gradients

Study site	No. of fruit species	Habitat	Elevation (m)	Author
KWFR	17	Submontane	565-1640	This study
Gishwati FR	23	Montane	2020-2500	(Chancellor *et al.,* 2012)
Bwindi NP	30	Montane	2000-2300	(Stanford & Nkurunungi, 2003)
Nyungwe NP	37	Montane	1600-2950	(Gross-Camp *et al.,* 2009)
Kahuzi-Biega NP	42	Montane	2050-2350	(Basabose, 2002),
Ngel Nyaki FR	52	Submontane	1400-1600	(Dutton & Chapman, 2015)
Mbam and Djerem NP	53	Forest-savannah mosaic (ecotone)	650 - 930 m	(Abwe *et al.,* 2020)
Ebo FR	63	Lowland Forest	100 - 1200	(Abwe *et al.,* 2020)

6.4.2 Effects of seasonality on diet composition

The volume of fibre (pith and leaves) in faecal samples was significantly higher in the dry season (possibly when fruit was scarce) than in the wet season in KWFR, suggesting that chimpanzees may consume them as fallback food. A similar dietary pattern was reported for the Nigeria – Cameroon chimpanzee at the Mbam and Djerem National Park in Cameroon, where fibre consumption was significantly higher in the dry season (Abwe *et al.,* 2020). At Kalinzu Forest, Uganda, chimpanzees migrated from mature forests to secondary forests that provided important fallback fruits like figs (*Ficus* sp.) and Musanga fruits in response to fruit scarcity (Furuichi *et al.,* 2001). It is likely that the chimpanzee of KWFR also moved to vegetation with abundant terrestrial haberceous plants like *Marantochloa filipes* during the dry season.

 6.4.3 Preferred fruits

Landolphia sp*. Cyclomorpha solmsii and Pseudospondias microcarpa* were preferred fruits for chimpanzees in KWFR. *Landolphia* sp*. and Cyclomorpha solmsii* were preferentially consumed during the wet season (possibly when fruit availability was high), suggesting that the chimpanzee of KWFR may select a small subset of fruits (a less diverse diet) in periods of high fruit availability (Carvalho *et al.,* 2015). Similarly, Nigeria – Cameroon chimpanzees in the Mbam and Djerem National Park in Cameroon preferentially consumed several species of *Landolphia* sp*. and Pseudospondias microcarpa* when fruit was abundant and clumped (Abwe *et al.,* 2020).

 6.4.4 Fallback food

Chimpanzees rely on wild fallback food like pith, leaves and figs (*Ficus* sp.) during periods of fruit scarcity (Abwe *et al.,* 2020; Basabose, 2002; Chancellor *et al.,* 2012). Figs and *Marantochloa filipes* were an important food for the chimpanzees of KWFR during the dry season, suggesting they are consumed as fallback food. Contrary to our results, figs are the preferred food for the Nigeria – Cameroon chimpanzee at Ngel Nyaki Forest Reserve, Nigeria (Dutton & Chapman, 2015) and other research sites (Newton-Fisher,1999; Yamagiwa & Basabose, 2009). These variations in food preference may be associated with the presence of plant species with asynchronous fruiting patterns at the different sites (Marshall *et al.,* 2009, Tweheyo & Lye, 2003). Yamagiwa and Basabose (2009) found that chimpanzees exploit insects such as ants and honey bees as fallback food during seasons of fruit scarcity at Kahuzi-Biega National Park in the Democratic Republic of Congo ("necessity hypothesis"). At Ngel Nyaki, the Nigeria – Cameroon chimpanzee consumed more small mammals, birds and selective invertebrates during the dry season when there was a low variety of fruit available (Dutton & Chapman, 2015). We found indirect evidence of tool use in driver ant exploitation by the chimpanzees of KWFR but did not

find their body part in faecal samples. Also, tool assistant driver ant predation was common during the two seasons of survey, suggesting that the insects may not be exploited as fallback food in KWFR. Further research on ant and fruit availability should be conducted in KWFR to verify the necessity hypothesis.

6.4 Conclusion

The chimpanzees of KWFR feed mainly on fruits, but they also consume leaves and piths. They prefer some fruits over others and seasonality significantly affect the amount of fibrous food consume but not fruits. *Landolphia* sp. *Cyclomorpha solmsii and Pseudospondias microcarpa* are preferred food, while *Ficus* sp. *and Marantochloa filipes* may be important fallback food. Kom-Wum chimpanzees tend to increase fibrous food consumption during the dry season probably in response to fruit scarcity. No animal prey was found in faecal samples but indirect evidence revealed that the chimpanzees exploit driver ant throughout the year by using tools. The diversity of fruits in the diet of chimpanzees is lower than those of other chimpanzee populations in published literature.

Chapter 7: Tool Use by Nigeria – Cameroon Chimpanzee for Driver Ant Predation in Kom – Wum Forest Reserve, North -West Region, Cameroon

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Tool use by Nigeria-Cameroon chimpanzees for driver ant predation in Kom-Wum Forest Reserve, North-West Region Cameroon

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Abstract

Chimpanzees feed on driver ants (*Dorylus* sp.) using different tools and predation techniques that vary among populations and can be affected by availability of ant species as well as ecological and social-learning factors. At the Kom–Wum Forest Reserve (KWFR) in Cameroon, we investigated tool use behavior in Nigerian-Cameroon chimpanzees (*Pan troglodytes ellioti)*, examining the characteristics of tools used in driver ant predation, looking for possible seasonal patterns and comparing our results to those from other study sites. We recovered 83 tools along line transects and recces (reconnaissance) during two seasons. We found that chimpanzees used tools with blunting and dirty ends (possible digging and probing tools) and tools without (dipping tools), in driver ant predation. Tools with dirty ends tended to be thicker (N = 52), and thinner tools were less likely to have dirt (N = 31). Tools recovered in the wet season (N = 62), were significantly shorter and thicker than those recovered in the dry season (N = 21). Furthermore, driver ant tools recovered at KWFR are on average the longest yet recorded insect dipping tools for chimpanzees comparable to those used in North Uele. We found no evidence of nut-cracking, tool-use for honey bee nor termite consumption and did not observe the potential prey remains in chimpanzee faeces despite their presence in the reserve. Our results suggest that seasonality significantly contributes to a divergence in the form of tools selected for driver ant predation.

7.1 Introduction

Chimpanzees exploit a broad range of food resources, such as insects and nuts, with the help of plant tools, stone tools, and wooden hammers (Boesch & Boesch, 1983; Luncz *et al.,* 2019). Tool types and tool-use techniques vary between chimpanzee populations (Boesch & Boesch, 1990). A number of distinct tool types have been described across equatorial Africa including ant dip, ant dig, termite fish, leaf napkin, honey dip, stone hammers and anvils, and leaf sponge (McGrew & McGrew, 1992). These tools can be distinguished and categorized based on their form and function (Sanz *et al.,* 2010). For example, At Seringbara in Guinea, Koops *et al. (*2015a) found that ant-digging tools were significantly wider than dipping tools. While ant-digging and perforating tools have only been reported from a few sites (Dutton & Chapman, 2015; Koops *et al.,* 2015a), ant-dipping tools have been reported at several chimpanzee research sites across Africa, including Assirik and Fongoli in Senegal(McGrew *et al.,* 2005), Bossou and Seringbara in Guinea (Humle & Matsuzawa, 2002; Koops *et al.,* 2015a), Taï National Park in Ivory Coast (Boesch & Boesch, 1990), Gombe National Park in Tanzania(McGrew, 1974), Goualougo in the Democratic Republic of Congo (Sanz & Morgan, 2007), Ngotto in Central African Republic

(Hicks *et al.,* 2005), Kalinzu Forest in Uganda (Koops *et al.,* 2015a) and Gashaka-National Park in Nigeria (Fowler & Sommer, 2007).

The length of ant-dipping tools varies across different chimpanzee populations depending on the availability of the harvested ant species, harvesting techniques, harvesting locations (nest or trail), and the characteristics of the ant nests (Hicks *et al.,* 2019; Humle & Matsuzawa, 2002; Schöning *et al.,* 2008). For example, Humle & Matsuzawa (2002) reported that chimpanzees used longer tools when harvesting ants at their nest, with tools used to *Dorylus nigricans* longer than those used to harvest *D. kohli* at Bossou in Guinea. They further showed that chimpanzees used shorter tools for the direct mouthing technique and longer tools for the pull-through technique. Humle & Matsuzawa (2002) found that chimpanzees used longer dipping tools when harvesting more aggressive epigaeic *Dorylus* ant species. In contrast, Koops *et al.* (2015a) reported no significant difference in the length of tools used to dip for *Dorylus* sp. between two neighboring chimpanzee populations at Kalinzu, Uganda, with similar ant species availability suggesting that the difference in tool length maybe culturally driven.

In some chimpanzee populations, two or more tools (so called tool sets) are used to harvest a particular food type (Sanz & Morgan, 2013). At Goaulougo, Sanz *et al. (*2010) reported that tools used as part of a set to perforate driver ant mounds were significantly thicker than the accompanying dipping used as part of the same set to collect the ants. As another example, chimpanzees use digging tools to enlarge ant nets and dipping tools as collectors at Seringbara in Guinea (Koops *et al.,* 2015a).

