Universitat Autònoma de Barcelona

Human-Chimpanzee Co-Existence in Non-Protected Areas in Sierra Leone, West Africa

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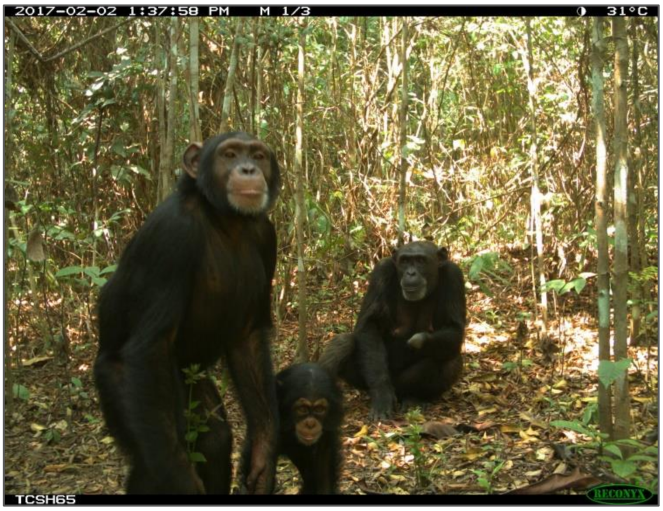

PhD Thesis

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HUMAN-CHIMPANZEE CO-EXISTENCE IN NON-PROTECTED AREAS IN SIERRA LEONE, WEST AFRICA

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Els doctors Ignasi Marco Sánchez, Professor Titular d'Universitat de l'Àrea de coneixement de Medicina i Cirurgia Animals de la Facultat de Veterinària de la Universitat Autònoma de Barcelona, Encarna Casas Díaz, Tècnic de Suport a la Recerca del Departament de Sanitat i d'Anatomia Animals, i Tatyana Humle, DICE, School of Anthropology and Conservation, University of Kent, UK.

Informen:

Que la memòria titulada "HUMAN-CHIMPANZEE CO-EXISTENCE IN NON-PROTECTED AREAS IN SIERRA LEONE, WEST AFRICA", presentada per Rosa Garriga Anguera per a l'obtenció del grau de Doctora en Veterinària per la Universitat Autònoma de Barcelona, s'ha realitzat sota la nostra direcció i, un cop considerat satisfactòriament finalitzada, autoritzem la seva presentació per tal de que sigui avaluada per la comissió corresponent.

I perquè així consti als efectes que siguin oportuns, firmem el present informe a Bellaterra, 24 de setembre de 2018.

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Abstract

Wild chimpanzees (*Pan troglodytes*) populations are facing a serious risk of extinction and the main global threat is habitat conversion for subsistence and commercial agriculture. The western chimpanzee subspecies (*Pan troglodytes verus*) has been recently categorised as Critically Endangered by the IUCN red list because in the past 50 years its population has drastically reduced of more than 80% as a result of poaching, loss of habitat and habitat fragmentation due to human activities. Sierra Leone harbors the third largest western chimpanzee population but more than half of it lives in unprotected areas with a significant competition between people and chimpanzees for resources in areas dominated by farming activities where wild chimpanzees forage on crops. This thesis explores the agricultural challenges facing farmers and their attitudes and perceptions towards chimpanzees in four rural areas of Sierra Leone. Wildlife was reported to be the main agricultural problem although chimpanzees were not ranked within the 3 most destructive species. Chimpanzees consumed semi-domesticated oil palm resources and cultivated fruits, and this is negatively viewed by farmers. In general farmers perceived chimpanzees more destructive than dangerous. Between April 2016 and May 2017, we conducted a camera trap survey in one of the rural areas previously surveyed with the aim to analyse the ecological and anthropogenic drivers of chimpanzee occurrence across a highly degraded and human-impacted landscape in the south-western district of Moyamba in Sierra Leone. The model showed that chimpanzee abundance across this landscape is affected by the distance to roads and proximity to swamps. However, settlements and human proximity did not influence in chimpanzee abundance. Farmers' tolerance and low hunting pressure are argued to be some of the reasons chimpanzees still persist in these degraded landscapes. Finally, this study also provides a preliminary insight into the demographics, group structure and ranging of unhabituated chimpanzees living in a non-protected landscape. Overall, we expect that the results of this thesis will contribute to a better understanding of how chimpanzees live in degraded landscapes and its implications for conservation actions including land use planning.

Resum

Les poblacions de ximpanzés (*Pan troglodytes*) afronten un greu risc d'extinció, i la principal amenaça mundial és la transformació de l'hàbitat cap a una agricultura de subsistència i comercial. La subespècie de ximpanzé occidental (*Pan troglodytes verus*) ha estat inclosa en la llista vermella de la IUCN, ja que en els últims 50 anys la seva població s'ha reduït dràsticament en més del 80% com a conseqüència de la caça furtiva, la pèrdua i la fragmentació de l'hàbitat a causa de les activitats humanes. Sierra Leone alberga la tercera població més gran de ximpanzé occidental, però més de la meitat viu en àrees desprotegides dominades per activitats agrícoles amb una considerable competència pels recursos entre les persones i els ximpanzés. Aquesta tesi explora els reptes dels agricultors i de les seves actituds i percepcions cap als ximpanzés en quatre zones rurals de Sierra Leone. Segons els agricultors, la fauna silvestre és el principal problema agrícola que pateixen, tot i que els ximpanzés no van ser inclosos dins de les 3 espècies més destructives. Els ximpanzés consumeixen els recursos que ofereixen les palmeres d'oli semidomesticades i les fruites conreades, la qual cosa és vista de forma negativa pels agricultors. En general, els agricultors perceben els ximpanzés més destructius que perillosos. Entre els mesos d'abril de 2016 i maig de 2017, vam realitzar un estudi amb càmeres de trampeig fotogràfic en una de les zones rurals prèviament enquestades amb l'objectiu d'analitzar l'impacte de factors ecològics i antropogènics sobre l'abundància de ximpanzés que viuen en un hàbitat molt degradat per l'home al districte sud-occidental de Moyamba a Sierra Leone. El model va mostrar que l'abundància de ximpanzés en aquest hàbitat es veu afectada per la distància a les carreteres i la proximitat als aiguamolls. No obstant això, els poblats i la proximitat humana no van influir. La tolerància dels agricultors i el baix nivell de caça es consideren algunes de les raons per les quals encara existeixen poblacions de ximpanzés en aquestes àrees tan degradades. Finalment, aquest estudi també proporciona una visió preliminar sobre la demografia, l'estructura del grup i l'àrea de distribució de ximpanzés no habituats que viuen en un hàbitat no protegit. Els resultats d'aquesta tesi contribueixen a una millor comprensió de com els ximpanzés sobreviuen en aquests hàbitats degradats i de les implicacions per a dur terme plans de conservació, que integrin una planificació agrícola i l'ús del sòl.

Resumen

Las poblaciones de chimpancés (*Pan troglodytes*) afrontan un grave riesgo de extinción, y la principal amenaza mundial es la transformación del hábitat hacia una agricultura de subsistencia y comercial. La subespecie de chimpancé occidental (*Pan troglodytes verus*) está incluida en la lista roja de la IUCN, ya que en los últimos 50 años su población se ha reducido drásticamente en más del 80% como consecuencia de la caza furtiva, la pérdida y fragmentación del hábitat debido a las actividades humanas. Sierra Leona alberga la tercera población más grande de chimpancé occidental, pero más de la mitad vive en áreas desprotegidas dominadas por actividades agrícolas con una considerable competencia por los recursos entre las personas y los chimpancés. Esta tesis explora los retos de los agricultores y sus actitudes y percepciones hacia los chimpancés en cuatro zonas rurales de Sierra Leona. Según los agricultores, la fauna silvestre es el principal problema agrícola que sufren, aunque los chimpancés no fueron incluidos dentro de las 3 especies más destructivas. Los chimpancés consumen los recursos que ofrecen las palmeras de aceite semidomesticadas y las frutas cultivadas, lo que se percibe de forma negativa por los agricultores. En general, los agricultores perciben a los chimpancés más destructivos que peligrosos. Entre abril de 2016 y mayo de 2017, realizamos un estudio con cámaras de trampeo fotográfico en una de las zonas rurales previamente encuestadas con el objetivo de analizar el impacto de factores ecológicos y antropogénicos sobre la abundancia de chimpancés que viven en un hábitat muy degradado por el hombre en el distrito suroccidental de Moyamba de Sierra Leona. El modelo mostró que la abundancia de chimpancés se ve afectada por la distancia a las carreteras y la proximidad a los humedales. Sin embargo, los poblados y la proximidad humana no influyeron. La tolerancia de los agricultores y el bajo nivel de caza se consideran algunas de las razones por las que aún persisten chimpancés en estos hábitats tan degradados. Finalmente, este estudio también proporciona una visión preliminar sobre la demografía, la estructura del grupo y el área de campeo de chimpancés no habituados que viven en un hábitat no protegido. Los resultados de esta tesis contribuyen a una mejor comprensión de cómo los chimpancés sobreviven en estos hábitats degradados y de las implicaciones para llevar a cabo planes de conservación, que integren una planificación agrícola y del uso del suelo.

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I never thought I would do a PhD and now that it is done, I feel relieved and proud. But this would have not been possible without the encouragement, support and guidance of many people because a thesis is never a work of one. Many people ends up involved in helping in many different ways. And I apologise beforehand, if I forget to mention someone.

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Tacugama Chimpanzee Sanctuary has been my home for many years. It has been a privilege and an honour to work with Bala Amarasekaran, director and founder of Tacugama, who I admire unconditionally for his persistence and strength. If there is someone that is doing all possible in the most difficult circumstances to help chimpanzees, is him, together with all the committed sanctuary staff. This thesis is dedicated to them and to all the chimpanzees at Tacugama. Unfortunately, all of the sanctuary chimpanzees have been orphaned from the wild and it is my hope this research helps a little to protect the remaining wild chimpanzees and to prevent more arriving to the sanctuary gates.

This project would have not been possible without the help and work of Tacugama's outreach team: Natalia Casado, David Momoh, Konkofa Marah, Joseph Marah, Bockarie and Yirah Koroma. They are wonderful and very hard working. Tanki, tanki.

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Sierra Leone is a wonderful country that has suffered greatly over the years but always shows a firm determination to resurface. I thank the Ministry of Agriculture, Forestry and Food Security of the Sierra Leone Government for granting the permission to conduct this research, the paramount chiefs, the local authorities and above all, the farmers of all the villages I worked in for their hearted welcoming.

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In memory of my father Josep

List of abbreviations and acronyms

CBD - Convention on Biological Diversity

CILSS - Comité Permanent Inter-états de Lutte contre la Sécheresse dans le Sahel

CITES - Convention on International Trade in Endangered Species of Wild Fauna and Flora

DRC - Democratic Republic of Congo

GIS – Geographic Information System

GoSL – Government of Sierra Leone

IUCN - International Union for Conservation of Nature

KDE - Kernel density estimator

MCP - Minimum convex polygon

NBSAP - National Biodiversity Strategic Action Plan

NP – National Park

SL – Sierra Leone

SLNCCP - Sierra Leone National Chimpanzee Census Project

SPSS – Statistical Package for the Social Sciences

SSC - Species Survival Commission

TCS - Tacugama Chimpanzee Sanctuary

UAVs - Unmanned aerial vehicles

UGFB - Upper Guinean Forest Block

UNDP - United Nations Human Development

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PART I

1 - Introduction

1.1. The Epoch of the Anthropocene

Coined by earth scientists in the early 2000s, the Anthropocene describes a new epoch characterised by the direct and indirect human-derived environmental changes to the Earth (Steffen et al. 2011). The rate of human population growth has increased dramatically since the last century reaching an alarming 7.6 billion people and growing at a rate of 50 million per year (United Nations DESA / Population Division 2017). The more people, the more ecosystem services are required, e.g. more food, more fuel, more land, etc., in turn irreversibly destroying, degrading and polluting natural habitats globally. Many scientists believe that the Sixth Mass Extinction is already happening due to the continuous pressures put onto the Earth by environmental changes associated with human activities (Barnosky et al. 2011; Dirzo et al. 2014; Pimm & Raven 2000; Sodhi & Ehrlich 2010). Human activities have without doubt exacerbated biodiversity loss (Aukema et al. 2017; Cahill et al. 2012). One of the most accepted environmental alterations occurring nowadays is global warming, linked to increased fossil fuel emissions and the release of green-house gasses (Solomon et al. 2009). The Earth's average surface temperature is increasing fast and triggering global environmental changes, such as the melting of the ice mass, rising sea levels and extreme weather events (Sodhi & Ehrlich 2010). How precisely these environmental changes will affect biodiversity globally is still a matter of debate; however, climate change is expected to increase and accelerate biodiversity loss for every degree rise in global temperatures (Cahill et al. 2012; Urban 2015; Wiederholt & Post 2010). Current main drivers for biodiversity loss are habitat degradation, fragmentation and destruction, unsustainable exploitation of natural resources and the displacement of native species by invasive ones (Butchart et al. 2010; Crooks et al. 2017). However, the greatest causes of biodiversity loss are habitat loss and degradation (Pimm & Raven 2000). The high demand for land and ecosystem resources are decimating natural habitats and consequently affecting adversely biodiversity (Aukema et al. 2017; Hoffmann et al. 2010).

1.2. Non-human primates in anthropogenic habitats

Approximately 60% of all non-human primates (hereafter primates) globally are threatened with extinction (Estrada et al. 2017). The main global threat is habitat loss due to habitat conversion for subsistence and commercial agriculture, but regional threats include logging, livestock farming and hunting (Estrada et al. 2017; Laurance et al. 2014). Consequently, habitats and protected forests are shrinking, becoming more fragmented and driving primates to live in forest-agricultural mosaics and in closer proximity to humans (Estrada 2013). Increased fragmentation of forest habitats negatively affects biodiversity globally and species in more fragmented habitats are at a greater risk of going extinct (Crooks et al. 2017). West Africa has one of the most fragmented tropical forest landscapes in the world due to deforestation (Rudel & Roper 1997). Some animal species can adjust to these changes and are able to survive and even flourish in human altered conditions (Wong & Candolin 2015). Indeed, many primate species show a certain degree of flexibility and adapt their dietary, socioecological behaviours to these human altered or also called anthropogenic habitats (Brncic et al. 2015; McLennan et al. 2017).

1.3. Chimpanzees (*Pan troglodytes*) and their conservation status

The Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) recognizes four subspecies of the common chimpanzee (*Pan troglodytes*) (Humle et al. 2016): the Western Chimpanzee (*Pan troglodytes verus*); the Nigeria-Cameroon Chimpanzee (*P. t. ellioti*); the Central Chimpanzee (*P. t. troglodytes*); and the Eastern Chimpanzee (*P. t. schweinfurthii*). All of them are listed as endangered and their populations are declining. Recently the IUCN status for the western subspecies was upgraded to critically endangered (Humle et al. 2016) because it is predicted that over the next three generations, i.e. 75 years, its population is likely to decline by more than 80% as a result of poaching, habitat loss and fragmentation due to human activities (Kühl et al. 2017).

The current estimates for the total chimpanzee population are between 172,700 - 299,700 individuals (Humle 2003). For each subspecies, current estimates are as follows:

- *P. t. ellioti*: Probably fewer than 6,000–9,000 (Morgan et al. 2011)
- *P. t. schweinfurthii*: 181,000–256,000 (Plumptre et al. 2010)
- *P. t. troglodytes*: approximately 140,000 (Maisels et al. 2016)
- *P. t. verus*: 15,000–65,000 (Kühl et al. 2017)

Chimpanzees are distributed in the tropical and subtropical belt of Africa from southern Senegal to western Tanzania and western Uganda (Fig. 1.1). Chimpanzees can occur in a variety of habitats from moist lowland to mountain forests, swamp forests, woodland savannahs and farmland (Williamson et al. 2013). In West Africa, chimpanzees are also found in fallow-agricultural matrixes dominated by wild or feral oil palms (Brncic et al. 2010; Humle et al. 2016).

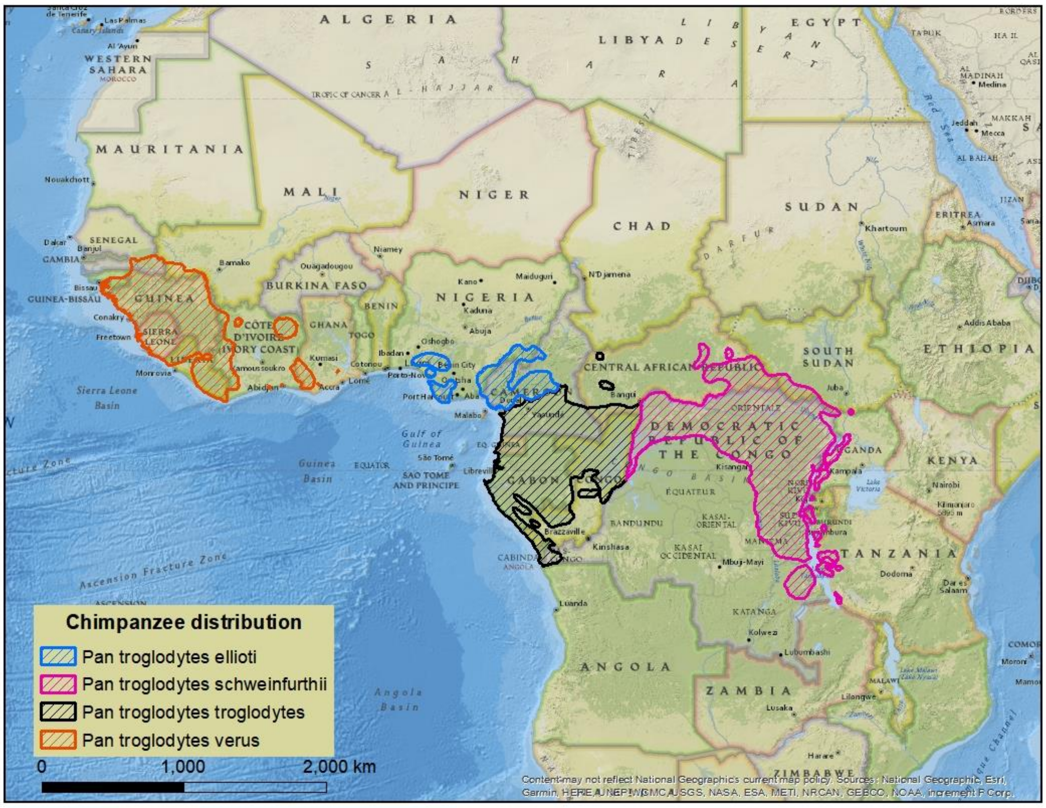

Figure 1.1. Chimpanzee distribution across Africa distinguishing the four known subspecies (Sourced Prado-Martinez et al. 2013).

Chimpanzees are semi-terrestrial, diurnal primates and spent approximately half of the day-time on the ground travelling, feeding and socialising, and sleep in nests built every night high in the canopy (Mittermeier et al. 2013). They are gregarious, territorial and live in multi-gender fission-fusion communities averaging 35 members, ranging from 16 to 82 (Mittermeier et al. 2013). Home ranges in forest habitats vary from 6-8 km^2 to 32 km^2 (Basabose 2005; Boesch & Boesch-Achermann 2000; Humle 2011). In savannah woodland their home range can exceed the 500 km^2 (Nakamura et al. 2013). Chimpanzees are omnivorous but basically frugivorous.

Fruit indeed forms about half the diet, typically supplemented with terrestrial herbaceous vegetation, leaves, stems, seeds, flowers, bark, pith, honey, mushrooms, resin, eggs, and animal prey such as insects and medium-sized mammals with variation across communities (Mittermeier et al. 2013). Chimpanzees are well-known tool users across most of their range with cultural variation between communities (Whiten et al. 1999). They make and use tools from plant parts to extract bees, ants and termites from their nests, and stone hammers or wooden clubs to crack nuts (Whiten et al. 1999), spears to hunt in hollow trees (Pruetz & Bertolani 2007) and stepping-sticks to climb thorny trees (Alp 1997).

The chimpanzee is protected by law across all range states where it occurs in the wild (Humle et al. 2016) and listed in Appendix I CITES. However, the laws protecting the species are often not enforced across most of its range, as evidenced by the continual influx of orphan chimpanzees into sanctuaries or rehabilitation centres, often by-products of wild-meat hunting (Faust et al. 2011) and the persistence of the illegal trade in live individuals (Stiles et al. 2013).

The rapid human population growth and agricultural expansion into forested areas have forced chimpanzee populations to live into anthropogenic habitats (Humle et al. 2016). However, to date, most conservation efforts have focused on protecting areas of high value for biodiversity that contain threatened species of international concern (Bermejo 1999; Chapman et al. 2018; Fleury-Brugiere & Brugiere 2010; Pusey et al. 2007). Most studies to date have therefore been carried out in or around protected areas (Ganas 2009; Hockings & Sousa 2013; Matthews & Matthews 2004), and comparatively few have investigated sympatry between chimpanzees and farmers in landscapes dominated by agriculture (Bryson-Morrison et al. 2017; Hockings et al. 2015; McLennan 2008; McLennan & Hill 2012).

1.4. Sierra Leone

Sierra Leone is located on the Atlantic coast of West Africa, bordering Guinea, Liberia and the Atlantic Ocean and it covers an approximate area of 72,500 km^2. Sierra Leone lies at the western end of the Upper Guinean Forest Block (UGFB) (Fig. 1.2) which is among one of the most biologically rich in the world but also highly threatened with extinction (Brooks et al. 2002). The UGFB has been designated as one of 25 global biodiversity hotspots (Myers et al. 2000) and one of the two highest priorities for primate conservation in the world (Mittermeier et al. 1999).

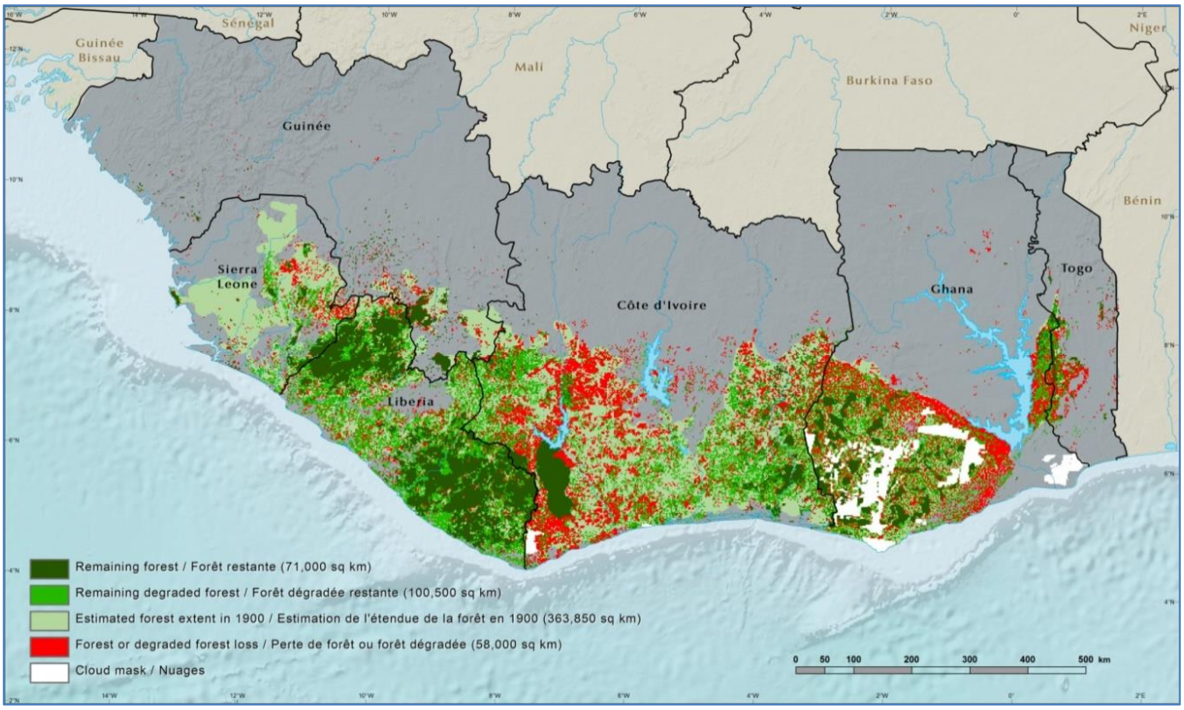

Figure 1.2. Upper Guinean Forest change from 1975 to 2013. Sourced: CILSS, 2016.

Sierra Leone has sustained a very fast human demographic growth rate since 1963 from approximately 2 million to a human population currently numbering 7 million, a rise of more than 250% (Statistics Sierra Leone 2017). More than half of the population (59%) lives in rural areas and the rest in urban areas (Statistics Sierra Leone 2017). Sierra Leone has suffered a vicious 10-year civil conflict which ended in 2002 and resulted in large numbers of internally displaced people, adding to the degradation and increased human pressure on important ecosystems (Squire 2001). When the country was slowly recovering economically and psychologically from the scars of the war, a deadly Ebola outbreak hit the country between 2014 and the start of 2016, which not only caused thousands of deaths, but compromised seriously the country's health system and had an adverse socio-economic impact (Elston et al. 2017). Currently, Sierra Leone is ranked 179th out of 188 countries on the United Nations Human Development Index (UNDP 2016), a very low index that shows the country's poor level of development. On paper, the Government of Sierra Leone (GoSL) is committed to the on-going protection and management of its biodiversity assets under the Convention on Biological Diversity (CBD), and has developed a National Biodiversity Strategic Action Plan (NBSAP). It is also a signatory to the

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). However, the GoSL has extremely limited resources available and is unable to implement effectively the majority of its desired environmental strategies without external support.

It is unknown how much forest cover Sierra Leone had over the last century but it is unlikely that the country was ever heavily covered by dense forests (Munro & van der Horst 2012). However, it is estimated that since 1975, the country has lost 36% of its forest and woodland habitats (CILSS 2016). 'Farm-bush', the degraded secondary forest growth that succeeds slash-and-burn agriculture, is increasingly the most dominant vegetation type in Sierra Leone (CILSS 2016).

Sierra Leone is home to 193 species of mammals of which 35 species are red listed by the IUCN as critically endangered (1), endangered (5) vulnerable (16) and near threatened (13). The country's diverse wildlife includes 15 species of primates, elephant (*Loxodonta Africana*), common and pygmy hippopotamus (*Hippopotamus amphibius* and *Choeropsis liberiensis)*, leopard (*Panthera pardus*), golden cat (*Caracal aurata*), water chevrotain (*Hyemoschus aquaticus*), bongo (*Tragelaphus eurycerus*), bushbuck (*Tragelaphus scriptus*), waterbuck (*Kobus ellipsiprymnus*) and ten species of duikers (*Cephalophinae*).

However, hunting for wild-meat is a common and serious issue across Africa affecting protected animal species (Schulte-Herbrüggen et al. 2013). Wild-meat is an important element in the diet of many Sierra Leoneans. Cane rats (*Thryonomys swinderianus)*, porcupines (Hystricidae), duikers, bushbuck and primates comprise the majority of wild caught meat in Sierra Leone (Subramanian 2012) (Fig. 1.3).

The taste for wild-meat has not decreased in Sierra Leone despite the laws protecting endangered species and despite the two-year long Ebola outbreak and the widespread campaigns against hunting/eating wild-meat across the country (Bonwitt et al. 2018).

Figure 1.3. Market stall selling wild-meat in Bo, Sierra Leone. Photo ©TCS.

Forty percent of the primates living in Sierra Leone are listed as threatened by the IUCN (Table 1.1). Sierra Leone harbours the third largest western chimpanzee population after Guinea and Liberia (Brncic et al. 2010; Kühl et al. 2017). The western chimpanzee subspecies ranges from the Dahomey Gap/Niger River westward to Senegal and is estimated to number between 15,000 and 65,000 individuals (Kühl et al. 2017). The subspecies has already gone extinct in three countries - Benin, Togo and Burkina Faso; populations in Senegal, Guinea Bissau and Ghana are extremely threatened and number fewer than 1,150 individuals (Kühl et al. 2017).

Tacugama Chimpanzee Sanctuary (TCS), the only chimpanzee rescue and rehabilitation centre in Sierra Leone, coordinated the Sierra Leone National Chimpanzee Census Project (SLNCCP) during 2009-2010. The census estimated a total population of 5,580 chimpanzees (range 3,052-10,446) across the country, with >50% located outside protected areas (Brncic et al. 2010). Chimpanzees face serious threats in Sierra Leone, including habitat loss, hunting, and retaliation as a result of competition with people for resources (Brncic et al. 2010). The census findings highlighted the extent of human–chimpanzee competition for resources, with 88% of villages that reported local presence of chimpanzees mentioning that chimpanzees foraged on crops.

Table 1.1. List of primates present in Sierra Leone and their IUCN status. CR: critically endangered, EN: endangered, VU: vulnerable, NT: near threatened, LC: least concern.

Species	Common names	Red List status	Year assessed	Population trend
Cercocebus atys	Sooty Mangabey	NT	2016	decreasing
Cercopithecus campbelli	Campbell's Monkey	LC	2016	unknown
Cercopithecus diana	Diana Monkey	VU	2016	decreasing
Cercopithecus petaurista	Spot-nosed Monkey	LC	2008	unknown
Chlorocebus sabaeus	Green Monkey	LC	2008	stable
Colobus polykomos	Western Black-and-White Colobus	VU	2008	unknown
Erythrocebus patas	Patas Monkey	LC	2008	decreasing
Galago senegalensis	Senegal Galago	LC	2008	stable
Galagoides demidoff	Demidoff's Galago	LC	2016	stable
Galagoides thomasi	Thomas's Galago	LC	2008	stable
Pan troglodytes verus	Chimpanzee	CR	2016	decreasing
Papio anubis	Olive Baboon	LC	2008	increasing
Perodicticus potto	West African Potto	LC	2016	stable
Piliocolobus badius	Western Red Colobus	EN	2016	decreasing
Procolobus verus	Olive Colobus	NT	2008	unknown

1.5. Chimpanzees adaptability to anthropogenic habitats and their co-existence with humans

Over the last decade there has been a growing interest in studying primates, and especially chimpanzees, living in anthropogenic habitats to understand how they behave and survive in these habitats and which conservation strategies can be implemented for the survival of the species (McLennan et al. 2017). Chimpanzees living in anthropogenic landscapes have featured in studies more often than any of the other great apes (McLennan et al. 2017). Chimpanzees seem capable of adapting to some level of human disturbances like agriculture and/or low levels of hunting (Brncic et al. 2015; Rist et al. 2009) adjusting their behaviour. Reported behavioural adjustments of chimpanzees to anthropogenic habitats include feeding in energy-rich crops when forest fruits are scarce (McLennan 2013), chimpanzees with longer exposure to agriculture, eat more variety of crops than chimpanzees with recent exposure (McLennan & Hockings 2014); consuming crops during the night to avoid the risks of encounters with farmers (Krief et al. 2014); raiding crops in more cohesive group parties instead of splitting into smaller groups (Hockings et al. 2012); feeding on terrestrial herbaceous vegetation along the roads, especially in times of fruit scarcity (Bortolamiol et al. 2016); feeding on novel food resources like eucalyptus bark (*Eucalyptus grandis*) (McCarthy et al. 2017); nesting in introduced tree species such as eucalyptus (McCarthy et al. 2017); and adapting their behaviour when crossing roads (Cibot et al. 2015; Hockings et al. 2012).

Usually, anthropogenic landscapes in which primates co-exist with humans consist of a complex mosaic of forest and agricultural habitat types intermixed with roads and settlements often bordering protected areas (McLennan et al. 2017). Some studies have shown similar density estimates for *Colobus guereza* and *Pan troglodytes* between a mixed agroforestry system and a bordering protected forest revealing the importance of this anthropogenic habitat for the conservation of primates (Blanco & Waltert 2013). Most of the primates found in the Kibale National Park in Uganda also use and live in small forest patches near the park; however, no predictor variables could explain suitably primates' ability to live in these forest patches (Onderdonk & Chapman 2000). Nevertheless, the absence of hunting and the proximity to a large forested and protected area may play an important role in sustaining primate presence and abundance in forest patches abutting the national park (Blanco & Waltert 2013). According to a global study on the relationship between number of species and forest fragment area (≤ 100 km^2), primate richness declined with area size except in Africa (Harcourt & Doherty 2005). The study discusses whether primates in Africa are more resilient to local extinction because they have been more exposed historically to human influence. In Sierra Leone, there are chimpanzee populations living in highly degraded anthropogenic landscapes without neighbouring protected areas and with only small remnant forest fragments left (Brncic et al. 2010). Typically, such forest fragments are riverine, flooded and swamp forests not suitable for agriculture and are important habitat refuges for wildlife (McLennan & Hill 2010). Some studies have highlighted the importance of swamp forests and mangroves for great apes in certain areas (chimpanzees and bonobos (*Pan paniscus*): Inogwabini et al. 2012; western lowland gorillas (*Gorilla gorilla gorilla*) and chimpanzees: Poulsen & Clark 2004; western lowland gorillas: Rainey et al. 2010; western lowland gorillas and chimpanzees: Stokes et al. 2010). Therefore, as human population grows and agriculture expands, the role of agroecosystems and habitat refuges within the landscape, such as swamps, should be evaluated in the context of the long-term persistence of primate populations in these locations (Estrada et al. 2012). However, one study in the Democratic Republic of Congo (DRC) showed that the swamps present in the study area were minimally used by chimpanzees (Basabose 2005). The author argued that when swamps form part of a mixed habitat where primary and secondary forests patches are dominant, chimpanzees use the swamp areas much less because the area is unsuitable for chimpanzees, and suggests that swamp areas might act as a separation between chimpanzee groups.

Non-human primates are often cited as one of the main culprits of crop foraging in the geographical ranges where they occur (Humle & Hill 2016). Foraging on crops by chimpanzees has also been reported across Africa (Hockings & Humle 2009; McLennan & Hockings 2014). The survival of chimpanzees in agricultural matrixes could be attributed to human tolerance in some areas due to religious and cultural taboos (Hockings & Sousa 2013), the access to highly nutritious cultivars (Hockings et al. 2009) and the importance of semi-domesticated oil palms (*Elaeis guineensis*) for nesting and food resource in some areas (e.g. Bossou, Guinea: Humle & Matsuzawa 2004; Guinea-Bissau: Bessa et al. 2015; Sousa et al. 2011). Semi-domesticated oil palms are not actively cultivated by farmers but are wild oil palms that are not felled in slash-and-burn cultivation systems (Gerritsma & Wessel 1997). Davies (1987) already noted that chimpanzees in Sierra Leone frequented agricultural land across the entire country, but few studies have explored at fine-spatial scale how chimpanzees survive in these human degraded landscapes, what type of adaptations have developed to survive in them, what is the future for these populations and which conservation measures can effectively be implemented to protect them in Sierra Leone (Brncic et al. 2010; Brncic et al. 2015).

