

THE CHIMPANZEES OF THE COMOÉ NATIONAL PARK, IVORY COAST. Status, distribution, ecology and behavior

DIE SCHIMPANSEN IM COMOÉ NATIONALPARK, ELFENBEINKÜSTE. Status, Verbreitung, Ökologie und Verhalten

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ABSTRACT

Although wild chimpanzees (Pan troglodytes) have been studied intensely for more than 50 years, there are still many aspects of their ecology and behavior that are not well understood. Every time that a new population of chimpanzees has been studied, new behaviors and unknown aspects of their ecology have been discovered. All this accumulated knowledge is helping us to piece together a model of how could last human and chimpanzee common ancestors have lived and behaved between seven and five million years ago. Comoé chimpanzees had never been studied in depth, until we started our research in October 2014, only a few censuses had been realized. The last surveys prior our work, stated that the population was so decimated that was probably functionally extinct. When we started this research, we had to begin with a new intensive survey, using new methods, to ascertain the real status and distribution of the chimpanzees living in Comoé National Park (CNP). During the last five years, we have realized a deep study aiming to know more about their ecology and behavior. We combined transects and reconnaissance marches (recces) with the use of camera traps, for the first time in CNP, obtaining a wealth of data that is not fully comprised in this dissertation. With this research, we determined that there is a sustainable continuous population of Western chimpanzees (Pan troglodytes verus) in CNP and the adjacent area of Mont Tingui, to the West, with a minimum of 127 weaned chimpanzees living in our main 900 km² study area, SW of CNP. We found that this population is formed by a minimum of eight different chimpanzee communities, of which we studied seven, four of them more in detail. These chimpanzees spent much more time in the forest than in the savanna habitats.

We also found that Comoé chimpanzees consumed at least 58 different food items in their dit, which they obtained both from forest and savanna habitats. Another finding was that insectivory had an important role in their diet, with at least four species of ants, three of termites and some beetle larvae. These chimpanzees also hunted at least three species of monkeys and maybe rodents and duikers and occasionally consumed the big land snails of genus *Achatina*. We found that, during the fruit scarcity period in the late rainy season, they intensely consumed the cambium of *Ceiba pentandra*, as fallback food, much more than the bark or cambium of any other tree species. Another interesting finding was that all the chimpanzees in the studied area realized this particular bark-peeling behavior and had been repeatedly peeling the trees of this species for years. This did not increase tree mortality and the damage caused to the trees was healed in two years, not reducing the growth, thus being a sustainable use of the trees. We found that Comoé chimpanzees produced and used a great variety of tools, mainly from wooden materials, but also from stone and herbaceous vegetation.

Their tool repertory included stick tools to dip for *Dorylus burmeisteri* ants, to fish for *Camponotus* and *Crematogaster* ants, to dip for honey, mainly from *Meliponini* stingless bees, but sometimes from honey bees (*Apis mellifera*). It also included the use of stick tools to fish termites of *Macrotermes subhyalinus* and *Odontotermes majus* (TFTs), to dip for water from tree holes and investigatory probes for multiple purposes. Additionally, these chimpanzees used leaf-sponges to drink from tree holes and to collect clayish water from salt-licks. They also used stones to hit the buttresses of trees during displays, the so called accumulative stone throwing behavior and probably used stones as hammers, to crack open hard-shelled *Strichnos spinosa* and *Afraegle paniculata* fruits and *Achatina* snails. The chimpanzees also used objects that are not generally accepted as animal tools, for being attached to the substrate, with different purposes: they drummed buttresses of trees with hands and/or feet to produce sound during male displays and they pounded open hard-shelled fruits, *Achatina* snails and *Cubitermes* termite mounds on stone or root anvils. We finally measured the stick tools and found significant differences between them

suggesting that they were specialized tools made specifically for every purpose. We studied more in detail the differences between apparently similar tools, the honey dipping tools and the water dipping tools, often with brushes made at their tips to collect the fluids. These last tools were exclusive from Comoé and have not been described at any other site. We found that total length, diameter and brush length were significantly different, suggesting that they were specialized tools. We concluded that Comoé chimpanzees had a particular culture, different from those of other populations of Western chimpanzees across Africa. Efficient protection, further research and permanent presence of research teams are required to avoid that this unique population and its culture disappears by the poaching pressure and maybe by the collateral effects of climate change.

ZUSAMMENFASSUNG

Obwohl wild lebende Schimpansen (*Pan troglodytes*) seit mehr als 50 Jahren intensiv untersucht werden, gibt es noch zahlreiche Aspekte ihrer Ökologie und ihres Verhaltens, die nicht gut verstanden werden. Jedes Mal, wenn eine neue Population von Schimpansen studiert wurde, wurden neue Verhaltensweisen und unbekannte Aspekte ihrer Ökologie entdeckt. All dieses gesammelte Wissen hilft uns, ein Modell zu erstellen, wie lange die gemeinsamen Vorfahren von Menschen und Schimpansen vor sieben bis fünf Millionen Jahren gelebt und sich verhalten haben könnten. Als wir im Oktober 2014 mit unserer Forschung begannen waren die Comoé-Schimpansen, bis auf einige Populations-Zensus von Schimpansen in der Elfenbeinküste, noch nie eingehend untersucht worden. Die letzte Zählung bevor unsere Arbeit began ergab, dass die Schimansenpopulation so stark dezimiert war, dass sie als funktionell ausgestorben erarchtet werden konnte. Zum Beginn unserer Forschung, führten wir zuerst mit neusten Methoden einen neuen detailierten Zensus durch, um den tatsächlichen Status und die Verteilung der im Comoé-Nationalpark (CNP) lebenden Schimpansen zu ermitteln. In den folgenden fünf Jahren haben wir zudem eine umfassende Studie durchgeführt, um mehr über ihre Ökologie und ihr Verhalten zu erfahren. Wir haben im CNP erstmals systematische Transekte und Datenerhebungen mittels Kamerafallen kombiniert, um eine Fülle von Erkenntnissen zu erhalten, die in dieser Dissertation nicht vollständig enthalten sind. Wir stellten fest, dass es in CNP und dem westlich angrenzenden Gebiet des Mont Tinqui nach wie vor eine nachhaltige und kontinuierliche Population westlicher Schimpansen (*Pan troglodytes verus*) existiert, wobei mindestens 131 adulte (entwöhnte) Schimpansen in unserem 900 km² großen Hauptuntersuchungsgebiet südwestlich des CNP leben. Diese Population besteht aus mindestens acht verschiedenen Schimpansengruppen, von denen wir sieben untersuchten, vier davon genauer. Wir konnten zeigen dass diese Schimpansen deutlich mehr Zeit im Wald als in den angrenzenden Savannenhabitaten verbringen. Wir stellten fest, dass Comoé-

Schimpansen mindestens 58 verschiedene Futtermittel aus Wald- als auch aus Savannenhabitaten nutzen. Zudem spielt der Konsum von Insekten, bestelhend aus mindestens vier Ameisen-, drei Termiten- und verschiedenene Käferlarven eine wichtige Rolle in ihrem Ernährungsreportoire. Die Comoé-Schimpansen jagen zudem mindestens drei Affena sowie möglicherweise Nagetiere und Duiker, und fraßen gelegentlich die großen Schnecken der Gattung Achatina. Wir fanden heraus, dass sie den typischen Mangel an reifen Fuechten in der \späten Regenzeit durch den intensiven Konsum der Rinde (Kambium) von *Ceiba pentandra* kompensieren. Alle Schimpansen im untersuchten Gebiet zeigten dieses besondere Verhalten, bei dem sie die Rinde von Ceiba Bäumen schälen. Wir konnte zeigen, dass die Schimpansen diese Bäume seit Jahren wiederholt geschält hatten, was offenbar den Bäumen keinen nachhaltigen Schaden zugefügte. Innerhalb von zwei Jahren ware die Schäden geheilt and das Wachstum nicht verringert, was schlussfolgern lässt dass die Nutzung der Baumrinde nachhaltig ist. Wir fanden heraus, dass Comoé-Schimpansen eine Vielzahl von Werkzeugen aus Vegetation aber auch Steinen herstellten und verwendeten. Das Werkzeugrepertoire umfasste Stöckchen zur Gewinning von on Ameisen der Art *Dorylus burmeisteri*, sowie Ameisen der Gattungen Camponotus und Crematogaster, aber auch von Bienenhonig produziert von der stachellosen Gattung *Melipoa* sowie von *Apis mellifera*. Die Schimpansen nutzen ausserdem Pflanzenwerkzeuge zum Termitenfischen von Macrotermes subhyalinus und Odontotermes majus, um an das Wasser in Baumvertiefungen zu gelangen, sowie für diverse andere Untersuchungszwecke. Zusätzlich verwenden die Comoé-Schimpansen Blattschwämme, um aus Baumlöchern zu trinken und lehmiges Wasser von den Salzlecken zu sammeln.

Im Rahmen ihres Imponierverhaltens schleuden sie Steine an die Brettwurzeln spezieller grosser Bäume, ein neu entdecktes Verhalten das als akkumulatives Steinerfen bezeichnet wird. Es ist wahrscheinlich dass sie Steine auch als Hammerwerkzeuge nutzen, um hartschalige Früchte wie *Strichnos spinosa* und *Afraegle paniculata* sowie grosse Landschnecken aufzubrechen. Die Schimpansen verwenden Gegenstände auch in anderen Zusammenhängen, die nicht unbedingt als Werkzeuggebrauch definiert werden können: Sie trommlen im Rahmen vom männlichen Imponierverhalten laut mit Händen und Füßen auf die Brettwurzeln von Bäumen, und zerschmettern harte Früchte, Schneckenhäuser und Cubitermes-Termitenhügel auf Ambossen aus Gestein oder Wurzeln.