Environmental factors such as seasonality and rainfall influence tool-use behaviour in chimpanzees (Sanz & Morgan, 2013; Schöning *et al.,* 2007). At Goualougo, driver ant predation was highly correlated with rainfall (Sanz & Morgan, 2013). At Gashaka, the encounter rate of driver ant (*D. rufescens*) trails was significantly higher in the wet season than in the dry season (Schöning *et al.,* 2007). Fowler & Sommer (2007) found that chimpanzees used longer dipping tools for driver ant predation in the dry season and shorter tools in the wet season.

Several hypotheses have been proposed to explain tool-use behaviour in chimpanzees. The "necessity hypothesis" states that the exploitation of insects by great apes is based on the scarcity of their preferred food resources, in particular fruits (Fox *et al.,* 1999). For example, in Kahuzi-Biega, Democratic Republic of Congo, honey bees and ants were consumed by chimpanzees as a fallback food during periods of fruit scarcity (Yamagiwa & Basabose, 2009). In contrast to this

prediction, however, fruit scarcity did not correlate with tool-mediated driver ant-predation by chimpanzees at Seringbara, nor Gashaka (Koops *et al.,* 2013; Sommer *et al.,* 2017). The "opportunity hypothesis" states that the exploitation of food resources using tools depends on the availability of the resources and the materials needed to make the tools (Fox *et al.,* 1999). Koops *et al.* (2013) showed that chimpanzees did not exploit termites at Seringbara due to the low density of Macrotermes termite mounds within their distribution range, supporting the opportunity hypothesis. In contrast, tool use for driver ant has been found to be absent in some chimpanzee populations despite the ant being present, suggesting the possibility of a cultural variation between populations. Boesch *et al.* (1994) surveyed 35 different sites in Ivory Coast and found that neither chimpanzee abundance, density of nut-producing trees, presence of anvils and hammers or forest types could explain the difference in the presence or absence of nut-cracking behaviour between sites. Furthermore, chimpanzees in the Northern Democratic Republic of Congo used tools to prey on army ants more frequently to the north than to the south of Uele River irrespective of ant availability (Hicks *et al.,* 2020).

Tool use in chimpanzees has been considered cultural because it differs across different populations and appears to be socially acquired (Whiten *et al.,* 1999, Boesch & Boesch-Achermann, 2000). For example, Boesch & Boesch (1990) showed the chimpanzees at Taï National Park in Ivory Coast, and Gombe in Tanzania exploit driver ants while those of Mahale mountains in Tanzania do not, even when they are available, suggesting that driver ant predation can be considered cultural., Boesch & Boesch (1990), further reported chimpanzees at Taï chimpanzees only use the direct mouthing technique in ant predation while Gombe chimpanzees mostly use the pull through and the direct mouthing technique occasionally (McGrew,1974). This suggests that the differences in ant-dipping techniques between Gombe and Taï maybe cultural (McGrew, 1992).

Several studies have documented tool-use behaviour of the Nigeria – Cameroon chimpanzees in Gashaka (Fowler, 2006; Fowler & Sommer, 2007), Ebo Forest Reserve in Cameroon (Morgan & Abwe, 2006), and Ngel Nyaki Forest Reserve in Nigeria (Dutton & Chapman, 2015). At Gashaka, chimpanzees use stick tools to exploit insects like termites (*Macrotermes bellicosus*), African honeybees (*Apis mellifera*), stingless bees (*Hypotrigona gribodoi*), and driver ants (*Dorylus* sp.) (Fowler & Sommer, 2007). At Ebo, indirect evidence indicates that the chimpanzees used sticks and flexible leaf midribs for subterranean termite fishing and appeared to use stone or wooden hammers and anvils to crack the nuts of *Coula edulis* (Abwe & Morgan, 2008; Morgan & Abwe,

2006). At Ngel Nyaki, chimpanzees used stick tools to probe for stingless bees and wands to dip for carpenter ants (*Camponotus nr. perrisii*) (Dutton & Chapman, 2015).

The Kom – Wum Forest Reserve in the North – West Region of Cameroon is a priority conservation site for the Nigeria – Cameroon chimpanzee (Morgan *et al.,* 2011) and a home to about 83 chimpanzees (Fotang *et al.,* 2021b). Driver ant tools have been reported in previous surveys at Kom-Wum Forest Reserve (KWFR) in Cameroon (Chuo *et al.,* 2017), but the authors provided no details on tool dimensions or wear-patterns nor on potential seasonal patterns of tool use. Our objective in this study was to examine the characteristics of the tools use by the Nigeria – Cameroon chimpanzee in KWFR in their driver ant (*Dorylus* sp.) predation, investigate possible seasonality in the behaviour and compare our results to those of other sites. We hypothesize that chimpanzees use shorter tools in the wet season, and longer tools in the dry season (Fowler & Sommer, 2007).

7.2 Materials & methods

7.2.1 Data collection

We first conducted a recce survey to identify core areas of chimpanzee activity focusing on chimpanzee signs, including sightings, nests, faeces, feeding remains, tool-use sites, footprints and vocalizations (Kühl, 2008). We used a grid with a 2x2 km cell size across the study area to place 23 line transects (each 2 km in length) equally spaced (1000 m) following Buckland *et al.* (2001). We surveyed all 23 transects for chimpanzee signs. Based on the results of the first survey, we re-surveyed only 13 line transects (23 km) and recces (42.09 km) monthly during the wet (June to September 2018) and dry seasons (November 2019 to March 2020) with at least one chimpanzee sign. At potential tool-use sites, we verified if they matched a number of criteria following Hicks *et al.* (2019): 1) associated with an insect mound, 2) projecting from an insect mound, 3) signs of modification (stripping of leaves, bark), 4) sources of tools found nearby, 5) signs of excavation of soil, and 6) associated with chimpanzee evidence. All the tools we used in our analyses matched at least two of the criteria except for one tool that we did include in our analyses (Table 7.1). We identified the targeted food source (driver ants, termites, stingless bees, and honeybees) by 1) inspecting their mounds (Figure A 7.1& 6.11), identifying the insects (Figure A 7.10 &12), and 3) the presence of holes at the bases of trees (Figure A 7.3, 6.4 & 6.5; Table 7.2). Once the target food source was confirmed, we collected samples when the insects were present. We marked the geographic location of the tool use sites with a handheld GPS device. We counted the number of tools per site and recorded the types of modification made on each potential tool (cut at one or two ends, remove side twigs, stripped of bark). We also estimated tool

age from the freshness of the stem and sap following Hicks *et al.* (2019). Tools were considered fresh when the stem was fresh, with green bark and sap still dripping; recent when the stem was fresh with dying bark; old when the stem was dry with brown bark; very old when tools had decaying stems with rotten bark but still distinguishable as a tool. We took pictures of the tools from several angles in situ before touching them with our hands. We measured all tool lengths from proximal (the end which was near to the stem, branch or root of the plant from which the tool was removed) to distal ends (the end furthest from the stem, branch or root of the plant) with a meter tape and their respective diameters with a digital vernier caliper (Fowler & Sommer, 2007). Additionally, we recorded the wear types of tool ends into five categories: sliced, blunt, frayed, pointed, and split, following (Fowler & Sommer, 2007). We further inspected termite mounds, honey hives and checked for nut cracking behaviour beneath nut producing trees. We identified the plant family whenever possible and classified tool sources into trees or herbs. We classified ant feeding tools into two classes following (Koops *et al.,* 2015a): those with blunted and dirty ends, with excavation of soil (tools with dirty ends), and those without (tools without dirty ends).

Table 7. 1 Criteria used to classify tools used by chimpanzees in KWFR with numbers and percentages

Projecting	Modified	Wear	Soil excavation	Source found	Total	Percentage	Tool status
Yes	Yes	Yes	Yes	No	49	55.68	Yes
No	Yes	Yes	Yes	No	5	5.6	Yes
Yes	Yes	Yes	No	Yes	34	38.6	Yes
Total					88		

* Yes: Criteria matched; No: Criteria not matched

Table 7. 2 Criteria used to identify tool use sites in KWFR with number of sites and percentages

Criteria	Number of sites per criteria	Percentage	Food source
Presence of mounds	5	41.7	Driver ant
Presence of the insects	8	66.7	Driver ant
Holes beneath roots of trees	11	91.7	Driver ant

7.2.2 Dung analysis

We collected chimpanzee faeces opportunistically at feeding, nesting, and tool-use sites looking for insect parts. We sluiced samples in sieves of 1 mm mesh, dried samples in sunlight, and manually searched for fragments of ants, bees and termites (Basabose, 2002). We separated the

component of each sample into fruits (seeds, pulp and fruit skin), plant fibre, and animal remains and stored them in plastic bags.

7.2.3 Data analyses

We inspected normality of residuals and homogeneity of variances using Shapiro-Wilk normality and Levene test, respectively. We calculated the relative abundance (encounter rate) of ant feeding sites as the total number of ant nests with tools (N) encountered during the survey divided by the total distance covered on transects and recces in kilometres (Mathot & Doucet, 2005). We used an independent t-test to compare tool length and diameter between seasons (wet versus dry) and a two-sided permutation t-test to compare the mean tool length between sites (Ho *et al.,* 2019). We performed a linear discriminant function analysis to predict whether tool types (tools with dirty ends versus tools without dirty ends) could be separated by length and diameter. We used the partimat function in the klaR package to display the results of the classification. We performed the dip test of unimodality using the library dip test (Hartigan & Hartigan, 1985), to investigate whether the mean tool length or diameter showed a multimodal pattern possibly indicative of a tool set (Sanz *et al.,* 2010). All analyses were done in R version 3.5.1 (Team, 2018).