To date, studies have primarily focused on evaluating the crops targeted by chimpanzees and their dietary contribution relative to wild foods (Bryson-Morrison 2017; Hockings et al. 2009; Hockings & McLennan 2012; McLennan & Ganzhorn 2017; McLennan & Hockings 2014), as well as chimpanzees' responses to interactions with people and associated infrastructure, such as roads (Cibot et al. 2015; Hockings et al. 2006; McLennan & Hill 2010, 2012). Local people who depend on natural resources often perceive conservation efforts to protect biodiversity as a threat to their livelihoods (Madden & Mcquinn 2014; Redpath et al. 2013). However, not all wildlife causes the same amount of damage and farmers may hold biased perceptions of damage linked to species attributes such as size, temporal and spatial activity patterns, sociality and/or traditional and related cultural taboos and beliefs (Humle & Hill 2016). Understanding local perceptions, attitudes and concerns regarding wildlife is crucial for appropriate conservation and management strategies, to reduce conflict and promote a sustainable coexistence between people and wildlife (Madden & Mcquinn 2014; Redpath et al. 2013).

1.6. Surveying chimpanzees

Historically field pioneer primatologists studied wild chimpanzees after habituating them (Imanishi 1960; Kortlandt 1962; Nishida 1968; Reynolds & Reynolds 1965; Van Lawick-Goodall 1968) and direct behavioural observations are still ongoing at many of these sites, some of which for more than 50 years (e.g. Taï Forest, Côte d'Ivoire: Boesch & Boesch-Achermann 2000; Gombe, Tanzania: Pusey et al. 2007; Bossou, Guinea: Matsuzawa et al. 2011; Mahale, Tanzania: Nakamura et al. 2015). This technique is highly efficient for individual identification and behavioural studies but requires years before the animals trust scientists to let them follow and observe them at close distance. However, there is currently controversy regarding the consequences of habituation and its negative impacts (Macfie & Williamson 2010; Williamson & Feistner 2011). Chimpanzees are physiologically and genetically very similar to humans and therefore highly susceptible to acquire and succumb to zoonotic diseases from researchers and visitors (Dunay et al. 2018; Köndgen et al. 2008; Scully et al. 2018).

Therefore, scientists have been using alternative indirect methods to study chimpanzee behaviour with remote heat and motion sensitive photography (hereafter camera traps) (e.g.: Boesch et al. 2017; Krief et al. 2014; Lapuente et al. 2017; Sanz et al. 2010) and to study chimpanzee diet (McLennan 2013) and disease (Köndgen et al. 2010) via faecal analysis. Other indirect techniques to survey and determine chimpanzee presence, density, distribution, composition and population size (Kühl et al. 2008) include line transect distance sampling (Buckland et al. 2010), reconnaissance trail surveys (recces) (Plumptre & Cox 2006), interviews with local people (Duvall 2008), dung sampling for genetic analysis (Arandjelovic & Vigilant 2018; Moore & Vigilant 2014), camera trapping (O'Connell et al. 2011) and unmanned aerial vehicles (UAVs) (van Andel et al. 2015). However, there is not a survey technique that does not have limitations and it is often recommended to use a combination to suit research purposes (Ancrenaz et al. 2012; Kühl et al. 2008).

In the last 20 years, the use of camera traps in primatology has grown in popularity for the survey of rare species, for population assessments, for behavioural studies and for species monitoring and identification (Pebsworth & LaFleur 2014). The use of camera traps in research presents various pros and cons. Camera traps are a non-invasive tool that can be used over large survey areas for several months at a time and are considered an efficient tool for research (Ancrenaz et al. 2012). However, they pose certain constraints that require consideration. Camera traps are better suited to detect medium to large terrestrial mammals, they have an initial high cost and their performance is very variable depending on the type of environment they are set (Ancrenaz et al. 2012; Newey et al. 2015; Pebsworth & LaFleur 2014). Added issues with the use of camera traps are the large amount of data gathered that needs to be processed and analysed, technical failures and theft (Meek et al. 2016; O'Connell et al. 2011). Despite these shortcomings, the use of camera traps to study animal species distribution and richness (Si et al. 2014), abundance (Nakashima et al. 2013), behaviour (Caravaggi et al. 2017) and social structure (Ahumada et al. 2011) amongst others has increased markedly in recent years.

For the study of chimpanzees, camera traps are utilised to identify unhabituated chimpanzees and to study their behaviour (e.g.: Boesch et al. 2017; Krief et al. 2014; Lapuente et al. 2017; Sanz et al. 2010; Boyer-Ontl & Pruetz 2014). However, capture-recapture methods to determine animal densities cannot be easily implemented with species like chimpanzees as it requires large number of images for their correct identification. To overcome this issue, occupancy models have been developed to estimate species abundances using camera traps when capture–recapture methods of estimation cannot be implemented (Després-Einspenner et al. 2017; Mackenzie et al. 2006) and can provide inferences of habitat use by a species and their distribution in relation to landscape variables such roads, settlements (Gerber et al. 2014).

2 - Objectives

The aims of this thesis were to investigate the attitudes and perceptions of farmers towards chimpanzees living in an unprotected and highly human modified habitat in the district of Moyamba in south-western Sierra Leone, and to analyse whether the different habitat features affect chimpanzees' habitat use and distribution across highly anthropogenic landscapes.

The specific objectives were:

- To analyse and understand farmers' perceptions and attitudes to the challenges to subsistence agriculture and crop foraging by wildlife and chimpanzees in particular in unprotected habitats in Sierra Leone.

- To study the potential influence of human disturbance on spatial (i.e. occupancy and detectability) patterns of chimpanzees in the Lawana study area, and to assess if variables like roads, settlements, swamps and mangroves influence the presence of chimpanzee based on camera trapping rates.

- To estimate chimpanzees' minimum group size and structure by individual identification. Infer the minimum home range area for the chimpanzee population living in the study area and to compare daily chimpanzees' activity patterns to daily human activity.

PART II- Studies

3 – Study I

Perceptions of challenges to subsistence agriculture, and crop foraging by wildlife and chimpanzees (*Pan troglodytes verus*) in unprotected areas in Sierra Leone

Garriga, R. M., Marco, I., Casas-Díaz, E., Amarasekaran, B., & Humle, T. (2017). Oryx, pp. 1–14. doi:10.1017/S0030605316001319

3.1. Abstract

The 2009-2010 Sierra Leone National Chimpanzee Census Project estimated there was a population of 5,580 chimpanzees (*Pan troglodytes verus)* distributed across the country, with >50% occurring outside protected areas. The census also highlighted the significance of competition between people and chimpanzees for resources in areas dominated by farming activities where wild chimpanzees forage on crops. We selected four study areas in two districts in Sierra Leone with high chimpanzee density in habitats dominated by agriculture, far from any protected areas. Our objectives were to assess farmers' perceptions of the main challenges to their agricultural yields, and the wildlife involved in crop foraging, and their perceptions of chimpanzees in particular, as well as the main crop protection measures used. We conducted 257 semi-structured interviews with local farmers across the four study areas. We found that (1) farmers reported wild animals as the main challenge to their agricultural practices; (2) most complaints concerned cane rats (*Thryonomys swinderianus)*, which targeted almost all crop types, especially rice and cassava; (3) chimpanzees reportedly targeted 21 of the 23 crop types cultivated, but did so less often than cane rats, focusing particularly on oil palm, cassava and domestic fruits; (4) overall, chimpanzees were not among the top three most destructive animals reported; (5) chimpanzees were generally perceived as being more destructive than dangerous and as having declined since before the civil war; and (6) the main crop protection measure employed was fencing interspersed with traps. Our findings show the importance of investigating farmers' perceptions to inform the development of appropriate conservation strategies aimed at promoting coexistence of people and wildlife in degraded landscapes.

3.2. Introduction

Competition for resources between wildlife and people is a widespread concern in places where they coexist (Woodroffe et al., 2005). Wild animals are an important part of the life and diet of many local people in developing countries (Hoffman & Cawthorn, 2012) but habitat loss, agricultural expansion (Maxwell et al., 2016) and human encroachment into wildlife habitat are key drivers of wildlife population decline and even local extinctions (Van Vliet et al., 2012). In anthropogenic landscapes wildlife may be compelled to consume cultivated foods or prey on domesticated animals to survive (McLennan, 2008; Hockings et al., 2009; Inskip & Zimmermann, 2009). Competition between wildlife and people is problematic in areas where farmers depend solely or predominantly on subsistence agriculture and natural resources, as it can affect peoples' livelihoods and their relationship with, and perceptions of, wildlife (Naughton-Treves, 1998; Webber & Hill, 2014; Humle & Hill, 2016).

Sierra Leone is home to the western chimpanzee (*Pan troglodytes verus)*, which is categorized as Critically Endangered on the IUCN Red List (Humle et al., 2016). In Côte d'Ivoire the wild chimpanzee population has declined by up to 90% in recent years (Campbell et al., 2008) and this highlights the importance of Sierra Leone for chimpanzee conservation in West Africa. However, chimpanzees face serious threats in Sierra Leone, including habitat loss, hunting, and retaliation as a result of competition with people for resources (Brncic et al., 2010). The chimpanzee is protected by law across all range states where it occurs in the wild (Humle et al., 2016). However, the laws protecting the species are often not enforced across most of its range, as evidenced by the continual influx of orphan chimpanzees into sanctuaries or rehabilitation centres, often by-products of bushmeat hunting (Faust et al., 2011) and the persistence of the illegal trade in live individuals (Stiles et al., 2013). Conservation efforts are often focused on protecting areas of high value for biodiversity that contain threatened species of international concern. Most studies to date have therefore been carried out in or around protected areas, and comparatively few have investigated sympatry between chimpanzees and farmers in landscapes dominated by agriculture (e.g. Halloran et al., 2013; McLennan & Hill, 2013; Hockings et al., 2015).

Tacugama Chimpanzee Sanctuary coordinated the Sierra Leone National Chimpanzee Census Project during 2009-2010. The census estimated a total population of 5,580 chimpanzees (range 3,052–10,446) across the country, with >50% located outside protected areas (Brncic et al., 2010). The findings highlighted the extent of human-chimpanzee competition for resources, with 88% of villages that reported local presence of chimpanzees mentioning that chimpanzees foraged on crops. The population and habitat viability assessment conducted following the census suggested the need for a better understanding of the costs and benefits of coexistence for both people and chimpanzees; the threats faced by chimpanzees in such landscapes; the attitudes and perceptions of the farmers regarding chimpanzees; and how and why these change over time (Carlsen et al., 2012).

Local people who depend on natural resources often perceive conservation efforts to protect biodiversity as a threat to their livelihoods (Redpath et al., 2013; Madden & McQuinn, 2014). However, not all wildlife causes the same amount of damage and farmers may hold biased perceptions of damage linked to species attributes such as size, temporal and spatial activity patterns, sociality and/or traditional and related cultural taboos and beliefs (Humle & Hill, 2016). Understanding local perceptions, attitudes and concerns regarding wildlife is crucial for appropriate conservation and management strategies, to reduce conflict and promote a sustainable coexistence between people and wildlife (Redpath et al., 2013; Madden & McQuinn, 2014). Non-human primates are often cited as one of the main perpetrators of crop raiding in the geographical ranges where they occur (Humle & Hill, 2016). Foraging on crops by chimpanzees has also been reported across Africa (Hockings & Humle, 2009; McLennan & Hockings, 2014). To date, studies have primarily focused on evaluating the crops targeted by chimpanzees and their dietary contribution relative to wild foods (Hockings et al., 2009; Hockings & McLennan, 2012; McLennan & Hockings, 2014), as well as chimpanzees' responses to interactions with people and associated infrastructure, such as roads (McLennan & Hill, 2010, 2012; Hockings, 2011; Cibot et al., 2015; McLennan & Asiimwe, 2016). Although reports of fatal attacks by chimpanzees on people are rare, there has been an increasing number of accounts of chimpanzees behaving aggressively towards people (McLennan & Hockings, 2016). Even if often attributable to prior provocation by people (Hockings et al., 2010), such instances can elicit or increase negative attitudes towards chimpanzees, generate resentment and accentuate the fear of attack (McLennan & Hockings, 2016). Nevertheless, few studies have explored people's perceptions and attitudes towards chimpanzees. It was found that chimpanzees in Tombali, Guinea-Bissau, were perceived as human-like and inedible but were also considered to be pests because of their crop foraging behaviour (Costa et al., 2013). In this region, non-Muslims appeared to be more tolerant than Muslims, and men perceived chimpanzees more positively than women. In the Budongo forest of Uganda, farmers perceived chimpanzees more positively than other primates, such as baboons *Papio* spp., although some farmers indicated they were afraid of chimpanzees (Webber & Hill, 2014). Farmers in Bulindi, Uganda, were found in general to have a positive perception of chimpanzees and tolerate occasional foraging of domestic fruits but not cash crops (McLennan & Hill, 2012). This latter study emphasized that alterations to the habitat and human encroachment can negatively affect chimpanzee behaviour towards people, thus ‘challenging residents’ traditionally benign attitude towards them’ (p. 219).

We selected four areas in unprotected landscapes with hardly any forest cover but with a high density of chimpanzees and with reported instances of human-chimpanzee competition for resources, based on national census data (Fig. 3.1) (Brncic et al., 2010). Our aims were to identify the key challenges to agricultural productivity for people in these landscapes, assess the mitigation strategies currently used by farmers to protect their crops from wildlife, and understand the farmers’ perceptions of chimpanzees and their current status in their locality, and evaluate the perceived impact of crop losses caused by chimpanzees relative to other wildlife in each study area.

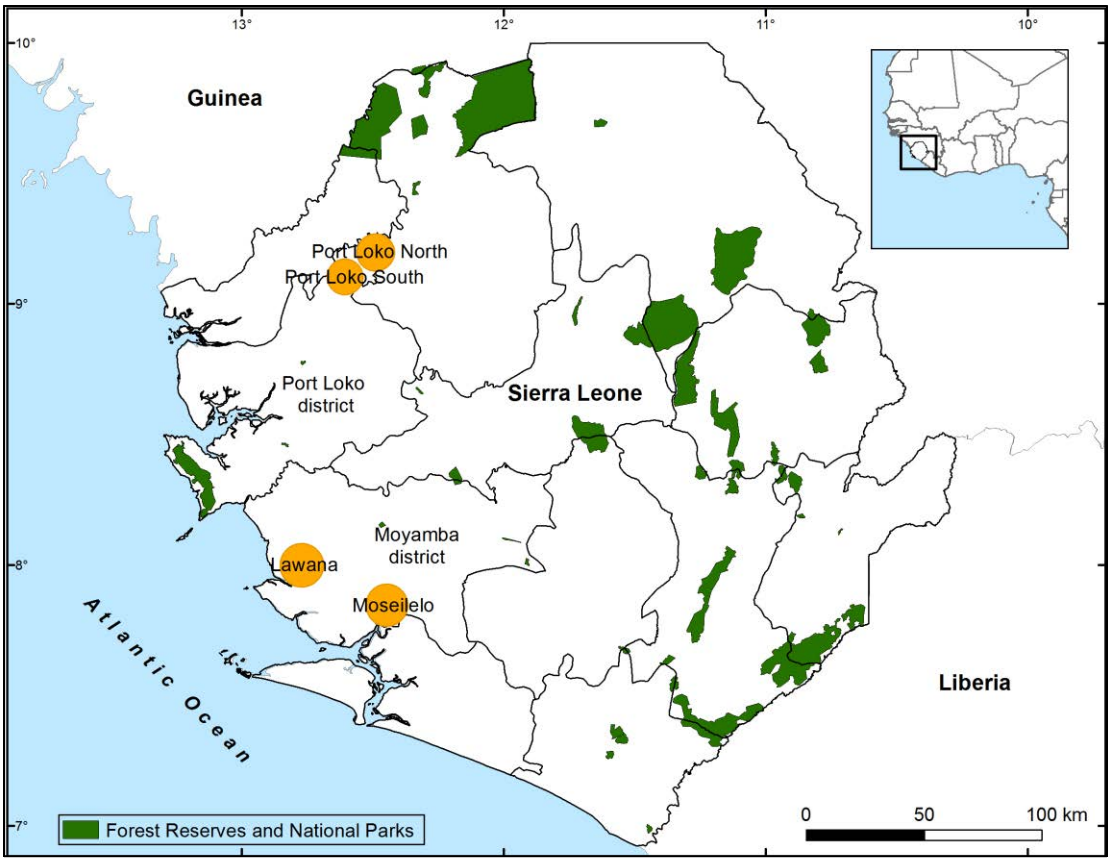

Figure 3.1. Location of the four study areas (Port Loko North, Port Loko South, Lawana and Moseilelo) in Sierra Leone

Table 3.1.Details of the four study areas in the Moyamba and Port Loko districts of Sierra Leone (Figure 3.1).

Study area	Altitude (m)	Study period	Nº of villages visited	Nº of interviews	M:F ratio of participants	Land characteristics	Types of cultivars
Moyamba district (46 people per km^2)*							
Lawana (80 km^2)	7–27	Dec. 2012–Feb. 2013	13	51	42:9	Swamp areas; cultivated & fallow farm land; abundance of wild oil palms throughout.	Swamps with rice, upland farms with rice & cassava intercropped with sesame, sorghum, beans & maize.
Moseilelo (35 km^2)	20–182	Feb.-Mar.2013	10	38	36:2	The Kasillah Hills lie in the centre of the study area, characterized by a highly degraded secondary forest. The surrounding landscape is composed of swamps, & cultivated & fallow farm land, with wild oil palms throughout.	Swamps with rice, upland farms with rice & cassava intercropped with sesame, sorghum, maize & potato.
Port Loko district (104 people per km^2)*							
Port Loko North (86 km^2)	40–80	Dec. 2013-Jan. 2014	14	71	53:18	Landscape dominated by grassland & woodland savannah. Cultivated & fallow farms. Wild oil palms throughout.	Upland farms are cultivated with cassava & upland rice intercropped with maize, sesame & sorghum. Peanut farms. Small-scale commercial oil palm plantations. Cattle farming.
Port Loko South (108 km^2)	30–75	Oct.-Nov. 2013	24	97	75:22	Swamps, cultivated & fallow farm land. Riverine forests. Small-scale oil palm farms. Wild oil palms throughout.	Swamps with rice, upland farms with cassava & rice intercropped with maize, sesame & sorghum in the upland farms. Peanut farms. Abundant small-scale commercial oil palm plantations.

M: male. F: female. *Statistics Sierra Leone (2016)

Figure 3.2. The characteristic landscape of the Lawana study area (Figure 3.1.), comprising agricultural land and swamp areas, with wild oil palms (Elaeis guineensis) abundant throughout. (© Josep M. Fortuny).

3.3. Study areas

The study took place in four locations in Sierra Leone: Lawana and Moseilelo in the Moyamba district, and Port Loko South and Port Loko North in the Port Loko district (Fig. 3.1 & Table 3.1).

Active and fallow farms at various stages of growth dominate these four areas. Wild or feral oil palms (*Elaeis guineensis)* are the most frequently encountered tree species across these agricultural matrices, together with rough-skin plum trees (*Parinari excelsa)* (Fig. 3.2.). Oil palms are an important non-cultivated resource that people harvest locally for palm oil, palm wine, nuts and construction materials. However, the sites differ in several ways: Lawana is located between mangroves and swamp areas (Fig. 3.2); Moseilelo harbours a small and highly degraded area of secondary forest, known as the Kasillah Hills; Port Loko North is dominated by grassland and woodland savannah, and also harbours small-scale oil palm plantations; whereas Port Loko South is more swampy and harbours a higher number of small-scale commercial oil palm plantations located primarily near human settlements. Both areas of Port Loko have multiple narrow riverine forests spanning the landscape. Moseilelo and both areas of Port Loko are also delimited by two large rivers, which form a fork and potentially act as a barrier to wildlife dispersal (Fig. 3.3). Both men and women are involved in farming activities in these areas, cultivating mainly seasonal crops (RMG, pers. obs.). Apart from the Sierra Leone National Chimpanzee Census Project (Brncic et al., 2010) there had been no previous research on chimpanzees in these areas.

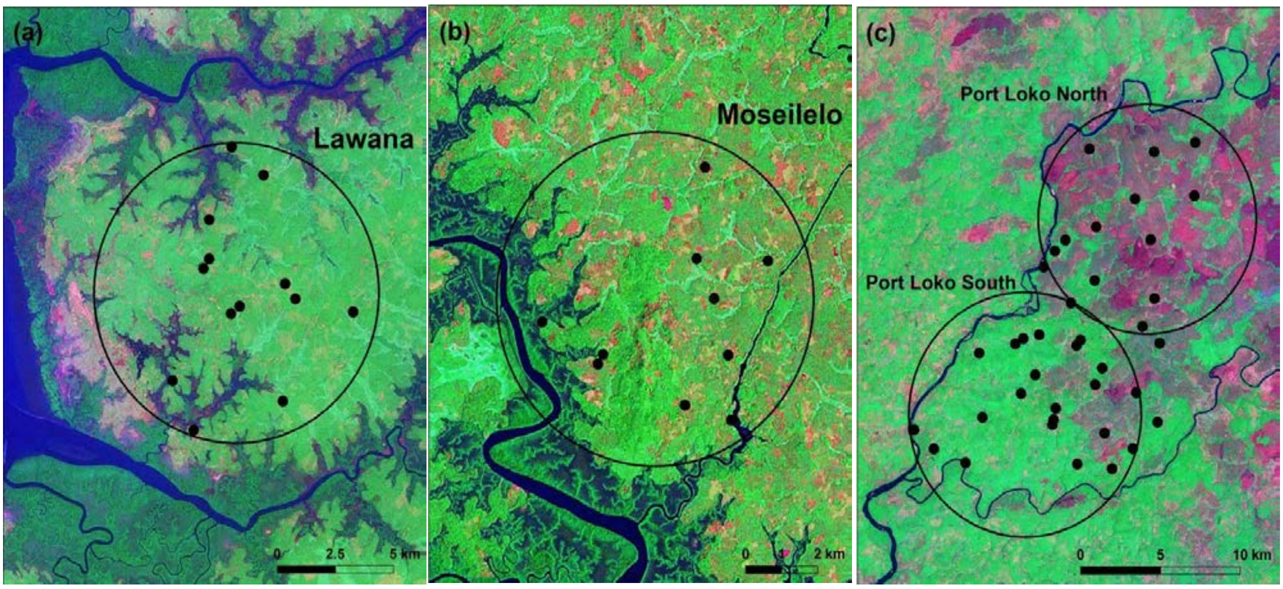

Figure 3.3. The locations of the villages where interviews were conducted in (a) Lawana, (b) Moseilelo and (c) Port Loko North and South. The locations in Sierra Leone are shown in Figure 3.1.

3.4. Methods

3.4.1. Semi-structured interviews

We conducted 257 semi-structured interviews with farmers in 61 villages (23 in the Moyamba district and 38 in the Port Loko district) during December 2012-January 2014 (Table 3.1). The mean time taken to complete an interview was 27±SD9 minutes (range 9–77). Among the participants, 80.2% were males and 19.8% were females. Given the significant sex-bias (Table 3.1.), we refrained from conducting any analysis exploring gender differences. The mean age of the participants was 43±SD14.08 years (range 19–90). The majority of the participants (93.9%) were farmers, and 3.8% of them combined farming with other occupations, including trading (n=4), teaching (n=3), fishing (n=2) and pot making (n=1). The dominant ethnicity varied across sites; the majority (95.7%) described themselves as Muslim. Nearly two-thirds (63.4%) of the participants reported not having received any formal education (Table 3.2.).

The study was approved by the Research Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK, and adhered to the code of best practices for field primatology issued by the International Society of Primatology. The interviews were anonymous and voluntary. We conducted one interview per household. We first asked permission from the village chief; interviewers then dispersed in various directions from the centre to the periphery of each village, selecting households at random. The interviews were conducted in the local language by four Sierra Leoneans from the Tacugama Chimpanzee Sanctuary field team, who had been trained by RMG. To cover a wide geographical area in each locality we conducted interviews in every second village as we passed through. The interviews were designed to determine (1) the socio-cultural profile of participants; (2) the types of crops cultivated locally and the causes of crop losses (this last question was inadvertently omitted in the questionnaire in the Moseilelo area, which was therefore not included in this analysis); (3) the local occurrence of wildlife, identified by means of a field guide, and the type of crops the identified wildlife were reported to consume; (4) which three species were considered to cause the most crop damage; (5) the measures of protection employed locally to deter wildlife from feeding on crops; and (6) people's perceptions of chimpanzees (i.e. do they perceive them to be dangerous and why, and how do they react when they encounter chimpanzees in the fields?) and the farmers' perceptions of the changes in chimpanzee numbers since before the civil war, which occurred during 1991–2002.

The identification guide compiled for use in the interviews contained 43 drawings of West African mammal species (Kingdon, 2001; Oates, 2010). The selection of images was tested on a pilot group of 10 Sierra Leoneans before the start of the study to ensure that people could recognize the species portrayed. When participants identified a species, they believed to exist in their area, we asked whether the species in question consumed crops, and which type. We then tallied the number of times each crop was reported as being consumed by each species to calculate percentages of reported crop foraging.

Table 3.2. Socio-cultural profile of farmers interviewed in the four study areas.

	No. of individuals (%)				
	Lawana (51 interviews)	Moseilelo (38 interviews)	Port Loko North (71 interviews)	Port Loko South (97 interviews)	Total
Education					
No formal education	36 (70.6)	27 (71.1)	53 (74.6)	47 (48.9)	163 (63.4)
Arabic school	7 (13.7)	6 (15.8)	11 (15.5)	31 (32)	55 (21.4)
English school	8 (15.7)	5 (13.2)	7 (9.9)	19 (19.6)	39 (15.2)
Religion					
Christian		2 (5.3)	7 (9.9)		9 (3.5)
Muslim	51 (100)	34 (89.5)	56 (78.9)	96 (99)	237 (92.2)
No response		2 (5.3)	8 (11.3)	1 (1)	11 (4.3)
Ethnic group					
Krio			2 (2.8)		11 (4.3)
Limba			42 (59.2)	3 (3.1)	45 (17.5)
Mende	1 (2)	33 (86.8)	1 (1.4)		35 (13.6)
Shabro	42 (82.4)	3 (7.9)			45 (17.5)
Temne	8 (15.7)	2 (5.3)	25 (35.2)	94 (96.9)	129 (50.2)
No response			1 (1.4)		1 (1.4)

3.4.2. Data analysis

We produced maps using ArcGIS 10.3 (ESRI, Redlands, USA) and analysed data using SPSS v. 23 (IBM, Armonk, USA). Chi-square tests were used to explore differences between sites in the types of crops grown, crop protection measures used, the perceived changes in the number of chimpanzees since before the civil war, people's perceptions of chimpanzees as being dangerous, and reports of how chimpanzees react when encountered in cultivated fields. For Chi-square tests with more than a 2x2 contingency design, the *z*-scores based on the adjusted standardized residuals were used to assess the cell contribution to significant Chi-square results with values ≥1.96 yielding statistical significance at $P<0.05$.

3.5. Results

3.5.1. Crops cultivated and reported causes of crop losses

Farmers reported cultivating a variety of seasonal crops using intercropping practices. Unlike swamp fields, which were planted exclusively with rice, upland farms were cultivated with a mixture of crops simultaneously (Table 3.3). Seasonal crops were the most reported cultivars grown by farmers in all areas (82.7±SD 6.7%). There was a significant difference in the types of crops reported across sites (Chi-square test: $\chi(6)=41.163$, $P<0.001$), with the *z*-scores indicating a significantly higher frequency of domestic fruit crops and cash tree crops at Port Loko South relative to the other sites, and significantly fewer than expected cash tree crops in both Lawana and Moseilelo. However, there was no significant difference in the reporting of seasonal crops being cultivated across the four sites (Table 3.3). In all cases the harvests were used for subsistence, although 66.1% (170 of 257) of participants reported selling any surplus, with farmers in Lawana reporting selling the least (25.5%) compared to the other three sites (Moseilelo: 60.5%; Port Loko North: 78.9%; Port Loko South: 80.4%).

In the Lawana area the reported challenges to agricultural productivity were crop foraging by wild mammals (76.5%), poor soil quality (51%), and plagues of grasshoppers (*Zonocerus variegatus*) (9.8%), whereas in the Port Loko district farmers reported crop foraging by wild mammals (Port Loko North: 98.6%; Port Loko South: 96.9%), grasshoppers (Port Loko North: 78.9%; Port Loko South: 83.5%), birds feeding on crops (Port Loko North: 7%; Port Loko South: 7.2%), poor soil quality (Port

Loko North: 4.2%; Port Loko South: 14.4%) and lack of fertilizer (Port Loko North: 1.4%; Port Loko South: 4.1%). Foraging by domestic animals was mentioned as a problem only once, in Port Loko South.

Rice and cassava, the two most reported cultivated crops (Table 3.3), were also the most reported as being damaged by wild mammals. In contrast, sesame and sorghum were rarely reported as being consumed by wild mammals (Table 3.3). Other cultivars, such as chilli pepper and okra, attracted fewer species, with duikers (*Cephalophus* and *Philantomba* spp.) and bushbucks (*Tragelaphus* spp.) mentioned most often as feeding on the leaves. Domestic fruit crops comprised only 9.6±SD2.9% of the cultivars reported to be cultivated across all four areas, and primates were considered to be the main consumers (75.6±SD12.7%), with 32.8±SD16.6% of consumption attributed to chimpanzees. Cash tree crops accounted for only 7.7±SD3.9% of the total cultivars reported. Small, commercial oil palm plantations were common in both areas of Port Loko district but not in Lawana or Moseilelo. However, farmers in all four areas regarded losses of oil palm to wildlife as a serious problem, and oil palm was reported as the third most frequently raided crop in all areas except Moseilelo, where it was ranked fifth (Table 3.4). Chimpanzees were the most frequently mentioned culprits, although up to 30 species of fauna were reported to exploit oil palms.

Chimpanzees reportedly targeted 21 types of crops, but with a lower frequency compared to cane rats, which were reported to target up to 20 crops (Table 3.5). Cane rats were reported to feed mainly on rice and cassava, and to a lesser extent on maize and peanuts, damaging all stages of the plants' growth. The giant-pouched rat (*Cricetomys emini)*, the green monkey (*Chlorocebus aethiops sabaeus)* and the fire-footed rope squirrel (*Funisciurus pyrropus)* consumed a similar number of crops (20–21), with a similar frequency. Green monkeys and sooty mangabeys (*Cercocebus atys)* were reported to target the same number of crops; however, sooty mangabeys were reported more frequently in Lawana and Moseilelo, and green monkeys in Port Loko. As a group, monkeys were reported to consume similar cultivars across all four study areas, primarily maize, rice, cassava and peanuts.

Table 3.3. No. of reports of crops cultivated in each of the four study areas.

	No. of reports (%)			
	Lawana	Moseilelo	Port Loko North	Port Loko South
Domestic fruit crops	13 (5.7)	15 (7.6)	47 (8.3)	90 (12.5)
Banana *Musa* spp.	4 (7.8)*	11 (28.9)*	14 (19.7)*	42 (43.3)*
Pineapple *Ananas comosus*	6 (11.8)*	4 (10.5)*	5 (7)*	21 (21.6)*
Orange *Citrus sinensis*	2 (3.9)*	*	8 (11.3)*	11 (11.3)*
Papaya *Carica papaya*	1 (2)*	*	10 (14.1)*	7 (7.2)*
Mango *Mangifera* spp.			7 (9.9)*	8 (8.2)*
Others			3 (4.2)	1 (1)
Cash tree crops	5 (1.6)	7 (3.6)	40 (7.6)	76 (10.9)
Oil palm *Elaeis guineensis*	3 (5.9)*	2 (5.3)*	34 (47.9)*	66 (68)*
Kola nut *Cola* sp.	1 (2)*		3 (4.2)	7 (7.2)
Cacao *Theobroma cacao*	1 (2)	4 (10.5)	1 (1.4)*	2 (2.1)
Others		1 (2.6)	2(2.8)	1 (1)
Seasonal crops	212 (92.2)	175 (88.8)	479 (84.5)	556 (76.9)
Rice *Oryza* spp.	50 (98)*	37 (97.4)*	71 (100)*	92 (94.8)*
Cassava *Manihot esculenta*	45 (88.2)*	35 (92.1)*	66 (93)*	81 (83.5)*
Sesame *Sesamum* sp.	32 (62.7)*	30 (78.9)*	41 (57.7)*	47 (48.5)*
Chilli pepper *Capsicum* spp.	4 (7.8)	2 (5.3)*	54 (76.1)	65 (67)
Peanuts *Arachis hypogaea*	9 (17.6)	2 (5.3)*	48 (67.6)*	65 (67)*
Maize *Zea mays*	9 (17.6)*	16 (42.1)*	35 (49.3)*	48 (49.5)*
Beans *Phaseolus* spp.	16 (31.4)*	4 (10.5)*	40 (56.3)*	42 (43.3)*
Potato *Solanum tuberosum*	5 (9.8)*	14 (36.8)	34 (47.9)	38 (39.2)*
Sorghum *Sorghum bicolor*	31 (60.8)	25 (65.8)	7 (9.9)	8 (8.2)
Okra *Abelmoschus esculentus*	7 (13.7)		26 (36.6)	30 (30.9)*
Yam *Dioscorea* spp.	1 (2)	9 (23.7)*	15(21.1)	14 (12.4)
Pumpkin *Cucurbita* spp.	2 (3.9)*	*	14 (19.7)	12 (12.4)*
Others	1 (2)	1 (2.6)	28 (39.4)	14 (14.4)

*Crops reported to be consumed by chimpanzees (*Pan troglodytes verus*) (this does not necessarily coincide with the crops people reported cultivating, as they sometimes omitted to mention domestic fruit such as mangoes, oranges and papaya).

The mean number of animal species identified per interview was 11±SD 4.25 (range 2–26). Of the species considered to be crop foragers, cane rats, chimpanzees, giant pouched rats and fire-footed rope squirrels were the most mentioned (Fig. 3.4), and in all four areas farmers perceived that cane rats caused the most damage to crops (Fig. 3.5). Overall, chimpanzees ranked as the fourth most destructive mammal; however, there was some variation across sites.

In Lawana chimpanzees were ranked second, and in Moseilelo fourth, whereas they were ranked seventh in Port Loko North and fifth in Port Loko South. One regular complaint of the farmers in the two Port Loko sites was the destruction of crops by grasshoppers, which was not mentioned at either of the sites in the Moyamba district (Fig. 3.5).

Table 3.4. No. of reports of wildlife foraging on various cultivars (N), and frequency of reported foraging (FF) and crop cultivation (FC) as percentages in each study area.