Wir haben signifikante Unterschiede beim Vermessen der Stabwerkzeuge festgestellt, was darauf hindeutet, dass es sich um Spezialwerkzeuge handelt, die speziell für verschiedene Zwecke hergestellt werden. Wir haben insbesondere die Unterschiede zwischen scheinbar ähnlichen Pinselwerkzeugen für den Konsum von Flüssigkeiten (H zu verhindern, sowie die möglichen Nebeneffekte des Klimawandels zu dokumentieren.onig, Wasser) genauer untersucht. Diese Pinselwerkzeuge der Comoé-Schimpansen sind offenbar einzigartig und bislang nicht in der Literatur beschrieben. Gesamtlänge, Durchmesser und Bürstenlänge weichen je nach Verwendungszweck der Pinsel erheblich voneinander ab, was darauf hindeutet, dass es sich um Spezialwerkzeuge handelt. Wir schlussfolgern, dass die Kultur der Comoé-Schimpansen einzigartig innerhalb der der westlichen Schimpansen ist. Um diese einzigartige Population von Schimpansen effektiv zu schützen benötigt es weitere Forschung sowie die ständige Präsenz von Forschungsteams, um Wilderei

For my parents, wife and daughters who always encouraged me despite the long distance from home that this work kept me

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CHAPTER ONE

1 INTRODUCTION

1.1 IMPORTANCE OF THE STUDY OF CHIMPANZEES IN THE WILD

"Chimpanzees are always new to me" (Toshisada Nishida, 1993)

Chimpanzees are, together with bonobos, our closest living relatives (Wildman et al. 2003, Watanabe 2004, Waterson et al. 2005), sharing between 98.6 % to 98.76% of our DNA (Watanabe, 2004, Waterson et al., 2005). This strikingly small genetic difference led some authors to suggest that chimpanzees and bonobos should be included in the genus Homo, as in Homo troglodytes and Homo paniscus (Wildman et al. 2003). Besides the molecular similarities, chimpanzees share with us a complexity of behavior that produces differentiated cultures (Wrangham, 1996, Whiten et al. 1999, 2001). Culture was once defined as a uniquely human characteristic, however, research in the last decades keeps broadening this conception to include any animal species that has socially transmitted behaviors which last generations and chimpanzees have shown to have a great variety of these (Wrangham, 1996, Boesch & Tomasello, 1998, Whiten et al. 1999, Boesch, 2012). These cultures quickly degrade under human pressure and habitat destruction (Kühl et al. 2017, 2019)). Therefore, studying these animals in the wild is of the upmost importance to try to understand how our last common ancestors could have lived and adapted to their environment (Wrangham, 1996, Boesch & Tomasello, 1998, McGrew, 2001, Carvalho et al. 2009, Carvalho & McGrew, 2012, Motes-Rodrigo et al. 2019), but also to try to understand our own connection with our wild past.

It has been realized that chimpanzees are our close cousins since the nineteenth century, Darwin himself compared chimpanzees and other nonhuman great apes with humans both morphologically and behaviorally and considered them as "the best representatives of our early progenitors" (Darwin, 1874) This idea led the American naturalist Richard Garner to try to study chimpanzees and gorillas in the wild for the first time by enclosing himself in a cage in the Gabonese jungle (Garner 1896). Nevertheless, until the mid-20th century, chimpanzees were mainly studied in captivity, advancing especially on the cognitive aspects (Yerkes, 1943) and most of the reports of their behavior in the wild were given by hunters that made comments about their "lack of bravery", although sometimes made interesting naturalistic observations (Aschemeier, 1922). In the meantime, a series of discoveries of *Australopithecus* fossils in South Africa (Dart, 1925) fueled the idea that fossil hominids had many features in common with chimpanzees.

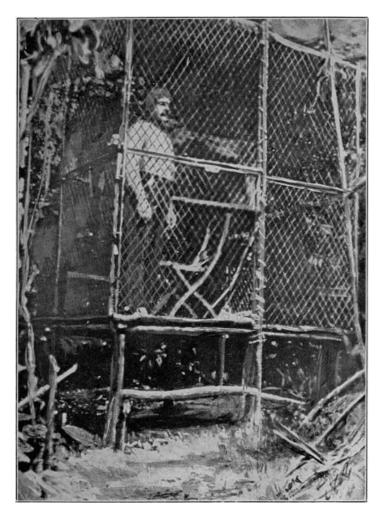


Fig. 1 Prof. Richard L. Garner in his cage in the jungle of Gabon, trying to make direct observations of wild gorillas and chimpanzees. Some of his statements have resulted to be incorrect, like the duration of pregnancy for female chimpanzees, but his effort to observe the natural behavior of great apes, in a time when this was considered to risk own life, was pioneering and opened the path for many others (Picture taken from Gorillas & Chimpanzees, R. L. Garner, 1896)

The famous anthropologist Louis Leakey, who had been looking for traces of human ancestors in Tanzania from the 1930s, found a series of puzzling fossils by the end of the 1950s and beginning of the 1960s (Leakey, 1959, 1964) but he soon realized that, to reconstruct the hypothetical ecology and behavior of those fossil hominids, he needed to know more about these aspects from the closest extant models available, the great apes. Leakey sponsored, among many other students, the famous "Trimates", Dian Fossey with mountain gorillas (*Gorilla gorilla beringei*) Birute Galdikas with orangutans (*Pongo pygmaeus*) and Jane Goodall with Eastern chimpanzees (*Pan troglodytes schweinfurtii*) that took research on free-living nonhuman great apes to a new level by habituating them and observing their behavior in the wild. Perhaps less famous in the Western countries, but no less important for the research of wild chimpanzees, Toshisada Nishida started an ongoing long term project in Mahale, Tanzania in 1965 (Nakamura et al. 2015), that rivals in longevity and scientific production with the one that Goodall created in Gombe, Tanzania, in 1960 (Goodall, 2010). Other pioneering works, like the one that Reynolds initiated in Uganda (Reynolds, 1963) had to wait until 1990 to become a stable long term

project (Reynolds, 2005). While in East Africa stable long term projects were created, in Central Africa there were also pioneering field works that widened the knowledge of Central chimpanzees (*Pan troglodytes troglodytes*) like the ones in the former Belgian Congo, now R.D.C. (Kortlandt, 1962) or Equatorial Guinea (Jones & Sabater Pi, 1969) which sadly did not have continuity, due to the troubled decolonization processes. Only much later, permanent long term projects have been established in this region to study chimpanzees of Goualogo, Congo (Sanz & Morgan, 2010) and important field work realized in previously unprospected areas such as Bili-Uéré (Hicks et al. 2014, 2019).

It was more than a decade later when research of wild West African chimpanzees (*Pan troglodytes verus*) started with projects in Senegal, Guinea and Ivory Coast that we detail in the next section. The last area where long term projects started to establish was the one inhabited by the most recently defined chimpanzee subspecies (*Pan troglodytes ellioti*), comprising part of Cameroon and Nigeria, where the Gashaka Primate Project is based (Sommer & Ross, 2011b).

Many other projects have developed along these years, both short and long term, to study different aspects of the ecology, behavior or human-chimpanzee interaction, the list of studies would be very long to summarize here, but they all contributed to the knowledge of wild chimpanzees by discovering new behaviors, interesting ecological adaptations, particularities of the diet or carrying out censuses or genetic research. A mega-project that aimed to collect as many data as possible from more than 40 different chimpanzee communities all across Africa, using a standardized methodology was the recent Pan African Programme – The Cultured Chimpanzee" (PanAf) (Arandjelovic et al. 2014). The aim of all this vast body of research was to search for variables, ecological, genetic, behavioral, human influence, etc. that could explain the diverse behavioral responses and ecological adaptations and solutions showed by wild chimpanzees. Every local project by itself can try to answer to mostly local questions with their research, while putting all the data of all this accumulated knowledge together, patterns can be detected and general explanations to general trends can be found. Thus, every contribution from every local study site has great importance to piece together the chimpanzee puzzle.

1.1.1 Research and conservation of wild chimpanzees

Finally, we have to consider that nowadays, human pressure, habitat destruction, poaching and even diseases, both natural and transmitted by humans are putting chimpanzees in the brink of extinction (Kühl et al. 2017, Hoffmann et al. 2017), while the permanent presence of research teams in the field has been proved to help to the conservation of the wild chimpanzees (Pussey et al. 2007, Wrangham & Ross, 2008, Campbell et al. 2011). Therefore, the only ethical way to keep learning from these great models of what could have been the behavior of our last common ancestors is by preserving them and field research of wild chimpanzees is an instrumental tool for this. The chimpanzee was once abundant and widely distributed across most of West, Central and East Africa (Butynski et al. 2001), but recently has seen a precipitous population decline across its range. In West Africa, populations of the Western chimpanzee have decreased by an 80 % in the last 24 years (Kühl et al. 2017) mainly due to habitat destruction and poaching. It is therefore urgent to study the remaining populations, not only to learn about their ecology and behavior, but also to learn how to implement managing measures to slow or stop their decline (Arandjelovic et al., 2014, Hicks et al. 2014, Lapuente et al. 2016, Hoffman et al. 2017, Kühl et al. 2017, 2019). It is ethically untenable for us to benefit from studying our closest cousins without taking steps to ensure their conservation and with them, their unique cultures, transmitted generation by generation for thousands of years.

1.2 PREVIOUS RESEARCH ON CHIMPANZEES IN COMOÉ AND NEARBY REGION

Western chimpanzees (*P. t. verus*) are the most threatened subspecies of chimpanzee (Kühl et al. 2017). Their range has been heavily reduced along the twentieth and the present centuries, to the point that they have been extirpated from several countries, Benin, Togo, Burkina Faso and in others are close to their extinction (Gahna, Mali). Even in Ivory Coast, where research projects have been working for several decades, their effectives have been reduced by a 90 % between 1991 and 2007 (Campbell et al. 2007) However, chimpanzees are thriving in Ivory Coast exclusively where research projects have sheltered them (Pussey et al. 2007, Campbell et al. 2011, N'Goran et al. 2013, Lapuente et al. 2016), thus, the establishment of sustainable research projects in the field is of instrumental importance for chimpanzee conservation.