7.2.4 Limitation of the study

We do not have any observations of the chimpanzees using these tools and therefore can only infer how the tools were used by the patterns of wear on the tools (peeled back, stripped leaves blunted ends) and close association with an insect nest (Hicks *et al.,* 2019). Additionally, we have no data on the number of chimpanzees that may have used these tools and can therefore not confidently assess how common or frequent the behaviours are. Furthermore, we did not identify most plant species that tools were made from, nor did we identify the termite or driver ant species that was present and exploited by chimpanzees in KWFR (Figure A 7.12 & 7.13). Further surveys should consider using wildlife camera traps, and a detailed taxonomy and identification of insect and plant species.

7.3 Results

6.3.1 Tool numbers, dimensions

During the two survey periods, we walked 700.1km and found 83 tools at 12 sites. The encounter rate was 0.2 tools per km and 0.01 tool sites per km. The number of tools per site ranging from 2 to 13 (6.92 ± SD 2.50). We found more tools with signs of blunting on the ends and coating with soil (N=52) than we did without (N=31). We found potential tool sets at two sites: tools with signs

of blunting and coating with soil (tools with dirty ends) and those without them together at the same tool use site (Figure. 2c & d). Mean tool length was 114.8 cm ± SD 51.8 cm (N = 83, range: 7.9–270 cm) and mean tool diameter was 10.1 mm ± 3.7 mm (N=83, range: 2.3 – 20.4). The mean diameter of tools with dirty ends was 10.9 mm ± SD 3.8 mm and those without was 8.9 mm ± SD 3.2 mm. The mean length of tools with dirty ends was 106.0 cm ± SD 56.7 cm and those without was 129.6 cm ± SD 38.7 cm. The discriminant function analyses showed that tools with dirty ends tended to be thicker and shorter, while those without dirty ends were more likely be thinner and longer (Figure 7. 3). The dip test revealed a binomial distribution for tool length (Dn = 0.037, P = 0.589, N = 83) and a unimodal distribution for tool diameter (Dn = 0.051, P = 0.104, N = 83).

Figure 7. 1 Driver ant predation site with a) tools with dirty ends already arranged with signs of excavation of soil and with ends encircled in red, b) tools projecting from a driver ant mound in situ c) tools with dirty ends (red) and without (blue) in situ, and d) tools with dirty ends (red) and without (blue) arrange.
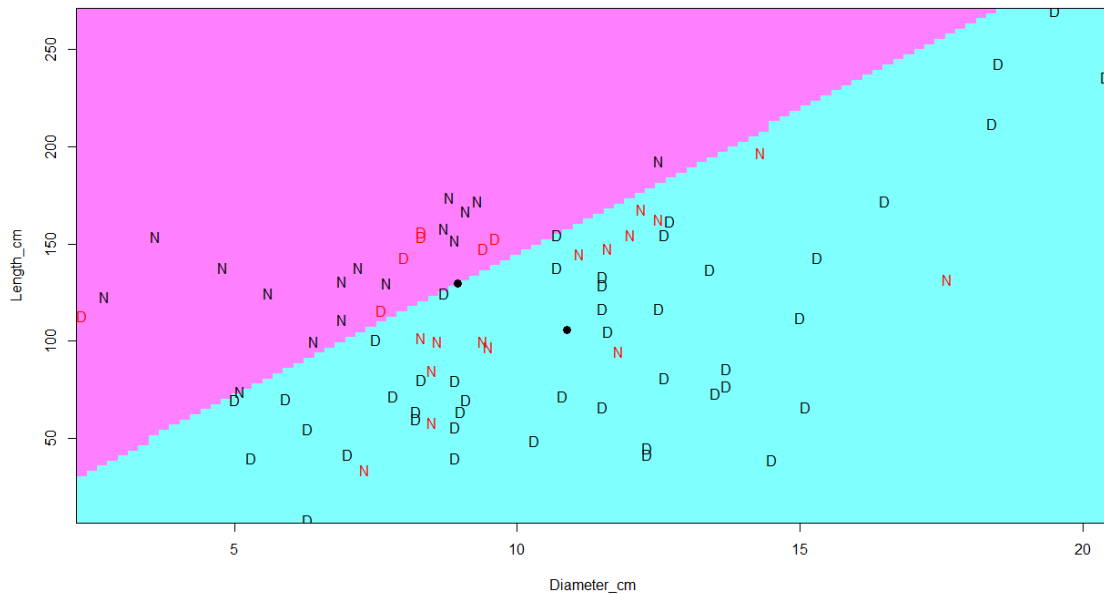
Figure 7. 2 Partition plot of tool length versus tool diameter analysed for tools with dirty ends (D) and tools without dirty ends (N) based on the linear discriminant analysis model. Black dots represent the centre of each group (tools with dirty ends and those without).

7.3.2 Seasonality

The tools recorded in our survey were either fresh or recent, suggesting they were made during the data collection season. Most tools were recorded in the wet season (62 of 83) with the same survey effort. The encounter rate of individual tools in the wet season was 0.2 tools per km and 0.1 tools per km in the dry season. More tools with dirty ends were recovered during the wet season (50 of 62) and more tools without dirty ends during the dry season (19 of 21). Tools recovered during the wet season were significantly shorter (106.7 cm $\pm$ SD 55.9 cm) than in the dry season (138.8 cm $\pm$ SD 25.8 cm, t = -3.53, P < 0.050). Tools recovered during the wet season were significantly thicker (10.7 mm $\pm$ SD 3.5 mm) than those recovered during the dry season (8.5 mm $\pm$ SD 3.8 mm, t = 2.45, df = 29.80 cm, P < 0.050).

7.3.3 Tool modifications and plant species

Tools had either blunt (N = 60), sharp (N = 18) or frayed (N = 5) ends and 98% of tools were used at their distal (Table A 6.1). Of the 52 tools with dirty ends, 34 were blunt, 13 were sharp and 5 were frayed. Of the 31 tools without dirty ends, 26 blunt and 5 were sharp (Table A 6.1). Tools with dirty ends were always stripped of leaves, whereas only 4 of 31 tools without dirty ends had leaves remaining. Only 3 of the 52 tools with dirty ends had been stripped of bark.

Similarly, only one tool without dirty ends had been stripped of bark . The few plant species (N=4) we could identify used to make the tools were from the families Zingiberaceae and Marantaceae (1 *Afromomum* sp. *without dirty ends* and 3 *Marantachloa* sp. with dirty ends) and the rest of the tools (N=79) were made up of unidentified sticks (Table 6.1).

7.3.4 Nut cracking, termite fishing and insect consumption

We recorded 17 Coula trees, 21 *Elaeis guineensis* trees, 43 termite mounds, and 14 honey hives but found no evidence of nut-cracking, termite fishing tools, nor honey or stingless bee extraction by chimpanzees. We found no prey remains of driver ants, termites, and honey bees after macroscopic examination of the 59 chimpanzee faecal samples collected during this survey.

7.4 Discussion

This study is the first report that describes the characteristics of tools used for driver ant predation by the Nigeria – Cameroon chimpanzees of KWFR. Tools with dirty ends (possible digging and probing tools) tended to be thicker and may have been used as enlargers, whereas clean-ended tools (dipping tools) were more likely to be thinner and may have been used as collectors. Chimpanzees preferentially used thicker and shorter tools for driver ant predation in the wet season. In contrast, longer and thinner tools were preferred in the dry season. The average length of tools used by chimpanzees of KWFR is similar to those of North Uele but differed significantly from other research sites, and this variation may be due to the depth of ant holes, ant behavior, raw material available to make the tools, or cultural., Additionally, nut-cracking was not observed, and no evidence of termite and honey bee exploitation was recorded, even though *Elaeis guineensis trees, Coula trees*, honey bees and termites mounds are present in the KWFR, suggesting that resource availability alone cannot explain variation in tool-use behaviour across different chimpanzee populations.

7.4.1 Tool sites

The number of driver ant predation tool sites varied between different research sites from 6 at Ngel Nyaki Forest Reserve (Dutton & Chapman, 2015), to 46 at Seringbara in Guinea (Koops *et al.,* 2015a), Table A 6.2). This suggests the possibility of cultural variation in tool use between the different populations of chimpanzees, although other possibilities, such as differences in the behaviors of the ant target species or the availability of plant material for tools must be considered as well (Möbius *et al.,* 2008).