Crop	Lawana			Moseilelo			Port Loko North			Port Loko South		
	N	FF %	FC %	N	FF %	FC %	N	FF %	FC %	N	FF %	FC %
Aubergine *Solanum melongena*	3	0.4	2.0	0	0.0	2.6	0	0.0	11.3	1	0.0	3.1
Banana	16	6.2	7.8	14	3.8	28.9	11	1.9	19.7	15	3.1	43.3
Bean	12	3.1	31.4	15	1.9	10.5	8	2.1	56.3	10	1.5	43.3
Cacao	0	0.0	2.0	2	0.1	10.5	4	0.3	1.4	0	0.0	2.1
Cassava	28	29.6	88.2	25	28.8	92.1	26	19.3	93.0	27	17.5	83.5
Chilli pepper	3	2.0	7.8	7	2.1	5.3	13	4.7	76.1	15	3.8	67.0
Coffee *Coffea* sp.	0	0.0	0.0	0	0.0	2.6	0	0.0	2.8	1	0.0	0.0
Cucumber *Cucumis sativus*	2	0.2	0.0	10	1.1	0.0	4	0.5	23.9	1	0.0	7.2
Kola nut	8	2.8	2.0	3	0.4	0.0	9	1.3	4.2	6	0.5	7.2
Maize	10	3.1	17.6	17	12.9	42.1	15	8.4	49.3	14	6.2	49.5
Mango	2	0.2	0.0	5	0.4	0.0	9	2.0	9.9	12	2.1	8.2
Millet *Pennisetum* sp.	0	0.0	0.0	0	0.0	0.0	3	0.3	4.2	3	0.2	4.1
Oil palm	14	10.5	5.9	15	5.9	5.3	21	11.6	47.9	27	14.0	68.0
Okra	5	3.8	13.7	5	2.6	0.0	7	1.5	36.6	7	1.6	30.9
Oranges	9	4.6	3.9	4	0.3	0.0	9	2.7	11.3	11	3.5	11.3
Papaya	5	1.1	2.0	5	0.6	0.0	8	1.3	14.1	5	1.1	7.2
Peanuts	14	10.3	17.6	18	9.6	5.3	19	11.6	67.6	22	13.9	67.0
Pineapple	6	1.3	11.8	3	0.8	10.5	1	0.3	7.0	8	0.9	21.6
Plum *Spondias dulcis*	0	0.0	0.0	0	0.0	0.0	7	0.8	4.2	9	0.6	0.0
Potato	10	1.9	9.8	13	2.4	36.8	17	6.7	47.9	18	5.2	39.2
Pumpkin	7	1.2	3.9	9	1.3	0.0	7	2.0	19.7	19	2.6	12.4
Rice	22	14.0	98.0	25	18.4	97.4	29	17.3	100.0	27	19.3	94.8
Sesame	5	0.6	62.7	8	1.1	78.9	8	1.4	57.7	7	1.0	48.5
Sorghum	8	3.3	60.8	8	1.4	65.8	1	9.9	0.1	2	0.1	8.2
Yam	0	0.0	2.0	16	4.1	23.7	9	2.1	21.1	7	1.2	14.4

Table 3.5. Number of different crops reported by farmers as being eaten by wildlife, and the frequency of reporting, for the 13 most reported species in the four study areas.

Species	**All areas**		**Lawana**		**Moseilelo**		**Port Loko North**		**Port Loko South**	
	No. of crops	Frequency (%)	No. of crops	Frequency (%)	No. of crops	Frequency (%)	No. of crops	Frequency (%)	No. of crops	Frequency (%)
Cane rat *Thryonomys swinderianus*	20	14.0	9	11.2	12	10.7	13	15.0	19	15.6
Chimpanzee *Pan troglodytes verus*	21	11.2	13	13.0	15	9.3	15	9.6	17	12.5
Giant pouched rat *Cricetomys emini*	20	9.4	6	4.6	10	6.6	13	10.2	17	11.6
Green monkey *Chlorocebus aethiops sabaeus*	21	8.8	9	2.1	13	5.6	16	9.9	20	11.7
Fire-footed rope squirrel *Funisciurus pyrropus*	20	7.8	7	6.9	10	6.0	17	8.9	13	7.9
Bushbuck *Tragelaphus scriptus*	14	6.3	9	9.2	8	7.4	7	6.1	12	5.0
Crested porcupine *Hystrix cristata*	17	4.9	7	4.5	11	2.9	13	6.7	12	4.5
Sooty mangabey *Cercocebus atys*	21	4.9	13	6.5	10	8.4	14	3.7	14	3.7
Red river hog *Potamochoerus porcus*	11	4.7	3	1.8	5	4.1	6	5.3	11	5.5
Brush-tailed porcupine *Atherurus africanus*	15	3.8	5	2.8	11	7.1	11	3.9	10	2.5
Giant forest squirrel *Protoxerus stangeri*	18	3.5	8	2.9	6	2.0	15	4.3	13	3.7
Maxwell's duiker *Cephalophus maxwellii*	14	3.0	8	3.5	9	5.3	8	3.1	5	1.6
Giant forest hog *Hylochoerus meinertzhageni*	12	2.7	7	5.9	5	2.0	7	2.8	7	1.9

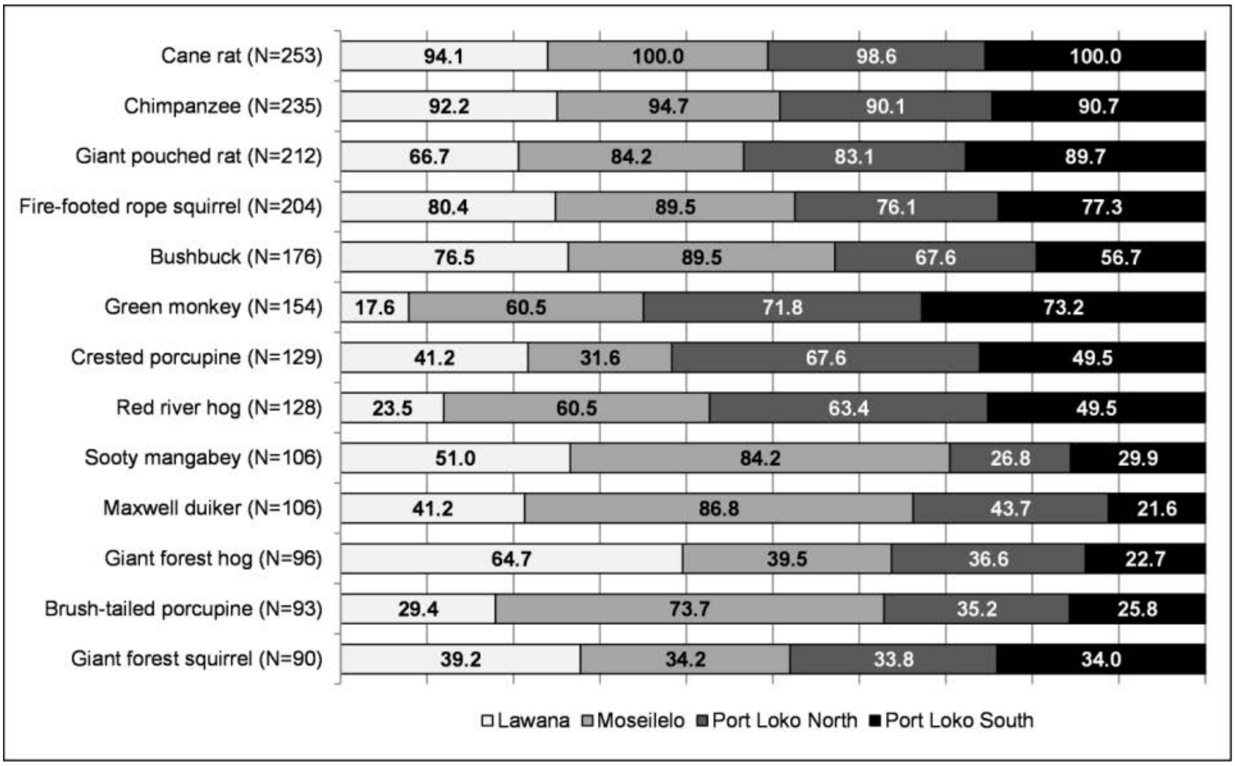

Figure 3.4. The total number of respondents across the four study areas (N) and the percentage of respondents in each study area who identified various species as crop raiders.

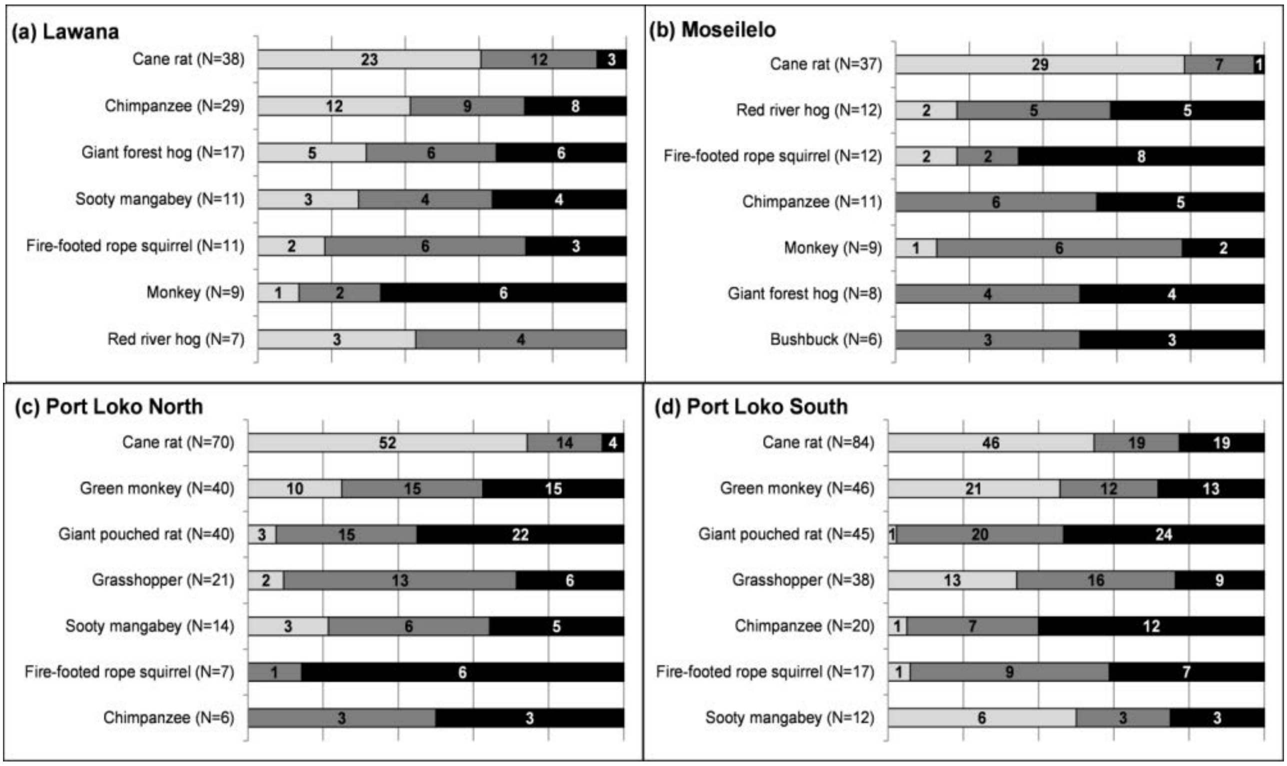

Figure 3.5. Ranking of the most destructive species in (a) Lawana, (b) Moseilelo, (c) Port Loko North and (d) Port Loko South, with the number of times each species was ranked as first, second or third most destructive, from left to right.

3.5.2. Crop protection measures

All but eight of the participants (249 of 257) reported using one or more mitigation measures against crop foraging by wild animals. More mitigation measures were reported at the Port Loko sites than at Lawana and Moseilelo (Table 3.6). Fencing (223 of 249) and traps (208 of 249) were the most common deterrents used to prevent wildlife from entering cultivated farms. Usually fences were hand-made with palm leaves and/or sticks interspersed with snares. Hunting with dogs was more common in the Port Loko district, with 49.4% (81 of 164) reporting use compared to only 7% (6 of 85) in the Moyamba district. However, if each measure is categorized as (potentially) lethal or non-lethal (Table 3.6), there were no differences among sites (Chi-square test: $\chi(3) = 2.243$, $P = 0.523$).

Table 3.6. Percentage of respondents who reported adopting various measures to protect farms in each of the four study areas.

Protection measure	Type	% reports			
		Lawana	Moseilelo	Port Loko North	Port Loko South
Fencing (n=223)	Non-lethal	92.2	71.1	97.2	82.5
Traps (n=208)	Lethal	88.2	86.8	74.6	79.4
Hunting with dogs (n=91)	Lethal	7.8	15.8	39.4	54.6
Scarecrows (n=24)	Non-lethal		2.6	12.7	14.4
Sling (n=26)	Lethal	7.8	5.3	9.9	13.4
Nets (n=17)	Non-lethal		5.3	8.5	9.3
Guarding (n=7)	Non-lethal				7.2
Poison (n=9)	Lethal			2.8	7.2
Stones (n=7)	Lethal				7.2
Brushing (n=5)	Non-lethal				5.2
Hunting with guns (n=4)	Lethal	2.0			3.1
Shouting (n=8)	Non-lethal	2.0	2.6	4.2	3.1

3.5.3. Farmers' perceptions of chimpanzees

Nearly all of the participants (253 of 257; 98%) stated that chimpanzees used to enter their farms before the civil war (1991–2002) and 63% (160 of 253) perceived that there were fewer chimpanzees now than before the war, mostly as a result of deforestation and hunting (118 of 160). Only 36.4% (92 of 253) thought there were more chimpanzees now and the only reason stated in 45% (41 of 92) of the responses was that they were not hunted. No other reasons were given. Whether farmers perceived there were more or fewer chimpanzees since before the civil war differed significantly among sites (Chi-square test: $\chi(3)=82.255$, $P<0.001$). Based on the *z*-scores, in Lawana significantly more people than expected thought there were more chimpanzees than before the civil war, whereas there was no significant difference for Moseilelo. However, at both Port Loko sites people thought there were significantly fewer chimpanzees than before the civil war.

Eighty seven percent (224 of 257) of respondents considered chimpanzees to be dangerous, the most common reason being that they destroy crops (48.7%, 109 of 224). They were also considered to be dangerous because they are destructive and frightening (5.8%, 13 of 224), frightening (28.1%, 63 of 224) or aggressive (2.7%, 6 of 224). There was no significant difference among sites regarding whether people perceived chimpanzees to be dangerous or not (Chi-square test: $\chi(3)=2.601$, $P=0.457$).

Ninety four percent (241 of 257) of participants reported currently encountering chimpanzees in their fields, with little variation across study areas (Lawana: 96%; Moseilelo: 94.7%; Port Loko North: 90.1%; Port Loko South: 96.9%). When asked how the chimpanzees respond when they are encountered, 81.7% (197 of 241) reported that chimpanzees run away, and 12.9% (31 of 241) reported that they threaten people. There was a significant difference in responses among sites (Chi-square test: $\chi(3)=9.702$, $P=0.021$). Although there was no significant difference in reports of chimpanzees running away, fewer people reported chimpanzees threatening people in Lawana, and significantly more in Port Loko South.

3.6. Discussion

We found that cane rats were perceived to be the most problematic mammal for farmers in the study areas. Other studies have reported the cane rat to be a problem species (Naughton-Treves & Treves, 2005), and it was found to cause the most severe damage to crops around a forest reserve in Cameroon (Arlet & Molleman, 2007). Cane rats are nocturnal, dependent on water, have high reproductive rates and can thrive in areas with abundant grasses (Hoffmann, 2008); the agricultural habitat present at our study sites is well suited to their needs.

No respondents ranked chimpanzees as the most destructive mammal species, and other species, such as the cane rat, the red river hog (*Potamochoerus porcus)*, monkeys and grasshoppers, were perceived as causing most damage. Nevertheless, there was variation across sites in the ranking of chimpanzees, possibly linked to variation in the occurrence and abundance of other destructive wildlife species and people's perceptions across sites. However, our results also suggest that farmers' perceptions vary depending on the crops grown and their dependence on agriculture for subsistence. Chimpanzees were ranked higher in Lawana and Moseilelo, where farmers mentioned growing more seasonal crops and fewer cash crops, and reported selling less surplus, indicating a higher dependency on seasonal cultivation for subsistence. The degree to which farmers viewed chimpanzees as a threat to their agricultural yield may also be related to the extent of overlap between the chimpanzees' home range and farmlands in the landscape, the contribution of various crop species to chimpanzees' diet locally (McLennan & Hill, 2012), whether farmers had direct experience of chimpanzee crop foraging (although there was no reported variation across sites in this study), and their level of tolerance of chimpanzee offtake (although chimpanzees were reportedly less likely to threaten people at Lawana, which indicates that perhaps farmers were more tolerant of chimpanzee crop foraging at this site; Webber & Hill, 2014). These alternative explanations warrant further investigation to reveal patterns of similarity or difference across sites.

We recorded significant evidence of chimpanzees using oil palms across all four study areas. The most visible and common use by chimpanzees was for nesting. Commercial oil palms are predominantly cultivated in the two Port Loko areas (Table 3.3) but during our time in the field we did not record any evidence of chimpanzees using them. Usually these plantations are cultivated near human settlements, potentially reducing their accessibility to chimpanzees. Based on our in situ observations, competition for oil palm mainly concerns wild oil palms, which are widespread and are an important resource to farmers. Chimpanzees at other sites have also demonstrated extensive reliance on oil palms for food and nesting (e.g. Bossou, Guinea: Humle & Matsuzawa, 2004; Guinea-Bissau: Sousa et al., 2011; Bessa et al., 2015). Further research is needed to assess the extent to which chimpanzees across various landscapes depend on the oil palm for food and nesting.

Hockings & McLennan (2012) found that cassava was not widely eaten by chimpanzees across their range and that they preferred sugar fruits. In our study, chimpanzees were reported to forage frequently on cassava, probably because of its wider and easier availability compared to other cultivars, such as banana, mango, pineapple or papaya. Domestic fruit crops comprised <10% of the crops cultivated in all four areas, although farmers tended to underreport these (Table 3.3). Chimpanzees may avoid coming close to the villages, preferring to consume cassava from the more distant fields. Despite occasional reports in Moseilelo and Port Loko South of farmers seeing chimpanzees near their villages, foraging on domestic fruit trees, such events were rarely reported. It is possible that farmers were more likely to report chimpanzee foraging on a valuable staple crop such as cassava than domestic fruits, which are typically grown around individual households and harvested mainly for self-consumption. A similar situation was described in Uganda (McLennan & Hill, 2012), where farmers tolerated chimpanzees consuming fruits such as guavas but not cash crops such as sugarcane, cocoa or bananas. Farmers in our study areas reported domestic fruits as being targeted especially by chimpanzees and monkeys. Monkeys seem to be more daring in approaching villages to feed on domestic fruit trees than chimpanzees, as we witnessed on several occasions during our field work. However, in Guinea and Uganda, chimpanzees have been reported entering villages to consume domestic fruits (Hockings & Humle, 2009; McLennan, 2013). This daring behaviour is potentially linked to people's tolerance of and behaviour towards chimpanzees and the extent to which they can meet their dietary requirements with wild food; habituation could also play a role in influencing the prevalence of such a behaviour (Naughton-Treves et al., 1998; Hockings et al., 2009; McLennan, 2013), although it is not a precondition (McLennan & Hill, 2010). Sesame, which was widely cultivated across all four areas, and sorghum in Lawana and Moseilelo, were rarely reported as being consumed by wild mammals. This suggests that these may be low-conflict crops (Hockings & McLennan, 2012; Hockings & Sousa, 2012) or else farmers may be more tolerant of these crops being consumed by wildlife. The intercropping system used in Sierra Leone provides wildlife with a choice of crops to feed on, and further assessment is required to identify differences between real and perceived damage in mixed vs mono-cultivated fields.

In our study areas, chimpanzees share the habitat with people but are not habituated; usually they run away during encounters with farmers. The absence or limited presence of forest cover at these sites potentially explains why wildlife is dependent upon cultivated and/or abandoned crops for their survival. Local farmers cannot recall seeing large tracts of forest in their area, suggesting that these landscapes were cleared many decades ago. The remaining wild fauna, including chimpanzees, appear to have adapted to this anthropogenic environment. We remain unsure why chimpanzees still persist in these degraded areas; future studies should help us identify more precisely the conditions favouring their persistence.

Almost all farmers interviewed reported adopting crop protection measures. The most common included snares, traps and fences. Fences are erected to prevent larger herbivores from entering cultivated fields, and snares and traps target small mammals. The traps are made of sticks and thin rope or wire. The use of mitigation measures was more prevalent at the Port Loko sites, where most farmers reported selling any harvest surplus, potentially indicating a relationship between monetary income and the ability to protect crops, corroborating findings elsewhere in Africa (Hill & Wallace, 2012) and South-east Asia (Campbell-Smith et al., 2012). Although some mammals, especially chimpanzees, may be able to escape by dislodging the wire from the trap, the wire could remain tight around the trapped limb and cause severe injury (Quiatt et al., 2002). The impact of wire traps on chimpanzees and other wildlife in our study areas has yet to be assessed. Farmers also reported occasionally hiring hunters to get rid of pests feeding on their crops, typically monkeys, as they are more difficult to catch with snares. Encouraging sustainable and more species-specific hunting practices using more specialized devices to capture rodents could not only decrease crop feeding but could also help improve yields and protect chimpanzees and other mammal species, whilst providing a supplementary source of protein to local people. Cane rats are a favoured and nutritious food source (Hoffman & Cawthorn, 2012).

Farmers from both study areas in Port Loko reported that plagues of grasshoppers were a significant challenge, destroying entire fields of cassava and potatoes. A biological insecticide called Green Muscle (Becker Underwood, South Africa) is available from the central government but a lack of resources to implement the project is preventing the product from reaching farmers across the country. Finding solutions for the distribution and implementation of this preventive crop protection measure could help farmers obtain better yields, which could promote greater tolerance of farmers towards key species, such as chimpanzees. However, a heightened expectation of preventability of crop loss could also backfire, lowering farmers' tolerance of damage caused by other species (Knight, 2000), and therefore implementation will require careful monitoring of farmers' tolerance levels. Furthermore, human population growth, which translates into a higher demand for resources (Barnes, 2002), forces farmers to shorten fallow periods, which results in impoverished soil and affects future agricultural productivity (Gaiser et al., 2011). Altogether, such agricultural practices are detrimental to human well-being, as people rely on natural resources provided by the forests, and habitat conversion can cause a decrease in the abundance and diversity of wildlife, which people also depend on for protein (Fa & Brown, 2009). In three of the four study areas farmers stated that chimpanzee numbers had decreased in the previous 2 decades as a result of deforestation and hunting. To protect wild chimpanzees under such habitat conditions there is a need to work closely with the local communities to help them develop more efficient and sustainable farming techniques to improve their yields, maintain soil fertility and minimize habitat loss as a result of slash-and-burn agriculture.

Almost all participants (94%) claimed to have seen chimpanzees in their fields. Farmers predominantly stated that chimpanzees run away when encountered in the fields, although some stated that chimpanzees can threaten people because they are not afraid, and could cause injury or death. However, only four participants reported incidents of physical aggression towards people (one in Lawana and three in Port Loko South), adults in all cases, in contrast to Bossou, Guinea, where such attacks mainly involve children (Hockings et al., 2010). Each of these participants felt that chimpanzees were dangerous. Differences between sites may be related to differences in encounter rates between people and chimpanzees (McLennan & Hockings, 2016) and/or people's behaviour towards chimpanzees (Hockings et al., 2010), and chimpanzees' perception of risk within their environment (Humle & Hill, 2016). Most participants (87%) considered chimpanzees to be dangerous. However, almost half argued that it was because chimpanzees were destructive of the crops rather than frightening or aggressive. Nearly two thirds (63%) of participants also perceived that there were fewer chimpanzees now than before the war; however, in Lawana farmers thought there were more chimpanzees now. This could reflect a local increase in chimpanzee numbers, or higher rates of chimpanzee crop foraging and sighting of chimpanzees in this area compared to other sites.

Although we focused on a subset of locations within Sierra Leone, our findings provide us with a better understanding of human-wildlife coexistence in agricultural landscapes and the factors influencing variability in sympatric relations between people, chimpanzees and other wildlife. Our results highlight variations across study areas, probably linked to differences in habitat types and crops cultivated, and historical patterns of habitat loss. We argue that conservation actions need to be context-specific based on an understanding of local people's perceptions, concerns and attitudes, as well as chimpanzee ecology and distribution in these landscapes. Conservation strategies should benefit and support farmers while promoting a positive coexistence between people and chimpanzees, thus favouring their protection and long-term survival. However, we still need to develop and assess with local and national stakeholders which actions can most effectively improve coexistence between people and chimpanzees, and tolerance levels towards crop-foraging.

4 – Study II

What factors influence wild chimpanzee (*Pan troglodytes verus*) occurrence in an agriculture-swamp matrix outside protected areas?

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(In preparation for journal submisssion)

4.1. Abstract

Human population growth and anthropogenic activities are exacerbating pressures on biodiversity globally. Land conversion is aggravating habitat fragmentation and non-human primates are increasingly compelled to live in forest-agricultural mosaics. In Sierra Leone, more than half of the wild chimpanzee population (*Pan troglodytes verus*) occurs outside protected areas and competes for resources with farmers. Our study area, in the Moyamba district in south-western Sierra Leone, is practically devoid of forest and is dominated by cultivated and fallow fields, swamps and mangroves. In this region, traditional slash-and-burn agriculture modifies annually the landscape, sparing swamps and mangroves and semi-domesticated oil palms (*Elaeis guineensis*). This study aimed to explore ecological and anthropogenic drivers of chimpanzee occurrence across this highly degraded and human-impacted landscape. Between 2015 and 2016, we deployed 24 camera traps systematically across 27 1.25x1.25 km grid cells. Cameras were operational over a period of 8 months. We used binomial iCAR models to understand the patterns of habitat use and how they are related to the distance to anthropogenic (roads, settlements, abandoned settlements) and habitat variables (swamps, farmland and mangroves). The model explained 43.16% of the variation and the best predictors of chimpanzee trapping rate were distance to roads and proximity to swamps. There was no significant effect of settlements, abandoned settlements or mangroves. Our results suggest that chimpanzees avoid roads and prefer to maintain proximity to swamps. We highlight the importance of studying chimpanzee populations living in anthropogenic habitats like agricultural-swamp matrixes to better understand factors influencing their distribution and inform conservation planning outside protected areas.

4.2. Introduction

It is estimated that approximately 60% of all world non-human primates (hereafter primates) are threatened with extinction and the main threats to their survival are habitat loss and fragmentation due to rapid human population growth and land conversion for agriculture (Crooks et al. 2017; Estrada et al. 2017; Laurance et al. 2014). Many primate species are having to live in forest-agricultural mosaics and in close proximity to people (Estrada 2013). West Africa has one of the most fragmented tropical forest landscapes in the world due to high levels of deforestation (Rudel &

Roper 1997). Some animal species are nevertheless able to adjust to these changes and survive and even flourish in human altered conditions (Wong & Candolin 2015). Some primates also have a certain degree of flexibility and can adapt their dietary, socioecological behaviours to these human altered landscapes (Brncic et al. 2015; McLennan et al. 2017). In recent years, there has been a growing interest in studying primates and especially chimpanzees (*Pan troglodytes*) living in human-modified habitats to understand how they behave and survive in degraded landscapes and which conservation strategies may be best suited for the species in areas outside protected areas (McLennan et al. 2017).

Chimpanzee populations across Africa are declining due to habitat loss, poaching and disease (Humle et al. 2016). They can occur in a variety of habitats from moist lowland to mountain forests, swamp forests and woodland savannas (Williamson et al. 2013), but rapid human population growth and agricultural expansion into forested areas have forced chimpanzee populations to survive in forest-agricultural mosaics (Humle et al. 2016). Chimpanzees are able to adjust their behaviour to some level of human disturbances like agriculture, selective logging and/or low levels of hunting (Brncic et al. 2015; Morgan et al. 2018; Rist et al. 2009). Behavioural adjustments include dietary (Bryson-Morrison et al. 2016; McLennan 2013; McLennan & Hockings 2014) and socioecological adaptations (Bryson-Morrison et al. 2017; Hockings et al. 2012; Krief et al. 2014; McCarthy et al. 2017), as well as behavioural responses to novel risks such as roads (Cibot et al. 2015; Hockings et al. 2006), and the presence of people, such as researchers and farmers (McLennan & Hill 2010).

Anthropogenic landscapes in which primates co-exist with people consist of a complex mosaic of forest and agricultural habitat types intermixed with roads and settlements often bordering protected areas (McLennan et al. 2017). Studies in Uganda have estimated similar densities of chimpanzees in an agroforestry landscape bordering a national park and within the national park, highlighting the importance of such anthropogenic habitat for the conservation of primates. However, the absence of hunting and the proximity to a large protected forest may explain primates' persistence in these fragmented forest blocks (Blanco & Waltert 2013). Nevertheless, many chimpanzee populations also occur in highly degraded anthropogenic landscapes away from protected areas and with only small remnant forest fragments left (Brncic et al. 2010). Typically, such forest patches are riverine, flooded or swamp forests usually unsuitable for agriculture but important habitats for wildlife (McLennan & Hill 2010).

Swamps can in places such as in the Kahuzi-Biega National Park in the Democratic Republic of Congo act as a barrier to chimpanzee dispersal (Basabose 2005). However, in other regions, swamp forests and mangroves can also act as critical habitat for great apes for feeding, nesting and as a refuge from hunters: Bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes troglodytes*): Inogwabini et al. 2012; Western Gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*P. t. troglodytes*): Poulsen & Clark 2004, Stokes et al. 2010; Western Gorillas: Rainey et al. 2010; Orangutans (*Pongo pygmaeus*): Singleton & Van Schaik 2001).

Road development in Africa is directly related to human expansion (Laurance et al. 2006, 2009) and extractive industries such as mining and logging (Ancrenaz et al. in press.; Vanthomme et al. 2013). It can exacerbate habitat loss and fragmentation, as well as wildlife mortality, including that of chimpanzees, directly via road kills (McLennan & Asiimwe 2016) or indirectly by facilitating hunting and the bushmeat trade (Laurance et al. 2009; Wilkie et al. 2000). In a nationwide study conducted in Gabon, Vanthomme et al. (2013) revealed that chimpanzee abundance is negatively affected by the presence of main roads (>15 m wide; tar and laterite coated). However, this study failed to find any significant relationship with proximity to secondary roads (typically sand coated and in poorer condition) and human settlements. Another study in a forest concession in Gabon showed that neither main roads nor settlements influenced chimpanzee distribution (Van Vliet & Nasi 2008). Duvall (2008) also highlighted the value of abandoned settlements for chimpanzees, as these areas provide highly nutritious food resources such as bananas (*Musa sp.*), oranges (*Citrus aurantifolia*), and mangos (*Mangifera indica*) long after abandonment. However, hunters and local people may also frequent such areas, potentially acting as deterrents to wildlife frequentation (Duvall 2008).

The IUCN status of the western subspecies of chimpanzee, *P. t. verus*, has been recently upgraded to critically endangered (Humle et al. 2016). Sierra Leone harbours the third largest chimpanzee population in West Africa with more than half living outside protected areas (Brncic et al. 2010; Kühl et al. 2017). It is estimated that since 1975, the country has lost 36% of its forest and woodland habitats (CILSS 2016). 'Farm-bush', the degraded secondary forest growth that follows slash-and-burn agriculture, is increasingly the most dominant vegetation type in Sierra Leone (Humle 2003). In the late eighties, Davies (1987) noted that chimpanzees in Sierra Leone frequented cultivated areas across the entire country. Only a few studies have since been published exploring how chimpanzees are able to persist in such agricultural matrixes (Brncic et al. 2010, 2015). Chimpanzees face serious threats in Sierra Leone, including habitat loss, hunting, and retaliation as a result of competition with people for resources (Brncic et al. 2010; Garriga et al. 2017). The persistence of chimpanzees in agricultural matrixes and their co-existence with farmers has been documented in other parts of Africa, but still remains largely understudied. It has mostly been attributed to human tolerance linked to religious and cultural taboos (Hockings and Sousa 2013), access to highly nutritious cultivars (Bryson-Morrison et al. 2016) and the importance of semi-domesticated oil palms (*Elaeis guineensis*) for nesting and food (e.g. Bossou, Guinea: Humle & Matsuzawa 2004; Guinea-Bissau: Bessa et al. 2015; Sousa et al. 2011).

Although chimpanzees occur across a wide range of habitat types, ranging from primary forest to woodland savanna, few studies have focused on chimpanzees inhabiting highly degraded landscapes devoid of forest and dominated by farmland and swamps, as well as human infrastructures such a roads and settlements. Our study aimed to fill this gap using camera trapping technology in an agricultural-swamp matrix in the Moyamba district in south-western Sierra Leone. We examined habitat preferences and the influence of human disturbance at a fine-spatial scale on wild chimpanzee abundance across this landscape. Our specific objectives were: (1) to determine the relative population abundance across the study area, and (2) to explore spatial variations in the abundance patterns in relation to anthropogenic (roads and settlements) and environmental (swamps and mangroves) features. Considering the extent to which chimpanzees occur outside protected areas in Sierra Leone, this study aims to contribute valuable insights into factors affecting persistence of chimpanzees in highly deforested landscapes to better inform current and future conservation efforts.

4.3. Material and methods

4.3.1. Study area

The study area, called Lawana, is located in the coastal plains in the Moyamba district in the south-western Sierra Leone in West Africa and it covers approximately 91 km^2 in the chiefdoms of Bumpeh and Kagboro (-12°46′31″N and 7°59′55″; Fig. 4.1) with elevation ranges of 1 to 37 m a.s.l. The habitat is characterised by active and fallow farms at various stages of regrowth, swamps and mangroves intermixed with settlements and unpaved roads with a forest cover of <1% as estimated during this study (see details below). Semi-domesticated oil palms are abundant and the most frequently encountered tree species across this agricultural matrix. The climate is tropical with a dry season which runs from November to May (Garriga et al. 2017). The total human population is rural with an average density of 51.5 hab/km^2 for Bumpeh and 55.9 hab/km^2 for Kagboro chiefdoms (Statistics Sierra Leone 2017). Subsistence farming is the main human activity in the study area. Farmers cultivate seasonal crops like rice (*Oryza spp*.), cassava (*Manihot esculenta)*, sesame (*Sesamum* sp.) and sorghum (*Sorghum bicolor*) using slash-and-burn intercropping practices (see chapter 3). Previous investigations in the study area confirmed the presence of chimpanzees through semi-structured interviews as well as direct observations (Brncic et al. 2010; Garriga et al. 2017).

4.3.2. Camera trap survey

We conducted a camera trap survey during 8 months between April 2016 and May 2017 divided in three time periods during the dry season months: April to May 2016, November 2016 to February 2017 and February to May 2017. We used ARCGIS 10.3 (ESRI, Redlands, USA) to design a sampling grid with cell sizes of 1.25x1.25 km^2. The chimpanzee home range in the study area was unknown, and we defined our grid cell size based on approximate average minimum day range from Basabose 2005; Bates and Byrne 2009 and unpublished data from released chimpanzees equipped with store-on-board tracking collars in a savanna dominated landscape (Humle, unpub. data). We set one camera within each block for each period. Due to limitations in the number of cameras, sampling was focused in the areas with expected presence according to triangulated farmers' confirmation across villages. In each selected grid, cameras were located within 100 m of the centre of the grid selecting the best place to install each camera trap to optimize captures. We asked village chiefs and farmers for permission to set cameras on their land. In some instances, we had to shift a camera's placement or remove it altogether because of ongoing slash-and-burn agricultural activities. Therefore, a few locations were not sampled during the entire sampling period. For analytical purposes, we selected cameras that were deployed in the same location at least during 2 of the 3 time periods. We used 24 infra-red digital camera traps Reconyx HC500, HC600 and PC800 (Reconyx Inc., Holmen, WI, USA) and all were programmed with the same settings, i.e. high sensitivity, three consecutive pictures and no delay, resolution of 3.1 MP, 24h operational, with date and time stamp and infra-red mode. In total, we surveyed 27 grids of which 17 locations were surveyed for three periods and 10 for two periods (Fig. 4.1).