Western chimpanzees have been studied in the rainforest by a few long term ongoing projects, such as the one in Bossou, Guinea, started in 1976 which investigated in detail many aspects of he ecology, the nut-cracking behavior and described other tool behaviors that have only be found there by now, such as pestle-pounding or push-pull leaf-sponging (Matsuzawa et al. 2011) or the one in Taï forest, Ivory Coast, that started in 1979 (Boesch & Boesch-Achermann, 2000, 2019). Savanna chimpanzees in West Africa started to be studied by the same time in Mont. Assirik, Senegal (Baldwin, 1979), although this site never developed the same habituation process as the previous and has not sustained a continuous long term project. However, also in Senegal, at the site of Fongoli, a long term project started in 2001, has habituated the chimpanzees and continues in the present, discovering behaviors such as the use of spears to hunt galagos, bathing in ponds or the use of caves to coold down (Pruetz, 2006).

Chimpanzee research in Ivory Coast has been mainly concentrated in Tal forest, through the Tal Chimpanzee Project that has worked continuously for 40 years, making major contributions to the knowledge of hunting, nut-cracking and other ecological aspects, tool and social behaviors (Boesch & Boesch-Achermann, 2000, Boesch, 2019). In the rest of the country, mostly general surveys have been realized with the aim to know about the status and distribution of chimpanzees (Hoppe-Dominik, 1991, Marchesi et al. 1995, Campbell et al. 2008). The exception was the study of Boesch et al. (1994) intended to search for the limits of nut-cracking behavior, through the indirect signs that the behavior leaves, such as nut cracking sites. The limit was found at Sassandra-Nzo rivers, West of which nut-cracking extends across Ivory Coast, Liberia, Guinea, reaching East Sierra Leone, while there are no traces of this behavior in Western chimpanzees East of these rivers (Boesch et al. 1994).

Apart from the long term research sites, many short term research initiatives have produced data about the behavior of Western chimpanzees living in forests: tool use and predatory behavior in Tenkere, Sierra Leone (Alp, 1993), habitat use and diet in Bafing, Mali (Duvall, 2008), tool use and ecology in Sapo, Liberia (Anderson, 1983), tool use and diet in Bakoun, Guinea (Boesch et al. 2016), the tool use and ecology in Mont Nimba and Seringbara (Humle, 2003, Matsuzawa et al. 2011), both in Guinea and the diet and ecology Cantanhez NP, Guinea-Bissau (Bessa et al. 2015). Besides the previous examples, many other shorter surveys, mostly censuses have been carried out across all the region, allowing to estimate population sizes and distribution in most countries of the region (Kormos et al. 2003) including the recent good new of finding a relic population of chimpanzees in Ghana (Tehoda et al. 2017). Adding to this body of knowledge, the larger scale initiative of the PanAf Programme has started to produce data that cover the whole region (Kühl et al. 2016, 2017, 2019).

The same general surveys that covered most of Ivory Coast can be applied as the only studies of chimpanzees in Comoé National Park (CNP) prior to the present one (Hoppe-Dominik, 1991, Marchesi et al. 1995, Campbell et al. 2008, Lapuente et al. 2016). Hoppe-Dominik did not actually survey CNP, but he estimated that a population of 250 chimpanzees probably lived in the park based on interviews and assuming that the density was similar to other savanna sites. Marchesi et al. (1995) and Campbell et al. (2008) used the same method, with limited survey effort, as we detail in chapter 3. There was an initiative that was frustrated by the Ivorian Civil War (2002) to create a primate laboratory to study chimpanzee behavior by French scientists of IRD, although they only provided an anecdotal description of chimpanzee behavior in Comoé within a publication that reported mainly the behavior of chimpanzees in Senegal (Galat et al. 2008). Apart from these surveys realized by primatologists, opportunistic observations of chimpanzees have been done in CNP by other zoologists or naturalists (GTZ, 1979, Galat & Galat Luong, 1985, Fischer & Gross, 1999, Lauginie, 2007). In 2013, while working for MPI-EVAN, the author realized a fast survey of CNP and the neighboring GEPRENAF area, to locate chimpanzees. We found many more chimpanzee traces in the latter than the former and thus advised MPI to work in GEPRENAF, where they sent a student for a one year study in 2013-2014, whose data became a part of some recent publications (Kühl et al. 2016, 2017, 2019). However, We are the first to research and publish specifically on the ecology and behavior of Comoé chimpanzees (Lapuente et al. 2016).

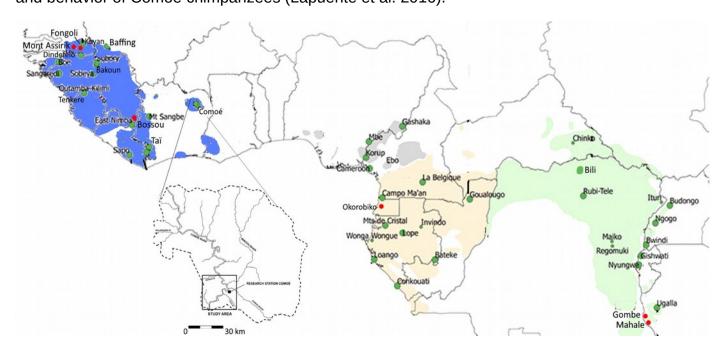


Fig. 2 Location of chimpanzee research sites across Africa. Green dots are temporal research sites where the PanAf programme collected data and samples for periods of around a year. Many of the sites marked with green dots are also older research sites mentioned in the text above. Comoé also provided data for the PanAfrican programme. Red dots indicate other famous long term research sites mentioned in the text that were not included in the programme. Shaded areas correspond to the current known distribution of the different subspecies of chimpanzees. Dark blue is Western chimpanzee (*Pan troglodytes verus*), grey is the Nigerian chimpanzee (*P. t. ellioti*), pink is the Central chimpanzee (*P. t. troglodytes*) and light green is the Eastern chimpanzee (*P. t. schweinfurtii*).

Modified from http://panafrican.eva.mpg.de/english/approaches and methods.php

1.3 RESEARCH QUESTIONS

When we began this research, we knew nothing about the ecology or behavior of Comoé chimpanzees and very little information was available from previous general surveys. Actually, the last three consecutive surveys of CNP had failed to find any significant traces of chimpanzees so the consultants even suggested that the population of the park was functionally extinct (WCF, 2009, 2010, 2012). However, the author had been doing a fast survey for MPI-EVAN in 2013 of the area where chimpanzees had been last seen (Lapuente et al., unpublished data). During this survey, the author found a few nests, indicating that there were at least some chimpanzees left to study. Thus, we had little hopes to find a healthy population that allowed to do a long term study and we were thinking about a few basic scientific questions that could be answered even if the population was really decimated:

- 1 What is the current status and distribution of Comoé chimpanzees?
- 2 What was their diet?
- 3 What use they do of their habitats and which ecological adaptations they presented?
- 4 What tool-use and other cultural behaviors are present in Comoé chimpanzees?
- 5 How can their particular behaviors help them to survive in the harsh savanna conditions of Comoé?

1.4 AIM OF THIS DISSERTATION

The aim of this dissertation is to present the knowledge that we accumulated over the last five years about the status and distribution of Comoé chimpanzees, their diet, habitat use and special behaviors and adaptations, including tool-use, which helped them to live in the particular conditions of the savanna-forest mosaic of Comoé. We also intend to propose management measures based in the conclusions of this dissertation that we hope should help to preserve this population of chimpanzees with the support of a sustainable long term project. This thesis was aimed to fill an absolute lack of knowledge on all the aspects of the life of the chimpanzees of Comoé. The results produced should be used as the base of all future studies of these chimpanzees and their habitat. Ideally, there should be a continuation of this effort through the maintenance of a long term project to study and protect Comoé chimpanzees.

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CHAPTER TWO

2 THE COMOÉ CHIMPANZEE CONSERVATION PROJECT (CCCP)

With the aim of documenting a new chimpanzee culture and improving our knowledge of the distribution of Western chimpanzees, we began this research project in October 2014 without the certainty of having a sizable population of chimpanzees in CNP to study (WCF, 2010, 2012, 2014, Lapuente et al. 2016). Excitingly, in the first weeks of our fieldwork, we acquired information that we had a healthy population with many scientifically interesting ecological and behavioral aspects. As we stated in the last chapter, it is no longer considered ethically acceptable to conduct research on the critically endangered Western chimpanzee (CR, IUCN) without contributing to its conservation. Thus, in 2014 Juan Lapuente created the Comoé Chimpanzee Conservation Project (CCCP) with the support of Prof. Linsenmair, as a scientific research project which would also aim to contribute to the conservation of this unique chimpanzee population.

2.1 STUDY AREA

2.1.1 Why the CNP? Some history

Covering 11,487.57 km², CNP is the largest protected area in Ivory Coast. Limiting with the park to the SW, there are the classified forest of Kinkené and the Special Zone of Biodiversity of Mont Tingui (fomer GEPRENAF) and limiting to the NW, the zone of Mont Warigué, adding, in total, a less protected natural area of around 3,000 km² more (OIPR, 2016, Lapuente, 2017, 2018). The park harbors relatively well preserved forest and savanna habitats that were influenced at some point by the long human presence in the park (Chenorkian, 1983, Raymaekers, 1998), but did not lose their diversity and integrity.

Comoé was declared a national park in 1968 on the basis of a previous Bouna Reserve which had itself replaced the hunting refuge of the same name created in 1927 (SCPN 1962, GTZ, 1979). The CNP was classified as a Biosphere Reserve in 1982 and a UNESCO World Heritage Site in 1983. This latter status passed to be considered in danger in 2003, due to surveillance problems and the great impact of illegal activities during the politico-military crisis (2002-2011). Heavy poaching pressure was already a problem in the 1980s and 1990s (Fischer et al. 2002) with reports complaining about the lack of efficient surveillance by the former service of "Eaux et Forêts". Poaching on elephants resulted in the reduction of their population in the park to a 10 % of what was estimated in 1982 (Lauginie, 2007, Lapuente 2017). After the crisis, the new manager of the park, the "Office Ivoirienne de Parcs et Reserves" OIPR slowly improved the surveillance and biomonitoring activities, with the support of their partners, the Comoé Research Station (CRS), the German cooperation (GIZ), the German bank for cooperation (KFW) and others. At the same time, the research carried out by the CCCP which showed that key species such as the elephant, chimpanzee, leopard and buffaloes still had sustainable populations, helped to regain World Heritage status for the park in 2017 (Lapuente, 2017, 2018). The author also helped the OIPR to improve their biomonitoring system with 11 training courses about sampling and analysis techniques and fauna identification CRS.