7.4.2 Tool dimensions and tool sets

The discriminant analysis revealed that tools with blunting and dirty ends tended to be thicker and shorter than those without suggesting that they were stronger and heavier and may have been used to break open the underground chambers (digging) or to stir up (probing) the insects and the cleaner tools for collecting them. At Seringbara, Koops *et al.* (2015a) suggested that chimpanzees use tool sets: thick digging tools for enlarging ant nests and thin dipping tools for collecting them, and at Goualougo, Sanz *et al.* (2010) found that chimpanzees used thick perforating tools for stimulating ants and thin dipping tools for collecting them. However, the perforating tools at Goualougo had leaves attached in contrast to tools with dirty ends tools at KWFR. Additionally, 94% of tools without dirty ends had woody stems in KWFR, contrary to findings at Goualougo, where all dipping tools were made from herbaceous plants. Furthermore, the dip test statistics for the tools recovered at KWFR showed a unimodal distribution for tool diameter and a binomial distribution for tool length, indicating that the tools may not have been used as tool sets. Further surveys with camera traps are required to investigate the use of tool sets in KWFR.

7.4.3 Seasonality

We found a clear effect of seasonality on the length and diameter of tool use for ant predation. This recalls the results of Fowler & Sommer (2007) who found that chimpanzees use longer tools more frequently in the dry season to collect ants that retreat deeper into their nests to avoid desiccation and shorter tools in the wet season to prey on driver ants that tend to spend more time outside their nest in the wet season (Schöning *et al.,* 2007).

7.4.4 Variation in tool length between sites

Mean dipping tool length recovered at KWFR are comparable to those used in North Uele but significantly different from those used in Gashaka and Ngel Nyaki (Figure 7.3). The length of the tools makes it likely that chimpanzees use the pull-through technique, thereby reducing contact and painful bites from the aggressive workers (Humle & Matsuzawa, 2002; McGrew, 1974). The consumption of an aggressive epigaeic driver ant in KWFR and North Uele may explain the use of longer tools by chimpanzees in ant predation compared to those at Ngel Nyaki where carpenter ants (*Camponotus nr. perrisii)* are consumed. However, the mean dipping tool length at KWFR and Northern Uele is relatively longer than those at other sites where driver ants are consumed suggesting the possibility of cultural differences in feeding techniques (Table 7.3). Future studies

should compare the depths of ant mounds, soil characteristics, ant species availability, and the behavior of the ants between sites before assuming a cultural explanation (Hicks *et al.,* 2019; 2020).
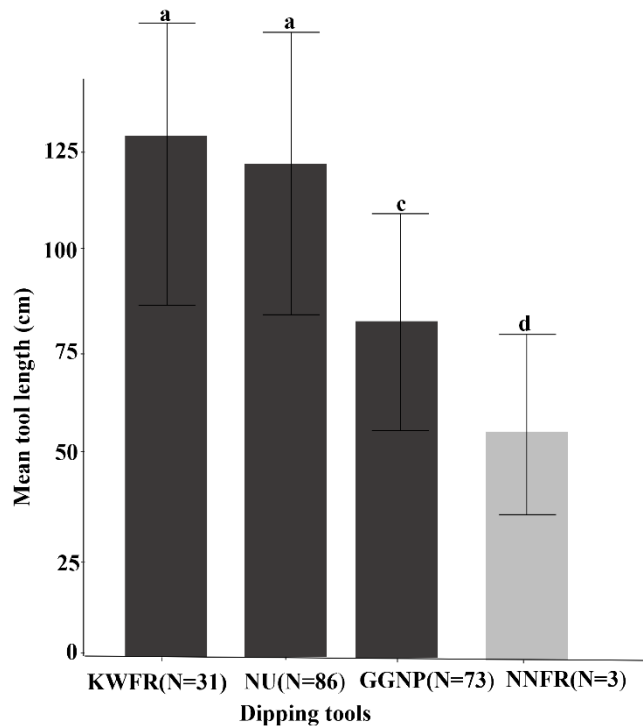
Figure 7. 3 Mean dipping tool length (cm) used to catch *Dorylus* sp. (dark grey bar) or *Camponotus* sp. (light grey bars) ants at KWFR (this study), Gashaka - Gumti National Park (GGNP, (Fowler & Sommer, 2007)), Ngel Nyaki Foret Reserve (NNFR, (Dutton & Chapman, 2015)) and Northern Uele (NU, (Hicks *et al.,* 2019)). Error bars are standard deviations and different letters indicate significant differences (P < 0.05).

Table 7. 3 Driver ants dipping tool length compared for different chimpanzees populations

Study site	Mean tool length (cm)	Country	Author and year
This study	129.6	Cameroon	
Northern Uele	122.0	DR Congo	(Hicks *et al.,* 2019)
Gashaka Gumti	83.8	Nigeria	(Fowler & Sommer, 2007)
Fongoli	79.3	Senegal	(McGrew *et al.,* 2005)
Gombe	66.0	Tanzania	(McGrew, 1974)

| Seringbara | 64.2 | Guinea | (Koops *et al.,* 2015a) |
| Bossou | 53.7 | Guinea | (Humle & Matsuzawa, 2002) |

7.4.5 Driver ant, termite, and honey bee consumption

While 42% of faecal samples (N = 381) contained body parts of ants at Gashaka – Gumti National Park, we did not find driver ants in chimpanzee faeces in KWFR after macroscopic examination of 59 faecal samples. The small number of faecal samples from KWFR could explain the absence of driver ants in the chimpanzee dung, given the abundance of tool sites we found to prey on these insects. The absence of driver ant body parts in chimpanzee faeces in KWFR also suggests that the chimpanzees do not collect ants on trails. Schöning *et al.* (2007) suggested that the proportion of ants in the chimpanzee diet at Gashaka was low when they did not collect ants on trails. Driver ants are available at Ngel Nyaki, but there was no evidence of their exploitation by the resident chimpanzees, and their body parts were not found in chimpanzee faeces (Dutton & Chapman, 2015). The different patterns in driver ant consumption between regions may reflect a complex mixture of cultural and ecological factors between populations of the Nigeria – Cameroon chimpanzees. We recommend collecting more faecal samples in future surveys to support our findings.

We frequently encountered termite mounds during our survey in KWFR (Figure A 7.13) but found no evidence of their exploitation using tools nor did we find the remains of termites in chimpanzee faeces. Chimpanzees may harvest termites using easily degradable tools like leaves and grasses similar to chimpanzee populations at Assirik (McGrew *et al.,* 1979). Similar findings were reported at Gashaka (Fowler, 2006; Fowler & Sommer, 2007; McGrew *et al.,* 1979), and the Bili-Uéré Landscape in northern Democratic Republic of where chimpanzees did not use tools to prey on Macrotermes but did pound open the mounds of Cubitermes and Thoracotermes (Hicks *et al.,* 2019).

Like at Ngel Nyaki (Dutton & Chapman 2015), termite mounds were also abundant at forest edges at KWFR, but chimpanzees did not visit termite mounds at forest edges because of high human disturbance (Fotang *et al.,* 2021a). We had few encounters with the nests of stingless and African honey bees, but found no evidence of bee harvesting tools in KWFR. In contrast to our results, stingless bee digging tools were found in Ngel Nyaki (Dutton & Chapman, 2015) and African honey bee dipping tools in the Gashaka (Fowler & Sommer, 2007). The lack of evidence of tools used for honey and stingless bee extraction at our site suggests that their nests are usually arboreal, and objects used for their exploitation are challenging to find by human observers compared with

ant predation tools (Fowler & Sommer, 2007). However, we cannot rule out the possibility that some of the tool sites encountered in our survey might have been used for underground honey exploitation because 4 of the 12 tool use sites did not contain insects.

7.5 Conclusion

We have shown that chimpanzees use tools with dirty blunted (possible digging and probing tools) ends and those without (dipping tools) for driver ant predation. Dirty blunted tools tended to be thicker and shorter and those without were more likely to be thinner and longer. Chimpanzees preferentially used thicker and shorter tools for driver ant predation in the wet season, while longer and thinner tools are used during the dry season. Tools characteristics (dipping tool length in particulars) used by chimpanzees at KWFR are comparable to those used at Northern Uele and significantly different from those at other sites. Our results suggest seasonality has a significant effect on the dimension of tool use for ant predation.

Chapter 8: General Discussion and Conclusion

8.1 Main findings

The research presented in this thesis has improved our understanding about the abundance and ecology of chimpanzees in general and the population status, habitat requirements, and food utilization of the Nigeria – Cameroon chimpanzee in particular. Up to 83 chimpanzees currently survive in KWFR, and this number of chimpanzees is among the lowest for a particular area in the published literature, highlighting the urgent need to protect them. Encounter rates for chimpanzee signs declined with increasing human activity as predicted and poaching was identified as the main threat to chimpanzees in the reserve. The number of chimpanzee signs is higher in mature forests compared to secondary forests and at higher elevations. Consequently, chimpanzees preferentially select tall mature forest trees at high elevations with slopes for nesting. Tree height is the most preferred tree trait for nesting and chimpanzees generally avoid nesting close to bare land, roads, and villages. Up to 92% of the study area is therefore unsuitable as habitat for chimpanzees and only 8% of the study area represents suitable habitats in the study area, with a high proportion of very suitable habitats located in unprotected areas outside the reserve. Fruits are the main food of chimpanzees. *Landolphia* sp., *Cyclomorpha solmsii,* and *Pseudospondias microcarpa* are preferred chimpanzee food in descending order. *Ficus* sp. and *Marantochloa filipes* are important fallback food. They also consume fiber (leave and pith) and the amount of fibre consumed in the dry season is significantly higher than that in the wet season. Indirect evidence reveals that chimpanzees exploit driver ants as food resource using probing, digging and dipping tools. The tools used in driver ant predation in the wet season are shorter and thicker than those used in the dry season. The tools recovered at KWFR are on average the longest recorded insect dipping tools for chimpanzees, only comparable to those used in North Uele in Democratic Republic of the Congo. This thesis has contributed to closing knowledge gaps in the Nigeria – Cameroon chimpanzee action plan which is important for the conservation success and will facilitate the development of successful conservation plans in the future. These results can improve conservation decisions to manage the remaining suitable habitat inside and adjacent to the protected areas and to avoid local extinction of this endangered chimpanzee subspecies.