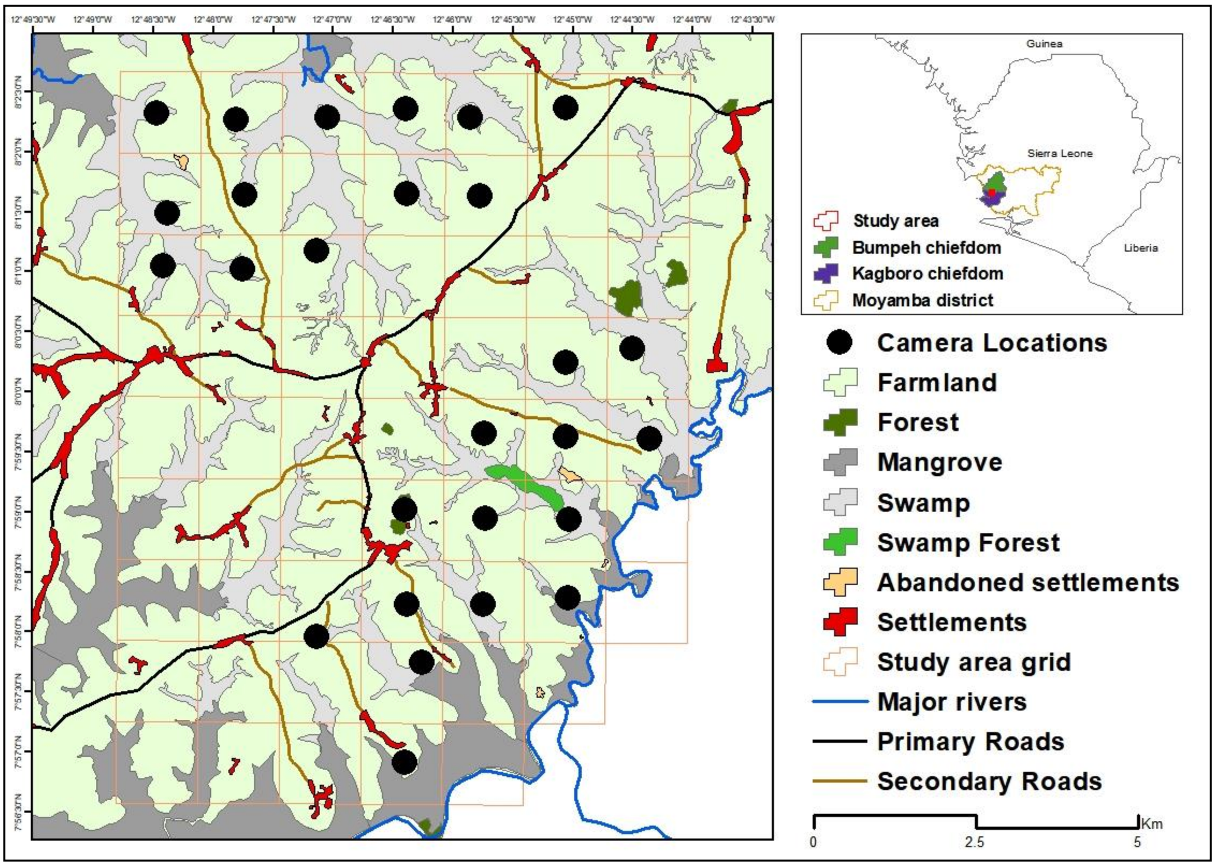

Figure 4.1. Study area showing the 27 camera traps locations and the habitat types in the district of Moyamba in Sierra Leone. Upper right map shows the location of the study area in the chiefdoms of Bumpeh and Kagboro.

4.3.3. Habitat classification

The habitat was classified manually using satellite imagery with a 30 m resolution (GeoEye, WorldView-2 and WorldView-3 satellites acquired between 2015 and 2017). The landscape is a mixture of habitat types, in which farmland is markedly predominant. Despite the area being relatively small, it is at the intersection of different satellite images for different time periods and the annual slash-and-burn farming practices consequently rendered it impossible to classify different farmland types (i.e. burnt land, new farm, young fallow and old fallow). Therefore, we classified all the farmland as one single type. Table 4.1 describes the habitats and vegetation types present in the study area. A large river, the Kagboro River, delimits the southern side of the study area and is presumed to act as a natural barrier to chimpanzee dispersal (Fig. 4.1). Human settlements were divided in two categories, 'small' with fewer than 25 households (ranging from 0.12 - 2.9 hectares) and 'large' with more than 25 households (ranging from 3 - 38 hectares). Hamlets that were less than 200 m away from each other were considered as part of the same settlement, unless the presence of a swamp warranted their separate categorisation. This classification system was also corroborated via ground-truthing observations.

Table 4.1. Habitat types and range in the study area.

Habitat type	Description	Total area in km^2	Percentage of the total area
Farmland	Includes: young fallow, mature fallow, cultivated land and burnt fields for cultivation	66.80	73.1 %
Swamp	Dominated by raffia palms	15.76	17.2 %
Mangrove	Dominated by mangrove shrubs	6.86	7.5 %
Urban	Settlements	1.34	1.5 %
Forest	Mature secondary regrowth of vegetation. 30+ years old with a closed canopy	0.36	0.4 %
Swamp Forest	Forest which is inundated with freshwater, either permanently or seasonally	0.27	0.3 %
Total		**91.39**	**100 %**

4.3.4. Anthropogenic and environmental variables

We hypothesized the spatial distribution of chimpanzees' relative abundance may be influenced by: a) the predominant habitat type; and b) the anthropogenic habitat variables such as road and human settlements (Table 4.2). Aside from the human camera trapping rate, all other anthropogenic predictor variables used in the analysis were based on the shortest Euclidean distance (Romero et al. 2012) between the camera trap and the road network, settlements, abandoned settlements, swamps and mangroves. All predictors were based at the grid-level using the '*raster*' package (Hijmans 2017) in the R software (R Core Team 2017). We used GIS Software ArcGIS 10.3 to calculate the percentage of habitat types in each grid and we created 5 categorical habitat variables depending on the dominant habitat types in each grid: farmland, swamps, mangroves and farmland/swamps and farmland/mangroves (these latter categories were created when none of the habitat types in the grid predominated however they were not included in the models as were highly correlated to distance to swamps and mangroves).

Table 4.2. Description of the habitat and anthropogenic variables used as predictors in the analysis.

Type	Variables	Description	Measure
Anthropogenic Variables	Small settlements	Fewer than 25 households.	Distance from camera location to nearest feature (m)
	Large settlements	More than 25 households.	Distance from camera location to nearest feature (m)
	Roads	Includes all motor-able roads. All were unpaved.	Distance from camera location to nearest feature (m)
	Abandoned settlements	Areas in which there was a settlement in the past. No houses remain but fruit producing orchards persist.	Distance from camera location to nearest feature (m)
	All urbanised areas	Small and large settlements merged.	Distance from camera location to nearest feature (m)
	Human trapping rate	Comparing human and chimpanzee TR	number of events x Trap-days per camera location
Habitat variables	Farmland	Cultivated land active and fallow	Distance from camera location to nearest feature (m)
	Swamp	Uncultivated land where water and raffia palms dominate	Distance from camera location to nearest feature (m)
	Mangrove	A tidal swamp which is dominated by mangrove shrubs	Distance from camera location to nearest feature (m)

4.3.5. Statistical modelling

Camera images were screened for species identification and analysed using the ZSL-CTAT open-access software developed at Zoological Society of London (ZSL) specifically to process images from camera trap arrays (Amin et al. 2017). In this analysis, the software was set to score a new independent event (IE) when a sequence of images of a target species appeared more than 60 minutes after the previous images of that species (Tan et al. 2013). Species trapping rates (TR) were calculated as the mean number of independent photographic events per trap day x 100, using cameras that operated for more than 75% of the survey period. We defined the sampling occasion as 5 consecutive days of monitoring. The same approach was used to derive trapping rates for both people and chimpanzees.

The chimpanzee home range in the study area was most probably greater than our grid cell size of 1,250 m^2 and therefore we expected some spatial autocorrelation in our data. To overcome this issue, we used the 'hSDM.binomial.iCAR' function of the 'hSDM' package (Vieilledent et al. 2014) within the R statistical environment (R Core Team 2017). This function performs a logistic regression model (events vs occasions) in a hierarchical Bayesian framework accounting for spatial autocorrelation using an intrinsic conditional autoregressive (iCAR) model. iCAR assumes that the probability for recording an event at one site depends on its probability on the neighbouring sites, in this case the eight cells around a target one. We performed the model selection using a forward stepwise procedure using deviance explained to select the final model; stepwise stops when the addition of a new variable in the model did not improve significantly the explained deviance (Spiegelhalter et al. 2002).

4.4. Results

Cameras were operational for 4,763 trap-days with an average of 176 operational trap-days (range: 119 - 207 trap-days) per location. We recorded 44 chimpanzee IE in 12 locations (44.4% of the total locations) and 65 human IE in 16 locations (59.3% of the total locations) during the study period. Chimpanzee and human TR for each camera location is shown in Fig. 4.2 as the number of IE per trap-day.

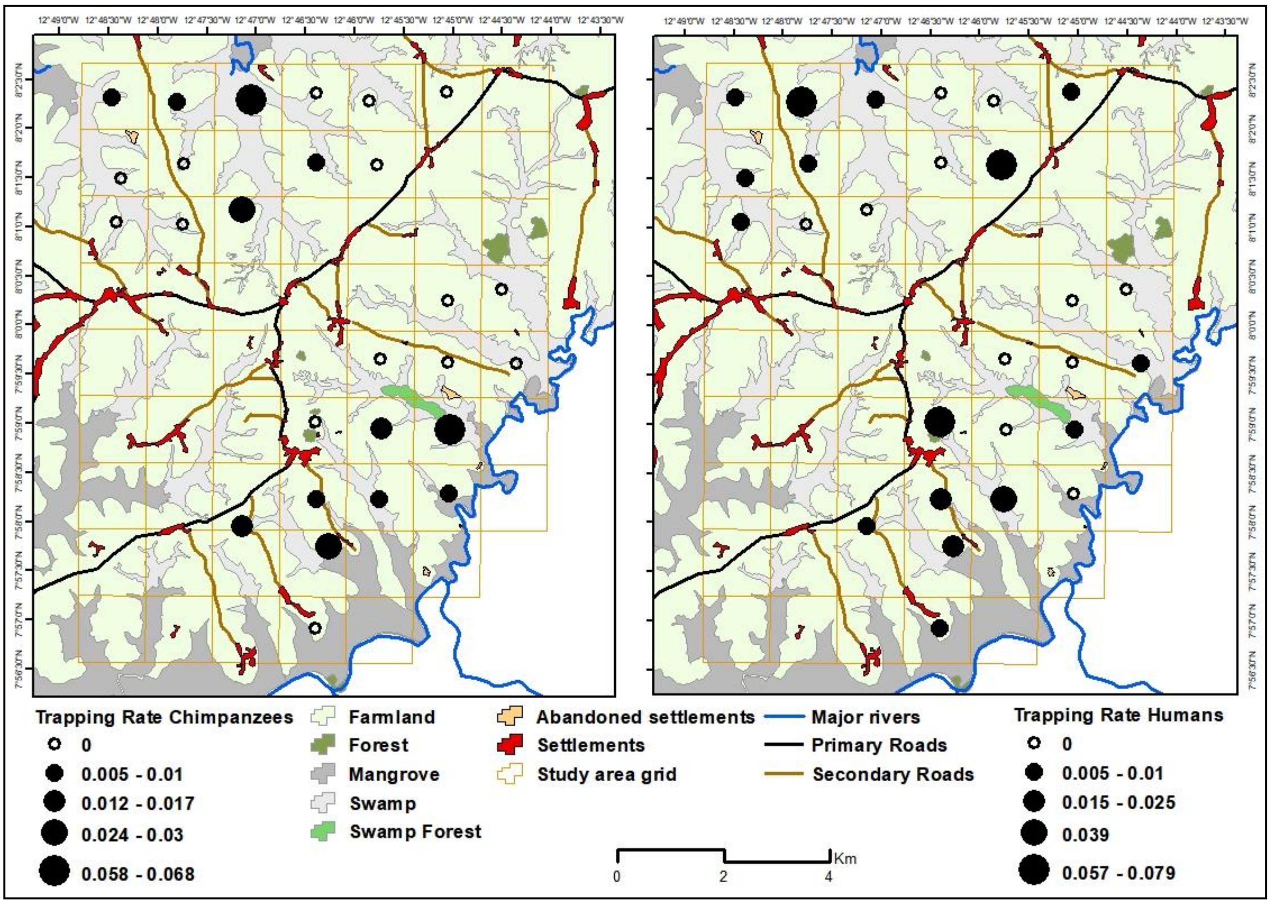

Figure 4.2. Chimpanzee and human trapping rates for each camera location.

4.4.1. Statistical modelling

Modelling showed that both anthropogenic and ecological features are relevant drivers of chimpanzee TR. However, only the distance to roads and the proximity to swamps served as good predictors of species TR, yielding a best final model explaining 43.16% of the total deviance and a relevant amount of variability in trapping rates was explained by the iCAR component (Table 4.3 & Fig. 4.3). The variables that were not included in the final model were human TR, distance to settlements and mangroves, and the habitat types.

Table 4.3. Results of the binomial – ICAR final model examining the contribution of roads and swamps to chimpanzee trapping rates. Vrho: Spatial random effect variance.

	Mean	SD Naive	SE	Time-series SE	Quantiles				
					2.5%	25%	50%	75%	97.5%
Intercept	-5.638	0.937	0.042	0.058	-7.774	-6.220	-5.506	-4.944	-4.184
Roads	0.748	0.399	0.018	0.019	0.034	0.481	0.725	1.011	1.505
Swamps	-2.830	1.572	0.070	0.101	-6.648	-3.837	-2.597	-1.712	-0.168
Vrho	6.716	2.076	0.093	0.093	2.290	5.334	6.891	8.482	9.940

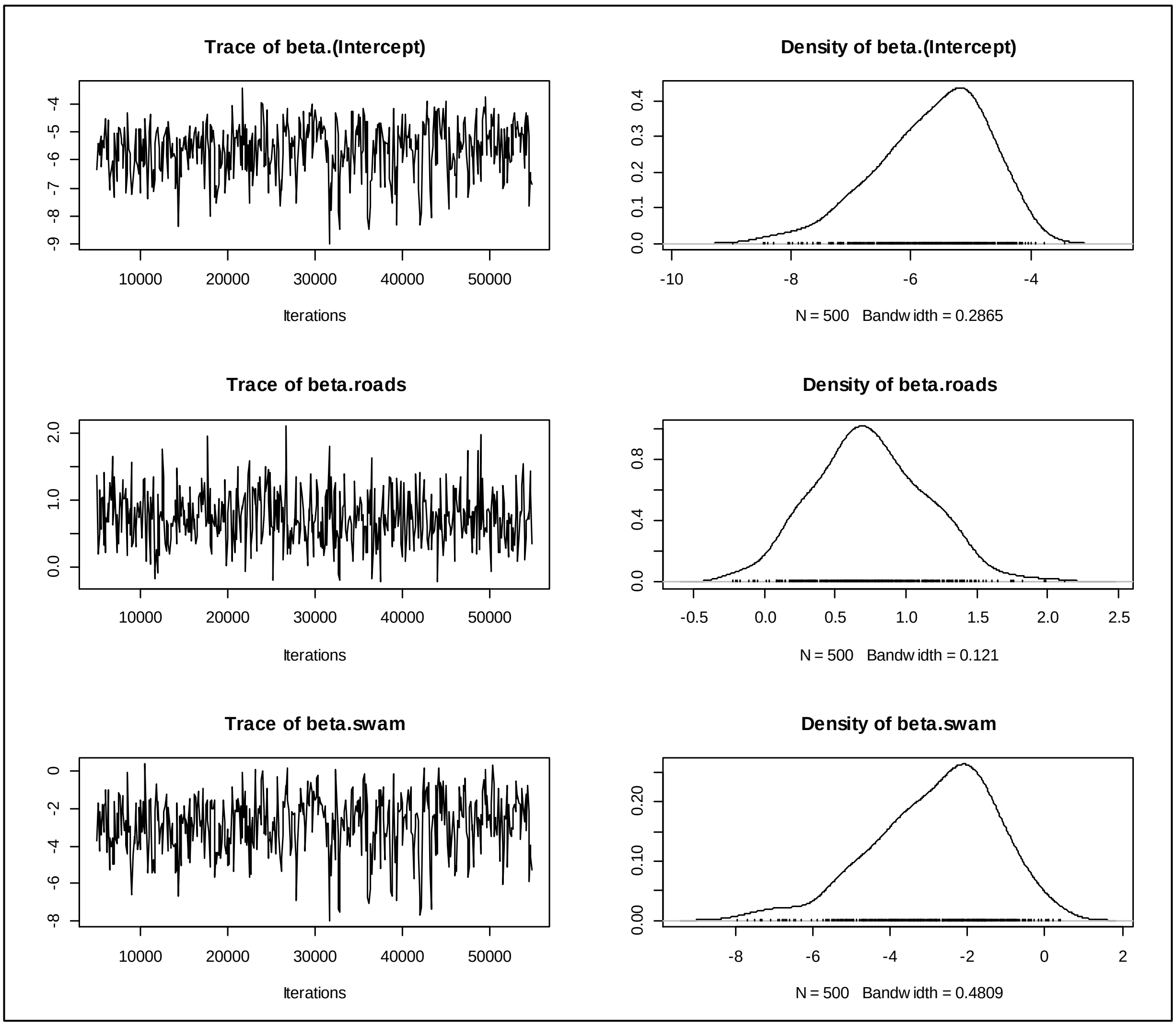

Figure 4.3. Trace and density estimates for the variables swamps and roads.

4.5. Discussion

This study provides an assessment of the relative importance of some habitat and anthropogenic variables on the abundance of chimpanzees across a predominantly farmland habitat at a fine-spatial scale. Our model shows that roads and swamps play an important role in chimpanzee abundance across this landscape. This finding corroborates large scale studies which have revealed reduced chimpanzee abundance near major roads in Sierra Leone (Brncic et al. 2015) and in Gabon (Vanthomme et al. 2013). However, these studies conclude that chimpanzee abundance was negatively associated to main primary roads but positively associated with secondary roads. In our study area all roads are untarmacked, with variable frequency of use by vehicles, motorcycles and pedestrians but their presence still influenced chimpanzee abundance. This is critical when one thinks of the rapid expansion of road construction across Africa

(Laurance et al. 2017) and highlights the fact that roads can certainly impact in chimpanzee distribution and abundance even along smaller secondary roads. Chimpanzees living in fragmented habitats typically cross roads to move from one area to another in their home range and often approach human settlements (Bortolamiol et al. 2016; Hockings and Sousa 2013; Laurance et al. 2006; Vanthomme et al. 2013). Chimpanzee abundance and distribution might be negatively influenced by the proximity to roads and therefore the risks associated with the probability of encountering people. A recent study revealed that the distance from roads was the best predictor of bonobo nest occurrence; however, this study argued that hunting of apes in proximity to the road rather than displacement of the bonobos, best explained this pattern (Hickey et al. 2013; Laurance et al. 2009). However, in our model, settlements and human presence did not influence chimpanzee abundance, possibly due to human tolerance for chimpanzees and low levels of hunting in our study area (Brncic et al. 2015). Although, even low rates of hunting can have an impact in slow reproducing animals like chimpanzees, our study failed to uncover any effect on chimpanzee distribution in this region of Sierra Leone. The study area is remote and there are no short-term plans by the government to improve road infrastructure; however, during our study, at least three footpaths leading to small settlements had been widened and cleared by the local people to allow car passage. Moreover, in the last 5 years, there has been a boom in motorcycles becoming the most common mean of local transportation. People use them as taxis and they can circulate at high speeds even along small footpaths, therefore increasing disturbance to wildlife and the risk of collision. The unpaved roads and the relatively low traffic levels in our study area probably explain why there have been no reported cases of chimpanzee road kills as in other parts of Africa such as Uganda (McLennan and Asiimwe 2016). Nevertheless, chimpanzees can adjust their behaviour (e.g. looking right and left before and while crossing, crossing in small subgroups and more cohesive, increased waiting time) to reduce the danger posed by roads and avoid the risk of collision (Cibot et al. 2015; Hockings et al. 2006), and similar adaptations could be occurring with the chimpanzees in our study area.

Proximity to swamps seems to be a good predictor of chimpanzee presence in this landscape. Swamps represent the second largest habitat in the study area, while forest patches were extremely rare. However, remnant swamps and swamp forests are not cultivated by farmers and they might act as a refuge for chimpanzees and other wildlife possibly due to their greater inaccessibility as argued by Poulsen & Clark (2004) in

Northern Congo. Semi-domesticated oil palms are widely distributed across this landscape including inside the swamps, offering chimpanzees a relative safe environment where to rest and feed (Bryson-Morrison et al. 2017; Garriga et al. 2017; Humle & Matsuzawa 2004) and possibly to find shade during days with high temperatures (e.g. use of caves in Senegal (Pruetz 2007) or to reduce thermoregulation costs by resting at higher positions during cooler periods by Bossou chimpanzees in Guinea (Takemoto 2004). Chimpanzees at other sites have demonstrated extensive reliance on oil palms for food and nesting (Bessa et al. 2015; Bryson-Morrison et al. 2016; Humle & Matsuzawa 2004; Sousa et al. 2011).

We theorised that there could be differences between large and small human settlements when it comes to predicting chimpanzee presence; however, our model did not support this hypothesis, possibly because most of the villages in the study area are relatively small and many are isolated hamlets. Also, around settlements, farmers grow fruits which might attract chimpanzees despite the risks associated with being detected and encountering people when foraging on orchards. In fact, we captured images of chimpanzees carrying domesticated fruits (i.e. mangoes, pineapples) in four different cameras that were set near orchards close to settlements.

We hypothesised that species' habitat use will be greater close to abandoned settlements because of the presence of domesticated fruit trees (Duvall 2008). However, our model did not support this prediction. Although we recorded nests in these areas, chimpanzees may only visit these sites occasionally when fruits are available. Local people visit these areas to harvest the fruits and hunters also venture in these areas which attract wildlife such as monkeys and duikers (R. M. Garriga pers. obs.) which might also deter regular chimpanzee presence.

This study revealed that chimpanzees have been coping and living in a challenging landscape where most of trees are semi-domesticated oil palms growing across a changing agricultural land intermixed with which act as a refuge for wildlife. The small settlements and the limited road network may be in the chimpanzees' favour. However, their long term future remains uncertain. Will chimpanzees still be present in this sort of landscape without the presence of the ubiquitous semi-domesticated oil palms in which chimpanzees nest and feed should the landscape be converted to oil palm plantations or other industrialised agricultural activity? What is the future of chimpanzees living in these degraded landscapes facing increased human growth and development? How will chimpanzees cope with wider paved roads and larger settlements? The fact that more than half of the chimpanzee population in Sierra Leone are found in similar anthropogenic habitats highlights the importance of our results and the need to include these chimpanzee populations in conservation programmes to secure their long term survival, especially in areas where they are tolerated and hunting pressure on the species is low, or areas prone to conversion to industrialised activities and associated infrastructures. Further studies are also required to better understand chimpanzees' ecological, demographic and social habits in similar anthropogenic habitats to inform chimpanzee responses to landscape changes and effective mitigation strategies aimed at improving people attitudes towards the species and balancing conservation efforts and development activities. There is also a growing need to understand what factors shape people's tolerance of chimpanzees to increase initiatives aimed at improving sustainable coexistence between people and chimpanzees. Successful protection measures should benefit people and chimpanzees alike. Conservation actions should be focus on helping farmers improve their agricultural practices and land use patterns, their behaviour towards chimpanzees and their understanding of the role of the species in the landscape and the drivers behind crop foraging. One valuable approach may also be to develop agreements with farmers to allow untouched strategic fallow areas to regenerate into community-managed forest refuges providing corridors for wildlife and vital natural resources for both species.

5 – Study III

Chimpanzee population structure, ranging and activity patterns in the Lawana study area

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(In preparation for journal submission)

5.1. Abstract

Little is known about the demographics and home range of unhabituated chimpanzee populations in landscapes dominated by human activities. Here we provide insights into the structure, range and activity patterns of two groups of unhabituated wild chimpanzees living in an agricultural-swamp matrix in south-western Sierra Leone. We conducted an 8-month camera trap survey between April 2016 and May 2017 which produced 1,725 images of chimpanzees totalling 125 independent events. We identified two groups of 24 and 14 individuals whose group sizes and age structure were comparable to the other African sites. However, the gender ratio was biased towards males. The minimum estimated home ranges differed depending on the analytical method used. The minimum convex polygon resulted in a home range (HR) of 15km^2 and 16km^2 for the northern and southern groups respectively and the Kernel density estimate resulted in a HR of 14.3 km^2 and 22.5 km^2 respectively. The estimated chimpanzee density considering the total study area of 91 km^2 was 0.4 individuals/km^2. Chimpanzees are a diurnal species, but recent studies have shown occasional chimpanzee night activity that are related to environmental factors (e.g. high day temperatures in Senegal) or anthropogenic factors (e.g. accessing crops when farmers are not present). In our analysis, we compared the chimpanzee day activity with that of humans based on camera trapping rates and we found a statistically positive correlation, indicating that human presence seems not to interfere with chimpanzees' day activity. This could indicate a certain degree of tolerance by farmers and low levels of hunting in the area. However, at a temporal level, chimpanzees tended to reduce their activity at midday when human activity was highest. Despite not finding statistically difference between chimpanzee party size and human presence at temporal level, we observed different activity patterns between both groups. The larger northern group decreased the average party size and the smaller southern group increased it at midday hours. Snare-traps are commonly used by farmers to protect their crops from small mammals but can also pose a risk to chimpanzees as seen in the camera trap images in which we identified three adult chimpanzees with amputated limbs.

5.2. Introduction

Demographic studies are valuable to understand the size, structure and behaviour of populations. A population defined by Berryman (2002, p.441) is '*a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and / or migration behaviour and in which numerical changes are largely determined by birth and death processes within a given area*'. Members of a population often rely on the same resources, are subject to similar environmental constraints, and depend on other members to persist over time. Demographics studies have two interrelated branches: population structure and population dynamics. Population structure focuses on how the population is organised by gender and age classes and how they are organised into social groups. Population dynamics focus rather on how the population changes over time (Lawler 2011).

Censuring total individuals in a population is often impracticable in large study areas and therefore, scientists use indirect statistical survey methods to estimate chimpanzee population parameters such population density and abundance (Kühl et al. 2008). However, study of chimpanzee demographics in small study areas can be achieved by direct observation of habituated groups (Imanishi 1960; Kortlandt 1962; Nishida 1968; Reynolds and Reynolds 1965; Sugiyama 2004; Van Lawick-Goodall 1968). Habituation allows collecting information of followed individuals in their habitat for long periods of time (Boesch & Boesch-Achermann 2000; Matsuzawa et al. 2011; Nakamura et al. 2015; Pusey et al. 2007). Habituation is highly efficient for individual identification and behavioural studies but requires years before the animals trust scientists to let them follow and observe them at close distance (Wilson & Wrangham 2003). However, close proximity to habituated chimpanzees can also have negative impacts (Macfie & Williamson 2010; Williamson & Feistner 2011), mostly related to the risks of zoonotic disease transmission between humans and chimpanzees (Dunay et al. 2018; Köndgen et al. 2008, 2010; Scully et al. 2018; Woodford et al. 2002). Therefore, scientists have been using indirect non-invasive methods to study chimpanzee demographics, behaviour, diet and disease based on the genetic and/or chemical analysis of hairs, urine and faecal samples (Arandjelovic et al. 2010, 2014; Arandjelovic & Vigilant 2018; Köndgen et al. 2010; McLennan 2013; Moore & Vigilant 2014). However, collection of samples and resampling can be challenging and typically requires large sample sizes to infer conclusive results and genetic analyses can also be expensive. Other indirect techniques to study chimpanzees' presence, density distribution, composition and population size, as well as behaviour, e.g. nesting or ranging patterns (Kühl et al. 2008), include line transect distance sampling (Buckland et al. 2010), reconnaissance trail surveys (recces) (Plumptre & Cox 2006), interviews with local people (Duvall 2008), camera trapping (O'Connell et al. 2011) and unmanned aerial vehicles (UAVs) (van Andel et al. 2015).

In recent years, researchers have increasingly relied on the use of more advanced technologies such as camera trapping to survey and observe wildlife, albeit significant inconsistencies in protocols and data analysis (Burton et al. 2015). Such technology has been used to study animal species distribution, abundance, behaviour and social structure amongst other aspects (Caravaggi et al. 2017; Steenweg et al. 2017). For the study of chimpanzees, camera traps have been utilised to identify unhabituated chimpanzees and to study their behaviour (Boesch et al. 2017; Boyer-Ontl & Pruetz 2014; Krief et al. 2014; Lapuente et al. 2017; Sanz et al. 2010), as well as to estimate their distribution and abundance (Nakashima et al. 2013; Si et al. 2014). Identification of individual chimpanzees from camera trap photographs relies on facial and body features as well as individual characteristics like injuries. It may not always be possible to identify all the individuals of a group if the chimpanzees are weary of the camera traps (McCarthy et al. 2018). However, with a large number photographs, it is possible to identify individual chimpanzees and to estimate group composition and number of chimpanzees when cameras are deployed for long periods of time and located in highly-frequented chimpanzee areas (Després-Einspenner et al. 2017). Combination of camera trapping and spatially explicit capture-recapture (SECR) techniques can provide detailed population assessments and density estimates (Head et al. 2013). Researchers have started to develop animal biometrics to semi-automatically detect ape faces in a way that can recognise the ape species but it cannot reliable identify the individual (Crunchant et al. 2017).

Chimpanzees are semi-terrestrial, diurnal, gregarious, territorial and live in multi-gender fission-fusion communities (Goodall 1986; Nishida 1968) averaging about 35 members, ranging from approximately 12 (Bossou, Guinea (Sugiyama 2004)) to 150 (Ngogo, Uganda (Mitani 2006)). Generally, in a chimpanzee community the proportion of adult females is greater than adult males (Boesch & Boesch-Achermann 2000; Matsuzawa et al. 2011; Nishida et al. 2003). Male chimpanzees tend to stay in their natal group, while, adolescent females can move either temporarily or permanently to other communities to avoid inbreeding (Pusey 1980). Chimpanzees' fission-fusion social organisation implies that at any time they can form subgroups or parties; the factors assumed to affect party size are food resource availability (Humle 2003; Nishida 1968) and the presence of cycling females (Goodall 1986; Matsumoto-Oda et al. 1998). In anthropogenic habitats, chimpanzees' party size can show socioecological adaptations to novel risks, e.g.: increasing party cohesiveness when feeding on crops (Hockings et al. 2012), forming larger parties of males when entering cropland and reducing their vocalisations (Wilson et al. 2007).

Chimpanzee home ranges vary greatly depending on the habitat type they live. In forest habitats, their home range spans from 6-8 km^2 to 32 km^2 (Basabose 2005; Boesch & Boesch-Achermann 2000; Humle 2011). In woodland-savanna, it can exceed 500 km^2 (Nakamura et al. 2013). In mixed forest-agricultural mosaics, chimpanzees range can exceed 20 km^2 but usually their core area is around 5-8 km^2 (5 km^2: Bulindi, Uganda (McLennan & Ganzhorn 2017); 8 km^2: Caiquene-Cadique, Guinea-Bissau (Bessa et al. 2015); 7 km^2: Bossou, Republic of Guinea (Hockings et al. 2017; Sugiyama 2004)). Typically ranging patterns are influenced by seasonal changes in food availability (Poulsen & Clark 2004) and territoriality (Herbinger et al. 2001). In general, male chimpanzees tend to range over larger areas than lactating females (Goodall 1986). Females usually use overlapping areas that are smaller than the whole community range (Williams et al. 2002). Males' chimpanzee ranging behaviour is associated to border patrolling and defense of their territory against other neighboring communities (Bates 2009; Herbinger et al. 2001; Mitani 2006).

Chimpanzees are considered a diurnal species; however, there are reports of chimpanzees' night activity. Nocturnal activities although infrequent are widespread in wild chimpanzees (Pruetz & Bertolani 2009; Tagg et al. 2013) and have been reported more recently thanks to the use of camera traps, which provides data from unhabituated animals and from areas that may be difficult for researchers to access. In south-eastern Senegal, Kharakhena chimpanzees were photo-captured visiting a water hole in the middle of the night (Boyer-Ontl & Pruetz 2014) and Sebitoli chimpanzees in Kibale National Park (NP), Uganda, were photo-captured feeding frequently at night in open croplands, hence minimising the risk of human detection and disturbance (Krief et al. 2014). A later study in this same area revealed that chimpanzee distribution was not influenced by the spatial proximity of humans, albeit differences in temporal activity patterns (Bortolamiol et al. 2016). A similar pattern of spatial overlap and temporal avoidance between people and wildlife was noted in tigers (*Panthera tigris*) in

Nepal (Carter et al. 2012). In general, there appears to be a global increase of nocturnality in wildlife in response to human disturbances (Gaynor et al. 2018).

Our study focused on determining the demographics of wild chimpanzees at a fine spatial scale using camera trap images. The specific objectives of our study were:

1. To define the number of distinct chimpanzees and the group composition and structure through individual identification of camera trap images.
2. To determine chimpanzees' minimum home range based on the locations where chimpanzee images were captured and other chimpanzee evidences (nests, dungs, feeding remains, trails and vocalisations) observed during the study period.
3. To compare the spatio-temporal activity patterns of chimpanzees and humans in the study area based on camera trap images,
4. To assess if human presence had an effect in chimpanzee party size.

5.3. Methods

5.3.1. Study area

The study area, called Lawana, is located in the coastal plains in the Moyamba district in the south-western Sierra Leone in West Africa and it covers approximately 91 km^2 in the chiefdoms of Bumpeh and Kagboro (-12°46′31″N and 7°59′55″; Fig. 5.1) with elevation ranges of 1 to 37 m a.s.l. The habitat is characterised by active and fallow farms at various stages of regrowth, swamps and mangroves intermixed with settlements and unpaved roads with less than 1% of forest cover. Semi-domesticated oil palms are abundant and the most frequently encountered tree species across this agricultural matrix, together with rough-skin plum trees (*Parinari excelsa)*. The climate is tropical with a dry season which runs from November to May. The total human population is rural with an average density of 51.5 hab/km^2 for Bumpeh and 55.9 hab/km^2 for Kagboro chiefdoms (Statistics Sierra Leone 2017). Subsistence farming is the main human activity in the study area. Farmers cultivate seasonal crops like rice (*Oryza spp*.), cassava (*Manihot esculenta)*, sesame (*Sesamum* sp.) and sorghum (*Sorghum bicolor*) using slash-and-burn intercropping practices (Study I). Previous investigations in the study area confirmed the presence of chimpanzees through semi-structured interviews as well as direct evidence (Brncic et al. 2010; Garriga et al. 2017).