Chimpanzees have been known to inhabit the park from shortly after its creation (GTZ, 1979) but were never studied apart from some nest counts in general surveys (Hoppe-Dominik, 1991, Marchesi et al. 1994, Campbell et al. 2008, Lapuente et al. 2016,

2017, 2018). Savanna chimpanzees had never been studied in Ivory Coast. From the results of nationwide surveys, we suspected that the chimpanzee population in the park and limiting area of GEPRENAF was the only significant population of savanna chimpanzees left in the country (Campbell, 2008, WCF 2009, 2014, Lapuente et al. 2016). Thus the study and preservation of these chimpanzees was of the highest importance. This led us to begin our study in CNP in 2014.

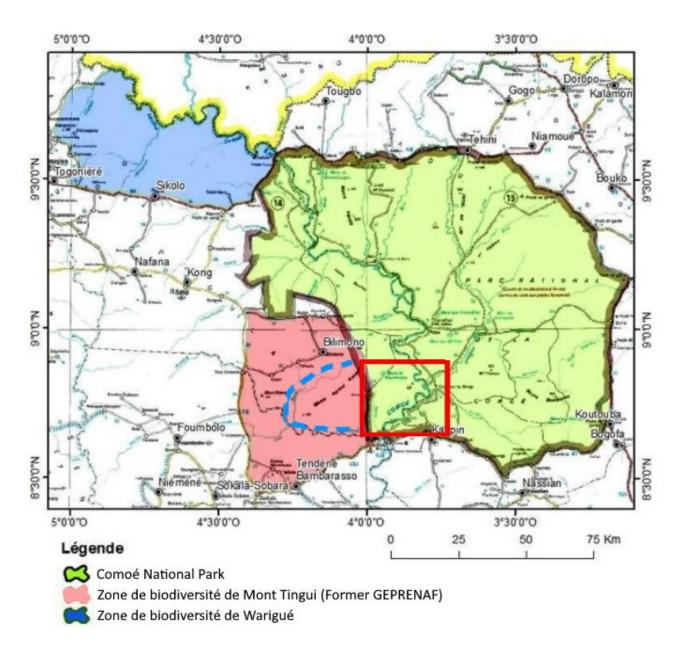


Fig. 1 Map of the Comoé National Park (green shade) with the neighboring areas of Mont Tingui (Pink shade) and Warigué (Blue shade). The red square indicates our main study area whitin the park, along the whole period, 2014-2019. The blue dashed line indicates the area of Mont Tingui where we started working with smaller sampling effort in 2018. Map modified from OIPR.

2.1.2 Physical environment, climate

The relief of the park is relatively flat, with an average altitude above sea level of around 230 m and some little ranges and hills that reach up to little more than 600 m (Hennenberg, 2005). The park is crossed from North to South by the Comoé river, which gives its name to the park. This big river receives its most important tributaries in the park from the left side, with rivers that never completely dry during the dry season, like Wabe, Boin or Iringou rivers. The tributaries coming from the right side within the park become completely dry during the dry season or just retain small puddles, but are the most used ones by the chimpanzees, like Gondo, Iberá or Kinkené. The climate is dry and warm with a mean annual temperature of 27 ° C and precipitation around 1090 mm, when estimating the average between the meteorological stations that are the closest to the park, Bouna, to the East and Dabakalá, to the West (Hennenberg, 2005). However, in our study site, SW of the park, a mean of 1010 mm was measured from 1993 to 2000 (Fischer, Gross, & Linsenmair, 2002) and during our five years study period (October 2014-October 2019), we recorded an annual mean precipitation of only 925.5 mm and a mean temperature of 26.79° C. The dry season lasts from the second half of October to the second half of April, with only some scattered rainstorms, while the rainy season lasts from mid April to mid October, with the highest precipitation peaks in May and September.

2.1.3 Habitat, vegetation and history of use

The CNP is located in the transition zone between the biogeographical Sudanian belt of savanna and the more forested formations of the Guinean domain. Due to its biogeographical situation and the passage of the Comoé river over a length of 230 kilometers, the CNP harbors a wide variety of habitats and a great biological diversity. Around 720 plant species have been described in the park (OIPR, 2016).

Within the park, the cover of forested habitats has been estimated to be 9 % (Hennenberg, 2005, OIPR, 2016), although in the Southwest, our main research area, the forest cover is around 13 % (Lapuente et al. 2016), while the rest of the surface is covered by savanna habitats that are mainly woody and bushy savanna, with a small proportion of open grassland (less than 5 %). The classification of the habitats that we followed is mostly inspired by the French school (Riou, 1995, Lauginie, 2007), since this is the one used by the park managers and applied in most reports of the park. All the habitats that have a discontinuous tree canopy and a continuous (unbroken) grass stratum are included in the category savanna. French botanists distinguished in this classification between treesavanna, bush-savanna and grass savanna, which are equivalent of the above mentioned woody savanna, bushy savanna and open grassland. In Comoé, there are only small portions of the savanna that are totally deprived of trees due to the extremely thin soil that cannot support the root system, these are locally called "boals". The rest of savanna habitats in Comoé have at least some tree cover. Therefore, when we speak about grasslands or grass-savanna (excluding the above-mentioned boals) we refer to savannas with a very small proportion of trees and/or shrubs, inferior to the 30 % of the cover, while grass covers 100 %. When we speak of bushy savanna, we have 30-60 % of shrubs, but very few trees and when we speak about tree savanna or woody savanna, we have usually between 30-60 % tree cover, with some shrubs and always a 100 % cover of grass. For habitats with higher cover of trees, with portions of semi-continuous tree canopy, even if they contain a more or less continuous grass layer, we would be speaking about open or clear forest, which in most cases in Comoé, appears associated to ancient human settlements. Some authors have used the term woodland to refer to this last type of tree dense savanna (Pruetz & Bertolani, 2007, Piel et al. 2017), however, this term has also been used to refer to more dense, forest-like habitats, which could lead to confusion. Therefore, for the rest of this dissertation, when we use just the term savanna without further details is to refer to all the different types of savanna in contrast with the closed forested habitats. To refer to any specific type of savanna, grassland, bushy or woody savannas, we will add the corresponding adjective.

There are two main types of forest habitats in Comoé, gallery forest and the forest islands. Gallery forest growing along the main rivers, the Comoé and Iringou, is dominated by *Cynometra megalophylla*, an evergreen tree which needs clay-rich soil. Gallery forest growing on the riverbanks of seasonally-drying streams is much more rich in deciduous species, such as *Cola cordifolia*, *Detarium senegalense*, *Berlinia grandifolia*, *Albizia zygia* and others. Forest islands are not linked to water courses, but grow on the interfluvia, atop plateaus ranging from a few meters in elevation to 80 m above the surrounding landscape. In addition, Comoé has semideciduous forest islands, including a high proportion of evergreen trees, such as *Cynometra megalophylla*, *Diospyros abissinica*, *Dialium guineense*, *Dripetes floribunda*, *Tapura fischeri*, as well as are dry forest islands, dominated by deciduous species, such as *Annogeissus leiocarpus*, *Albizia adianthifolia*, *Celtis integrifolia*, *Celtis zenkeri*, *Antiaris toxicaria*. In both types of forests, there can be up to three strata, with the largest canopy-breaking trees exceeding 40 m, such as *Ceiba pentandra* and *Millicia excelsa* (Mühlenberg, 1990, Hennenberg, 2005, Lapuente et al. 2016).

In our study area, we found signs of recent forest disturbance by illegal logging of *Millicia excelsa* (Iroko) during the political-military crisis (2002-2011). Based on interviews with locals, most of this logging happened between 2003-2006. Illegal loggers entered with machines only West of the Comoé river, but reached every forest patch, extracting the biggest trees. During our study we found that the forest had in many places completely overgrown the traces of logging, while in a few places, there were still visible dirt roads or ditches. Secondary vegetation growing in these disturbed areas was rich in vines and herbs and produced attractive fruits, thus, it was intensely used both by elephants and chimpanzees.

The park was inhabited prior to its declaration in 1968, mostly consisting of small settlements of less than 100 people, with a few exceptions such as Gawi, Komandimi or Timingo (these can still be found on road maps which have not yet been updated). All these villages were evacuated following the declaration of the park; people then settled in the periphery. The exception was the small village of Gorowi which resisted relocation and is still at its former position in our main study area, inside an indentation of the park limit. Older and smaller settlements can be detected by the presence of baobab trees (Adansonia digitata) which are not native to this area, but planted by settlers when creating a new camp. In some cases, we could still find traces of old settlements such as cleared forest with mounds of earth which were once old mud-brick houses. It is difficult to evaluate the impact that all of this human activity had on the structure of the vegetation, since there are many degrees of recovery. Further research would be needed to establish the chronology. Nevertheless, in many forest patches, we can find "holes" of several hectares in the canopy covered by lianas and bushy vegetation which, in most cases, could have originated from the slash and burn agriculture practiced by the previous inhabitants. We need to take into consideration that the park has been inhabited since at least the Neolithic Era, around 3500-3700 B.P., as demonstrated by the abundant pottery remains and lithic tools that can be found all across the park (Chenorkian, 1983, Raymaekers, 1998).



Fig. 2.2 Aerial view from a drone (300 m above the ground) of a dry forest island used by the chimpanzees in the home-range of Aeneid community. Image was taken in the first half of the rainy season, when all the trees have full grown leaves. The more open vegetation that surrounds the island is bushy savanna, with less than thirty percent of tree cover, and the grayish vegetation on the upper part is woody savanna with high tree cover (Photo Christophe Servant).