8.2 Population estimates and threats

This thesis provides the first estimates of chimpanzee abundance in KWFR jointly using four widely used methods. Estimated chimpanzee numbers ranged from 10 (direct observation) to 83 individuals (distance sampling). As predicted, chimpanzee sign encounter rates decreased with increasing human activities in KWFR (Bryson-Morrison *et al.,* 2017; Morgan *et al.,* 2018). Chimpanzees avoided secondary forests, low

elevation areas, perforated areas, and forest edges due to high human activities, particularly illegal hunting. These results also support previous findings that chimpanzees occur at low densities in KWFR and surrounding forest reserves in the North – West Region of Cameroon (Morgan *et al.,* 2011). The low density is due to poaching, harvesting of non-timber forest products, illegal logging, and grazing activities (Humle *et al.,* 2016). Chimpanzee signs were more prevalent in mature forests and higher elevations than in secondary forests and low elevations. Mature forests provide important feeding trees and secured nesting sites for chimpanzees (Potts *et al.,* 2011, Abwe *et al.,*2020). Our results concur with previous findings from other areas that chimpanzees prefer mature forests with a closed canopy (Koop *et al.,* 2012; Bryson-Morrison *et al.,* 2017; Junker *et al.,* 2012). Conservation effort should focus on reducing poaching and habitat degradation through law enforcement patrols to protect the small chimpanzee population in KWFR against these emerging threats.

8.3 Nesting behaviour

As predicted, the chimpanzees of KWFR selected tall and large mature forest trees located at higher elevations and steep slopes for nesting similar to populations in other regions (Koops *et al.,* 2012; Hernandez-Aguilar & Reitan, 2020; Carvalho *et al.,* 2021; Granier *et al.,* 2014; Koops *et al.,* 2012; Njukang *et al.,* 2019). The preference for tall trees for nest location in KWFR may be related to high human activities such as poaching and harvesting timber and non-timber forest products within the reserve. These results support the human avoidance hypothesis that arboreal nesting increases with increasing human disturbance (Carvalho *et al.,* 2015; Hakizimana *et al.,* 2015; Last & Muh, 2013; Stewart *et al.,* 2011). The preference for mature forests over secondary nesting may be due to the presence of a high density of large fleshy fruits trees in mature forests (e.g. Balcomb *et al.,* 2000; Chitayat et *al.,* 2021; Potts *et al.,* 2011) and the low impact of human activities (e.g. Strindberg *et al.,* 2018). Additionally, most mature forest patches remaining in KWFR are found at a higher elevation and on steep slopes that are rarely used by humans and harbor tall and mature forest trees that are important for nesting. Chimpanzees avoided nesting at low elevation areas in KWFR because these habitats are made up of rich soils suitable for farming, especially along the banks of three rivers that flow through the reserve (Chuo *et al.,* 2017; Kah, 2015). Chimpanzees further avoided nesting close to villages and on bare land. Areas close to villages are not suitable for nesting because they are frequently cultivated by small-scale farmers. The avoidance of bare land may also be due to the absence of nesting trees. The chimpanzees of KWFR used some tree species for nesting in their habitat more than others. *Strombosia sp., Pseudospondias microcarpa, Musanga cercropioides and Monodonra myristica* were the most preferred nesting tree species of chimpanzee in KWFR in descending order. Similar findings were reported at other research sites (Brownlow *et al.,* 2001; Furuichi & Hashimoto, 2004; Hakizimana *et*

al., 2015; Stanford & O'Malley, 2008). Overall, primary forests at higher elevations with slopes are essential for chimpanzee conservation in KWFR and should be protected with high priority.

8.4 Suitable habitats

The results presented in this thesis support the previous findings that most African great apes live outside protected areas (Strindberg *et al.,* 2018) and that areas with suitable environmental conditions are decreasing (Junker *et al.,* 2012). In contrast, our finding does not support previous work that the suitable habitats for chimpanzees in the North – West Region of Cameroon will remain intact in the next six decades (Sesink-Clee *et al.,* 2015). Suitable chimpanzee habitats in KWFR only represented 8% of the study area, with a high proportion of suitable habitats located in unprotected areas outside the forest reserve. This proportion is very low compared to those at other research sites across its distribution range (Ginath *et al.,* 2020; Kehou *et al.,* 2021; Mwambo *et al.,* 2010). The low suitability value for KWFR may be due to increasing human activities like illegal gun hunting, trapping, harvesting of timber and non-timber forest product, extensive cattle grazing, and bushfires associated with cattle rearing (Morgan *et al.,* 2011).

Our findings support previous work that elevation is the top predictor of suitable chimpanzee habitat (Jantz *et al.,* 2016; Tédonzong *et al.,* 2020). Elevation, secondary forest density and distance to villages were the major predictors of habitat suitability for the Nigeria – Cameroon chimpanzee in KWFR in decreasing order. The probability of chimpanzee occurrence increased between 800 to 1200 m and was highest above 1200 m. In KWFR, high elevation areas (> 1000 m) are suitable for chimpanzees because they are rocky and are very difficult to access by farmers, illegal timber exploiters and poachers. In contrast, low elevation areas are unsuitable habitats for chimpanzee as they are often cultivated and suffer from logging, fishing, and hunting (Chuo *et al.,* 2017; Kah, 2015). Similar findings were reported at other research sites in Africa. For example, at Seringbara, Nimba Mountains, chimpanzee occurrence increased above 700 m because of the absence of cultivated fields (Fitzgerald *et al.,* 2018). At Tofala Hill Wildlife Sanctuary, Cameroon, chimpanzees preferred nesting at higher altitudes (800–1000 m) because of the low encounter rates of agricultural and logging activities (Njukang *et al.,* 2019). Secondary forest density was the second most important variable in predicting chimpanzee habitat suitability in KWFR. The likelihood of seeing chimpanzee signs increased with secondary forest density. The positive relationship between chimpanzee sign occurrence and secondary forest density suggests that secondary forest are suitable habitats for chimpanzees in KWFR. White & Edwards *et al.* (2000) reported that old secondary forests tends to resemble mature forests as their tree density increases. Consequently, chimpanzee occurrence may increase as the density of old secondary forest increases. Similarly, Tédonzong *et al.* (2020) demonstrated that the likelihood of chimpanzee occurrence increased with the density of their preferred nesting habitat at the northern periphery of the Dja Faunal Reserve in Cameroon.

Distance to villages was an important variable in our model. The probability of chimpanzee occurrence decreased with increasing proximity to villages, roads, and bare lands. The low occurrence of chimpanzees close to villages, roads, and bare land is likely due to the conversion of suitable chimpanzee habitats to farms and the establishment of new settlements (Kah, 2015). Similarly, chimpanzees avoided areas close to human settlements at the northern periphery of the Dja, Cameroon (Tédonzong *et al.,* 2020). Additionally, chimpanzees were less likely to forage close to villages at Cantanhez, Guinea-Bissau, and their densities were low close to human settlements in non-protected areas of Tanzania (Bersacola *et al.,* 2021; Ogawa *et al.,*2013). Taken together suitable chimpanzee habitats are scarce in KWFR. The adoption of sustainable land-use to stop the conversion of suitable habitats into agricultural fields is crucial for the conservation of this endangered chimpanzee subspecies.

8.5 Feeding behaviour

This study is the first to report on the dietary ecology of chimpanzees in KWFR. As predicted, faecal analyses showed that the chimpanzees of KWFR feed mainly on fruits. The diversity of fruits in the diet of chimpanzees in KWFR was lower than described in the previously published literature. The KWFR is a submontane forest habitat with elevations between 565-1640 meters above sea level. Higher elevations have been linked to a lower diversity of vascular plants (Grytnes *et al.,* 2007). Consequently, the diets of chimpanzee populations living at higher elevations and savanna-ecotone are less diverse (Basabose, 2002*;* Gross-Camp *et al.,* 2009; Stumpf, 2011) compared to those living in lowland rainforest habitats with a high diversity of plants (Abwe *et al.,* 2020; Morgan & Sanz, 2006; Potts *et al.,* 2011). In line with our hypothesis (Basabose, 2002), the was inter-seasonal variation in chimpanzee diet at KWFR. The volume of fibre consumption (pith and leaves) increased significantly during the dry season (possibly the season of fruit scarcity). Our results are similar to findings at Ganga in the Mbam and Djerem National Park, Cameroon, where the Nigeria – Cameroon chimpanzees relied on fibrous fruits, especially pith of Marantaceae during the dry season when fruits were scarce (Abwe *et al.,* 2020). At Kahuzi, Democratic Republic of Congo, chimpanzees largely depended on leaves and pith during the wet season when fruits were scarce (Basabose, 2002). Similarly, chimpanzee boosted their diet with fibrous food when fruits were scarce at Gishwati Forest Reserve, Rwanda (Chancellor, 2012). The chimpanzees of KWFR preferred some fruit species over others. For example, *Landolphia* sp., *Cyclomorpha solmsii,* and *Pseudospondias microcarpa* were highly preferred chimpanzee food. *Figs* (*Ficus* sp.) and *Marantochloa filipes* appeared in feacal samples only in the dry season, suggesting that they were consumed as fallback food. Figs were observed as fallback foods at Budongo forest, Uganda (Tweheyo & Lye, 2003) but were preferred food at Ngel Nyaki Forest Reserve, Nigeria (Dutton & Chapman, 2015, Yamagiwa & Basabose, 2009). This variation in fruit preference may

be due to the variation in the fruiting cycle of plants at different study sites (Basabose, 2005; Tweheyo and Lye, 2003).