5.3.2. Survey design and camera deployment

We completed a camera trap survey across 8 months divided into 3 study periods during the dry season (April-June 2016; Nov. 2016-Feb. 2017; Feb.-May 2017). We used ARCGIS 10.3 (ESRI, Redlands, USA) to design a sampling grid with cell sizes of 1.25x1.25 km^2 across the study area. We deployed 39 - 41 infrared digital camera traps Reconyx HC500, HC600 and PC800 (Reconyx Inc., Holmen, WI, USA) across the study area and all were programmed with the same settings, i.e. high sensitivity, three consecutive pictures and no delay, resolution of 3.1MP, 24h operational, with date and time stamp and infra-red mode. We set 24-26 camera traps in targeted locations at approximately the centre point of each 1.25 km^2 grid covering the study area. Not all grids within the study area were targeted as triangulated information gathered from villagers indicated absence of chimpanzees in certain areas and some cameras had to be relocated or removed because of slash and burn agricultural activities. We placed the remainder of the cameras in locations with evidence of chimpanzee activity to maximize the chances of obtaining images of chimpanzees (Fig. 5.1).

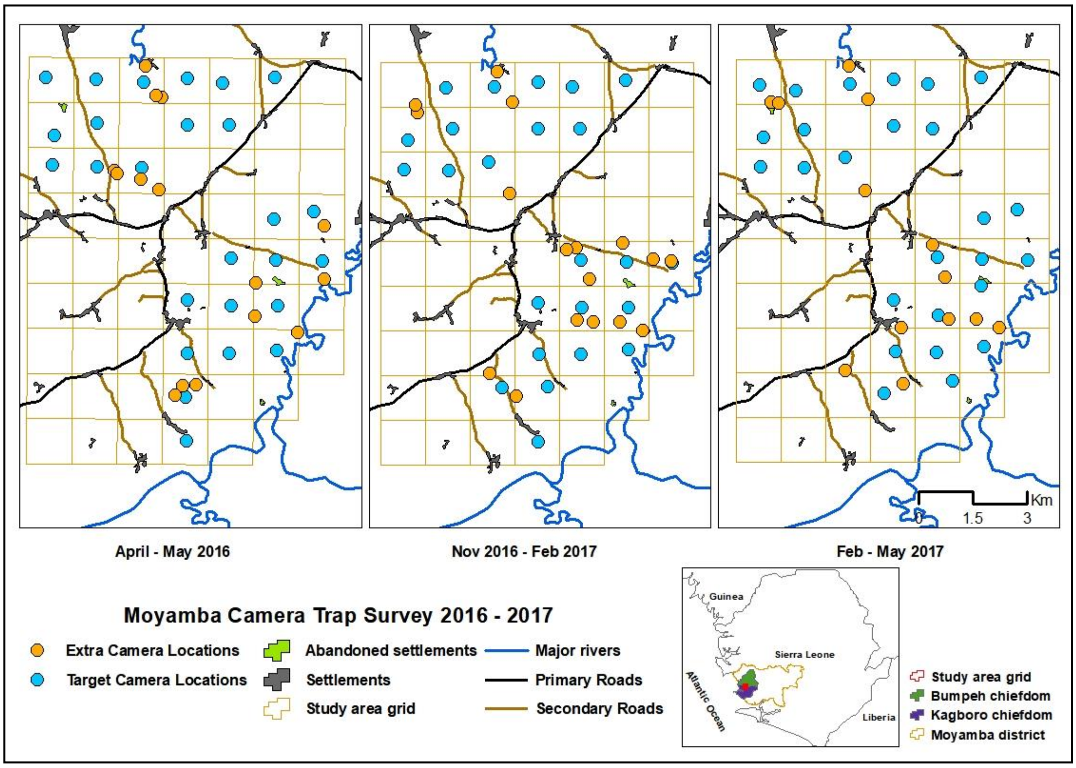


Figure 5.1. Camera trap distribution in the Lawana study area showing target and extra locations for each study period. Inset shows the location of the study area in Sierra Leone.

We also recorded chimpanzee evidences (nests, feeding remains, dung, trails and vocalisations) during recce walks to reach camera trap locations and these data were imported into ARC-GIS as an additional layer for evidence of chimpanzee presence across the study area.

5.3.3. Data analysis

Camera images were screened for species identification and analysed using the ZSL-CTAT open-access software developed at Zoological Society of London (ZSL) specifically to process images from camera trap arrays (Amin et al. 2017). The software was set to score a new species independent 'event' when a sequence of images of a target species appeared more than 60 minutes after the previous images for that species. Three independent recorders, expert in chimpanzees whether in captive or wild settings, identified the chimpanzee images based on facial and body features as well as individual characteristics such as injuries, and estimated their number, gender and approximate age. Recorders reiterated the process of identification until they reached 100% agreement on the final identifications, with any uncertainties left as 'unidentified'. Age-class categories followed those employed by Sugiyama (1999): 1) Adults (fully matured: >11 years old); 2) Adolescents (immature: 8-11 years old); 3) Juveniles (4-7 years old) and 4) Infants (dependent offspring: 1-3 years old). We calculated the chimpanzees' minimum home range in the study area based on chimpanzee camera trap captures (Kühl et al. 2008; Nakamura et al. 2013) and chimpanzee evidences (nests, dungs, feeding remains, trails and vocalisations) observed during the study period. The chimpanzee evidences were attributed to one of the chimpanzee groups based on the proximity to a camera trapping site. We used two different methods a) the convex-hull feature in ArcGIS 10.3 (ESRI, Redlands, USA) to determine the minimum convex polygon (MCP) and b) the kernel density estimator (KDE) in Geospatial Modelling Environment (Version 0.7.4.0) (Beyer 2015) and ArcGIS 10.3. Both methods construct polygons defining the occupied range. The difference between both techniques is how they join the nearby points. MCP is the smallest area polygon to encompass all observed locations, but it is biased by outer locations and does not define ranging structure as does KDE (Boyle et al. 2009). KDE is a non-parametric method that estimates the distribution probability of a set of points and models the home range using the observed locations (Chirima & Owen-Smith 2017). KDE requires defining an optimal bandwidth to determine the density distribution for the species being studied and depending of the species ranging behaviour, this technique might overestimate the ranges (Chirima & Owen-Smith 2017). Recent variations for the MCP method (characterised-hull base and local neighbour convex hull techniques) produce more accurate ranges than the simple MCV and the KDE for large spatial scale studies with large data sets (Chirima & Owen-Smith 2017; Downs & Horner 2009). But at fine spatial scales, it has been noted that MCP and KDE can produce similar results (Newton-Fisher 2003) and considering the small size of our study site and with limited dataset based on camera trapping images and recce observations, we used the simplest methods to estimate the minimum home range and compare their results. We used a Gaussian (bivariate normal) fixed kernel type with the smoothed cross validation (SCV) bandwidth (Kie et al. 2010). The bandwidths are calculated using the default settings for these estimators in the 'ks' library in R (R Core Team 2017). We used 95% isopleths as best representing the extent of the area occupied and 75% isopleths to demarcate core regions (Chirima & Owen-Smith 2017).

We used the time of the day from the camera trap events and the number of events in each location for chimpanzees and humans to extract their temporal and spatial activity patterns. To analyse correlation between patterns, we selected only the active hours for both species i.e. between 5 am until 19 pm. We used a Pearson Product Moment Correlation and Spearman Rank Correlation Coefficient tests depending whether the data was or not normally distributed. The analysis was performed with the software IBM SPSS Statistics v23.0 (SPSS, Chicago, USA).

5.4. Results

5.4.1. Camera trap survey effort

Capture trapping effort totalled 210 days and 7,785 trap nights between April 2016 and May 2017. We covered approximately 47 km^2 (30 grids) of the study area and collected 75,178 images of which 1,725 were of chimpanzees totalling 125 independent events and 12,930 images of humans in 223 independent events (Table 5.1).

Table 5.1. Summary of the camera trap findings in each study period.

	Period			TOTAL
	16/04/2016 - 01/06/2016	25/11/2016 - 02/2017	02/2017 - 10/05/2017	
Cameras total	41	41	39*	
Target cameras	26	24	26	
Non-target cameras	15	17	13	
Grids covered	26	26	27	
Total days deployed	1,664	3,220	3,150	8,034
Total days operational	1,625	3,148	3,030	7,803
Total images	14,583	24,119	36,476	75,178
Total wildlife images	3,836	4,858	4,719	13,413
Total human images	8,766	829	3,335	12,930
Total human events	126	21	76	223
Total chimpanzee images	348	486	891	1,725
Total chimpanzee events	34	32	59	125
Target cameras with chimpanzees	5	6	7	
Total images with chimpanzees from target cameras	75	102	237	414
Non-target cameras with chimpanzees	7	8	7	
Total images with chimpanzees from non-target cameras	273	384	654	1,311

*one camera trap failed

5.4.2. Minimum number of individuals per community

We determined the presence of two different groups, one in the north and one in the south of the study area. We assumed the presence of two different groups because no individual recorded in the North was ever recorded in the South and vice-versa. Of the total 125 chimpanzee IE recorded, 77 IE (61.6%) were captured in the northern site and 48 IE (38.4%) in the southern site (Fig. 5.2). In total, we identified 38 different individuals: the northern group formed by a minimum of 24 individuals and the southern group by a minimum of 14 individuals (Table 5.2). Images of the chimpanzees identified are shown in annex 9.2.

Table 5.2. Chimpanzee demographics in the study area for both chimpanzee communities.

Age-gender	Northern community Number of individuals (%)	Southern community Number of individuals (%)	Total number of individuals (%)
Adult male	6 (25)	2 (14)	8 (21)
Adult female	5 (21)	3 (21)	8 (21)
Adolescent male	1 (4)	1 (7)	2 (5)
Adolescent female	2 (8)	2 (14)	4 (11)
Juvenile male	4 (17)	1 (7)	5 (13)
Juvenile female	2 (8)	1 (7)	3 (8)
Juvenile gender unknown	-	1 (7)	1 (3)
Infant male	1 (4)	2 (14)	3 (8)
Infant female	1 (4)	1 (7)	2 (5)
Infant gender Unknown	2 (8)	-	2 (5)
Total	**24**	**14**	**38**

The maximum number of different individuals recorded in one event in the northern site was 17 and in the southern site was 11 (Table 5.3 and 5.4).

Table 5.3. Number of camera locations with the maximum number of events and the maximum number of different chimpanzees captured in the northern chimpanzee community.

Northern community											
Number of camera locations	**Maximum number of events**	**Maximum number of different chimpanzees recorded**									
		1	**2**	**3**	**4**	**6**	**7**	**8**	**9**	**16**	**17**
9	1	6	2			1					
3	4			1			1	1			
1	5				1						
1	7		1								
1	8						1				
2	9								1		1
1	18									1	

Table 5.4. Number of camera locations with the maximum number of events and the maximum number of different chimpanzees captured in the southern chimpanzee community.

Southern community										
Number of camera locations	**Maximum number of events**	**Maximum number of different chimpanzees recorded**								
		1	**2**	**3**	**4**	**5**	**7**	**8**	**10**	**11**
12	1	4	1	1	2	1		2	1	
3	2	1			1				1	
3	3			1			1	1		
1	4				1					
2	5		1							1
1	7				1					

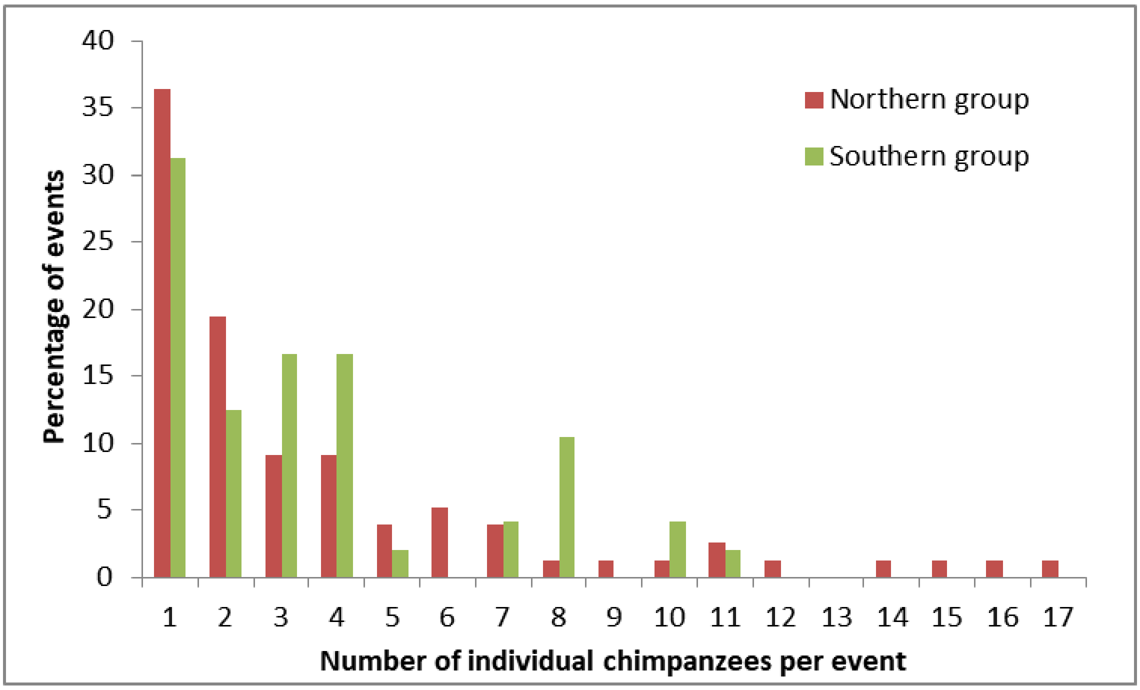


Figure 5.2. Percentage of events according to the number of chimpanzees captured per event. Number of IE in the northern site=77 and in the southern site=48.

On average, each identified chimpanzee was captured on 8 different days (range: 2-15 days). Even if 'unidentified chimpanzees' could not be individually identified, we could determine their age-class and gender. Therefore, when examined by gender and age-class, adult females were more often photo-captured (mean: 9.6 days; range: 4-15 days) than adult males (mean: 8.5 days; range: 6-11 days) (Fig. 5.3).

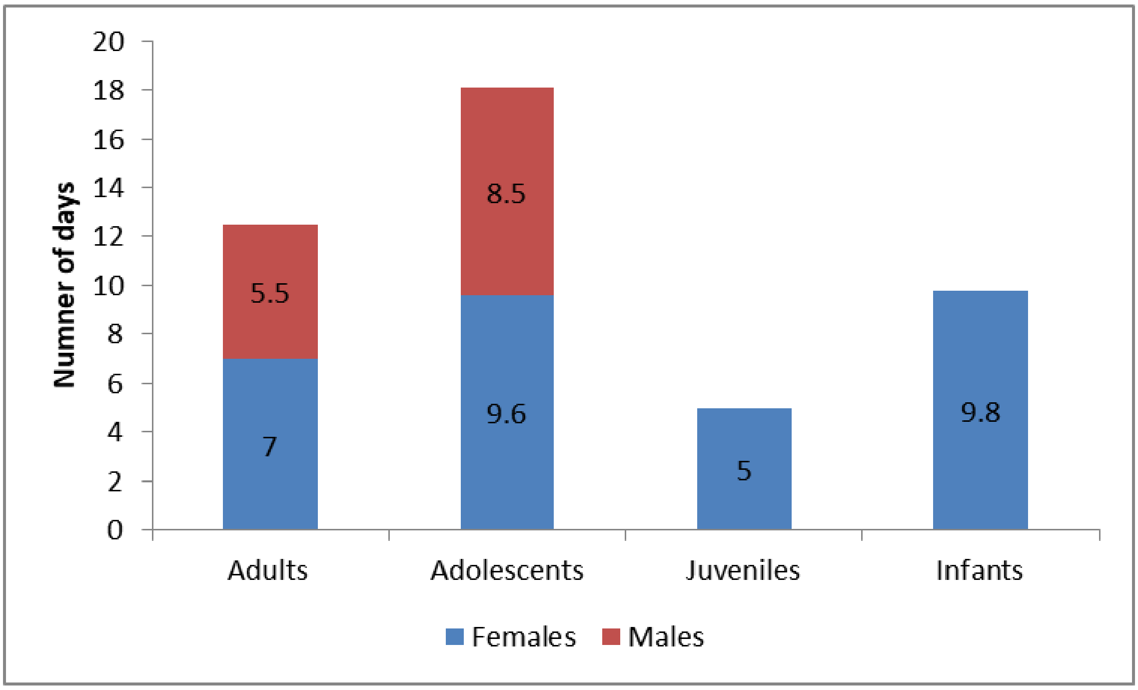


Figure 5.3. Average number of days individual chimpanzees grouped according to their age-class and gender were captured with the camera traps. The gender for some infants and juveniles could not be determined and we grouped them according to their age-class only.

It took 8 days following the installation of the first cameras until we captured the first chimpanzee and in 39 days we had captured 76% of the total identified chimpanzees (29/38). All adults except one female were captured within these initial 39 days. There were six months during the rainy season (June to November) in which cameras were not deployed. All identified chimpanzees were confirmed as captured on camera traps at 93 days following the beginning of the second period in November 2016. Adding the total days, but not including the six-month period with no cameras, the 38 chimpanzees were identified in 138 days (Fig. 5.4). Adult and adolescent males were captured in less time compared to adolescent and adult females (Fig. 5.5).

The northern community harboured three times more adult males and twice the number of juveniles when compared to the southern community; however, the age-class structure did not differ significantly between groups $t=1.814$ ($p=0.1$) (Fig. 5.6).

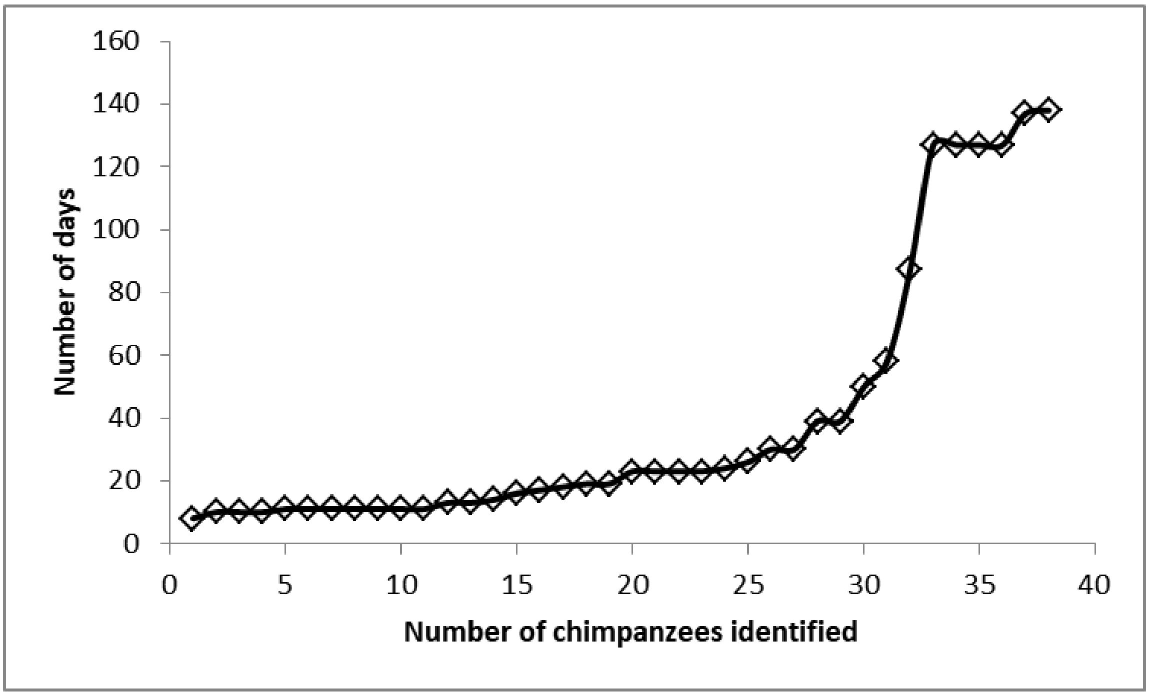


Figure 5.4. Number of days it took to identify each chimpanzee (N=38 individuals). No more chimpanzees were identified after 138 days (Total capture trapping effort = 210 days).

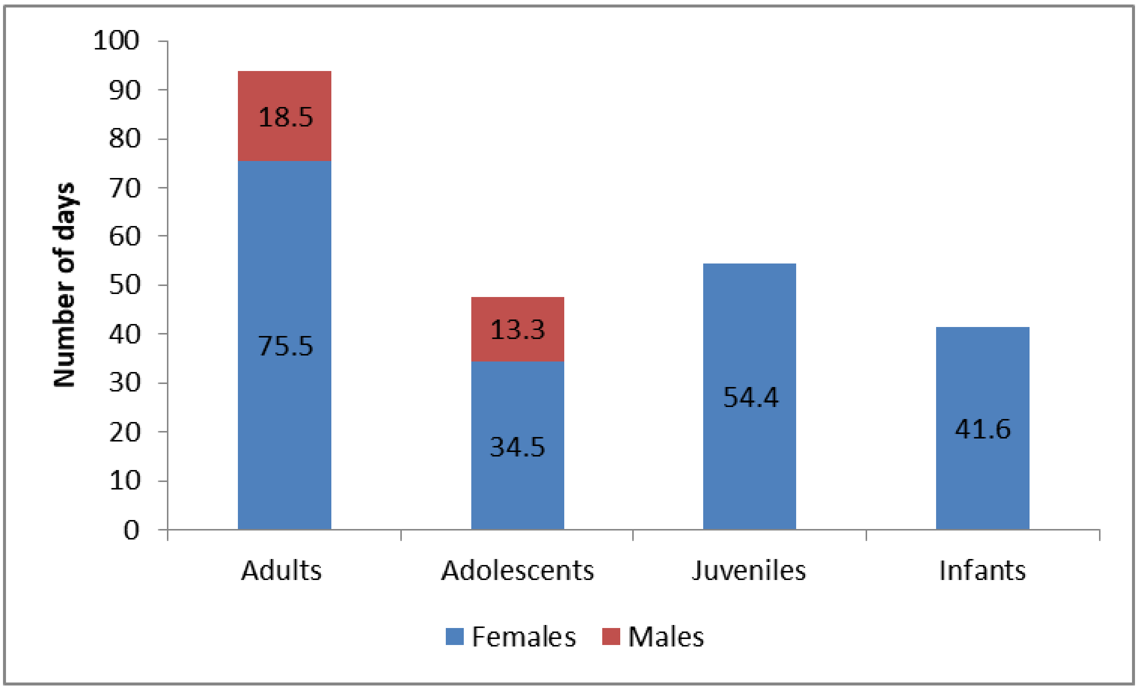


Figure 5.5. Average number of days required to identify individual chimpanzees grouped according to their age-class and gender. The gender for some infants and juveniles could not be determined and we grouped them according to their age-class only.

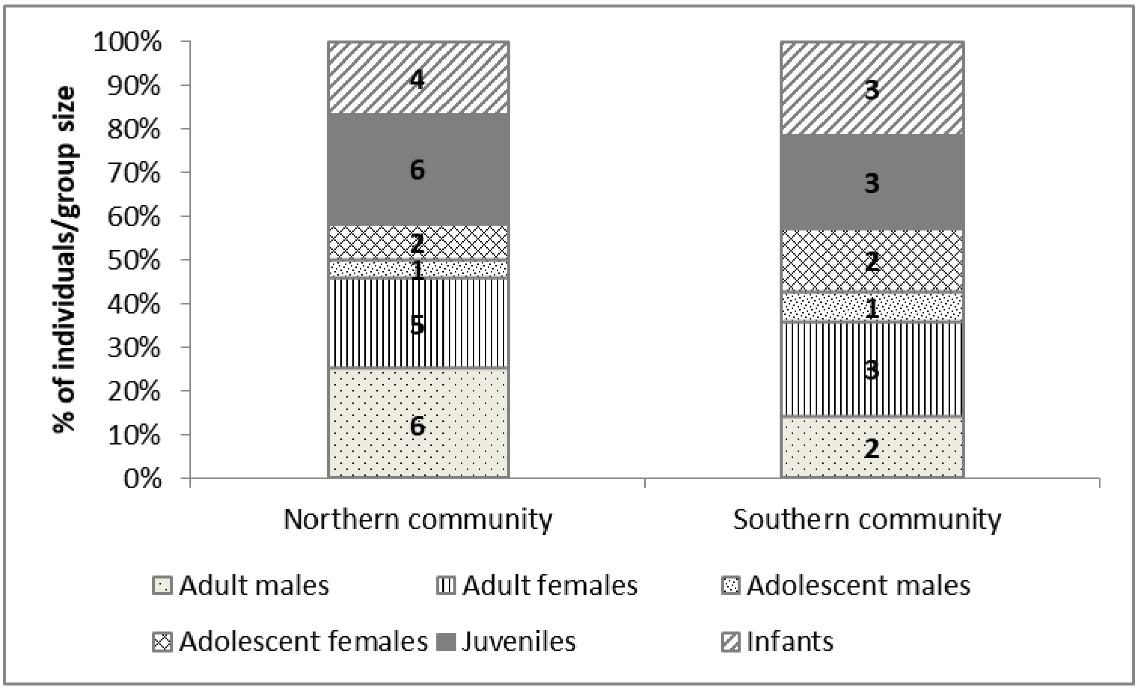


Figure 5.6. Percentage of chimpanzees for each community relative to their group size (northern community N=24; southern community N=14). The numbers inside the columns show the number of individuals for each category.

Nearly all adult females (87.5 %; 7/8) in both communities were carrying an infant and all were associated with at least one weaned juvenile. While no sub-adults showed signs of injury, three adults had amputated limbs: one male in the north was missing his lower right limb below the knee, one female in the south was missing her left hand and a male his right arm above the elbow. Almost 8% of the chimpanzees in the study area therefore showed injuries compatible with wire-snare trapping (Fig. 5.7).

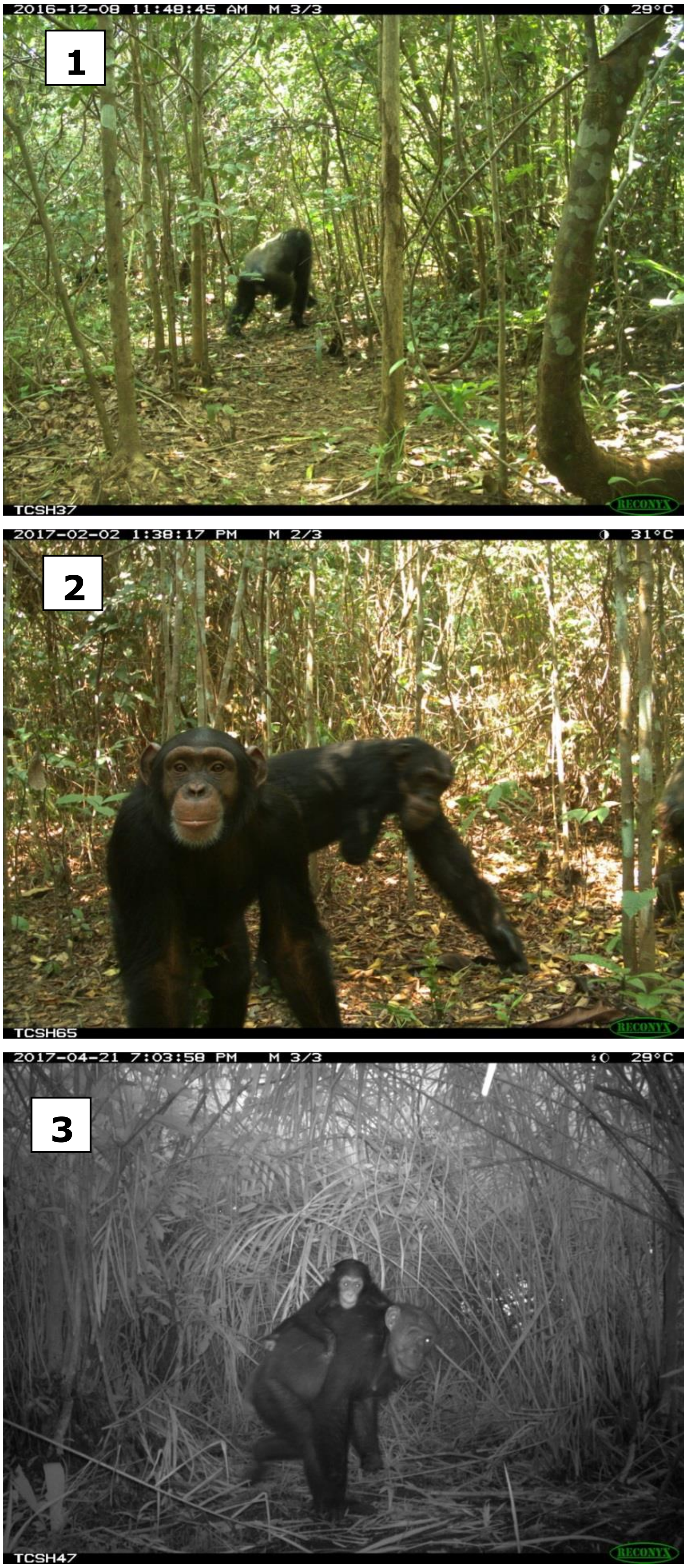


Figure 5.7. Injuries compatible with wire-snare trapping: 1. Adult male, Black, with amputated right leg. 2. Otto, adult male with amputated right arm. 3. Granny, adult female with no left hand.

5.4.3. Minimum home range (MHR)

The average MHR for the northern chimpanzee community was 9 km^2 (SD: 4.1, range: 3.5-14.3) and for the southern community was 14.6 km^2 (SD: 6.6, range: 5.2-22.5). The northern chimpanzee community exhibited a smaller range compared to the southern community (Table 5.5). When compared between methods, KDE produced a larger MHR than the MCP, being markedly larger for the southern community (Table 5.5 and Figure 5.8).

Table 5.5. Minimum home ranges for both chimpanzee communities based on the results obtained with the minimum convex polygons (MCV) and kernel density estimates (KDE) for each quantile. We used 95% isopleths as best representing the extent of the area occupied and 75% isopleths to demarcate core regions. CT: only trapping locations were included. CT-Observations: includes trapping locations and observations.

Group	**CT**	**CT - observations**				
	MCP (km^2)	**MCP (km^2)**	**KDE (km^2)**			
			95%	90%	75%	50%
Northern group	7.4	15	14.3	11.2	6.9	3.5
Southern group	10.6	16	22.5	18.8	11.9	5.2

Based on trapping captures and using the MCP method, the minimum range for adult females was smaller compared to the adult males for both communities (Fig. 5.9).

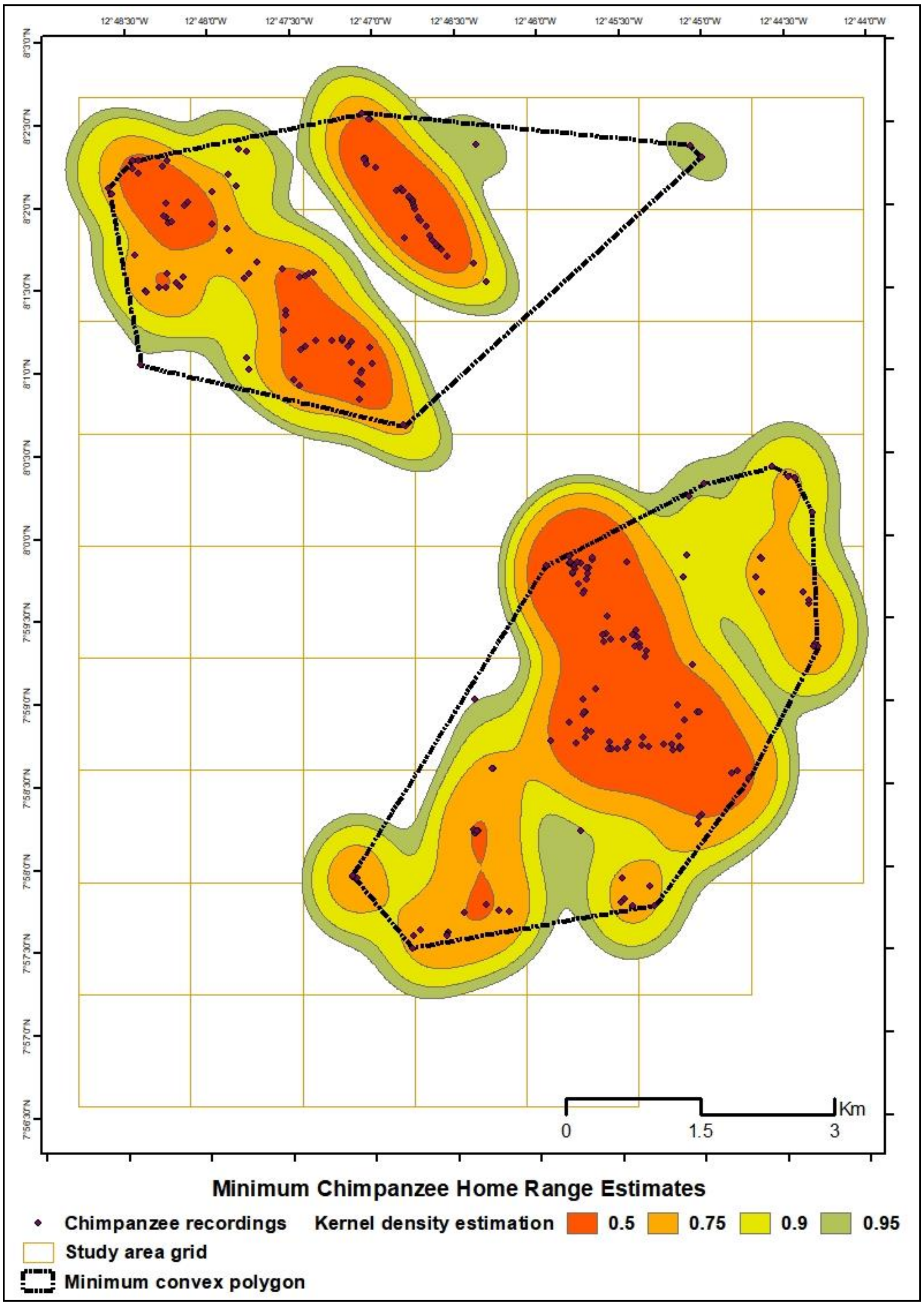


Figure 5.8. MCP and KDE home range estimates for each chimpanzee community pooling camera trap captures and observational data for the whole study period.