Another practice that has surely influenced the structure of the vegetation is the seasonal burning of the savanna, which is carried out traditionally at the beginning of the dry season when the forest is still moist. This means that the fire only burns the savanna grass and stops at the edge of the forest. Nowadays, park rangers have taken over this work and burn the savanna in a controlled manner to avoid later uncontrolled burning by poachers (Mühlenberg, 1990, OIPR, 2016). Much discussion has taken place regarding the role of fire in creating anthropic savannas in these areas (Maley & Livingstone, 1983, Mühlenberg, 1990, Hennenberg, 2005). Further research is needed to understand to what extent the fire has changed the forest cover in this region, which is already climatologically favorable to savanna habitats.

It is difficult to know also the impact that historical human presence in the park might have had on the chimpanzees and their behavior. Locals avoid consuming the meat of chimpanzees because they consider them too similar to humans, although they sometimes kill chimpanzees to avoid damage to the crops or to use their bones in their traditional medicine (Fischer et al. 2002, interviews to locals). We found that chimpanzees did not avoid the historically inhabited areas, but given that the settlers left the park more than 50 years ago, this is not surprising. However, we cannot discard the possibility that chimpanzees inhabited areas of the park that are currently without them, since according to elder we interviewed, they also inhabited forests close to nearby villages such as Zamu, until 50 years ago, while they are absent from these areas now.

Apart from the illegal logging of Iroko, other illegal activities that caused disturbance after the creation of the park have been: 1. poaching, which has been constant, peaking during periods of unrest or neglected surveillance (Fischer et al. 2002, 2004); 2. illegal

fishing along the Comoé and Iringou Rivers; 3. artisanal gold mining, especially in hilly areas; and 4. cattle herding, which, although not common in our research zone, was very active in the north and east of the CNP and across the entire Mont Tingui zone. Luckily, encroachment of farming activities has not been a problem in the CNP, although a few illegal farms of "manillet" and cashew nut have sprung up in forested areas close to the western limit of the park (Amaradougou and Gorowi Villages). Since the condition imposed by UNESCO for the CNP to recover its World Heritage status was the elimination of illegal farming within the park limits, the solution found by park managers to avoid conflict was to change the limits of the park, giving away 74 km² to these villages, which came from within our study area.



Fig. 2 Woody savanna in CNP in the dry season (March). Only the blackened portion in the middle has been burnt, while the ocher color areas correspond to unburnt elephant grass. We can see a forest patch in the top left corner, where most of the trees have no leaves yet. Image taken by a drone flying at around 60 m above the ground.

2.1.4 Fauna

The CNP is home to around 152 mammal species, including 11 primates, 12 carnivores and 21 artiodactyls. There are also 35 species of amphibians and 500 species of birds living in the reserve, and in the waters of the Comoé River and its tributaries are found 70 species of fish and three species of threatened crocodiles: *Osteolaemus tetraspis, Crocodylus suchus* and *Mecistops cataphractos* (Fischer et al. 2002, Lapuente, 2018).

Among the mammals, the forest elephant, *Loxodonta cyclotis*, has been confirmed via DNA studies to be the sole proboscidean species to inhabit the park (Lapuente et al. unpublished). Elephants share the same habitats with the chimpanzees, although the latter avoid the former. Other large mammals include the hippopotamus *Hippopotamus* amphibius, the buffalo, Syncerus caffer and many antelopes, including roan antelope Hippotragus equinus, hartebeest, Alcelaphus bulselaphus, waterbuck, Kobus ellypsiprimnus, the kob Kobus kob, bushbuck, Tragelaphus scriptus and bongo, Tragelaphus euryceros (the latter species we confirmed to be present in the park for the first time with our camera traps). Five species of of duikers are present: Cephalophus sylvicultor, C. niger, C. dorsalis, C. rufilatus and Philantomba maxwelli and royal antelope *Neotragus pygmaeus.* Among the carnivores, we have confirmed the presence of twelve species of small and medium size: common cusimanse, Crossarchus obscurus, white tailed mongoose, *Ichneumia albicauda*, marsh mongoose, *Atilax paludinosus*, ichneumon, Herpestes ichneumon, three genets, Genetta genetta, G. pardina and G. thyerri, honey badger, Mellivora capensis, golden cat, Profelis aurata, serval, Leptailurus serval, civet, Civettictis civetta and jackal, Canis adustus. Two larger carnivores capable of eating chimpanzes are present as well: the leopard, Panthera pardus and the hyena, Crocuta crocuta. Three species of pangolins are present witin the park: the giant pangolin, Smutsia gigantea, the white-bellied pangolin, Manis tricuspis and the black-bellied pangolin, Pathaginus tetradactyla. Aardvarks, Orycteropus afer, are present as well. There are three species of hogs, the giant hog *Hilochoerus meinertzeghani*, red river hog, *Potamochoerus* porcus and warthog, *Phacochoerus africanus*. Among the larger rodents, we confirmed the presence of seven species: crested porcupine, *Histrix cristata*, brush-tailed porcupine, Atherurus africanus, greater cane rat, Thrionomys swinderianus, giant poached rat, Cricetomys gambianus and three squirrels Funisciurus pyrropus, Heliosciurus rufobrachium and Protoxerus stangeri.

Primate abundance and diversity is high, but was likely reduced by hunting over the last decades. Besides the Western chimpanzee, *P. t. verus*, we confirmed the presence of the olive baboon, *Papio anubis*, the white naped mangabey, *Cercocebus lunulatus*, the green monkey, *Chlorocebus sabaeus*, Lowe's monkey, *Cercopithecus lowei*, lesser putty nose monkey, *C. petaurista*, olive colobus, *Procolobus verus*, white thighed colobus, *Colobus vellerosus and prosimians*, *Perodicticus potto*, *Galago senegalensis* and *G. demidovi*. Other species that had been cited previosuly as occurring in the park, such as *Cercopithecus nictitans* and *C. roloway* (Fischer et al. 2002), could not be confirmed by us (Lapuente, 2016, 2017, 2018).

2.2 THE WORK OF THE CCCP

As we mentioned above, this research project has been conducted within the framework of the project CCCP, which was created by the author with the support of Prof. Linsenmair. During most of the study period, the base camp was the Comoé Research Station (CRS) where we slept, worked on logistics and conducted laboratory work and data analysis. We selected our field assistants from the village of Kakpin. We began in 2014 with two assistants, had hired four by the end of 2015, reaching up to seven assistants by the end of 2016 which in 2019 was reduced to a smaller team of four. We trained the assistants to use GPS, to enter data onto paper datasheets, to take photos and measurements, to identify a number of plant and animal species and to check the camera traps and change their batteries and SD cards (Lapuente et al. 2016, 2017, 2018). This hard-working team of local assistants made the field work possible along the whole study

period and our work benefited greatly of their traditional knowledge on animals and plants and their tracking ability.

For transportation along the few roads that fell within our study area, we used CRS project cars. However, we walked most of the time, when we traveled into chimpanzee territory, since there were no roads in the main area inhabited by the chimpanzees. We crossed the Comoé River thousands of times (literally) using inflatable boats when the water was high. Luckily, a few months per year when the water was low, we could cross the river by foot..

Once per month we organized trips using the project vehicle to the nearest town of Bondoukou to buy materials and food. We created two main field camps, a semi-permanent one at the core of the home-range of the Odyssey community (Camp Nord), that was semi-permanent, with students and assistants using it for several months in a row, and the other, a permanent camp, was located at the limit between the home-ranges of the Achean and the Trojan communities, with assistants and/or students occupying it all year around (Camp Ouest). We carried all of the equipment and food to these camps in backpacks, which was a day-long march. From there, we operated in all the directions by foot, carrying only the basic daily equipment. When the team was large enough, we divided up into up to four sub-teams to carry out a wide range of tasks.

Many students from different countries participated in the project to do their own research, PhD, Masters, graduate thesis, or to get field experience as volunteers. We devoted a lot of time to their training, sampling design, research conception, general supervision...in exchange, they helped to collect data and analyze some samples and mainly contributed to keep the project going on. Special attention deserve the African students who got involved in our research, since they should take over in the future of the protection of the natural resources of their country.

The collaboration of the CCCP with local authorities and park managers has been constant, since they should take care of the surveillance and management of the chimpanzee population. We shared with them all the data, including coordinates, of the illegal activities that we detected, trying to get the park rangers in the spot as soon as possible. We also realized 11 training courses for the park rangers and the biomonitoring team of OIPR at the CRS, contributing to their knowledge of the resources of the park and giving them some scientific management tools.

Between October 2015 and April 2017, we worked in collaboration with The Max Planck Institute for Evolutionary Anthropology (MPI-EVAN). They provided economical support and materials with which we could sample more intensively a wider area collecting many of the ecological data that have been used for this dissertation. The author also got research grants from Fundació Barcelona Zoo, Arcus Foundation, US Fish & Wildlife Service, which helped to keep the research going on for the five years, and support in 2019 from KFW for a great predator survey which indirectly helped to get some of the data used for this dissertation.

2.2.1 Selection of the specific study area

To decide the placement of our main study area, where most of the work included in this dissertation was realized, we took into consideration several factors:

- 1 The area where chimpanzees had been located for the last time by previous surveys
- 2 The area with the highest potential amount of chimpanzee habitat
- 3 The area that allowed us easiest access from our CRS operation base

All the previous chimpanzee transect surveys that had located chimpanzee traces, found them in the southwest corner of the CNP (Marchesi et al. 1995, Campbell et al. 2008, WCF, 2009). These researchers also found some traces in the northwest of the park, around the Kolonkoko River Valley, but this area was extremely difficult to access during our study, requiring a two days car trip to reach it from our base, so we did not make use of it for most of the aspects of our study. Nevertheless, in 2016 we made a quick exploration with 45 km of recces. In 2017, we collaborated with OIPR, searching for chimpanzee traces during the elephant surveys, including this area (Lapuente et al. 2017, 2018). We also conducted a large carnivore survey in this area in 2019, during which we again looked for chimpanzees. We found no traces of chimpanzees in any of these surveys, which reinforced our decision to focus our efforts in the southwest.