Stanford (2003) reported that chimpanzees include animal prey in their diet. Animal food like insects and mammals provide primates with proteins and lipids (Deblauwe & Janssens, 2008; Lambert & Rothman, 2015). Two hypotheses have been proposed to explain the exploitation of animals by primates. The "necessity hypothesis" states that the exploitation of insects by great apes is based on the scarcity of their preferred food resources, in particular fruits (Fox *et al.,* 1999). For example, Yamagiwa & Basabose (2009) showed that chimpanzees consumed ants and honey bees as a fallback food, and their exploitation increased during seasons of fruit scarcity at Kahuzi-Biega National Park, Democratic Republic of Congo. At Ngel Nyaki Forest Reserve, the Nigeria – Cameroon chimpanzee consumed more small mammals, birds and selected invertebrate prey during the dry season when there was a low variety of fruit available (Dutton & Chapman, 2015). We found indirect evidence of driver ant exploitation by chimpanzees using tools, but did not find ant prey remains in chimpanzee faeces. Additionally, tool-assisted ant predation in KWFR was common during the two seasons of this survey, suggesting that our results are unlikely to support the "necessity hypothesis" that chimpanzees exploit driver ants due to the scarcity of their food (fruits in particular). The "opportunity hypothesis" states that the exploitation of food resources using tools depends on the availability of the resources and the materials needed to make the tools (Fox *et al.,* 1999, Koops *et al.,* 2013). It is impossible from the presented data to tell if chimpanzees of KWFR consume fruits based on their availability because neither fruits nor insect availability were assessed. Therefore, further studies on fruit and insect availability are required to fully understand if the feeding habits of chimpanzees in KWFR changes depending on the availability of food resources. Our finding suggest that the chimpanzee of KWFR consume mainly fruits but also include leaves and pith in their diet.

8.6 Tool used behavior

Indirect evidence revealed that chimpanzees exploit ants using tools in KWFR. On average, tools recovered at KWFR were the longest yet recorded insect dipping tools for chimpanzees, only comparable to those used in North Uele, but different from chimpanzee tools observed at other research sites across Africa. Ant behaviour, the depth of the ant holes, the raw materials used to produce the tools, or cultural factors may explain why chimpanzees use longer tools to exploit ants at these sites (Hicks *et al.,* 2019, 2020). It is likely that the chimpanzees of KWFR employ the pull-through method to minimize contact and painful bites from aggressive workers (Humle & Matsuzawa, 2002; McGrew, 1974). The presented results further revealed that tools with blunted ends and coating with dirt were thicker and shorter than those without (possible dipping tools). These results suggest that tools with dirty ends may have been used in enlarging

ant nests or stimulating them and those without for collecting the ants (Koops *et al.,* 2015). Further surveys with camera traps are required to verify how tools are used for ant predation in KWFR. Seasonality significantly affected the selection of tools used by chimpanzees in army ant predation (Fowler & Sommer, 2007; Schöning *et al.,* 2007). The chimpanzee of KWFR used longer and ticker tools for driver ant predation in the wet season and short and thinner ones in the dry season resembling the patterns observed for army ant predation by Fowler & Sommer (2007). Future studies recording tool use for ant predation should simultaneously record the depths of ant mounds, soil characteristics, and the behavior of the ants to better understand if these factors affect the tool use techniques.

8.7 Conclusion

The research results presented in this thesis show an alarmingly low population size of chimpanzees in KWFR that is further highly threatened by human activities which also affect the nesting ecology and feeding behaviour of the species. Poaching is a major threat to this small population and mature forests at a higher elevation are of prime importance for the future protection and conservation. Suitable chimpanzee habitats are scarce in the study region and restricted to high elevation areas with slopes outside the reserve. Chimpanzees preferentially select tall trees for nesting in these areas that are located far away from villages, bare land and roads. The chimpanzees of KWFR mainly consume fruits and increase fibre consumption during the dry season. Indirect evidence further revealed the exploitation of driver ants as prey by chimpanzees using tools that on average are the longest yet recorded insect dipping tools for chimpanzees, comparable only to those used at Northern Uele. Future conservation measures should focus on reducing poaching by 1) conducting regular anti-poaching patrols within the reserve and surrounding unprotected forest and 2) generating alternative livelihood activities such as goat rearing, fish farming, poultry farming, and market gardening. Mature forests at higher elevations should be protected with high priority, and suitable habitats in the surrounding unprotected forests should be included in future management plan.

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Appendices

Appendix Chapter 3

Table A 3. 1 Transect number (2 km long); nest counts per category. New nests (recent or fresh nests) are nests constructed during the inter-survey period.

Transect	New	Old	Total
1	6	28	34
2	32	2	34
3	1	8	9
4	0	3	3
5	2	6	8
6	31	4	35
7	0	5	5
8	0	10	10
9	1	7	8
10	5	9	14
11	0	0	0
12	0	0	0
13	0	0	0
14	0	0	0
15	0	0	0
16	2	6	8
17	0	0	0
18	3	22	25
19	30	48	78
20	0	0	0
21	0	0	0
22	0	0	0
23	0	0	0
Total	113	158	271

Table A 3. 2 Number of signs and encounter rate of chimpanzee signs in Kom-Wum Forest Reserve.

TID	NVT	TL	TE (km)	N	FR	TUS	Fe	V	TNS
1	5	2	10	34	13	1	0	5	53
2	5	2	10	34	0	0	0	0	34
3	5	2	10	9	0	0	0	0	9
4	5	2	10	3	0	0	0	0	3
5	5	2	10	8	0	0	0	0	8
6	5	2	10	35	0	0	24	0	59
7	5	2	10	5	6	1	0	1	13
8	5	2	10	10	0	0	0	0	10
9	5	2	10	8	0	0	0	3	11
10	5	2	10	14	9	1	6	8	38
11	1	2	2	0	0	0	0	0	0
12	1	2	2	0	0	0	0	0	0
13	1	2	2	0	0	0	0	0	0
14	1	2	2	0	0	0	0	0	0
15	1	2	2	0	0	0	0	0	0
16	5	2	10	8	11	1	0	3	23
17	1	2	2	0	0	0	0	0	0
18	5	2	10	25	29	1	3	2	60
19	5	2	10	78	0	0	2	4	84
20	1	2	2	0	0	0	0	0	0
21	1	2	2	0	0	0	0	0	0
22	1	2	2	0	0	0	0	0	0
23	1	2	2	0	0	0	0	0	0
Total		46	150	271	68	5	35	26	405
ER				1.8	0.45	0.03	0.23	0.2	2.7

TID: Transect ID; NVT: Number of visit per transect; TL: Transect length; TE: Total effort; N: Nest; FR: Feeding remains; TUS: Tool used site; Fe: Faeces; TS: Total signs per transect; ER: Encounter rates.

Table A 3. 3 Number of signs and encounter rate of human activities signs in Kom–Wum Forest Reserve.

TID	NV	TL (km)	TE (km)	H	F	G	NTFPC	L	TS
1	5	2	10	1	0	0	0	0	1
2	5	2	10	4	3	0	0	0	7
3	5	2	10	1	0	2	0	0	3
4	5	2	10	15	0	3	0	0	18
5	5	2	10	0	0	0	0	0	0
6	5	2	10	21	0	0	0	0	21
7	5	2	10	15	1	2	0	0	18
8	5	2	10	2	3	9	0	3	17
9	5	2	10	1	0	0	0	0	1
10	5	2	10	2	0	0	1	0	3
11	1	2	2	5	0	2	0	0	7
12	1	2	2	11	0	4	0	0	15
13	1	2	2	4	0	0	1	5	10
14	1	2	2	8	9	0	1	7	25
15	1	2	2	3	7	0	2	0	12
16	5	2	10	1	0	0	0	0	1
17	1	2	2	11	5	0	5	1	22
18	5	2	10	0	0	0	0	0	0
19	5	2	10	4	0	0	0	0	4
20	1	2	2	9	9	0	0	5	23
21	1	2	2	10	10	0	0	11	31
22	1	2	2	3	4	0	3	6	16
23	1	2	2	11	1	0	1	3	16
Total		46	150	142	52	22	14	41	271
		ER		0.95	0.35	0.15	0.09	0.27	1.90

TID: Transect identity; NV: Number of visits; TL: Transect length; TE: Total effort; H: Hunting; F: Farming; G: grazing; NTFPC: Non timber forest products collection; L: Logging; TS: Total sign per transect; ER: Encounter rates.