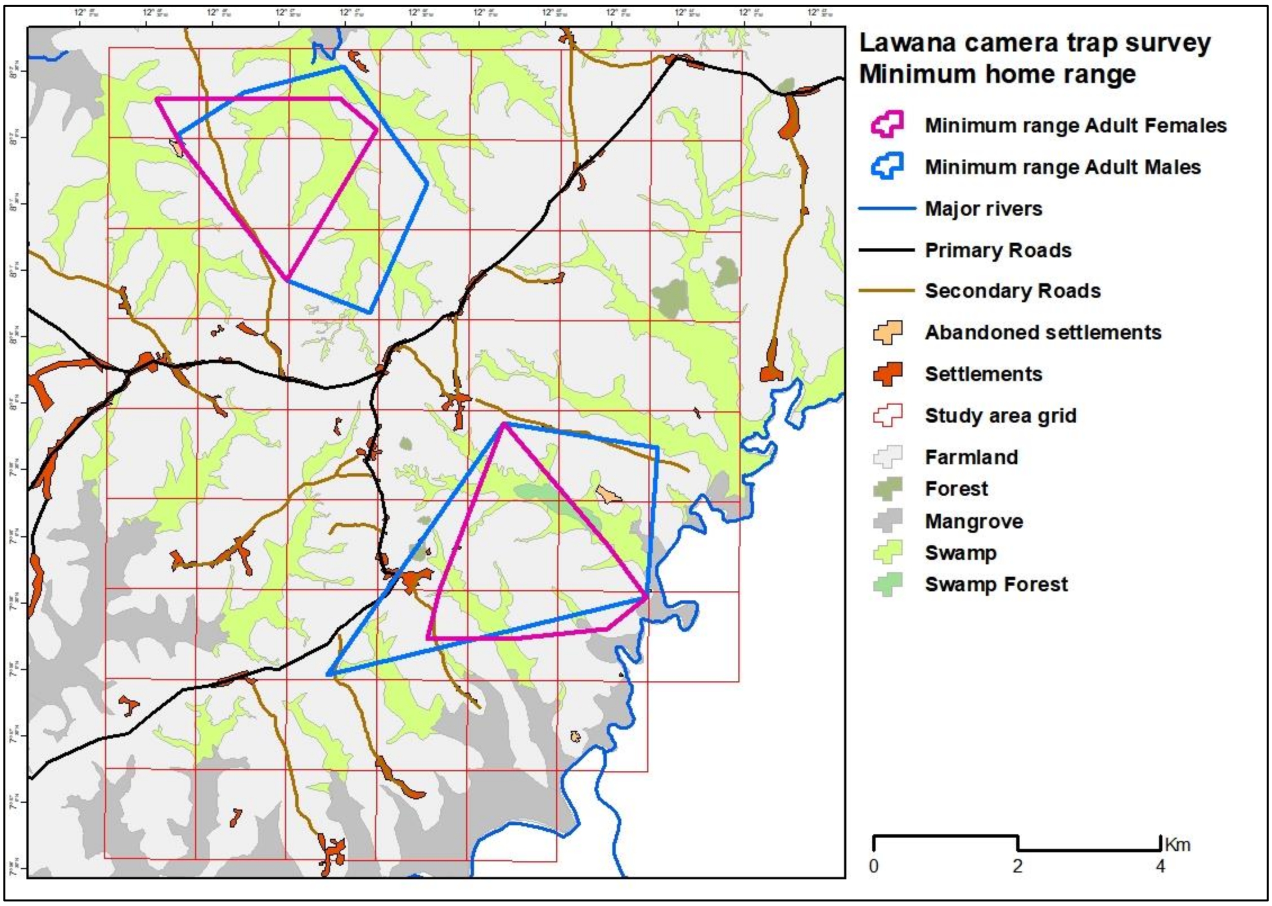


Figure 5.9. Adult chimpanzees' minimum home range according to their gender based on camera trap captures and using the MCP method.
Northern group: Adult females = 4 km^2 and adult males = 7 km^2; Southern group: adult females = 5 km^2 and adult males = 9 km^2.

The density estimate for the northern group was 1.6 individuals/km^2 and for the southern group it was 0.9 individuals/km^2. If we consider the total study area of 91 km^2, the chimpanzee density was of 0.4 individuals/km^2.

5.4.4. Spatial and temporal chimpanzee party size

The average party size relative to all trapping locations was similar for both groups, i.e. northern group=3.8 individuals/event (range 1-17) and southern group=3.6 individuals/event (range 1-11).

When analysed the average party size by hour, the northern group showed more activity between 7-9 am and 5-6 pm with an average party size slightly increasing towards midday (Fig. 5.10). The number of events for the southern community varied along the day with no activity between 11am and 12pm but with larger average party size the previous hours, i.e. at 10am and between 2pm and 3pm (Fig. 5.11).

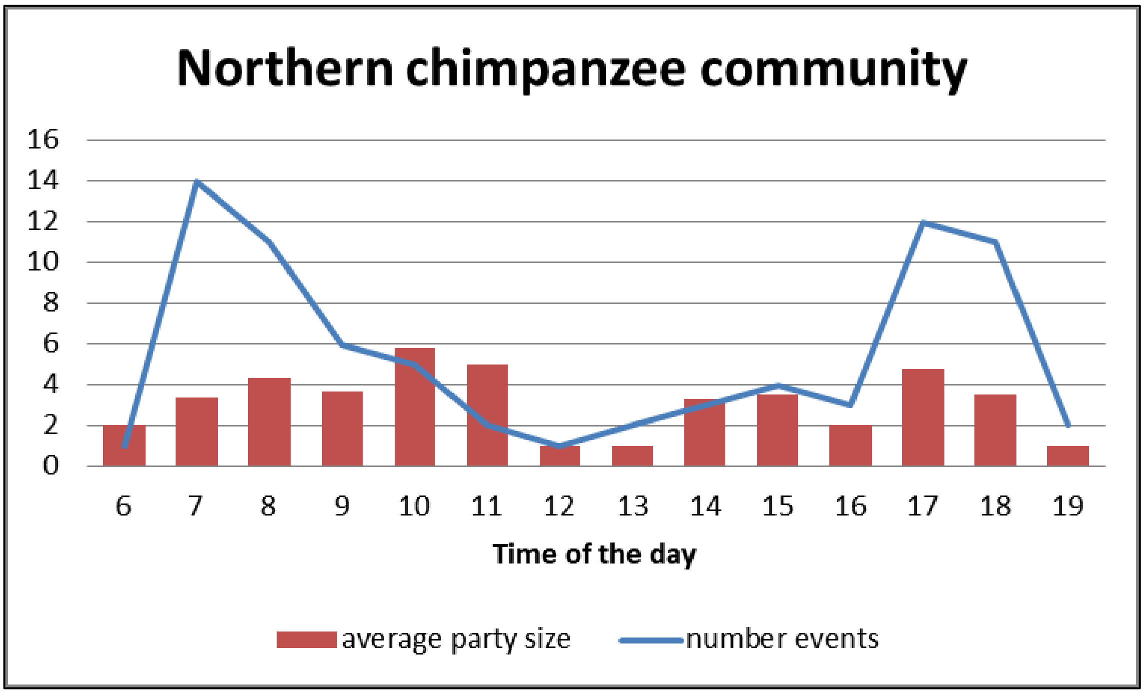


Figure 5.10. Comparison of the average party size and number of events at each hour of the day for the Northern chimpanzee group.

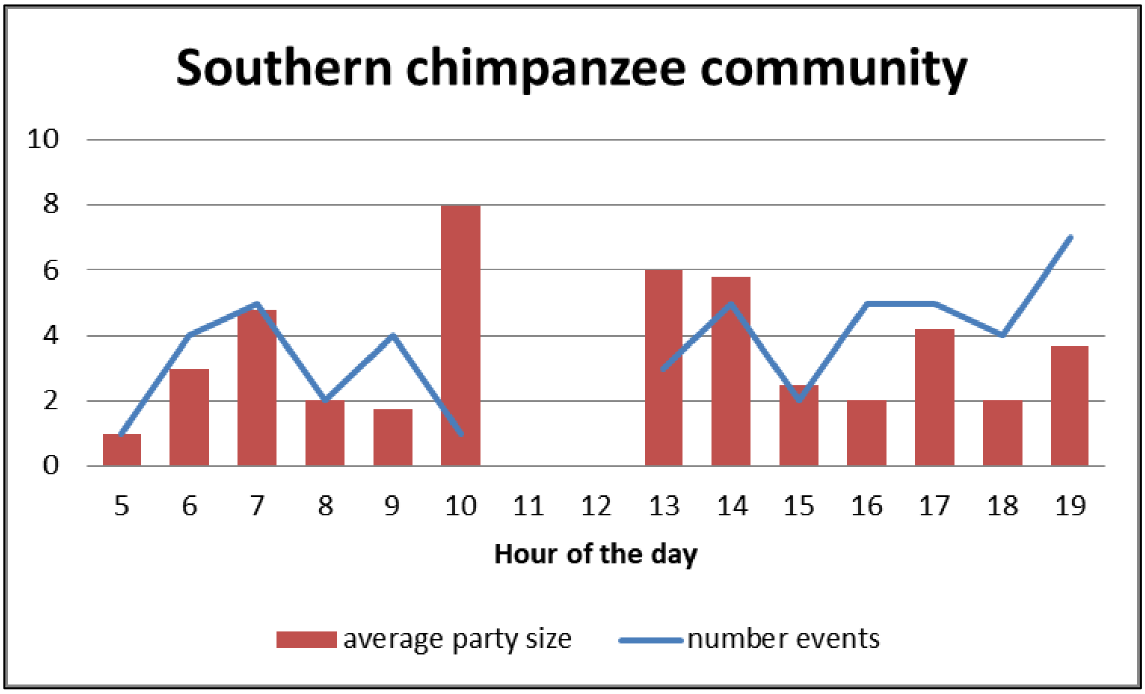


Figure 5.11. Comparison of the average party size and number of events at each hour of the day for the Southern chimpanzee group.

There was no significant correlation between average party size accounting for group size by hour between both groups; nevertheless, the southern group showed a more cohesive party size towards midday compared to the northern group (Fig. 5.12).

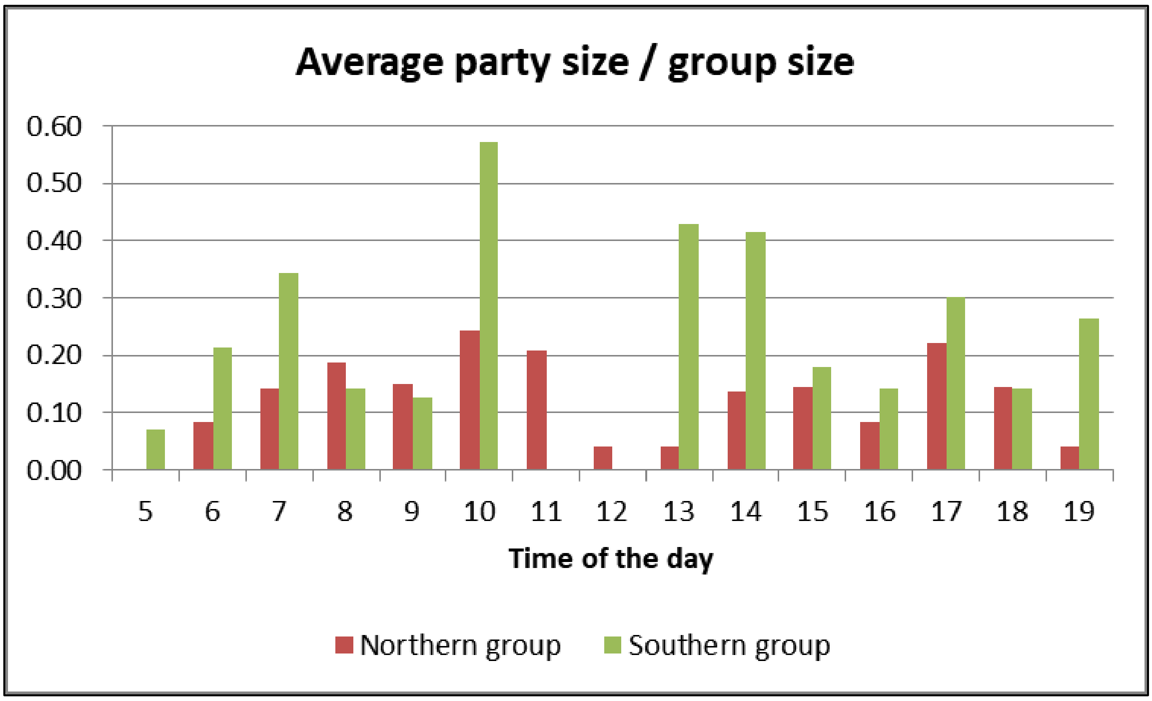


Figure 5.12. Average party size divided by group size as recorded at the different times of the day for each group (Northern group=24 individuals, Southern group=14 individuals).

5.4.5. Chimpanzee and human spatio-temporal activity patterns

5.4.5.1. Chimpanzee-human spatial activity pattern

Chimpanzees and humans were captured in 40 camera locations and humans in 42 camera locations across all three periods. Both species were photo-captured from the same location at 18 camera trapping sites. When we analysed the spatial correspondence between human and chimpanzee number of events and trapping rate per all trapping locations it showed a positive association (Spearman Rank Correlation: r_s= 0.188, $p<0.05$ and r_s= 0.198, $p<0.05$ respectively), suggesting that human presence seem not to interfere with chimpanzee presence at a spatial level.

But when we analysed the spatial correlation for the number of events and trapping rates for both species in the 18 trapping locations in which both were captured, we found no significant correlation (Spearman Rank Correlation r_s=0.224 and r_s=0.343 respectively).

5.4.5.2. Chimpanzee-human temporal activity pattern

The chimpanzee temporal activity pattern analysis revealed a diurnal pattern of behaviour; however, chimpanzees were more active during early and later hours of the day (5am-9am; 5pm-7pm). Human activity overlapped partially with the chimpanzee activity pattern but was more frequent in the mid hours of the day (9am-5pm) (Fig. 5.13). However, when we analysed the temporal correspondence between the number of events for human and chimpanzee activity patterns by the active hours for all trapping locations there was no correlation between the two (Pearson Correlation: R = -0.130).

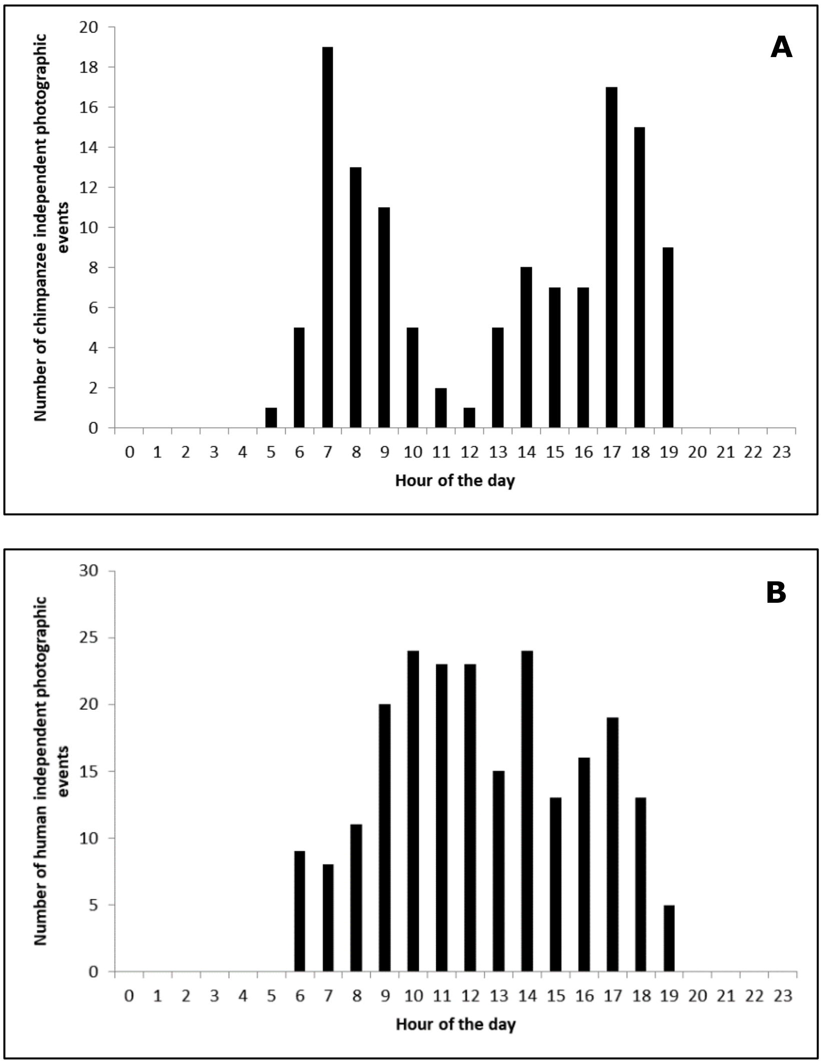


Figure 5.13. Number of events per hour of the day for chimpanzees (A) and humans (B).

There was also no correlation between the number of events by active hours between humans and chimpanzees independent events according to captures at each site of the study area (i.e. northern and southern sites). Pearson correlation: R=-0.244 for the northern site and R=-0.203 for the southern site (Fig. 5.14).

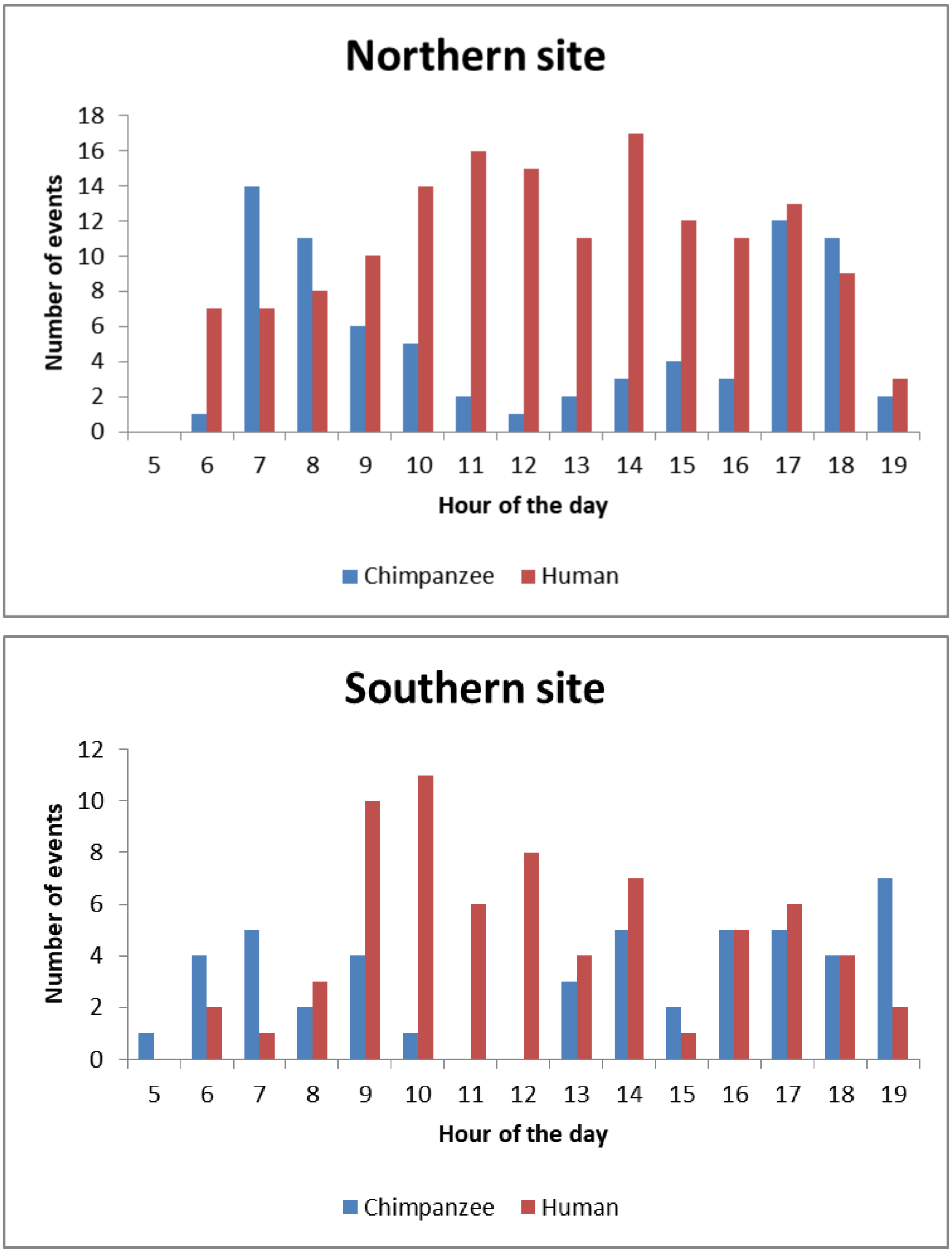


Figure 5.14. Number of events for chimpanzee and humans for all trapping locations according to whether they were captured in the northern or southern sites of the study area.

5.4.5.3. Temporal chimpanzee average party size in relation to human captures

The average chimpanzee party size during active hours does not seem to be influenced by the number of human captures when considering all trapping locations (Pearson correlation: northern site: R=0.361 and southern site: R=0.204) (Fig.5.15) nor when considering only the 18 cameras in which both species were captured (Pearson correlation: northern site: R=-0.009 and southern site: R=-0.141)(Fig.5.16); however, for this latter scenario, the negative correlation factor indicated certain degree of avoidance by chimpanzees when there was more human activity.

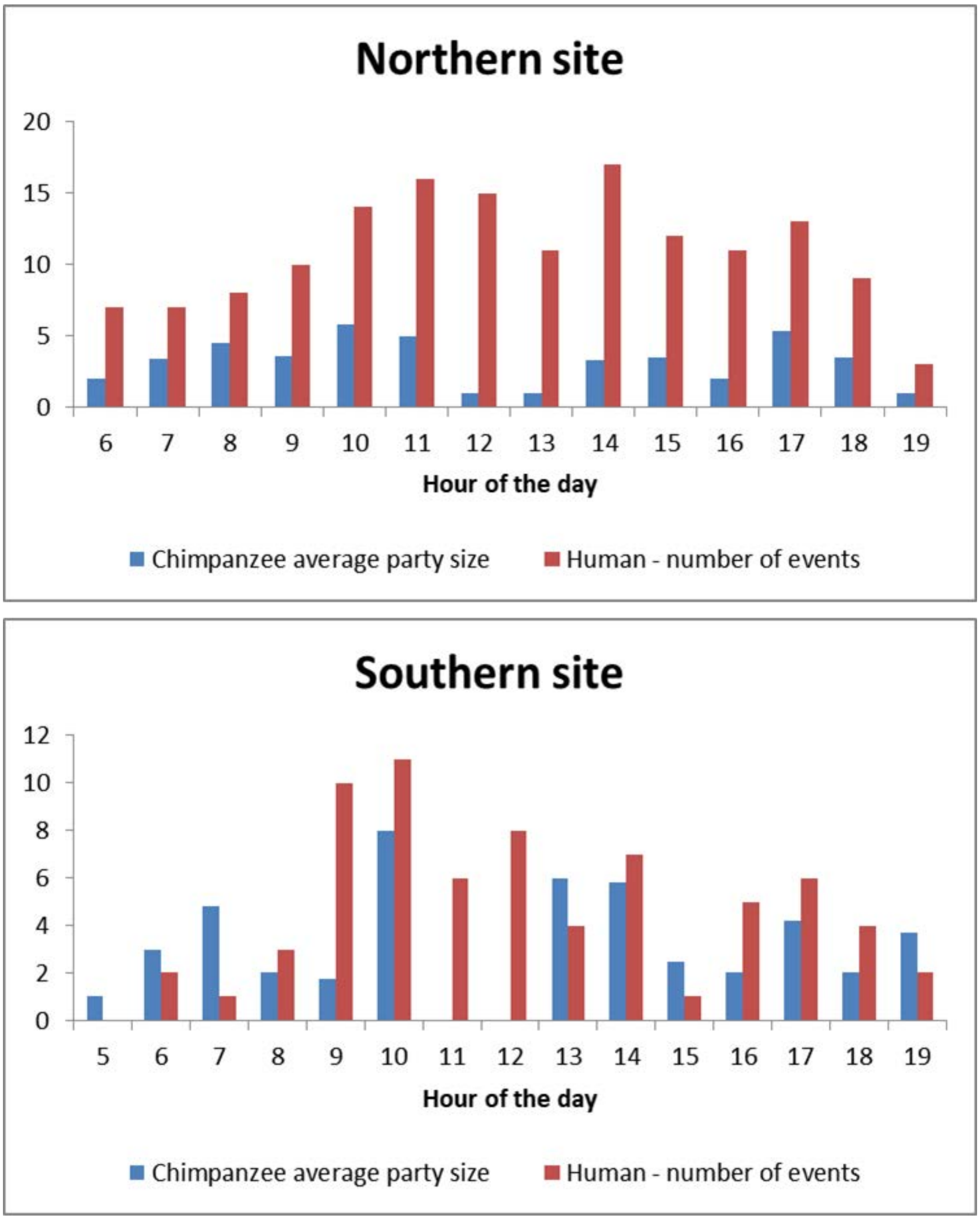


Figure 5.15. Chimpanzee average party size and number of human events by hour for all trapping locations according to northern or southern site captures.

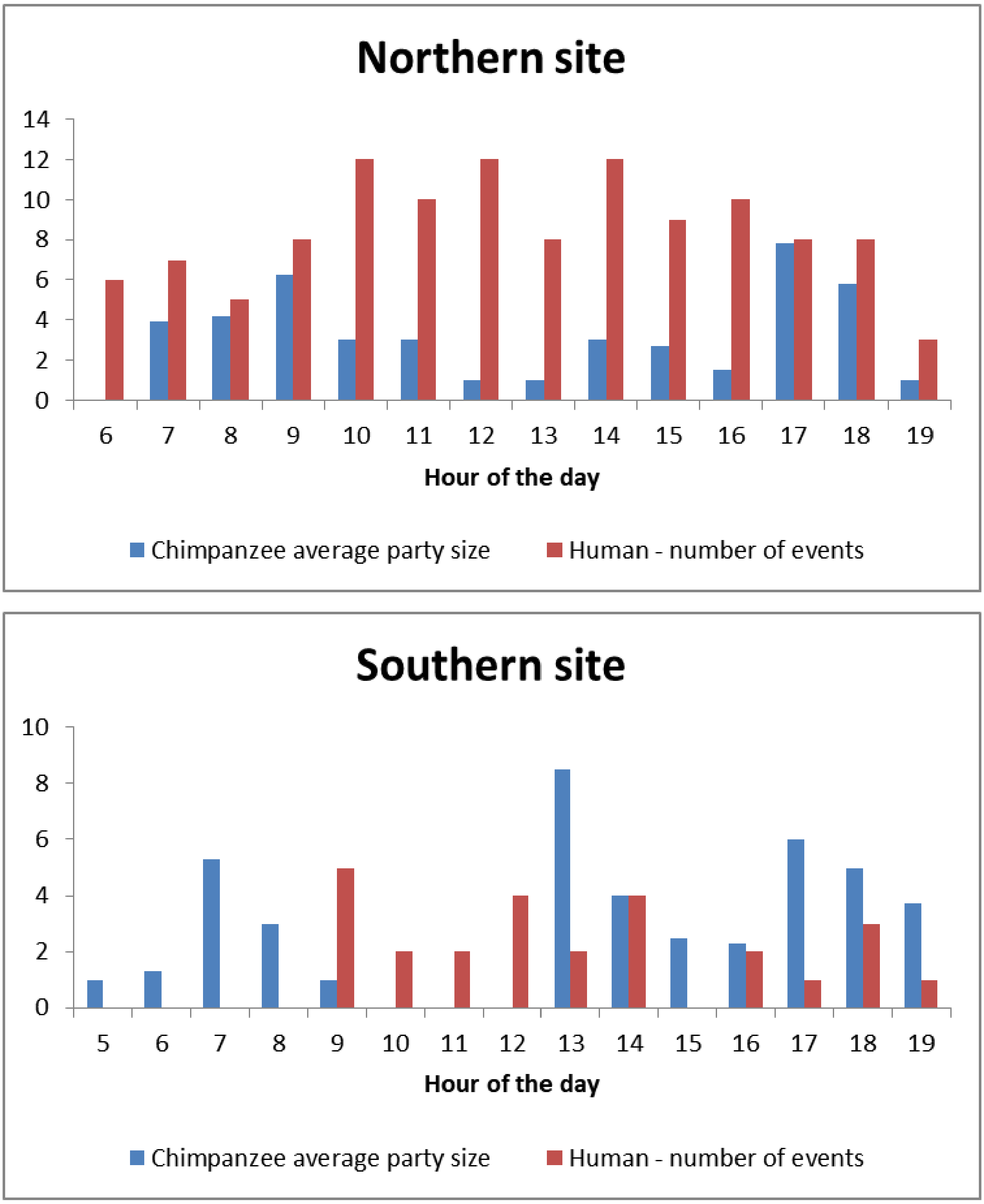


Figure 5.16. Chimpanzee average party size and number of human events by hour for the 18 trapping locations in which both species were captured and according to northern or southern site captures.

5.5. Discussion

5.5.1. Chimpanzee group sizes and structure

This study gives a preliminary insight into the demographics of unhabituated chimpanzees living in a non-protected and highly degraded landscape. Camera trapping allowed us to identify 38 individual chimpanzees divided in two distinct groups of 24 and 14 ranging across a study area dominated by farmland and swamps and in close proximity to human settlements. None of the chimpanzees in one group were captured in the other and vice-versa, and therefore we assumed the existence of two different chimpanzee groups. McCarthy et al. (2018) in the Taï National Park in Côte d'Ivoire compared the camera trap efficiency versus observational data in a group of habituated chimpanzees and concluded that camera data underestimated measures of party size but had similar community demographic composition. We cannot confirm if there were more individuals present in the study area that were not identified, because they are not habituated and therefore we do not know their total number; however, we did not identify new chimpanzees after 138 days from the total 210 days study period suggesting that we had potentially identified all members of both groups. It took us longer compared to the only 49 days it took in a camera trap study in Taï National Park with a group size of 37 chimpanzees (McCarthy et al. 2018). In our study, it took longer to capture all adult and adolescent females than males, but on average females were captured more often, which was not the case in Taï National Park where males were captured more often (Després-Einspenner et al. 2017). Perhaps males in our study were more wary of the cameras after the first encounter and tended to avoid them after; instead females became more accustomed after first encountering them. Future chimpanzee demographic camera trap studies should consider a long enough minimum study period to capture all individuals in their study area.

Our group sizes are comparable to the ones found in Bulindi in Uganda and Bossou in Guinea, both characterised by a human–dominated fragmented agroforestry matrix (Table 5.6). Group size differed between both communities but not their age-class structure. However, the gender ratio for the northern group was equal for adult and adolescents males and females, with proportionally more adult males than adult females. This is unusual in chimpanzee communities where adult females typically outnumber adult males (Nishida et al. 2003; Matsuzawa et al. 2011; Boesch & Boesch-Achermann 2000). There is a fine line between adolescent and adult males and these may be difficult to discern with only images captured in a short period of time. Therefore, we might have classified some adolescent males as adults. Yet, the proportion male-female does not follow reported patterns. The southern group had more adult females than males with a ratio of 1:1.5 which was half what other chimpanzee communities have (Boesch & Boesch-Achermann 2000; Nishida et al. 2003). Reasons for these differences could be due to higher female mortality because of disease and/or hunting, due to higher female dispersal, or simply a novel group structure pattern adapted to this type of degraded habitat, where higher number of males protect the females and therefore ensure breeding continuity. Adult females showed good reproductive rates, as all of them, except one from the northern group, were bearing an infant and all were associated with one juvenile, which we assumed to be their weaned offspring. The difference in group size between both communities could be attributed to disease (Leendertz et al. 2004; Hill et al. 2001), to less human tolerance or higher hunting pressure in the southern area or to less food resource availability. During the study we encountered hunters carrying dead monkeys in two occasions in the southern site (Fig. 5.17) and we had an unconfirmed report of the recent killing of two chimpanzees during the interviews carried out in one of the villages located in the southern group ranging area 2 years previously to the camera trapping (Garriga, pers. obs.).

Figure 5.17. Local hunter with recently caught monkeys in the study area. ©Rosa Garriga

Moreover, in both groups, we captured chimpanzees with amputated limbs compatible with wire-snare trapping (Waller & Reynolds 2001). Three adult chimpanzees, a female and two males, photo-captured had amputated limbs. Farmers protect their crops from small mammals using wire-snares (Garriga et al. 2017) however hunting with guns also occurs (Fig. 5.18).

Figure 5.18. Hunter with a gun captured with camera trap. ©TCS

Usually adolescent females are the ones emigrating to other groups to avoid inbreeding (Pusey 1980) but during our study period, we did not capture a northern chimpanzee in the southern group or vice-versa; however, a longer study period would be necessary to observe emigrations between groups. Interestingly, it took more days to capture adult and adolescent females than other age and gender class of individuals (Fig. 5.5). This could be explained by trap-shyness (individual heterogeneity behaviour to camera traps) (McCarthy et al. 2018), peripheral behaviour (spending time alone in the periphery of their territory) or shifting behaviour (adolescent females move from one community to another) (Williams et al. 2002).

5.5.2. Chimpanzee party size and spatio-temporal activity pattern

Both communities showed similar average party size with a positive correlation in the number of individuals per event and number of events despite the difference in group number. Camera trapping tends to underestimate party size compared to observational data (McCarthy et al. 2018), and this circumstance could also be occurring in our study. Camera detection angle is limited and chimpanzees could easily avoid passing in front of the camera. When comparing the spatial and temporal activity patterns between capture rates of chimpanzees and humans, we expected to find a negative correlation that is chimpanzees avoiding areas frequently used by humans and being more nocturnal. However, our findings show a positive spatial correlation with humans (almost 50% of the locations are frequented by both species). There was a spatial overlap between humans and chimpanzees indicating that human presence does not interfere with chimpanzee presence. It is speculated that smaller group size leads to party cohesion (Lehmann & Boesch 2004). Moreover, chimpanzees living in anthropogenic habitats usually acquire behavioural adaptations to overcome the risks associated with human presence. In Bossou, Guinea, chimpanzee party size and cohesiveness increased when feeding on crops compared with wild fruits, the difference attributed to higher degree of perceived risk (Hockings et al. 2012).

In our study, chimpanzee daily activity patterns also showed a certain degree of adaptation, decreasing their activity at hours when there was more risk to encounter humans, with some differences between groups. The southern group showed larger average party sizes by hour of the day as compared to the northern group being more marked towards the central hours of the day. When examined the temporal activity pattern for the same trapping locations in which humans and chimpanzees were captured, the southern group showed no activity between 10 am and 12 am when human activity was prevalent. Therefore, the smaller group size in the southern group could explain why they travel more cohesively at times when there was a higher risk of encountering people. Instead, the northern group was generally also less active at midday hours, but the average party sizes were smaller, when one would expect them to be larger due to the possible risk of encountering humans at this time.