The author had also completed a quick survey in 2013 while working with the MPI-EVAN PanAfrican Project, looking for chimpanzees within the CNP and the neighboring area of GEPRENAF. While we located abundant chimpanzee traces in the latter, we found only six nests in the former, thus, we adviced the MPI to work in GEPRENAF. They sent a student that worked for a year there. Local villagers also insisted that the chimpanzees only lived in that part of the park and Prof. Linsenmair and his students had seen them a few times in that area before the civil war (Fischer et al. 1999, 2002). Therefore, when Prof. Linsenmair and the author decided to look for a chimpanzee population to study in CNP, the first option to start searching was this area in the SW and specifically, the area where Juan Lapuente had found the last chimpanzee nests in 2013. We updated our methodology with respect to the ones used by previous surveys, combining the use of camera traps with reconnaissance walks (recces) focused on forest patches, which we localized with coordinates obtained from the Geo-referentation of satellite images. In the majority of the forest patches we explored West of the Comoé River, we found a healthy population of chimpanzees, documenting abundant traces, nests, tools, faeces and footprints, as well as numerous vocalizations and drummings, along with videos. We wanted to know how widespread this population was, so we decided to install a study area of 900 km² at the SW corner of the CNP, which left the CRS close to the center of the area, conveniently strategic. Both the villagers and all the researchers that made previous surveys stated that chimpanzees never lived permanently East of Comoé river, within the park (Marchesi et al. 1995, Fischer et al. 1999, 2002, Campbell et al. 2008, WCF, 2009), but, after his first surveys, the author did not find ecological differences in the forests that would justify the absence of chimpanzees East of the river, thus, we included as much study area East as West of the river. A few months after starting the study, the author did find chimpanzees East of the river, which resulted a small community that lived permanently there, as we confirmed along our study (Lapuente et al. 2016, 2017, 2018).

During the final years of this study, (2018, 2019) we continued working in our main study area, within the CNP, but we added the neighboring in the Zone de Biodiversité Special de Mont Tingui (former GEPRENAF), where we worked with smaller sampling effort . We found that poaching and gold mining had greatly increased in that zone out of the park and cattle herders roamed the area for the whole dry season. Despite all these disturbances, we found that at least one chimpanzee community was still thriving there and decided to include them in our study.

2.2.2 Work with camera traps

The author had previous experience working with camera-traps in Spain and just before this study, he used them, while working for two years for MPI-EVANin the study wild chimpanzees in Taï NP, Ivory Coast,. The author knew from experience the potential of camera-traps to reveal secretive and cryptic animals. Most of the fauna in CNP had

become invisible prior to our work, partly due to the politico-military crisis (2002-2011) that had left the park unsurveyed for several years. Actually, surveillance was not fully implemented yet and fishermen's and poachers' camps were found very frequently, especially along the gallery forest of Comoé river (Lapuente et al. 2016, 2017, 2018). Many species were assumed extinct or almost extinct as most surveys failed to find their traces, including the chimpanzees, elephants and great predators (Fischer, 2004, WCF, 2010, 2012, 2014). Camera traps had never been used before in CNP, thus, the author was confident to obtain footage of many species that survived the civil war and were still hiding in the bush. As a matter of fact, we started collecting footage of species that had not been directly observed for years, including hyenas, hippopotamuses, elephants and chimpanzees within the first two weeks of work. We recorded even the bongo (Tragelaphus euryceros) that had never been confirmed in CNP before and was only suspected to live there from doubtful dung and footprints. We also obtained the first footage in the wild of white naped mangabeys (Cercocebus torquatus) we confirmed the survival of the giant pangolin (Smutsia gigantea) and we described, for the first time, the presence of black bellied pangolin (Pathaginus tricuspis) in the park (Gudehus et al. 2019).

Camera-traps were instrumental to obtain many of the results of this research, but also to convince authorities of the diverse fauna that had survived the war and was worth to preserve. We started the study using 20 cameras, we used up to 80 during the collaboration with MPI-EVAN and we continued with 40 cameras for the rest of the study. More details can be found in next chapters. Our research was decisive to take CNP back to the World Heritage list in 2017 and we also provided images to the Environment and Tourism ministries that helped them to start promoting the park for ecotourism again (Lapuente et al. 2016, 2017, 2018).

2.2.3 The study subjects, the Comoé chimpanzees

Comoé chimpanzees belong to the most threatened chimpanzee subspecies, the Western chimpanzee, *Pan troglodytes verus* (Kühl et al. 2017). In Ivory Coast, this subspecies has been previously studied, as we said above, in Ivory Coast rainforest, mainly in Taï NP, but savanna chimpanzees had never been studied before in this country and they were less studied, across the region in general, than chimpanzees living in the rainforest (see section 1.2).

Previous observations of Comoé chimpanzees were not aimed to study them, but made only opportunistically (Gallat-Luong & Galat, 1985, Fischer et al. 1999, 2002, Galat et al. 2008). The exception to this was the one year long study in GEPRENAF mentioned in sections 1.2 and 2.2.1, that is contributing to region-wide studies in which we participated (Kühl et al. 2016, 2017, 2019) but has not produced any specific research on the particularities of the site. CNP chimpanzees had never been studied apart from the above mentioned nest counts, thus, they were completely wild and their behavior largely unknown when we started this study. As a result of poaching pressure and other intrusive illegal activities in the park (logging, farming, fishing, gold-mining), they had become extremely weary of human presence. They were very reluctant to allow us to approach them and were very hard to observe directly (Lapuente et al. 2016, 2017, 2018). We cannot know exactly the total impact of direct poaching on chimpanzees during the lack of surveillance caused by the crisis (2002-2011) although we learned from villagers that at least six chimpanzees were killed in what is today our study area during that period of unrest. (interviews to villagers). Obviously, this did not make any easier to study them. We decided to avoid any further disturbance by approaching them, because we wanted them

to behave naturally. We used the camera-traps instead, which allowed us to cover simultaneously many different interesting spots, which is not possible when following directly the chimpanzees. During the first years 2014-2016, following an Ebola epidemic, the Ivorian government declared a total ban on the trade and consumption of bushmeat as a way to prevent the spread of the epidemic. Poachers did not care about Ebola, but were unable to sell their product, thus, they had to turn to more profitable activities, such as gold-mining. As a result, during this period, poaching was practiced only for local consumption, with the consequent reduction of hunting pressure. Fauna in general became progressively less wary and more easy to view during this period and chimpanzees became also more confident.

By the beginning of 2017 we had already data that suggested that we had a minimum of six different communities in our main study area. We studied four of them more in detail, since they were logistically more accessible: the Odyssey, Achean, Trojan and Aeneid communities. Two other areas, the Theogony and Argonaut communities (originally referred to as the A and K communities), were studied only a week per month during the dry season of each year, thus, our knowledge is not as complete as for the others(see map in chapter 7, page). From our work with camera-traps (chapter 3), we know that the latter community is the largest, although it could also be two different ones. This also happened with Achean and Trojan communities, which we thought were a single community at the beginning of the study (Lapuente 2018). The last area in which we started to work with camera traps, Mont Tingui, could also harbor several communities, although we need further research to confirm it. All the known communities, with the exception of Aeneid, which is a very small one living East of Comoé river, are formed by all sex/age classes and seem well structured, with some adult males, abundant adult females with infants, many juveniles and some adolescents (chapter 3, Appendix I)

During 2017-2018, the effect of gold rush, that attracted most young people not fond of farming to gold mining sites, such as Wendené, far from our study area, allowed the poaching pressure to remain relatively low, combined with the fact that the permanent presence of our teams in the field and the collaboration with OIPR deterred the poachers from approaching the chimpanzees (Pussey et al. 2007, Campbell et al. 2011, Lapuente et al. 2016, 2017, 2018). With the area better secured, we decided to start testing the lengthy process to habituate the chimpanzees of the Achean community. These chimpanzees were a little more confident than the others, we knew the structure of the group and the home-range very well and it was logistically favorable for the proximity of their home-range to our permanent camp. Anyway, the process has just started, the habituation of a full community can take more than seven years (Goodall, 2010, Boesch & Wittig, 2019), so we did not include any results of this habituation work in this dissertation, only direct observations made during these initial phases of the process.

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CHAPTER THREE (Artcle 1)

3 STATUS AND DISTRIBUTION OF COMOÉ CHIMPANZEES: COMBINED USE OF TRANSECTS AND CAMERA-TRAPS TO QUANTIFY A LOW DENSITY POPULATION IN SAVANNA-FOREST MOSAIC

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ABSTRACT

The West African chimpanzee is critically endangered (CR). From 1990 to 2007. Ivory Coast lost 90% of its population to habitat destruction and poaching. In order to effectively implement conservation measures, we need to determine the status of any remaining populations in the country. Chimpanzee population of Comoé National Park (CNP) was assumed to have been severely depleted following the politico-military crisis of 2002-2011. Surveys in 2007, 2010, 2012 and 2014 failed to find significant evidence of chimpanzees in the park, leading managers to believe that no sustainable population was left. To evaluate status and distribution of chimpanzees in CNP, in 2015 we conducted a stratified survey in our study area in the southwest of the park. Over the next 3 years we conducted recce walks in the north, east and center of the park and in 2017 we collected additional data on distribution of chimpanzees during the full park survey for elephants. Additionally, for the first time in Northern Ivory Coast, we carried out a local nest decay study. In our main study area, we estimated a density of 0.14 weaned chimpanzees/km², with an abundance of 127 (92-176) weaned chimpanzees, representing a sustainable population in CNP. We identified 123 individual chimpanzees via parallel camera-trap survey. We discovered a resident chimpanzee population to the east of the Comoé River, an area previously assumed devoid of chimpanzees. This study confirms the viability of a population key for the conservation of Western chimpanzee. We stress the importance of concentrating stratified surveys in potential wildlife habitat to determine the distribution of this and other cryptic threatened species.