Figure A 3. 1 Principal investigator installing a camera trap in KWFR.

Figure A 3. 2 Threat to chimpanzee in KWFR with a) illegally hunted monkeys and pangolins, b) illegally logged timber,c) a fence trap and d) a wire trap.

Appendix Chapter 4

Table A 4. 1 Plant species used in nest construction (May 2018 to March 2020).

Scientific names	Common names/local name	Family	Percentage
Strombosia sp	Strombosia	Olacaceae	22
Pseudospondias microcarpa	Anghem	Anacardiaceae	20
Musanga cercropioides	Umbrella tree	Myristicaceae	16
Monodonra miristica	Groundnute spice	Annonaceae	10
Marantochloa filipes	-	Marantacees	8
Albizia ferruginea	Small leave	Fabaceae	6
Khaya grandifoliola	Mohoghany	Meliaceae	6
Myranthus arboreus	Bush pineapple	Moraceae	3
Palisota barteri Hook	-	Commelinaceae	3
Unidentified	-	-	3
Unidentified	Mbei	-	2
Pycnanthus angolensis	Umbrella tree	Myristicaceae	1
Canarium schewinfurthii	Bush plum	-	1
Kola nitidia/acuminate	Kola tree	Malvaceae	1
Staudtia kamerouniensis	-	Myristicaceae	1
Carapa procera	-	Zingiberacees	1
Aframomum daniellii	-	Zingiberaceae	1
Elaeis guineensis	Palm nut	Arecaceae	1
Phoenix reclinata	Date palm	Arecaceae	1
Unidentified	-	-	1
Unidentified	-	-	1

Figure A 4. 1 The Nigeria – Cameroon chimpanzee sitting in a nest in KWFR (Fotang, 2018).

Figure A 4. 2 Chimpanzee fresh ground nest in KWFR (Fotang, 2018).

Appendix Chapter 5

Figure A 5. 1 Landscape of KWFR showing different vegetation types (Fotang, 2018).

Appendix Chapter 6

Figure A 6. 1 chimpanzee dung dominated by the seeds of *Landolphia* sp. fruits (Fotang, 2018).
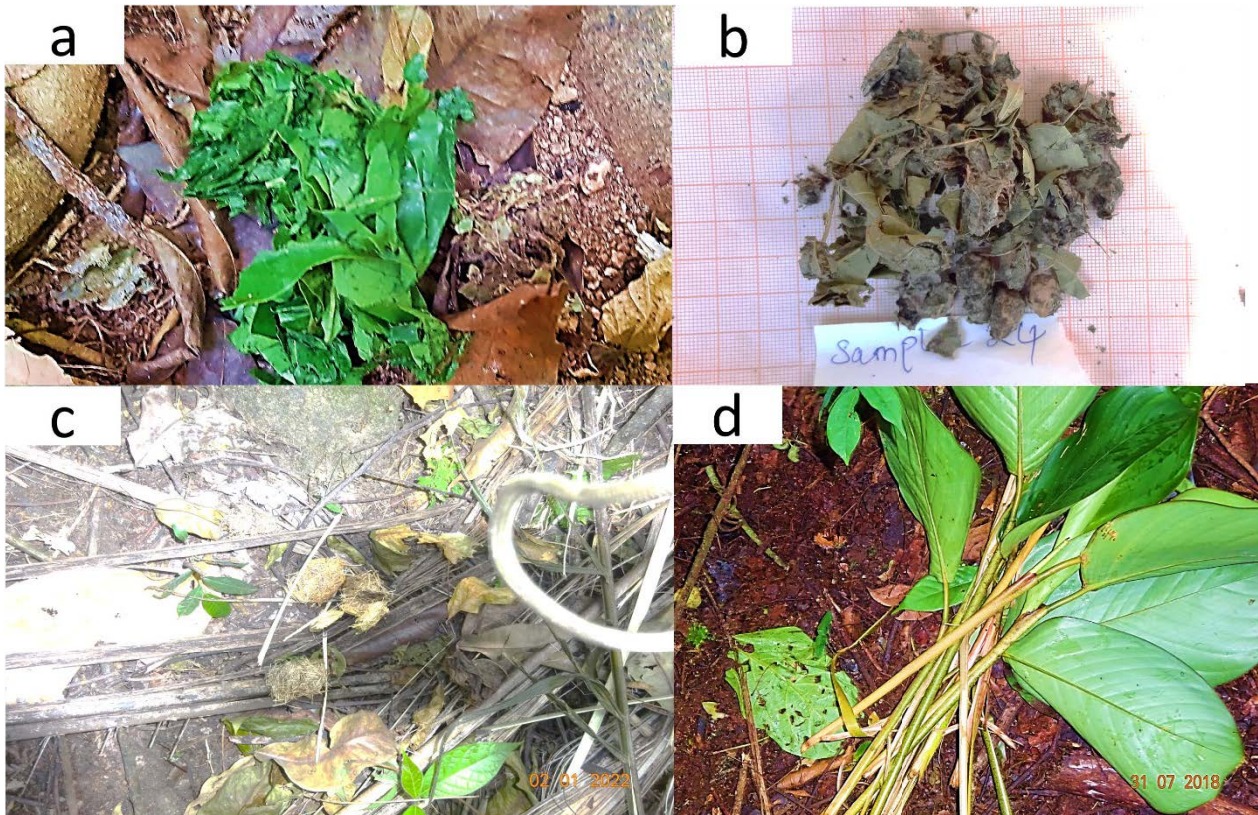
Figure A 6. 2 Chimpanzee feeding signs on a) unidentified plant,b) leaves and seed of *Pseudospondias macrocarpa*, c) pith of the branches of *Elaeis guineensis* and d) *Marantaceae* sp (Fotang, 2018).

Appendix chapter 7

Table A 7. 1 Number of individual tools recorded per site, tool dimensions, tool modification, and plant type per category (dirty & not dirt), used per season (wet &dry).

Tool ID	Tools per site	Length (cm)	Proximal diameter	Middle diameter (mm)	Distal Diameter (mm)	Average diameter (mm)	Wear	Plant type	Tool type	Season
1	13	66	15.1	15.3	14.9	15.1	Blunt	Wood	Dirty	Wet
2		81	14.2	12.7	10.9	12.6	Blunt	Wood	Dirty	Wet
3		100	8.5	10	7.3	8.6	Blunt	Herb	Not dirty	Wet
4		155	12.4	12.7	12.6	12.6	Fray	Herb	Dirty	Wet
5		97	10	10	8.5	9.5	Blunt	Wood	Not dirty	Wet
6		117	10.7	10.4	13.5	11.5	Blunt	Wood	Dirty	Wet
7		73	14.1	13.7	12.8	13.5	Blunt	Wood	Dirty	Wet
8		111	6.3	5.1	9.4	6.9	Sharp	Herb	Not dirty	Wet
9		117	12.7	12.8	12	12.5	Blunt	Wood	Dirty	Wet
10		85	7	6	12.6	8.5	Sharp	Wood	Not dirty	Wet
11		86	14.4	13.9	13	13.7	Sharp	Wood	Dirty	Wet
12		66	12.6	12.1	9.7	11.5	Blunt	Wood	Dirty	Wet
13		39	15.8	15.7	12	14.5	Sharp	Wood	Dirty	Wet
14	6	155	11.3	10.7	10	10.7	Blunt	Wood	Dirty	Wet
15		162	12.6	13.6	12	12.7	Blunt	Wood	Dirty	Wet
16		129	13.4	12	9	11.5	Blunt	Wood	Dirty	Wet
17		133	12.5	13	9	11.5	Sharp	Wood	Dirty	Wet
18		148	12.1	10	6	9.4	Sharp	Wood	Dirty	Wet
19		105	10.5	11	13.2	11.6	Blunt	Wood	Dirty	Wet
20	5	40	7	6	3	5.3	Fray	Wood	Dirty	Wet
21		64	9.5	8.3	9.3	9	Sharp	Wood	Dirty	Wet
22		49	12.9	10.3	7.6	10.3	Blunt	Herb	Dirty	Wet
23		56	8.3	8.5	9.8	8.9	Sharp	Wood	Dirty	Wet
24		64	9.3	7.3	8	8.2	Blunt	Wood	Dirty	Wet
25	6	42	17.2	11	8.8	12.3	Sharp	Wood	Dirty	Wet
26		270	17.8	18.7	22	19.5	Blunt	Wood	Dirty	Wet
27		236	16.3	20.4	24.5	20.4	Blunt	Wood	Dirty	Wet
28		243	13.4	18.5	23.5	18.5	Blunt	Wood	Dirty	Wet
29		212	21.7	18.9	14.5	18.4	Blunt	Wood	Dirty	Wet
30		143	11	8.7	4.5	8	Blunt	Wood	Dirty	Wet
31	6	156	5.1	9.4	10.4	8.3	Sharp	Wood	Dirty	Wet
32		143	11	19.7	15.1	15.3	Sharp	Wood	Dirty	Wet