5.5.3. Chimpanzee minimum home range

The two methods to calculate minimum home range differs for both communities. MCP and KDE (considering 95% isopleths as the area occupied by the chimpanzees) minimum home range estimates for the northern community are similar but vary for the southern group. KDE is regarded as more reliable to determine home ranges (Nilsen et al. 2008) but MCP has been traditionally used by researchers and therefore we compare our MCP results with other sites (Table 5.6).

There was great variability between community and range size between sites, most probably related to the habitat type and food availability. Similar community size can have small home ranges in forest type (Budongo, Uganda: 38-46 individuals and HR: 6.8 km^2, Newton-Fisher 2003) and large home ranges in savanna-woodland habitat (Fongoli, Senegal: 35 individuals and HR: 65 km^2, Pruetz & Betolami, 2009). Most of the study sites described in Table 5.6 are in forest habitats with variable anthropogenic impact around the forest edges. Our HR estimates are comparable to those from Bossou: 15 km^2 (Hockings et al. 2009), Taï-Middle: 12.1 km^2, and Taï-North / Côte d'Ivoire: 16.8 km^2 (Herbinger et al. 2001). Only Bossou and Bulindi have habitats comparable to our study site i.e. small forest patches in a fragmented and human impacted landscape. Bossou also has oil palms widespread across the landscape which is an important resource for chimpanzees (Matsuzawa et al. 2011).

Table 5.6. Comparison of home range areas, chimpanzee community sizes and density estimates at different project sites in Africa arranged in descending order of home range area. For comparison purposes, it is only included the sites where home ranges (HR) were calculated using the 100% MCP. The density was calculated with the largest community number and largest HR size.

Site name/country	HR area (km^2)	Community size	Density chimpanzees/km^2	Source
Mahale M/Tanzania	25.2 - 27.4	40 - 70	2.6	Nakamura 2013
Budongo/Uganda	6.8	38 - 46	6.8	Newton-Fisher 2003
Nyunwe-Cyamudongo /Rwanda	8.2	35 - 40	4.9	Moore et al. 2018
Taï Middle/Côte d'Ivoire	12.1	11	0.9	Herbinger et al. 2001
Bossou/Guinea	15	12 - 14	0.9	Hockings et al. 2009
Lawana–North/Sierra Leone	15	24	1.6	This study
Lawana–South/Sierra Leone	16	14	0.9	This study
Taï North/Côte d'Ivoire	16.8	35	2.1	Herbinger et al. 2001
Goualougo/Rep.Congo	19.2	54	2.8	Morgan et al. 2006
Bulindi/Uganda	20	18 - 21	1.1	McLennan & Ganzhorn 2017
Taï South/Côte d'Ivoire	26.5	63	2.4	Herbinger et al. 2001
Kibale-Ngogo/Uganda	28.7	148	5.2	Mitani 2006; Mitani et al. 2010
Kibale-Kamyawara/ Uganda	37.8	50	1.3	Wilson et al. 2007
Nyungwe-Mayebe /Rwanda	61.0	50 - 60	1.0	Moore et al. 2018
Fongoli/Senegal	>65	35	0.5	Pruetz & Bertolami 2009

5.5.4. Chimpanzee density

The density estimates based on our chimpanzee identifications and extrapolated to the whole study area, gives us a 0.4 individuals/km^2 which is equivalent to the results obtained from a drone nest survey carried out parallel to this study in the same study area (Humle et al. in prep.). Compared to chimpanzee densities in other West African countries (Table 5.7), our estimate was higher than other densities in forested areas and markedly higher to the density estimates in non-protected areas in Sierra Leone and Liberia. The entire Moyamba district where our site is located is covered by the same type of degraded habitat, entirely dominated by active and fallow farmlands widespread wild oil palms with relatively little forest cover and no protected areas (Brncic et al. 2010). Chimpanzee groups are present in other areas across this district (Garriga, unpublished data) indicating that our study site is not an isolated case and that this degraded landscape could harbour a significant chimpanzee population. Our result shows the importance of habitats other than forests for the survival of chimpanzees.

The relatively high chimpanzee density at our study site, a landscape nearly devoid of forest and harbouring limited sources of wild fruits, suggests that swamps might offset forest absence and the abundance of crops and oil palms constitute the main source of the chimpanzees' diet. Oil palms are capable of surviving the fires when fields are burnt for cultivation and are an important resource for the local people. They harvest the fruits for the production of palm and kernel oil and extract the sap of the trunk to obtain what they call 'palm wine', while using the fronds to fence off their fields and other constructions. The concomitant use of the oil palms by the chimpanzees for nesting and feeding was typically perceived negatively by farmers, who consider that these activities harm the trees (Garriga et al. 2017), although some studies conducted at Bossou, Guinea, suggest otherwise (Humle & Matsuzawa 2004; Soumah et al. 2014. Both sites in our study area shared the same type of landscape, human activity, shifting cultivation and cultivated crops. It would seem more logical that the largest northern chimpanzee group had a larger range to obtain more food resources. We based our HR calculation only on trapping rates and non-systematic observational recordings and therefore we might be underestimating their range. Yet, mangroves and the year-round inundated swamps might constitute a natural barrier for larger ranges. Savanna chimpanzees show adaptations to conditions of extreme heat and limited food resources (Pruetz & Bertolani 2009), so it is possible that these chimpanzees have also developed some specific skills to survive in this swamp habitat that we do not know of yet.

Table 5.7. A comparison of western chimpanzee densities (individuals/km^2) across West Africa in ascendent order.

Country	Study site	Density (ind/km^2)	Source
Guinea-Côte d'Ivoire	Nimba Mountains	0.14-0.65	Granier et al. 2014
Sierra Leone	Non-protected areas	0.03	Brncic et al. 2010
Liberia	Non-protected areas	0.05	Tweh et al. 2015
Côte d'Ivoire	Marahoue NP	0.05	N'Goran et al. 2007
Liberia	Grebo NF	0.10	Kouakou, unpubl.data in Tweh et al. 2015
Senegal	Niokolo Koba NP	0.13	Pruetz et al. 2002
Guinea-Bissau	Lagoas de Cufada Natural Park	0.22	Carvalho et al. 2013
Ghana	Bia-Goaso Forest Block	0.26	Danquah et al. 2012
Mali	Bafing FR	0.27	Pavy 1993
Sierra Leone	Gola Forest NP	0.27	Ganas 2009
Mali	Faragama	0.30	Granier & Martinez 2004
Sierra Leone	WAPNP	0.36	Brncic et al. 2010
Mali	Djakoli	0.39	Granier & Martinez 2004
Sierra Leone	**Lawana**	**0.40**	**This study**
Sierra Leone	Tingi	0.59	Brncic et al. 2010
Côte d'Ivoire	Tai NP – East	0.67	Després-Einspenner et al. 2017
Liberia	Sapo NP	0.86	N'Goran, unpubl.data in Tweh et al. 2015
Guinea	Haut Niger NP 2001-2002	0.87	Fleury-Brugiere & Brugiere 2010
Côte d'Ivoire	Tai NP	0.89	Kouakou et al. 2009
Sierra Leone	OKNP	0.97	Brncic et al. 2010
Sierra Leone	Loma Mountain NP	2.69	Brncic et al. 2010

Chimpanzees' progressive adaptation to this degraded environment together with certain level of human tolerance might be the influential factors to their survival. However, they are not free of risks as seen by the number of chimpanzees showing limb amputations. Moreover, the widespread presence of semi-domesticated oil palms and the access to cultivars across the landscape might compensate for the lack of more natural forest resources but this poses greater threats to chimpanzees' survival as they are competing for the same human resources.

We conclude that even though visual identification of the chimpanzees is time consuming and requires several expert reviewers, intensive camera trapping effort in a small study area is an effective tool in determining chimpanzee demographics, relative abundance and distribution. Further studies using alternative indirect methods like faecal genetic censusing would provide accurate estimates to corroborate our findings as well as determine whether there is genetic flow between communities (Arandjelovic & Vigilant 2018; McCarthy et al. 2015).

More research should focus on studying chimpanzee populations living in degraded landscapes as they might constitute an important part of the total chimpanzee population left in the wild that should not be neglected.

PART III

6 - General discussion

Chimpanzee populations across Africa are fast declining and western chimpanzees are listed as Critically Endangered by the IUCN with more than 70% occurring outside protected areas and in anthropogenic habitats (Humle et al. 2016). It is estimated that its population will decline more than 80% in just three generations (Kühl et al. 2017) and main reasons will be poaching, habitat loss and fragmentation due to human activities. The third largest western chimpanzee population is found in Sierra Leone; however, more than half occurs outside protected areas and often living in forest-agricultural mosaics in close proximity to humans (Brncic et al. 2010). The objective of this thesis was to investigate how wild chimpanzees survive in these anthropogenic habitats at a fine-spatial scale in Sierra Leone following an interdisciplinary approach combining social science and camera trapping technology, to obtain insights into the co-existence, tolerance and adaptation of chimpanzees to highly degraded landscapes.

Social science

The integration of social science research in our study enabled us to ask farmers directly about their challenges to subsistence agriculture and assess their perceptions of crop foraging by wildlife and chimpanzees. We explored farmers' attitudes and behaviours towards chimpanzees and the degree of conflict between both species. To do this we conducted semi-structured interviews with local farmers in four different agricultural areas in Sierra Leone. The habitat of all four areas was dominated by the presence of active and fallow farms, swamps and the ubiquitous semi-domesticated oil palms. There were differences between areas but in general terms our findings showed that farmers' main agricultural challenge was crop consumption by wildlife; however, chimpanzees were not among the top three most destructive animals, i.e. cane rats, red river hogs and monkeys. Mostly, farmers perceived chimpanzees as more destructive than dangerous. Being the most abundant tree, semi-domesticated oil palms are used extensively by chimpanzees for nesting and feeding and this was not well perceived by farmers who also rely on this resource. We had only a few accounts of chimpanzee's' aggression towards humans which were all dated years back. However, increased human pressure and land development could increase co-existence conflicts between both species as is the case in parts of Africa (McLennan & Hockings, 2016) and end up in retaliation actions against these chimpanzee communities undermining their survival. The inter-variability between study areas could be attributed to differences in the ecology of the landscapes, but also on factors influencing tolerance such as the type of crops grown and socio-economic and cultural context of the people living in the locality, indicating the need to carry out research at local level to prevent generalisations. Studies aimed at understanding the factors influencing tolerance towards chimpanzees are essential to implement informed conservation plans locally, as well as in areas outside and around protected sites with greater conservation potential. We found local knowledge to be a useful research tool which provided information that could not be gathered with conventional ecological methods.

Factors affecting chimpanzees' habitat use

We selected one on the four previous study areas to carry out a camera trapping survey. We used this technology as it is a non-invasive research tool that can be used efficiently to study unhabituated chimpanzee populations in a relatively short period of time. The aim was to explore ecological and anthropogenic drivers of chimpanzee occurrence across a highly degraded and human-impacted landscape. We used binomial iCAR models to understand the patterns of habitat use and how they are related to the distance to anthropogenic (roads, settlements, abandoned settlements) and habitat variables (swamps, farmland and mangroves). The results suggested that chimpanzees avoid roads and prefer to maintain proximity to swamps. This study also highlighted the fact that roads can certainly negatively impact chimpanzee distribution and abundance and corroborates the findings from other large-scale studies in Sierra Leone and in Gabon (Brncic et al. 2015; Vanthomme et al. 2013). Road development across Africa is increasing and this study highlights the need to include appropriate impact assessments and mitigation measures to protect chimpanzee populations living in non-protected habitats with road development plans or changes in land-uses (Humle 2015).

There is limited research done on chimpanzees living in agricultural-swamp matrixes and the importance of this type of habitat when forest habitat is scarce for their survival. Chimpanzees' adaptability to human driven environmental changes (Humle and Hockings 2009) reveals the need to invest time and resources in investigating chimpanzees living in unusual habitats at finer-spatial scales and to evaluate the importance of these habitats for the survival of the species. We found that local knowledge provides accurate information of the presence and location of chimpanzees groups living in the surroundings which is extremely helpful to define areas requiring special attention.

Chimpanzee demographics living in an agricultural-swamp matrix

The camera trap survey provided a large amount of images and allowed for the identification of unhabituated individual chimpanzees living in the study area. We identified two groups of chimpanzees, one in the northern site of the study area with 24 individuals and one in the southern site with 14 individuals. Despite the difference in group sizes, their age-class structure was correlated between both groups but not their gender ratio, which was male biased among adults. It would require a longer-term study to determine which intrinsic (e.g. female dispersal with unknown fate) and/or extrinsic factors (e.g. females being easier target for hunters than males) could explain this gender structure pattern and their survival implications.

According to farmers' reports, chimpanzees have been living in the area for decades (Study I), suggesting that chimpanzees have progressively adapted to the habitat changes caused mainly by farming activities. We expected to find a negative correlation between chimpanzee and human presence based on trapping rates, but instead it seems that human presence does not significantly affect chimpanzees' activity patterns, showing a certain degree of adaptation (Study II). In chimpanzee social systems, males tend to stay in their natal group while adolescent females usually migrate to other communities (Pusey 1980). In our study area, unpaved roads and the relatively small settlements are probably not a limiting conditioning factor for female migration, yet an increase in human and land development, would possibly impair dispersal, limit genetic exchange and increase inbreeding.

Chimpanzees in non-protected habitats in Sierra Leone

The density estimates based on the number of identified individuals and the minimum home ranges, are comparable to other studies carried out in similar anthropogenic habitat types (Bossou, Guinea and Bulindi, Uganda) and similar to forested sites (Taï

Forest, Côte d'Ivoire). Our estimates provide a unique baseline for chimpanzees living in a highly degraded landscape characterised by swamps and farmland. The extrapolated density estimates for the entire study area resulted in 0.4 individuals/km^2, an unexpected relatively high density estimate similar to other protected and non-protected areas across Africa (Table 5.7 in Study III). The chimpanzee communities we have studied here are not an isolated case. In Sierra Leone, chimpanzees are found almost across the whole country (Brncic et al. 2010). Bearing in mind that half of the chimpanzee population in Sierra Leone is found in non-protected habitats (Brncic et al. 2010) and that most of the country harbours similar degraded habitat (CILSS 2016) to our study site, it can well be that the national census had significantly underestimated chimpanzee numbers outside protected areas. Chimpanzees living in fragmented agricultural matrixes have not been a conservation priority, but we argue that they should be included in national conservation action plans. Chimpanzees show a great deal of adaptability to changing habitats but the fast human population growth and development in chimpanzees' country ranges, will increase their risk of extinction (Estrada et al. 2017) if these populations cannot adapt fast enough to the changes. If we want to preserve the species in the country, it is also paramount to further explore the factors influencing human tolerance towards chimpanzees and the anthropogenic and habitat factors influencing chimpanzee presence in agricultural matrixes at other sites. This knowledge will help define more specific conservation measures at local level with the aim to minimize the impact on chimpanzees and people's livelihoods as well as integrating them in the planning of development projects such as road constructions, commercial plantations, mining concessions, etc. in non-protected areas where chimpanzees occur.

Future directions and recommendations

The limited time period to carry out a thesis restricts the amount of studies that can be accomplished; however, this thesis not only add to our understanding of chimpanzees outside protected areas but also highlights the gaps in knowledge and reveals future research directions. Sierra Leone is currently developing rapidly in many parts of the country and the survival of chimpanzees living in non-protected areas could be threatened by new developments, such as the construction of roads, the establishment of industrial or commercial plantations such as oil palms.

Our research confirms the importance of the social science knowledge and we suggest that studies in anthropogenic habitats should start by carrying out preliminary interviews with local people at regional level and any other relevant stakeholders. Such interviews can provide accurate details of the location of chimpanzees, if present, on their land. This information is essential and would allow drawing a map with the distinct chimpanzee groups living in a relatively large area, which will help determine where research efforts should be directed.

Once chimpanzee key areas have been determined, carrying out more detailed interviews with farmers will provide information on their agricultural challenges, attitudes towards and perceptions of wildlife, specially chimpanzees. These data would be key to inform and monitor conservation plans locally that could favour farmers and chimpanzees alike.

We suggest using non-invasive methods such as camera trapping, drones and faecal genetic studies (Arandjelovic & Vigilant 2018; McCarthy et al. 2015) to perform assessments of the study areas where non-habituated chimpanzees occur which would provide information on their demographics, health and the characteristics of the habitats they live.

In our study, we have acquired more independent events of chimpanzees in non-target camera locations than targeted. Després-Einspenner et al. (2017), who compared the efficacy of non-target locations frequently visited by chimpanzees versus target cameras based on a systematic design, concluded that focusing studies in non-target locations provided reliable chimpanzee density estimates. We therefore suggest to use camera traps at targeted instead of systematic locations to increase the number of study sites and optimise the obtention of data when there are limited resources and time constraints.

We also suggest improving camera trapping methodology using paired cameras at each trapping location, which would increase the chances of capturing more accurately the chimpanzee party sizes as well as providing different views of the chimpanzees to help with the individual identifications.

Finally, we conclude that combining social science and fine-scale chimpanzee demographic studies are powerful tools to be incorporated in environmental impact assessments for projects prospected in non-protected sites, to minimise impact on chimpanzees and to develop appropriate mitigation measures.

7 - Conclusions

1- Interviews are a useful tool to establish farmers' main concerns on agricultural challenges in Sierra Leone, which are crop consumption by wildlife i.e. cane rats, red river hogs and monkeys, poor soil quality and plagues of grasshoppers. Unexpectedly, chimpanzees were ranked as the fourth most destructive mammal and the main reported consumed crops by chimpanzees were semi-domesticated oil palms and domestic fruits.

2- Fencing and traps were the most common mitigation measures used by farmers against crop foraging by wild animals, targeting small mammals. However, chimpanzees are not free of the risk as seen by the number of them showing limb amputations.

3- The persistence of chimpanzee populations in these highly human-impacted areas is probably related to a certain level of tolerance by farmers, the access to crops, the presence of swamps and the widely distribution of semi-domesticated oil palms.

4- The increasing human population, the shortening of fallow time and the risks associated with complete habitat conversion to industrialized plantations could signify chimpanzee extinction in these areas if better agricultural practices and land use management are not implemented.

5- Abundance of chimpanzees in the study area was influenced by distance to roads and proximity to swamps. Swamps may offer chimpanzees a safe environment in light of the scarcity of forests, so it is important to protect this type of habitats and to include appropriate impact assessments and mitigation measures in road development plans.

6- Camera trapping allowed us to identify two distinct groups of chimpanzees, totalling 38 individuals, whose group sizes and age structure are comparable to the other African sites characterised by a human–dominated fragmented agroforestry matrix. However, the gender ratio is biased towards males, which is unusual in chimpanzee communities where females outnumber males.

7- At a spatial level, human presence do not to interfere with chimpanzee activity, however at a temporal level, chimpanzees tended to reduce their activity at midday when human activity is more prevalent, indicating a certain degree of adaptation to human-impacted habitats.

8- The minimum home ranges estimated for both chimpanzee communities are within similar ranges to other African sites characterised by forested habitats with variable human impact, suggesting that the agricultural-swamp habitat can sustain chimpanzee communities despite the scarcity of forest and without the need to range over large distances.

9- The estimated density of 0.4 chimpanzees /km^2 in our study, ten times higher than the density estimate for non-protected areas in the whole of Sierra Leone, suggests that the national census underestimated the chimpanzee population in these areas.

8 - References

Ahumada, J., Silva, C., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., et al. (2011). Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1578), 2703–2711.

Alp, R. (1997). “Stepping-sticks” and “seat-sticks”: new types of tools used by wild chimpanzees (*Pan troglodytes*) in Sierra Leone. American journal of primatology, 41(June 1996), 45–52.

Amin, R., Davey, K., & Wacher, T. (2017). Camera Trap Data Management and Analysis Package - user guide. ZSL. https://www.zsl.org/zsl-camera-trap-data-management-and-analysis-package

Ancrenaz, M., Cheyne, S. M., Humle, T., & Robbins, M. M. (n.d.). Impacts of infrastructure on apes, indigenous peoples and other local communities. In Arcus Foundation (Ed.), Volume 3. State of the Apes: Infrastructure Development and Ape Conservation. Cambridge University Press.

Ancrenaz, M., Hearn, A. J., Ross, J., Sollman, R., & Wilting, A. (2012). Handbook for wildlife monitoring using camera-traps. BBEC Publication.

Arandjelovic, M., & Vigilant, L. (2018). Non-invasive genetic censusing and monitoring of primate populations. American Journal of Primatology, 80(3), e22743.

Arandjelovic, M., Boesch, C., Campbell, G., Hohmann, G., Junker, J., Célestin, K., et al. (2014). Pan African Programme The cultured chimpanzee: Guidelines for research and data collection, 1–105.

Arandjelovic, M., Head, J., Kühl, H., Boesch, C., Robbins, M. M., Maisels, F., & Vigilant, L. (2010). Effective non-invasive genetic monitoring of multiple wild western gorilla groups. Biological Conservation, 143(7), 1780–1791.

Arlet, M. E. & Molleman, F. (2007) Rodents damage crops more than wildlife in subsistence agriculture on the northern periphery of Dja Reserve, Cameroon. International Journal of Pest Management, 53, 237–243.

Aukema, J. E., Pricope, N. G., Husak, G. J., & Lopez-Carr, D. (2017). Biodiversity areas under threat: Overlap of climate change and population pressures on the world’s biodiversity priorities. PLoS ONE, 12(1), e0170615.

Barnes, R. F. W. (2002) The bushmeat boom and bust in West and Central Africa. Oryx, 36, 236–242.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., et al. (2011). Has the Earth's sixth mass extinction already arrived? Nature, 471(7336), 51–57.

Basabose, A. K. (2005). Ranging Patterns of Chimpanzees in a Montane Forest of Kahuzi, Democratic Republic of Congo. International Journal of Primatology, 26(1), 33–54.

Bates, L. A., & Byrne, R. W. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): Foraging and border checking. Behavioral Ecology and Sociobiology, 64(2), 247–255.

Bermejo, M. (1999). Status and conservation of primates in Odzala National Park, Republic of the Congo. Oryx, 33(4), 324–332.

Berryman, A. A. (2002). Population: A central concept for ecology? *Oikos*, *97*(3), 439–442.

Bessa, J., Sousa, C. & Hockings, K. J. (2015) Feeding ecology of chimpanzees (*Pan troglodytes verus*) inhabiting a forest-mangrove-savanna-agricultural matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau. American Journal of Primatology, 77, 651–665.

Beyer, H. L. (2015). Geospatial Modelling Environment (Version 0.7.4.0). (software). http://www.spatialecology.com/gme

Blanco, V., & Waltert, M. (2013). Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda. Journal for Nature Conservation, 21(6), 383–393.

Boesch, C., & Boesch-Achermann, H. (2000). The chimpanzees of the Taï Forest: Behavioural ecology and evolution. Oxford University Press. Oxford.

Boesch, C., Kalan, A. K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., & Kühl, H. S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. American Journal of Primatology, 79(3), 1–7.

Bonwitt, J., Dawson, M., Kandeh, M., Ansumana, R., Sahr, F., Brown, H., & Kelly, A. H. (2018). Unintended consequences of the 'bushmeat ban' in West Africa during the 2013–2016 Ebola virus disease epidemic. Social Science and Medicine, 200, 166–173.

Bortolamiol, S., Cohen, M., Jiguet, F., Pennec, F., Seguya, A., & Krief, S. (2016). Chimpanzee non-avoidance of hyper-proximity to humans. Journal of Wildlife Management, 80(5), 924–934.

Boyer-Ontl, K. M., & Pruetz, J. D. (2014). Giving the Forest Eyes: The Benefits of Using Camera Traps to Study Unhabituated Chimpanzees (*Pan troglodytes verus*) in Southeastern Senegal. International Journal of Primatology, 35(5), 881–894.

Boyle, S. A., Lourenço, W. C., Da Silva, L. R., & Smith, A. T. (2009). Home range estimates vary with sample size and methods. Folia Primatologica, 80(1), 33–42.

Brncic, T., Amarasekaran, B. & McKenna, A. (2010) Sierra Leone National Chimpanzee Census. Final report. Pp. 115. Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone.

Brncic, T., Amarasekaran, B., McKenna, A., Mundry, R., & Kühl, H. S. (2015). Large mammal diversity and their conservation in the human-dominated land-use mosaic of Sierra Leone. Biodiversity and Conservation, 24(10), 2417–2438.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology, 16(4), 909–923.

Bryson-Morrison (2017) Habitat use and nutrition of chimpanzees in an anthropogenic landscape: A case study in Bossou, Guinea, West Africa. PhD Thesis. University of Kent, UK

Bryson-Morrison, N., Matsuzawa, T., & Humle, T. (2016). Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa. American Journal of Primatology, 78(12), 1237–1249.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and Habitat Use of Chimpanzees (*Pan troglodytes verus*) in the Anthropogenic Landscape of Bossou, Guinea, West Africa. International Journal of Primatology, 38(2), 282–302.

Buckland, S. T., Plumptre, A. J., Thomas, L., & Rexstad, E. a. (2010). Line Transect Sampling of Primates: Can Animal-to-Observer Distance Methods Work? International Journal of Primatology, 31(3), 485–499.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., et al. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology.

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., et al. (2010). Global biodiversity: Indicators of recent declines. Science, 328(5982), 1164–1168.

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., et al. (2012). How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences, 280(1750), 20121890–20121890.

Campbell, G., Kuehl, H., N'Goran Kouamé, P. & Boesch, C. (2008) Alarming decline of West African chimpanzees in Côte d'Ivoire. Current Biology, 18, R903–R904.

Campbell-Smith, G., Sembiring, R. & Linkie, M. (2012) Evaluating the effectiveness of human-orangutan conflict mitigation strategies in Sumatra. Journal of Applied Ecology, 49, 367–375.

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., et al. (2017). A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation, 3(3), 109–122.

Carlsen, F., Leus, K., Traylor-Holzer, K. & McKenna, A. (eds) (2012) Western Chimpanzee Population and Habitat Viability Assessment for Sierra Leone: Final Report. IUCN/SSC Conservation Breeding Specialist Group - Europe, Copenhagen, Denmark.

Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. Proceedings of the National Academy of Sciences of the United States of America, 109(38), 15360–5.

Carvalho, J. S., Marques, T. A., & Vicente, L. (2013). Population Status of *Pan troglodytes verus* in Lagoas de Cufada Natural Park, Guinea-Bissau. *PLoS ONE*, *8*(8).

Chapman, C. A., Bortolamiol, S., Matsuda, I., Omeja, P. A., Paim, F. P., Reyna-Hurtado, R., et al. (2018). Primate population dynamics: variation in abundance over space and time. Biodiversity and Conservation, 27(5), 1221–1238.

Chirima, G. J., & Owen-Smith, N. (2017). Comparison of Kernel Density and Local Convex Hull Methods for Assessing Distribution Ranges of Large Mammalian Herbivores. Transactions in GIS, 21(2), 359–375.

Cibot, M., Bortolamiol, S., Seguya, A., & Krief, S. (2015). Chimpanzees facing a dangerous situation: A high-traffic asphalted road in the Sebitoli area of Kibale National Park, Uganda. American Journal of Primatology, 77(8), 890–900.

CILSS (2016). Landscapes of West Africa: a window on a changing world. 479U.S. Geological Survey EROS 14 252nd St, Garretson, SD 57030, UNITED STATES.

Costa, S., Casanova, C. & Sousa, C. & Lee, P.C. (2013) The good, The bad and the ugly: perceptions of wildlife in Tombali (Guinea-Bissau, West Africa). Journal of Primatology, 2, 110.

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., Di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences, 114(29), 7635–7640.

Crunchant, A. S., Egerer, M., Loos, A., Burghardt, T., Zuberbï¿½hler, K., Corogenes, K., et al. (2017). Automated face detection for occurrence and occupancy estimation in chimpanzees. American Journal of Primatology, 79(3), 1–12.

Danquah, E., Oppong, S. K., Akom, E., & Sam, M. (2012). Preliminary Survey of Chimpanzees and Threatened Monkeys in the Bia-Goaso Forest Block in Southwestern Ghana, *7*(2), 163–174.

Davies, A. G. (1987). Conservation of primates in the Gola Forest Reserves, Sierra Leone. Primate Conservation, 150–153.

Després-Einspenner, M. L., Howe, E. J., Drapeau, P., & Kühl, H. S. (2017). An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. American Journal of Primatology, 79(7), 1–12.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Antrhopocene. Science, 401(6195), 401–406.

Downs, J. A., & Horner, M. W. (2009). A characteristic-hull based method for home range estimation. Transactions in GIS, 13(5–6), 527–537.

Dunay, E., Apakupakul, K., Leard, S., Palmer, J. L., & Deem, S. L. (2018). Pathogen Transmission from Humans to Great Apes is a Growing Threat to Primate Conservation. EcoHealth, 2050, 1–15.

Duvall, C. S. (2008). Human settlement ecology and chimpanzee habitat selection in Mali. Landscape Ecology, 23(6), 699–716.

Elston, J. W. T., Cartwright, C., Ndumbi, P., & Wright, J. (2017). The health impact of the 2014–15 Ebola outbreak. Public Health, 143, 60–70.

Estrada, A. (2013). Socioeconomic Contexts of Primate Conservation: Population, Poverty, Global Economic Demands, and Sustainable Land Use. American Journal of Primatology, 75(1), 30–45.

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Fiore, A. Di, et al. (2017). Impending extinction crisis of the world's primates: Why primates matter. Science Advances.

Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and Primate Conservation in The Tropics: A Review. American Journal of Primatology.

Fa, J. E. & Brown, D. (2009) Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. Mammal Review, 39, 231–264.

Faust, L. J., Cress, D., Farmer, K. H., Ross, S. R., & Beck, B. B. (2011). Predicting Capacity Demand on Sanctuaries for African Chimpanzees (*Pan troglodytes*). International Journal of Primatology, 32(4), 849–864.

Fleury-Brugiere, M. C., & Brugiere, D. (2010). High population density of *Pan troglodytes verus* in the Haut Niger national park, Republic of Guinea: Implications for local and regional conservation. International Journal of Primatology, 31(3), 383–392.

Gaiser, T., Judex, M., Igué, A.M., Paeth, H. & Hiepe, C. (2011) Future productivity of fallow systems in Sub-Saharan Africa: is the effect of demographic pressure and fallow reduction more significant than climate change? Agricultural and Forest Meteorology, 151, 1120–1130.

Ganas, J, 2009. Population status survey and monitoring of western chimpanzees (*Pan troglodytes verus*) in the Gola Forest Reserve, Sierra Leone, Report to the U.S. Fish and Wildlife Service, (November 2008).

Garriga, R. M., Marco, I., Casas-Diaz, E., Amarasekaran, B., & Humle, T. (2017). Perceptions of challenges to subsistence agriculture, and crop foraging by wildlife and chimpanzees *Pan troglodytes verus* in unprotected areas in Sierra Leone. ORYX, pp. 1–14.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. Science, 360(6394), 1232–1235.

Gerber, B. D., Williams, P. J., & Bailey, L. L. (2014). Primates and Cameras: Noninvasive Sampling to Make Population-Level Inferences While Accounting for Imperfect Detection. International Journal of Primatology, 35(5), 841–858.

Gerritsma, W., & Wessel, M. (1997). Oil palm: domestication achieved? Netherlands Journal of Agricultural Science, 45(October), 463–475.

Goodall, J. (1986). The chimpanzees of Gombe: patterns of behavior. Harvard University Press. Cambridge (Massachusetts).

Granier, N. and Martinez, L. (2004). Premiere reconnaissance des *chimpanzes Pan troglodytes verus* dans la zone transfrontaliere entre la Guinee et al Mali. Primatologie. 6:423-447

Granier, N., Hambuckers, A., Matsuzawa, T., & Huynen, M. C. (2014). Density estimates and nesting-site selection in chimpanzees of the Nimba Mountains, Côte d'Ivoire, and Guinea. *American Journal of Primatology*, *76*(11), 999–1010.

Halloran, A. R., Cloutier, C. T. & Sesay, P. B. (2013) A previously undiscovered group of chimpanzees (*Pan troglodytes verus*) is observed living in the Tonkolili district of Sierra Leone. American Journal of Primatology, 75, 519–523.

Harcourt, A. H., & Doherty, D. A. (2005). Species-area relationships of primates in tropical forest fragments: A global analysis. Journal of Applied Ecology, 42(4), 630–637.

Head, J. S., Boesch, C., Robbins, M. M., Rabanal, L. I., Makaga, L., & Kühl, H. S. (2013). Effective sociodemographic population assessment of elusive species in ecology and conservation management. Ecology and Evolution, 3(9), 2903–2916.

Herbinger, I., Boesch, C., & Rothe, H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. International Journal of Primatology, 22(2), 143–167.

Hickey, J. R., Nackoney, J., Nibbelink, N. P., Blake, S., Bonyenge, A., Coxe, S., et al. (2013). Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. Biodiversity and Conservation, 22(13–14), 3085–3104. doi:10.1007/s10531-013-0572-7

Hijmans, R. J. (2017). raster: Geographic Data Analysis and Modeling. R package version 2.6-7. https://cran.r-project.org/web/packages/raster/index.html

Hill, C. M. & Wallace, G. E. (2012) Crop protection and conflict mitigation: reducing the costs of living alongside non-human primates. Biodiversity and Conservation, 21, 2569–2587.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., & Wrangham, R. (2001). Mortality rates among wild Chimpanzees. Journal of Human Evolution, 40(5), 437–450.

Hockings, K. & Humle, T. (2009) Best Practice Guidelines for the Prevention and Mitigation of Conflict Between Humans and Great Apes. IUCN/SSC Primate Specialist Group, Gland, Switzerland.

Hockings, K. J. & McLennan, M. R. (2012) From forest to farm: systematic review of cultivar feeding by chimpanzees. Management implications for wildlife in anthropogenic landscapes. PLoS ONE, 7(4), e33391.

Hockings, K. J. & Sousa, C. (2012) Differential utilization of cashew—a low-conflict crop—by sympatric humans and chimpanzees. Oryx, 46, 375–381.

Hockings, K. J. (2011) Behavioural flexibility and division of roles in chimpanzee road-crossing. In The Chimpanzees of Bossou and Nimba (eds T. Matsuzawa, T. Humle & Y. Sugiyama), pp. 221–229. Springer, London, UK.

Hockings, K. J., & McLennan, M. R. (2012). From forest to farm: systematic review of cultivar feeding by chimpanzees--management implications for wildlife in anthropogenic landscapes. PloS one, 7(4), e33391.

Hockings, K. J., & Sousa, C. (2013). Human-Chimpanzee Sympatry and Interactions in Cantanhez National Park, Guinea-Bissau: Current Research and Future Directions. Primate Conservation, 26(1), 57–65.

Hockings, K. J., Anderson, J. R. & Matsuzawa, T. (2009) Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. American Journal of Primatology, 71, 636–646.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. Current Biology, 16(17), 668–670.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2009). Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. American journal of primatology, 71(8), 636–46

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. Animal Behaviour, 83(3), 801–810.

Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W., et al. (2015). Apes in the Anthropocene: flexibility and survival. Trends in Ecology & Evolution, 1–8.

Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W. et al. (2015) Apes in the Anthropocene: flexibility and survival. Trends in Ecology & Evolution, 30, 215–222.

Hockings, K. J., Yamakoshi, G., & Matsuzawa, T. (2017). Dispersal of a Human-Cultivated Crop by Wild Chimpanzees (*Pan troglodytes verus*) in a Forest–Farm Matrix. International Journal of Primatology, 38(2), 172–193.

Hockings, K. J., Yamakoshi, G., Kabasawa, A. & Matsuzawa, T. (2010) Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. American Journal of Primatology, 72, 887–896.

Hoffman, L. C. & Cawthorn, D. M. (2012) What is the role and contribution of meat from wildlife in providing high quality protein for consumption? Animal Frontiers, 2, 40–53.

Hoffmann, M. (2008) Thryonomys swinderianus. The IUCN Red List of Threatened Species 2008: e.T21847A9323360. Http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T21847A9323360.en [accessed 14 September 2016].

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., et al. (2010). The impact of conservation on the status of the world's vertebrates. Science, 330(6010), 1503–1509.

http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15935A17989872.en
Downloaded on 29 August 2018.

Humle, T. & Hill, K. (2016) People-primate interactions: implications for primate conservation. In Introduction to Primate Conservation (eds. S. Wich & A. Marshall), pp. 219–240. Oxford University Press, Oxford, UK.

Humle, T. & Matsuzawa, T. (2004) Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. International Journal of Primatology, 25, 551–581.

Humle, T. (2003). Behavior and Ecology of Chimpanzees in West Africa. In R. Kormos, C. Boesch, M. I. Bakaee, & T. M. Butynki (Eds.), West African Chimpanzees. Status Survey and Conservation Action Plan. IUCN/SSC Primate Specialist Group. (p. 219). Gland, Switzerland and Cambridge, UK.

Humle, T. (2011). Location and ecology. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), The Chimpanzees of Bossou and Nimba (pp. 13–21). Springer London.

Humle, T. (2015). The dimensions of ape-human interactions in industrial agricultural landscapes. State of the apes: Industrial agriculture and ape conservation, Cambridge University Press.

Humle, T., & Hill, C. (2016). People–primate interactions: implications for primate conservation. In S. A. Wich & A. J. Marshall (Eds.), An Introduction to Primate Conservation (pp. 219–240). Oxford University Press.

Humle, T., & Hockings, K. J. (2009). Best Practice Guidelines for the Prevention and Mitigation of Conflict Between Humans and Great Apes. Gland, Switzerland: IUCN SSC Primate Specialist Group (PSG).

Humle, T., & Matsuzawa, T. (2004). Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. International Journal of Primatology, 25(3), 551–581.

Humle, T., Boesch, C., Campbell, G., Junker, J., Koops, K., Kuehl, H., & Sop, T. (2016). Pan troglodytes ssp. verus. (errata version published in 2016). *The IUCN List of Threatened Species*: e.T15935A102327574.

Humle, T., Maisels, F., Oates, J. F., Plumptre, A. & Williamson, E.A. (2016). *Pan troglodytes* (errata version published in 2018). *The IUCN List of Threatened Species*: e.T15933A129038584. Downloaded on 29 August 2018.

Imanishi, K. (1960). Social Organization of Subhuman Primates in Their Natural Habitat. Current Anthropology. The University of Chicago PressWenner-Gren Foundation for Anthropological Research.

Inogwabini, B. I., Abokome, M., Kamenge, T., Mbende, L., & Mboka, L. (2012). Preliminary bonobo and chimpanzee nesting by habitat type in the northern Lac Tumba Landscape, Democratic Republic of Congo. African Journal of Ecology, 50(3), 285–298.

Inskip, C. & Zimmermann, A. (2009) Human-felid conflict: a review of patterns and priorities worldwide. Oryx, 43, 18-34.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., et al. (2010). The home-range concept: Are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1550), 2221–2231.

Kingdon, J. (2001) The Kingdon Field Guide to African Mammals. 4th edition. A&C Black Publishers Ltd, London, UK.

Knight, J. (2000) Introduction. In Natural Enemies: People-Wildlife Conflicts in Anthropological Perspective (ed. J. Knight), pp. 1–35. Routledge, London, UK.

Köndgen, S., Kühl, H., N'Goran, P. K., Walsh, P. D., Schenk, S., Ernst, N., et al. (2008). Pandemic Human Viruses Cause Decline of Endangered Great Apes. Current Biology, 18(4), 260–264.

Köndgen, S., Schenk, S., Pauli, G., Boesch, C., & Leendertz, F. H. (2010). Noninvasive monitoring of respiratory viruses in wild chimpanzees. EcoHealth, 7(3), 332–341.

Kortlandt, A. (1962). Chimpanzees in the Wild. Scientific American, 206(5), 128–138.

Kouakou, C. Y., Boesch, C., Kühl, H. (2009). Estimating Chimpanzee Population Size with Nest Counts: Validating Methods in Taï National Park, American Journal of Primatology 71:447–457.

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J. M., & Masi, S. (2014). Wild chimpanzees on the edge: Nocturnal activities in croplands. PLoS ONE, 9(10).

Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., et al. (2017). The Critically Endangered western chimpanzee declines by 80%. American Journal of Primatology, 79(9).

Kühl, H., Maisels, F., Ancrenaz, M., & Williamson, E. (2008). Best practice guidelines for surveys and monitoring of great ape populations. Gland, Switzerland: IUCN SSC Primate Specialist Group (PSG).

Lapuente, J., Hicks, T. C., & Linsenmair, K. E. (2017). Fluid dipping technology of chimpanzees in Comoé National Park, Ivory Coast. American Journal of Primatology, 79(5), 22628.

Laurance, W. F., Campbell, M. J., Alamgir, M., & Mahmoud, M. I. (2017). Road Expansion and the Fate of Africa's Tropical Forests. Frontiers in Ecology and Evolution, 5(July), 1–7. doi:10.3389/fevo.2017.00075

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., et al. (2006). Impacts of roads and hunting on central African rainforest mammals. Conservation Biology, 20(4), 1251–1261.

Laurance, W. F., Goosem, M., & Laurance, S. G. W. (2009). Impacts of roads and linear clearings on tropical forests. Trends in Ecology and Evolution, 24(12), 659–669.

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution, 29(2), 107–116.

Lawler, R. R. (2011). Demographic concepts and research pertaining to the study of wild primate populations. American Journal of Physical Anthropology, 146(SUPPL. 53), 63–85.

Leendertz, F. H., Ellerbrok, H., Boesch, C., Couacy-Hymann, E., Mätz-Rensing, K., Hakenbeck, R., et al. (2004). Anthrax kills wild chimpanzees in a tropical rainforest. Nature, 430(6998), 451–452.

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. Behavioral Ecology and Sociobiology, 56(3), 207–216. Macfie, E. J., & Williamson, E. A. (2010). Best Practice Guidelines for Great Ape Tourism. IUCN Species Survival Commission. http://www.iucn.org/knowledge/publications_doc/publications/?6052/Best-practice-guidelines-for-great-ape-tourism

Macfie, E. J., & Williamson, E. A. (2010). Best Practice Guidelines for Great Ape Tourism. IUCN Species Survival Commission. http://www.iucn.org/knowledge/publications_doc/publications/?6052/Best-practice-guidelines-for-great-ape-tourism

Mackenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). Occupancy Estimation and Modeling. IEEE Transactions on Geoscience and Remote Sensing (Vol. 42). Elsevier.

Madden, F. & McQuinn, B. (2014) Conservation's blind spot: the case for conflict transformation in wildlife conservation. Biological Conservation, 178, 97–106.

Maisels, F., Strindberg, S., Greer, D., Jeffery, K., Morgan, D., & Sanz, C. (2016). Pan troglodytes ssp. troglodytes. The IUCN Red List of Threatened Species 2016:e.T15936A102332276. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15936A17990042.en Downloaded on 29 August 2018

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale mountains. International Journal of Primatology, 19(6), 999–1011.

Matsuzawa, T., Humle, T., & Sugiyama, Y. (Eds.) (2011). The Chimpanzees of Bossou and Nimba. (T. Matsuzawa, T. Humle, & Y. Sugiyama, Eds.) Primatology Monographs (Springer, Vol. 82). Tokyo: Springer Japan.

Matthews, A., & Matthews, A. (2004). Survey of gorillas (Gorilla gorilla gorilla) and chimpanzees (*Pan troglodytes troglodytes*) in Southwestern Cameroon. Primates, 45(1), 15–24.

Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. (2016) Biodiversity: the ravages of guns, nets and bulldozers. Nature, 536, 143–145.

McCarthy, M. S., Després-Einspenner, M.-L., Samuni, L., Mundry, R., Lemoine, S., Preis, A., et al. (2018). An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). American Journal of Primatology, (January), e22904.

McCarthy, M. S., Lester, J. D., & Stanford, C. B. (2017). Chimpanzees (*Pan troglodytes*) Flexibly Use Introduced Species for Nesting and Bark Feeding in a Human-Dominated Habitat. International Journal of Primatology, 38(2), 321–337.

McCarthy, M. S., Lester, J. D., Howe, E. J., Arandjelovic, M., Stanford, C. B., & Vigilant, L. (2015). Genetic censusing identifies an unexpectedly sizeable population of an endangered large mammal in a fragmented forest landscape. BMC Ecology, 15(1).

McLennan, M. R. & Asiimwe, C. (2016) Cars kill chimpanzees: case report of a wild chimpanzee killed on a road at Bulindi, Uganda. Primates, 57, 377–388.

McLennan, M. R. & Hill, C. M. (2010) Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western Uganda. American Journal of Primatology, 72, 907–918.

McLennan, M. R. & Hill, C. M. (2013) Ethical issues in the study and conservation of an African great ape in an unprotected, human-dominated landscape in western Uganda. In Ethics in the Field: Contemporary Challenges (eds. J. MacClancy & A. Fuentes), pp. 42–66. Bergham, New York, USA.

McLennan, M. R. & Hockings, K. J. (2014) Wild chimpanzees show group differences in selection of agricultural crops. Scientific Reports, 4, 5956.

McLennan, M. R. & Hockings, K. J. (2016) The aggressive apes? Causes and contexts of great ape attacks on local persons. In Problematic Wildlife: A Cross-Disciplinary Approach (ed. F.M. Angelici), pp. 373–394. Springer International Publishing, Cham, Switzerland.

McLennan, M. R. (2008) Beleaguered chimpanzees in the agricultural district of Hoima, western Uganda. Primate Conservation, 23, 45–54.McLennan, M.R. (2013) Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest-farm interface. International Journal of Primatology, 34, 585–614.

McLennan, M. R. (2008). Beleaguered Chimpanzees in the Agricultural District of Hoima, Western Uganda. Primate Conservation, 23(1), 45–54.

McLennan, M. R. (2013). Diet and Feeding Ecology of Chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging Strategies at the Forest-Farm Interface. International Journal of Primatology, 34(3), 585–614.

McLennan, M. R., & Ganzhorn, J. U. (2017). Nutritional Characteristics of Wild and Cultivated Foods for Chimpanzees (*Pan troglodytes*) in Agricultural Landscapes. International Journal of Primatology, 38(2), 122–150.

McLennan, M. R., & Hill, C. M. (2010). Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western Uganda. American journal of primatology, 72(10), 907–18.

McLennan, M. R., & Hill, C. M. (2012). Troublesome neighbours: Changing attitudes towards chimpanzees (*Pan troglodytes*) in a human-dominated landscape in Uganda. Journal for Nature Conservation, 20(4), 219–227.

McLennan, M. R., & Hockings, K. J. (2014). Wild chimpanzees show group differences in selection of agricultural crops. Scientific Reports, 4, 5956.

McLennan, M. R., Spagnoletti, N., & Hockings, K. J. (2017). The Implications of Primate Behavioral Flexibility for Sustainable Human–Primate Coexistence in Anthropogenic Habitats. International Journal of Primatology, 38(2), 105–121.

Meek, P. D., Ballard, G. A., & Falzon, G. (2016). The higher you go the less you will know: placing camera traps high to avoid theft will affect detection. Remote Sensing in Ecology and Conservation, 2(4), 204–211.

Mitani, J. C. (2006). Demographic influences on the behavior of chimpanzees. Primates; journal of primatology, 47(1), 6–13.

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current Biology, 20(12), 507–508.

Mittermeier, R. A., Myers, N., Mittermeier, C. G., & Robles Gil, P. (1999). Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. Mexico City: CEMEX, S.A., Agrupación Sierra Madre, S.C.

Mittermeier, R. A., Rylands, A. B., & Wilson, D. E. (Eds.). (2013). Handbook of the Mammals of the World. Volume 3: Primates. Lynx Edicions, Barcelona, Spain.

Moore, D. L., & Vigilant, L. (2014). A population estimate of chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic capture-recapture methods. American Journal of Primatology, 76(4), 335–346.

Moore, J. F., Mulindahabi, F., Gatorano, G., Niyigaba, P., Ndikubwimana, I., Cipolletta, C., & Masozera, M. K. (2018). Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda. American Journal of Primatology, e22897.

Morgan, B., Adeleke, A., Bassey, T., Bergl, R., Dunn, A., Fotso, R., et al. (2011). Regional Action Plan for the conservation of the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*). IUCN/SSC Primate Specialist Group and Zoological Society of San Diego. San Diego, CA, USA.

Morgan, D., Mundry, R., Sanz, C., Ayina, C. E., Strindberg, S., Lonsdorf, E., & Kühl, H. S. (2018). African apes coexisting with logging: Comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. Biological Conservation, pp. 277–286. Elsevier. doi:10.1016/j.biocon.2017.10.026

Morgan, D., Sanz, C., Onononga, J. R., & Strindberg, S. (2006). Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. International Journal of Primatology (Vol. 27)

Munro, P., & van der Horst, G. (2012). The Domestic Trade in Timber and Fuelwood Products in Sierra Leone: Current Dynamics and Issues.

Myers, N., Mittermeier, R. A. R., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853–858.

N'Goran, K. P., Yapi, F., Herbinger, I., Boesch,C., Tondossama, A. (2007). Etat du Parc National de Tai: Rapport de resultants de Biomonitoring, phase II (septembre 2006 – avril 2007). Rapport pour Wild Chimpanzee Foundation, Abdijan.

Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., et al. (2013). Ranging behavior of Mahale chimpanzees: A 16 year study. Primates, 54(2), 171–182.

Nakamura, M., Hosaka, K., Itoh, N., & Zamma, K. (2015). Mahale chimpanzees: 50 years of research. Cambridge University Press.

Nakashima, Y., Iwata, Y., Ando, C., Nze Nkoguee, C., Inoue, E., Akomo, E. F. O., et al. (2013). Assessment of landscape-scale distribution of sympatric great apes in African rainforests: Concurrent use of nest and camera-trap surveys. American Journal of Primatology, 75(12), 1220–1230.

Naughton-Treves, L. & Treves, A. (2005) Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In People and Wildlife: Conflict or Coexistence? (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 252–277. Cambridge University Press, Cambridge, UK.

Naughton-Treves, L. (1998) Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conservation Biology, 12, 156–168.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998) Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. Journal of Applied Ecology, 35, 596–606.

Newey, S., Davidson, P., Nazir, S., Fairhurst, G., Verdicchio, F., Irvine, R. J., & van der Wal, R. (2015). Limitations of recreational camera traps for wildlife management and conservation research: A practitioner's perspective. Ambio, 44, 624–635.

Newton-Fisher, N. E. (2003). The home range of the sonso community of chimpanzees from the Budongo Forest, Uganda. African Journal of Ecology, 41(2), 150–156.

Nilsen, E. B., Pedersen, S., & Linnell, J. D. C. (2008). Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research, 23(3), 635–639.

Nishida, T. (1968). The Social Group of Wild Chimpanzees in the Mahali Mountains. Primates, 9, 167–224.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., et al. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. American Journal of Primatology, 59(3), 99–121.

O'Connell, A. F., Nichols, J. D., & Karanth, K. U. (Eds.). (2011). Camera traps in animal ecology: Methods and analyses. Tokyo: Springer Japan.

Oates, J. F. (2010) Primates of West Africa: Pocket Identification Guide. Conservation International, Arlington, USA.

Ohashi, G., & Matsuzawa, T. (2011). Deactivation of snares by wild chimpanzees. Primates, 52(JANUARY 2011), 1–5.

Onderdonk, D. A., & Chapman, C. A. (2000). Coping with forest fragmentation: The primates of Kibale National Park, Uganda. International Journal of Primatology, 21(4), 587–611.

Pavy, J. M. (1993). Bafing faunal reserve. Biodiversity and human resource: survey and recommendations. Unpublished report, Cheverly, Maryland, USA.

Pebsworth, P. A., & LaFleur, M. (2014). Advancing Primate Research and Conservation Through the Use of Camera Traps: Introduction to the Special Issue. International Journal of Primatology, 35(5), 825–840.

Pimm, S. L., & Raven, P. (2000). Extinction by numbers. Nature, 403(6772), 843–845.

Plumptre, A. J., & Cox, D. (2006). Counting primates for conservation: Primate surveys in Uganda. Primates, 47(1), 65–73.

Plumptre, A. J., Rose, R., Nangendo, G., Williamson, E. A., Didier, K., Hart, J., et al. (2010). Eastern Chimpanzee (*Pan troglodytes schweinfurthii*): Status Survey and Conservation Action Plan 2010–2020. IUCN, Gland, Switzerland.

Poulsen, J. R., & Clark, C. J. (2004). Densities, distributions, and seasonal movements of gorillas and chimpanzees in swamp forest in northern Congo. International Journal of Primatology, 25(2), 285–306.

Prado-Martinez, J., Sudmant, P. H., Kidd, J. M., Li, H., Kelley, J. L., Lorente-Galdos, B., et al. (2013). Great ape genetic diversity and population history. Nature, 499(7459), 471–475.

Pruetz, J. D. (2007). Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: Implications for thermoregulatory behavior. Primates, 48(4), 316–319.

Pruetz, J. D., & Bertolani, P. (2007). Savanna Chimpanzees, *Pan troglodytes verus*, Hunt with Tools. Current Biology, 17(5), 412–417.

Pruetz, J. D., Marchant, L. F., Arno, J., & McGrew, W. C. (2002). Survey of savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *American Journal of Primatology*, *58*(1), 35–43.

Pruetz, J., & Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) Behavioral Responses to Stresses Associated with Living in a Savannah-Mosaic Environment: Implications for Hominin Adaptations to Open Habitats. PaleoAnthropology, 2009 (Potts 1998), 252–262.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. Animal Behaviour, 28(2), 543–552.

Pusey, A. E., Pintea, L., Wilson, M. L., Kamenya, S., & Goodall, J. (2007). The contribution of long-term research at Gombe National Park to chimpanzee conservation. Conservation Biology, 21(3), 623–634.

Quiatt, D., Reynolds, V. & Stokes, E.J. (2002) Snare injuries to chimpanzees (*Pan troglodytes*) at 10 study sites in east and west Africa. African Journal of Ecology, 40, 303–305.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org

Rainey, H. J., Iyenguet, F. C., Malanda, G.-A. F., Madzoké, B., Santos, D. Dos, Stokes, E. J., et al. (2010). Survey of Raphia swamp forest, Republic of Congo, indicates high densities of Critically Endangered western lowland gorillas Gorilla gorilla gorilla. Oryx, 44(01), 124.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A. et al. (2013) Understanding and managing conservation conflicts. Trends in Ecology & Evolution, 28, 100–109.

Reynolds, V., & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In I. DeVore (Ed.), Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart and Winston.

Rist, J., Milner-gulland, E. J., Cowlishaw, G., & Rowcliffe, J. M. (2009). The Importance of Hunting and Habitat in Determining the Abundnace of Tropical Forest Species in Equatorial Guinea, 41(6), 700–710.

Romero, D., Olivero, J., & Real, R. (2012). Comparative assessment of different methods for using land-cover variables for distribution modelling of Salamandra salamandra longirotris. Environmental Conservation, 40(1), 48–59.

Rudel, T., & Roper, J. (1997). Forest fragmentation in the humid tropics: A cross-national analysis. Singapore Journal of Tropical Geography, 18(1), 99–109.

Sanz, C. M., Caspar, S., & Morgan, D. (2010). Chimpanzees prey on army ants with specialized tool set. American Journal of Primatology, 72(1), 17–24.

Schulte-Herbrüggen, B., Rowcliffe, J. M., Homewood, K., Kurpiers, L. a., Whitham, C., & Cowlishaw, G. (2013). Wildlife Depletion in a West African Farm-Forest Mosaic and the Implications for Hunting Across the Landscape. Human Ecology, 41(6), 795–806.

Scully, E. J., Basnet, S., Wrangham, R. W., Muller, M. N., Otali, E., Hyeroba, D., et al. (2018). Lethal respiratory disease associated with human rhinovirus C in wild Chimpanzees, Uganda, 2013. Emerging Infectious Diseases, 24(2), 267–274.

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. PeerJ, 2, e374.

Singleton, I., & Van Schaik, C. P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. International Journal of Primatology, 22(6), 877–911. doi:10.1023/A:1012033919441

Sodhi, N. S., & Ehrlich, P. R. (2010). Conservation Biology for All. (N. S. Sodhi & P. R. Ehrlich, Eds.) Conservation Biology for All (Vol. 1). Oxford University Press.

Solomon, S., Plattner, G.-K., Knutti, R., & Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. Proceedings of the National Academy of Sciences, 106(6), 1704–1709.

Soumah, A. G., Humle, T. & Matsuzawa, T. (2014). Oil palm use among the people and wild chimpanzees of Bossou, Guine, West Africa. Presented at: International Primatological Society, 25th Congress Paper August 11-16, 2014, Hanoi, Vietnam.

Sousa, J., Barata, A. V, Sousa, C., Casanova, C. C. N., & Vicente, L. (2011). Chimpanzee oil-palm use in southern Cantanhez National Park, Guinea-Bissau. American journal of primatology, 73(5), 485–97.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society. Series B: Statistical Methodology, 64(4), 583–616. doi:10.1111/1467-9868.00353

Squire, C. B. (2001). Sierra Leone's Biodiversity and the Civil War: A Case Study Prepared for the Biodiversity Support Program. Washington, D.C.: Biodiversity Support Program.

Statistics Sierra Leone. (2017). Sierra Leone 2015 Population and Housing Census National analytical report. Http://www.statistics.sl.

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., et al. (2017). Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment, 15(1), 26–34.

Steffen, W., Grinevald, J., Crutzen, P., & McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 369(1938), 842–867.

Stiles, D., Redmond, I., Cress, D., Nellemann, C., & Formo, R. K. (2013). Stolen Apes - The Illicit Trade In Chimpanzees, Gorillas, Bonobos And Orangutans. A Rapid Response Assessment. United Nations Environment Programme. United Nations Environment Programme, GRID-Arendal. Arendal, Norway. www.grida.no

Stokes, E. J., Strindberg, S., Bakabana, P. C., Elkan, P. W., Iyenguet, F. C., Madzoké, B., et al. (2010). Monitoring Great Ape and Elephant Abundance at Large Spatial Scales: Measuring Effectiveness of a Conservation Landscape. PLoS ONE, 5(4), e10294.

Subramanian, M. (2012). Zoonotic disease risk and the bushmeat trade: Assessing awareness among hunters and traders in Sierra Leone. EcoHealth, 9(4), 471–482.

Sugiyama, Y. (1999). Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates, 40(1), 61–68.

Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. American Journal of Physical Anthropology, 124(2), 154–165.

Tagg, N., Willie, J., Petre, C. A., & Haggis, O. (2013). Ground night nesting in chimpanzees: New insights from central chimpanzees (*Pan troglodytes troglodytes*) in South-East Cameroon. Folia Primatologica, 84(6), 362–383.

Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. American Journal of Physical Anthropology, 124(1), 81–92.

Tan, C. L., Yang, Y., & Niu, K. (2013). Into the night: Camera traps reveal nocturnal activity in a presumptive diurnal primate, *Rhinopithecus brelichi*. Primates, 54(1), 1–6.

Tweh, C. G., Lormie, M. M., Kouakou, C. Y., Hillers, A., Kühl, H. S., & Junker, J. (2014). Conservation status of chimpanzees *Pan troglodytes verus* and other large mammals in Liberia: a nationwide survey. *Oryx*, (August 2013), 1–9.

UNDP. (2016). Human development report 2016. United Nations Development Programme. http://hdr.undp.org/sites/default/files/2016_human_development_report.pdf

United Nations DESA / Population Division. (2017). World Population Prospects: The 2017 Revision, Volume II: Demographic Profiles (ST/ESA/SER.A/400). https://esa.un.org/unpd/wpp/

Urban, M. C. (2015). Accelerating extinction risk from climate change. Science, 348(6234), 571–573.

Van Andel, A. C., Wich, S. A., Boesch, C., Koh, L. P., Robbins, M. M., Kelly, J., & Kuehl, H. S. (2015). Locating chimpanzee nests and identifying fruiting trees with an unmanned aerial vehicle. American Journal of Primatology, 77(10), 1122–1134.

Van Lawick-Goodall, J. (1968). The Behaviour of Free-living Chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs, 1, 161-IN12.

Van Vliet, N., & Nasi, R. (2008). Mammal distribution in a Central African logging concession area. Biodiversity and Conservation, 17(5), 1241–1249.

Van Vliet, N., Mertz, O., Heinimann, A., Langanke, T., Pascual, U., Schmook, B. et al. (2012) Trends, drivers and impacts of changes in swidden cultivation in tropical forest-agriculture frontiers : a global assessment. Global Environmental Change, 22, 418–429.

Vanthomme, H., Kolowski, J., Korte, L., & Alonso, A. (2013). Distribution of a Community of Mammals in Relation to Roads and Other Human Disturbances in Gabon, Central Africa. Conservation Biology, 27(2), 281–291.

Vieilledent, G., Merow, C., Guelat, J., Latimer, A. M., Marc, K., Gelfand, A. E., et al. (2014). Hierarchical Bayesian species distribution models with the hSDM R Package, 1–99.

Waller, J. C., & Reynolds, V. (2001). Limb injuries resulting from snares and traps in Chimpanzees (*Pan troglodytes schweinfurthii*) of the Budongo Forest, Uganda. Primates, 42(2), 135–139.

Webber, A. D. & Hill, C. M. (2014) Using participatory risk mapping (PRM) to identify and understand people's perceptions of crop loss to animals in Uganda. PLoS ONE, 9(7), e102912.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in Chimpanzees. Nature, 399(6737), 15–18.

Wiederholt, R., & Post, E. (2010). Tropical warming and the dynamics of endangered primates. Biology letters, 6(2), 257.

Wilkie, D., Shaw, E., Rotberg, F., Morelli, G., & Auzel, P. (2000). Roads, development, and conservation in the Congo basin. Conservation Biology, 14(6), 1614–1622. doi:10.1046/j.1523-1739.2000.99102.x

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Animal Behaviour, 63(2), 347–360.

Williamson, E. A., & Feistner, A. T. C. (2011). Habituating primates: Processes, techniques, variables and ethics. Field and Laboratory Methods in Primatology: A Practical Guide, Second Edition, 33–50.

Williamson, E. A., Maisels, F. G., Groves, C. P., Fruth, B., Humle, T. H., Morton, F. B., et al. (2013). Hominidae. In R. A. Mittermeier, A. B. Rylands, & D. E. Wilson (Eds.), Handbook of the Mammals of the World. Lynx Edicions, Barcelona, Spain.

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup Relations in Chimpanzees. Annual Review of Anthropology, 32(1), 363–392.

Wilson, M. L., Hauser, M. D., & Wrangham, R. W. (2007). Chimpanzees (*Pan troglodytes*) modify grouping and vocal behavior in reponse to location-specific risk. Behavior, 144, 1621–1653.

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. Behavioral Ecology.

Woodford, M. H., Butynski, T. M., & Karesh, W. B. (2002). Habituating the great apes: The disease risks. Oryx, 36(2), 153–160.

Woodroffe, R., Thirgood, S.J. & Rabinowitz, A. (eds) (2005) People and Wildlife: Conflict or Coexistence? Cambridge University Press, Cambridge, UK

9 - Annexes

9.1. Sample of the semi-structured interview

INTERVIEW NUMBER		**DATE**	
LOCATION NAME		**INTERVIEWER ASKING**	
INTERVIEW START TIME		**INTERVIEWER WRITING**	
INTERVIEW FINISH TIME		**WHICH LANGUAGE IS THE INTERVIEWEE USING?**	ENGLISH KRIO MENDE LIMBA TEMNE KURANKO OTHER________
HOW MANY ADULTS PRESENT DURING THE INTERVIEW?			

What is your position in your family?	HEAD OF FAMILY FATHER MOTHER OTHER______________	
Gender / Religion	MALE FEMALE	CHRISTIAN MUSLIM OTHER
What tribe are you?	KRIO MENDE TEMNE KURANKO LIMBA OTHER_____________	
How old are you?	______________YEARS	
Where are you from?	BORN HERE	NOT BORN HERE NUMBER OF YEARS LIVING HERE________
Have you been to school?	YES/NO	**Which school have you been to?** ARABIC ENGLISH BOTH **Which level did you finish at?** PRIMARY SECONDARY TERTIARY
How many people do you get in your house?	MEN ___________ WOMEN_________ CHILDREN_______ OTHER__________	
Which work do you do?	FARMER OTHER_____________	
Which plants do you grow now?	Banana Beans Benni Cacao Cassava Coffee Corn Cucumber Eggplant Groundnut Kola Mango Orange Oil palm Okra Papaya Pepper Pineapple Plum Potato Pumpkin Rice Sorghum Yam	
THREE crops that you value the most?	1______________________2______________________3________________________	
What do you do with the crops?	SELL _______________ EAT ____________SEEDS________________	
What are the problems in the farm? Rank by order of problem (1 is the worst)	____ANIMALS ____INSECTS ____LAND QUALITY ____LACK OF FERTILIZER ______ OTHER	

Code No	**Name of the animal**	**Does it raid your crops?**	**How often?**	**Which crop does the animal raid?** **Which part of the crop?** Don't know (DK) Seed (S) Leaf (L) Stem(St) Root (R) Fruit (F)
		YES NO Don't know	Daily Weekly Monthly Don't know	Banana Beans Benni Cacao Cassava Coffee Corn Cucumber Eggplant Groundnut Kola Mango Orange Oil palm Okra Papaya Pepper Pineapple Plum Potato Pumpkin Rice Sorghum Yam
		YES NO Don't know	Daily Weekly Monthly Don't know	Banana Beans Benni Cacao Cassava Coffee Corn Cucumber Eggplant Groundnut Kola Mango Orange Oil palm Okra Papaya Pepper Pineapple Plum Potato Pumpkin Rice Sorghum Yam
		YES NO	Daily Weekly	Banana Beans Benni Cacao Cassava Coffee Corn Cucumber Eggplant Groundnut Kola Mango

Code No	Name of the animal	Does it raid your crops?	How often?	Which crop does the animal raid? Which part of the crop? Don't know (DK) Seed (S) Leaf (L) Stem(St) Root (R) Fruit (F)
		Don't know	Monthly Don't know	Orange Oil palm Okra Papaya Pepper Pineapple Plum Potato Pumpkin Rice Sorghum Yam
		YES NO Don't know	Daily Weekly Monthly Don't know	Banana Beans Benni Cacao Cassava Coffee Corn Cucumber Eggplant Groundnut Kola Mango Orange Oil palm Okra Papaya Pepper Pineapple Plum Potato Pumpkin Rice Sorghum Yam

Which ones are the THREE most destructive animals?	1_________________2___________________3_________________

Do you protect your crops?	YES / NO	STICK FENCE PALM FENCE TRAPS SLING IMAGES POISON SHOUTING STONES HUNTING WITH DOGS GUNS OTHERS_________
What do people in the village when they trap an animal?	I don't hunt Eat them Sell them Discard them	
Have you ever reported the crop damage to the authorities?	YES / NO	**If yes, to whom?** CHIEF VILLAGE HEADMAN SECTION CHIEF GROUP DISCUSSION OTHER____________
How many chimpanzees have you seen coming to your fields?	INDIVIDUALS / IN GROUPS	**If in groups, HOW MANY?** _____________
Where do you see them? Write the location name and the direction / degrees		
What is their behavior when you find them in your fields?		
What do you do when you see chimpanzees in the field?		
What do you know about chimpanzees?		
Do you think they are dangerous?	YES / NO	**Why?**
Did you see chimps before the war?	YES / NO	
Do you think there are now more or less chimpanzees than before the war?	MORE chimps now LESS chimps now	**Why?**
Do you know they are protected by Sierra Leone's law?	YES / NO	**If yes, how do you know?**

9.2. Images of each individual chimpanzee identified in the study area

Northern chimpanzee group	
Adult males	*Alpha*
	Black
	Spot
	Fool
	Bobo
	Roi
Adult females and infants	*Judit & Julia & Junior*
	Molly & Mall
	Monie & Moises
	Mont & Monica
	Mina
Adolescents	*Tanya*
	Pin
	White eyebrows
Juveniles	*Jaws*
	Rosa
	Junior
	Morris
	Marc
	Neo

Southern chimpanzee group	
Adult males	*Patchy*
	Otto
Adult females and infants	*Granny & Mask*
	Meg & Pit
	Mary & Awe
Adolescents	*Curious*
	Eh
	John
Juveniles	*Cher*
	Heart
	Luna

9.2.1. Northern chimpanzee group

Adult Males

Alpha

Black

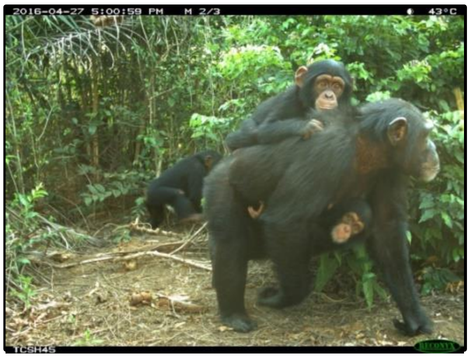
Spot

Fool

Bobo

Roi

Adult Females and infants



Judit, Julia & Junior

Molly & Mall

Monie & Moises

Mont & Monica

Mina

Adolescents

Tanya

Pin

White eyebrows

Juveniles

Jaws

Rosa

Marc

Junior

Morris

Neo

9.2.2. Southern chimpanzee group

Adult males

Otto

Patchy

Adult females and infants

Granny & Mask

Meg & Pit

Mary & Awe

Adolescents

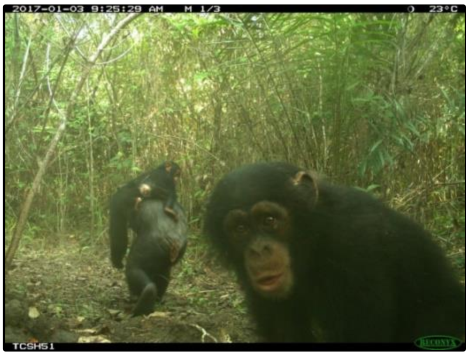
Curious

Eh

John

Juveniles

Cher



Luna

Heart