KEYWORDS

West African chimpanzee; Comoé National Park, census, distribution, cryptic species, camera trap

3.1 INTRODUCTION

The former range of West African chimpanzee, *Pan troglodytes verus*, has been reduced 100 fold due to habitat destruction for industrial and subsistence crops, forestry and poaching (Kormos et al. 2003, Kühl et al. 2017). The subspecies has still significant populations in Ivory Coast (IC), Guinea-Conakry, Liberia, Sierra Leona, Guinea-Bissau and Senegal (Kühl et al. 2017) with small or residual populations surviving in Mali (Duvall, 2008) and Ghana (Tehoda et al. 2017). The most recent regional estimate states that the chimpanzee population across the whole of the West African range has declined by 80% (Kühl et al. 2017) while it had been previously estimated that in IC, numbers had declined a 90% between 1990 and 2007 (Campbell et al. 2008). West African chimpanzees are being thoroughly studied in a few long-term research sites dating from the 1970s. Bossou, Guinea (Matsuzawa, 2011) and Taï Forest, IC (Boesch & Boesch-Achermann, 2009) focused on forest populations, while in savanna habitats, only the Senegalese chimpanzees at Mt. Assirik and Fongoli have been studied on a long term basis (Baldwin et al. 1983, Pruetz et al. 2002, 2008).

The chimpanzees in CNP had never been studied, except for a few partial nest surveys, prior to our project in October 2014. Chimpanzees were reported to be present in CNP some years after its declaration in 1968 (GTZ, 1979, Lauginie, 2007). Hoppe Dominik (1991) was the first to publish an estimation of the CNP chimpanzee population size. based only on interviews and an assumed density of 0.02 chimpanzees per km², proposing 250 chimpanzees living in the entire park. A higher density was proposed by the first tentative census carried out in 1990 by Marchesi et al. (1995) with three T-shaped transects totaling 30 km through the accessible areas, close to roads: Gansé, beside a main road and east of the Comoé River; Amaradougou, to the southwest; and Kolonkoko, to the northwest. The researchers stressed that they found no nests to the east of the Comoé River, despite intense prospection (12 km), leading them to assume that, even though the chimpanzees could occasionally cross the Comoé River to forage, they did not live permanently in that part of the park. Marchesi et al. (1995) used the nest decay and production rates from the Taï rainforest and applied them to the whole of IC, including the very different savanna-forest mosaics of Comoé. They drew the forest patches by hand from satellite images to estimate the percentage of forest cover and then calculated density and abundance for the forest, arriving at an estimate of 470 weaned chimpanzees for the section of the park west of Comoé River. Campbell et al. (2008) repeated the same transects in 2007, using the same methodology to make results comparable, and found that chimpanzee density had dropped by 90% at both sites. Meanwhile, Fischer et al. (1999, 2002) reported direct observations of chimpanzee individuals and groups in the park on the west bank of Comoé River and once spotted a solitary male crossing the savanna east of the river. Also in 2007, the Wild Chimpanzee Foundation (WCF) in collaboration with the Office Ivoirien du Parcs et Reserves (OIPR), did an aerial survey, combined with 6 terrestrial transects in which they detected no chimpanzees (WCF, 2008). In 2008, WCF carried out a new survey with an updated methodology that used 143.5 km of transects regularly placed in squares across the portion of the park west of Comoé river and the buffer area called GEPRENAF. They detected 55 chimpanzee nests along the transects, of which 14 nests were found within the park. They used the Distance program (Thomas et al. 2010) to estimate a density of 10.26 nests/km², including the park and the neighboring GEPRENAF area. They avoided estimating chimpanzee density since they lacked the specific nest decay rate for Comoé. They also considered that poaching was posing a serious threat to the survival of this population (WCF, 2009). WCF/OIPR's last terrestrial survey of 2012, using 74 4-km long transects across the whole park, failed to

find any chimpanzee signs, the same as the aerial survey of 2010. In the last aerial survey prior to our work in 2014, two chimpanzees were reported to have been spotted from the plane (WCF, 2010, 2012, 2014). All these discouraging results made WCF express their concern about the fate of the dwindling chimpanzee and elephant populations left in Comoé (WCF, 2010, 2012, 2014); their densities appeared too low for them to survive in the long-term. This concern was acknowledged by UNESCO inspectors, influencing their decision to keep the park classified as World Heritage Site in danger (UNESCO, 2013).

When we began the current research project in October 2014, we aimed to address the following questions:

- 1 Is there a sizable chimpanzee population in CNP?
- 2 Can we map the distribution of this chimpanzee population?
- 3 Is there one or several communities of chimpanzees and what is its/their structure?
- 4 Which habitats do they use preferentially for nesting?

Our main objectives were not only to find results comparable with previous studies, but to detect the current distribution of chimpanzees across the park, to locate concrete communities; to study the habitat selection, ecology and behavior of these chimpanzees, and to be able to implement much more precise conservation measures in the frame of a long-term study, for which, we created the Comoé Chimpanzee Conservation Project, CCCP. (Pussey et a. 2007, Campbell et al, 2011, Lapuente et al. 2017). The positive results that we present in this article helped UNESCO and IUCN to make the decision of returning the CNP to the World Heritage List.

3.2 MATERIAL AND METHODS

3.2.1 Study area

CNP is the largest national park in IC and one of the largest in Africa, with almost 11,500 km². It is located in the northeast of the country, between 8°30' to 9°40' N and 3°10' to 4°20' W. Its topography is mostly flat, with plains averaging 200 m.a.s.l. and some hills reaching up to 635 m. The mean annual precipitation is 1090 mm with a mean annual temperature of 27° C (Hennenberg et al. 2005). Most of the precipitation is concentrated in the rainy season, May-October, and is rare from December to April. The Comoé River divides the park from north to south. The savanna-forest mosaic presents only a 9 % of forest cover across the park. There are two types of gallery forest: the evergreen one, dominated by Cynometra megalophyla, that grows along the bigger rivers. Comoé and Iringou, and the deciduous gallery forest that grows along the smaller, seasonally dry rivers. Special attention must be paid to forest islands as potential chimpanzee habitats Mühlenberg et al. 1990, Lapuente et al. 2016). These are forest patches ranging from 1 ha to several km² which grow on higher elevation plateaus and are not linked to water courses. The dry deciduous forest islands are rich in fruiting trees on which chimpanzees feed, such as Dialium guineense, Diospyros abysinica, D. mespiliformis, Celtis integrifolia, Drypetes floribunda, Afraegle paniculata, Tamarindus indica and Ficus spp. They can have 2 to 3 layers of canopy, and often an emergent stratum of trees over 40 m formed by Ceiba pentandra, Antiaris africana and Milicia excelsa. Annogeissus leiocarpus is a fastgrowing pioneering species that colonizes the forest edge (Mühlenberg, 1990, Hennenberg et al. 2005, Lapuente et al. 2016).

The park contains a high animal diversity, including at least 152 mammal species affected by intense poaching for decades (Fischer et al. 2002). Chimpanzees share the forest with African forest elephants *Loxodonta cyclotis*, more than twenty ungulate species and eleven primate species. Among large carnivores, the lion, *Panthera leo*, has not been

confirmed since 2002, whereas spotted hyena, *Crocuta crocuta* and leopard, *Panthera pardus*, are still common across the park (Fischer 2002, Lapuente et al. unpublished data).

Local villagers traditionally believed that chimpanzees did not inhabit the part of the park east of Comoé River (Marchesi et al. 1995, Fischer et al. 2002, personal observation). After preliminary reconnaissance walks (recces), we found no apparent ecological difference justifying the supposed absence of chimpanzees to the east of Comoé River, moreover, during the dry season, low water level could allow the chimpanzees to cross it easily at many points (Fischer et al. 2002, personal observation). Therefore, we included a significant portion of the park to the east of the river in our study area.

We selected a 900 km² area in the southwest of the park which has a relatively high percentage of forest cover, 13 % (Fig. 1, 2). Since the aim of this study was to ascertain the distribution of the few chimpanzees thought to remain in the park, we included in our study area most of the zones where their signs had been detected in earlier surveys (WCF, 2009).

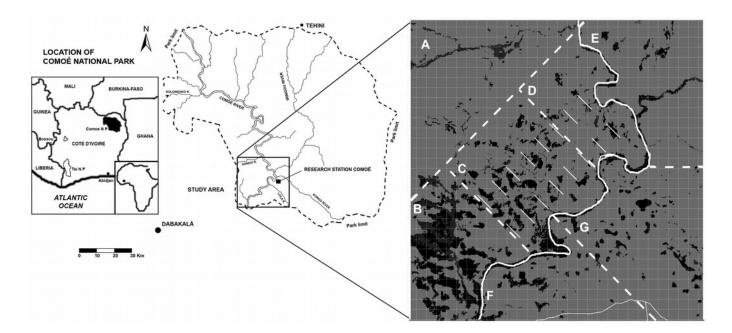


Figure 1. Location of the CNP and study area (to the left). The map on the right shows the division of the study area into the 7 strata (A-G) and 1 km² grid cells used for the camera trap survey. We can see the layout of the regular transects with random origin of coordinates placed on strata C and D. The limit between strata E, F, G and all the others is the irregular line formed by the Comoé River. The dashed lines on the map on the right demarcate the limits of of the remaining contiguous strata.

3.2.2 NEST SURVEY

The work was carried out in two different phases:

- 1 Preliminary phase: intensive survey of the 900 km² study area in the southwest of the park, from October 2014 to May 2015.
- 2 Second phase: global survey of the entire park in collaboration with OIPR within an elephant survey, complemented by quick surveys of the CCCP in the center, east and north of the park, in 2016 and 2018.

During both phases, we carried out a continuous camera-trap survey.

3.2.2.1 Nest counts, preliminary phase

When we began preparing our study, we analyzed the methods and results of previous surveys in Comoé, finding that most of the terrestrial transect walks carried out by WCF in 2007, 2009 and 2012 (WCF, 2008, 2009, 2012) fell in the savanna due to the regular systematic design (having only 9 % of forest cover, the probability of a transect to fall in the forest by chance in such a vast park is very low). As we would later confirm during our own surveys, chimpanzees oddly nest in savanna in Comoé (see table 1). Additionally, the surveys of WCF, Marchesi and Campbell omitted a number of potentially important areas, due to logistical reasons or sampling design. Therefore, we decided to conduct a double-stratified survey: the study area of 900 km² was divided in 7 strata (see fig. 2), with the aim of estimating density and abundance per stratum (see table 1); a second stratification was applied to concentrate the survey effort in forested habitats that were more likely to be used by chimpanzees: gallery forest and forest islands.