33		153	14.2	9.2	5.5	9.6	Sharp	Wood	Dirty	Wet
34		80	11.7	10.5	4.6	8.9	Blunt	Wood	Dirty	Wet
35		40	8.3	9	9.3	8.9	Blunt	Wood	Dirty	Wet
36		70	13	9.3	4.9	9.1	Blunt	Wood	Dirty	Wet
37	10	137	14.6	15.6	10.1	13.4	Blunt	Wood	Dirty	Wet
38		172	18.2	16.2	15.2	16.5	Blunt	Wood	Dirty	Wet
39		77	12	15	14	13.7	Blunt	Wood	Dirty	Wet
40		45	10	14	13	12.3	Sharp	Wood	Dirty	Wet
41		101	5.5	10	7	7.5	Sharp	Wood	Dirty	Wet
42		154	7	11	7	8.3	Fray	Wood	Dirty	Wet
43		125	5	11	10	8.7	Blunt	Wood	Dirty	Wet
44		138	6	12	14	10.7	Blunt	Wood	Dirty	Wet
45		112	12	16	17	15	Blunt	Wood	Dirty	Wet
46		70	2	4	9	5	Blunt	Wood	Dirty	Wet
47	8	42	6	6	9	7	Blunt	Wood	Dirty	Wet
48		72	13.4	10.2	8.7	10.8	Blunt	Wood	Dirty	Wet
49		72	4.5	7.1	11.7	7.8	Blunt	Wood	Dirty	Wet
50		70.5	3.8	6.4	7.4	5.9	Frayed	Wood	Dirty	Wet
51		60	7.7	8.7	8	8.2	Blunt	Wood	Dirty	Wet
52		55	3	11	5	6.3	Sharp	Wood	Dirty	Wet
53		80.3	1	9	15	8.3	Blunt	Wood	Dirty	Wet
54		7.9	7.5	5.8	5.8	6.3	Blunt	Wood	Dirty	Wet
55	8	148	15	12.4	7.4	11.6	Sharp	Wood	Not dirty	Wet
56		193	8.9	15.2	13.4	12.5	Blunt	Wood	Not dirty	Wet
57		34	8.8	7.5	5.5	7.3	Sharp	Wood	Not dirty	Wet
58		58	4.9	11	9.6	8.5	Blunt	Wood	Not dirty	Wet
59		95	10.3	13.1	12	11.8	Blunt	Wood	Not dirty	Wet
60		172	7.6	9.6	10.6	9.3	Blunt	Wood	Not dirty	Wet
61		167	8.3	10.3	8.5	9.1	Blunt	Wood	Not dirty	Wet
62		74	5.2	5.1	5	5.1	Blunt	Wood	Not dirty	Wet
63	7	125	1.8	6.8	8.1	5.6	Blunt	Wood	Not dirty	Dry
64		113	3.3	2.3	1.3	2.3	Frayed	Wood	Dirty	Dry
65		138	8.5	5.4	0.6	4.8	Blunt	Wood	Not dirty	Dry
66		123	1.9	1.4	4.8	2.7	Blunt	Wood	Not dirty	Dry
67		100	8.1	8.2	3	6.4	Blunt	Wood	Not dirty	Dry
68		116	10.9	7.5	4.3	7.6	Blunt	Wood	Dirty	Dry
69		154	3.9	4.3	2.5	3.6	Sharp	Wood	Not dirty	Dry
70	9	158	9.2	8.9	8	8.7	Blunt	Wood	Not dirty	Dry
71		132	23.5	16.3	13.1	17.6	Blunt	Wood	Not dirty	Dry
72		145	11.6	14.7	7.1	11.1	Blunt	Wood	Not dirty	Dry
73		163	14.7	12.6	10.1	12.5	Blunt	Wood	Not dirty	Dry
74		174	8.8	10.8	7	8.8	Blunt	Wood	Not dirty	Dry
75		130	7.9	8.6	6.4	7.7	Blunt	Wood	Not dirty	Dry
76		138	5.7	7.2	8.6	7.2	Blunt	Wood	Not dirty	Dry
77		131	6.4	8.5	5.7	6.9	Blunt	Wood	Not dirty	Dry
78		102	11.3	7.4	6.2	8.3	Blunt	Wood	Not dirty	Dry

79	3	197	17.7	14.6	10.7	14.3	Blunt	Wood	Not dirty	Dry
80		168	14.5	14	8.3	12.2	Blunt	Wood	Not dirty	Dry
81		100	9.4	9.5	9.2	9.4	Blunt	Wood	Not dirty	Dry
82	2	152	6.2	12.1	8.3	8.9	Blunt	Wood	Not dirty	Dry
83		155	10.6	14.4	10.9	12	Blunt	Wood	Not dirty	Dry

Table A 7. 2 Comparison of the number of tool sites and number of tools recovered at KWFR with some chimpanzee populations.

Parameters	Driver ant predation tools				
Study site	This study	GGNP	NNFR	N U L	SE
Ant species	*Dorylus sp.*	*Dorylus sp.*	*Camponotus sp.*	*Dorylus sp.*	*Dorylus sp.*
Sites (N)	12	17	6	22	46
Number (N)	83	73	13	86	191

* 1 GGN: Gashaka Gumti National Park (Fowler & Sommer, 2007), NNFR: Ngel Nyaki Forest Reserve (Dutton & Chapman, 2015), NUL: Northern Uele Landscape (Hicks *et al.,* 2019; 2020), SE: Seringbara (Koops *et al.,* 2015b).

Figure A 7. 1 Driver ant probing tools projecting from an ant mound in situ in KWFR, May 2018.

Figure A 7. 2 Principal investigator inspecting driver ant mound for the insects in KWFR, May 2018.

Figure A 7. 3 Driver ant tools projecting from under a tree in situ with signs of excavation of soil in KWFR, May 2018.

Figure A 7. 4 Driver ant tools site with signs of excavation of soil in KWFR, July 2018.

Figure A 7. 5The principal investigator inspecting driver ant tools projecting from a

mound in situ with signs of soil excavation in KWFR, May 2018.

Figure A 7. 6 Driver ant probes projecting from a nest in situ with the insects seen crawling on sticks in KWFR, May 2018.

Figure A 7. 7 Driver ant tools site consisting of tools with dirty ends (red) and those without (blue) (possible tool set) in KWFR.

Figure A 7. 8 Potential driver ant dip completely stripped off back with the insects
seen crawling on it at an ant nest in KWRF, August 2018. The painful bites of the driver
ants prevented us from taking the tools with the hand.

Figure A 7. 9 The principal investigator(right) and field assistant(left) measuring
the length of a tool (2.70cm) used to prey on driver ant in KWFR, June 2018.

Figure A 7. 10 Driver ant swarm in KWFR, May 2018.

Figure A 7. 11 Termite mound in the KWFR, December 2019.

Figure A 7. 12 Termite workers in a mound pounded open by an assistant in the KWFR, May 2018.

Figure A 7. 13 Termite workers, soldier, nymph and reproductive queen from a termite in the KWFR, May 2018.

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Individual contribution to manuscripts

Manuscript 1 (Chapter 3): Human Activity and Forest Degradation Threaten Populations of the Nigeria – Cameroon Chimpanzee (*Pan troglodytes ellioti*) in Western Cameroon

1. Conception/design of the work: Lead (100%)
2. Acquisition of data: Lead (100 %)
3. Analysis of data: Lead (75 %)
4. Interpretation of data: Lead (80 %)
5. Drafting the manuscript: Lead (95 %)
6. Reviewing it critically for important intellectual content: Equal (60 %)

Manuscript 2 (Chapter 4): Environmental and anthropogenic effects on the nesting patterns of Nigeria-Cameroon chimpanzees in North – West Cameroon

1. Conception/design of the work: Lead (100%)
2. Acquisition of data: Lead (100 %)
3. Analysis of data: Lead (75 %)
4. Interpretation of data: Lead (80 %)
5. Drafting the manuscript: Lead (95 %)
6. Reviewing it critically for important intellectual content: Equal (60 %)

Manuscript 3 (Chapter 5): Mapping suitable habitat for Nigeria–Cameroon chimpanzees in Kom-Wum Forest Reserve, North-Western Cameroon

1. Conception/design of the work: Lead (100 %)
2. Acquisition of data: Lead (100 %)
3. Analysis of data: Lead (75 %)
4. Interpretation of data: Lead (90 %)
5. Drafting the manuscript: Lead (100 %)
6. Reviewing it critically for important intellectual content: Equal (75 %)

Manuscript 4 (Chapter 6): Feeding Habits of Chimpanzees in Kom – Wum Forest Reserve

1. Conception/design of the work: Lead (100 %)

2. Acquisition of data: Lead (100 %)

3. Analysis of data: Lead (100 %)

4. Interpretation of data: Lead (100 %)

5. Drafting the manuscript: Lead (100 %)

6. Reviewing it critically for important intellectual content: Lead (80 %)

Manuscript 5 (Chapter 7): Tool use by Nigeria-Cameroon chimpanzees for driver ant predation in Kom-Wum Forest Reserve, North-West Region Cameroon

1. Conception/design of the work: Lead (100 %)

2. Acquisition of data: Lead (100 %)

3. Analysis of data: Lead (95 %)

4. Interpretation of data: Lead (80 %)

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