3.2.2.1.1 Recces and non-random transects

From October 2014 to May 2015, we walked 823 km of recces and non-random linear transects through all forest patches larger than five hectares, to achieve a detailed understanding of chimpanzee distribution. As we expected gallery forests to be an important habitat for chimpanzees (McLennan & Plumptre, 2012), we maximized the probability of detection by sampling longer distances across the gallery forests, placing transects parallel to the rivers. This was a similar methodology to the one used in Senegal by Pruetz et al. (2002) and in Tanzania by Piel et al. (2015), where they also have a little proportion of potential habitat for chimpanzees. The reduced width of gallery forest makes it impossible to find a gradient of concentration of chimpanzee nests based on distance to the water. The chimpanzees did not nest close to the water, but in secluded parts of the forest where they possibly felt safer (personal observation). To survey as much forested habitat as possible, coordinates were selected from Landsat 2012 images and georeferenced using Qantum GIS, so that the non-random transects crossed the maximum length of each forest patch. Along both recces and transects, we recorded all signs of chimpanzees, including nests, dung, feeding traces, tool use sites, vocalizations and direct observations, locating every observation with a handheld Garmin GPS 64st. We measured the perpendicular distances of the nests from the line along transects, we identified tree species of the nests and estimated the nests' heights. We also collected data on sympatric fauna, changes in habitat type along the transects, human signs and fruit trees. During the approximation walks to arrive to every forest patch, we crossed long distances of savanna in straight line, along which we always looked for nests and other chimpanzee signs and recorded the rest of observations, from which we calculated relative abundance indexes, or encounter rates per km walked (ER).

Between January and February 2015, we walked a total of 61.4 km of non-random transects across forest patches, doing standing crop nest counts (SCNC) with the method of Tutin & Fernandez (1984). Since these transects were walked exclusively in forests, the densities and abundances estimated considered only the area covered by forest within our study area. We calculated the percentage of forest cover in each stratum by digitizing each forest patch in QuantumGIS. Using these percentages, we could estimate also the density and abundance across the total area, including the savanna. In order to make our results comparable with earlier ones, we used a similar method to that used by Marchesi et al. (1995) and Campbell et al. (2008), but we walked more km of transects across more different areas and used GIS to calculate the forest cover and to plot the transects in the forest patches.

3.2.2.1.2 Regular transects and Distance sampling

To corroborate the quality of the estimations made using non-random transects, in March 2015 we walked an additional 32 km of transects placed regularly using a random origin of coordinates within the strata C and D of our main study area (see fig. 1), in which we had previously detected the highest concentration of chimpanzee signs. We used Distance software (Thomas et al. 2010) to analyze data from these transects and to confirm our effective strip width (ESW) for the non-random transects. We chose the half-normal model as the one with the better fitting.

3.2.2.1.3 Standing Crop Nest Counts (SCNC)

We followed the SCNC method (Tutin & Fernandez, 1984) for density and abundance estimation. Instead of measuring distances to the center of every group of nests, we measured distances of individual nests to the line. We applied the following formula:

$$Dch = \frac{Dn}{dPr}$$

Dch= chimpanzee density; Dn= Density of nests; d=decay rate; Pr= production rate Plumptre & Reynolds (1996, 1997) and Kouakou et al. (2009) stressed the importance of knowing the nest production rate to avoid overestimation of density. Weaned chimpanzees usually produce 1 sleeping nest per night, although occasionally they also produce day nests in which they nap. Kouakou et al. (2009, 2011) found an average production rate in Taï N. P. of 1.17 nests/day. Nevertheless, Plumptre & Reynolds (1997) consider that the reuse of a small percentage of night nests in practical terms cancels the effect of the additional nap-nest production rate. These last authors obtained a production rate balanced with reuse of 1.09 nests/day in Budongo, Uganda. Since the real production and reuse rates can only be estimated from habituated chimpanzees, we based ours on these previous studies to assume a production rate of 1.1 nests/day for the current study.

3.2.2.1.4 Nest Decay rate

To estimate decay rate, we considered the 4 categories described by Tutin & Fernandez (1984) and used by most other authors. A nest was considered degraded when it was no longer identifiable as a nest and had lost its original structure. From our recces during the first month, we determined that the five tree species most frequently used by chimpanzees to build their nests in Comoé were *Annogeissus leiocarpus*, *Celtis integrifolia*, *Cynometra megalophylla*, *Dialium guineense* and *Diospyros abysinica*. We selected 50 freshly built nests (stage 1) between late November and beginning of December 2014, 10 nests for each of the five above-mentioned tree species. We visited the selected nests quarterly for six months and for the eight nests that survived for longer, we visited them every month up to total degradation.

3.2.2.2 Second phase, nest counts during elephant survey

We collaborated with the managers of CNP, the OIPR, on the design, organization and data analysis of an elephant survey. Since the sampling effort of this survey was concentrated in the forested habitats, we took the opportunity to collect data on chimpanzees across the whole park. Local villagers and park rangers were trained in the

SCNC method and Distance sampling. In April 2017, we placed 25 sampling blocks across the park, of 100 km² each. Out of these, we sampled the 14 blocks which contained forest, within which we placed regularly 115 transects, 2 km long each, that crossed the forest and were perpendicular to the main water courses. The main aim of the study was to census the elephants, so the personnel did not seek for chimpanzee nests as actively as they did for elephant dung.

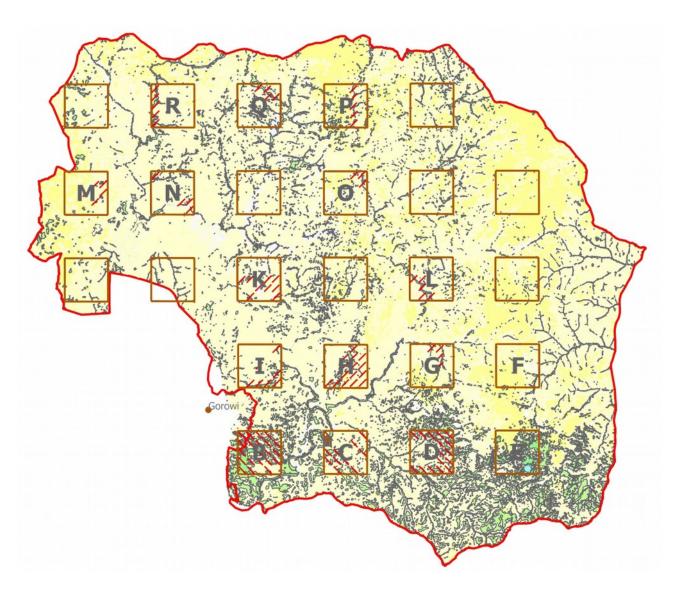


Fig. 2 Sampling design of the 2017 elephant survey. Sampling blocks with letters contain transects that cross forest and therefore were sampled. We contrasted the map with visits on the ground, allowing us to optimize the sampling effort by walking only the transects that crossed forest patches. Block E is an exception; it was not sampled due to the risk posed to the survey teams by extensive poaching and gold mining activities. The vegetation map used in this figure is the most recent one available for the CNP, but it contains errors, such as the inclusion of wide areas of woody savanna as forest.

3.2.3 Camera-trap survey

During the two phases of the study, we conducted a parallel camera trap survey of our 900 km² study area in the southwest. We plotted on the map a grid of 1 km² cells which we used as sampling units for camera trapping. While walking recces and transects we located promising places to install camera traps, such as paths, natural bridges and chimpanzee tool-use sites. We sampled all of the grid cells where we detected chimpanzee activity during a minimum of one month each. Cameras were programmed to take 60 second videos and operated 24 h/day. We checked them monthly for maintenance and collection of the videos recorded. Some of the cameras were shifted once or more within the same cell and some were shifted to different cells. Camera-trap survey was carried out in two phases:

- 1) First phase: from November 2014 to May 2015, we installed 20 Bushnell HD Trophy cams in forest patches within 25 different cells of the strata C, D and G (Fig. 1).
- 2) Second phase: from May 2017 to December 2018, we used a total of 42 camera-traps, 24 Browning SPEC OPS and 18 Bushnell HD Trophy cam, to sample 115 grid cells, across all the strata, except F, where we had never found chimpanzee signs. Our aim was to confirm the extent of home-ranges, collect data on the group structure of the different communities, and to study behavior. Of all the grid-cells covered, 86 cells were sampled for a minimum of three months, 67 for a minimum of six months and 14 cells were permanently sampled for the entirety of the study period (2014-2018).

During the sampling period, two cameras were stolen by poachers and three were destroyed by elephants. Nine more stopped working. We replaced these missing cameras to keep our sampling going on.

In order to individually identify the chimpanzees, two trained observers watched the videos independently, assigning identities based on sex, age and physical features of the faces and bodies. Cohen's Kappa test was applied to compare the coincidence and reliability of identifications. (Head et al. 2013)

3.2.3.1. Communities and home-range identifications

Chimpanzees live in fussion-fission societies called communities, but rarely all the members of the community are together. We determined that the individuals identified in the camera-trap videos consistently associated, over several years, with other known individuals belonged to the same community. When individuals where never associated with members of a known community, we determined that they did not belong to that community. Knowing what we do about chimpanzee xenophobia (Lemoine et al. 2019), individuals belonging to different neighboring communities should never be found together in mixed groups.

We recorded continuously the communities living in strata C, D and G, while the ones living in A and B were studied only during the dry season, due to the distance and difficulty of working in this further strata (Fig. 1).

The concentration of signs of chimpanzee activity, such as nests, dung, tools, footprints, feeding remains, vocalizations and direct observations was combined with the results of the camera traps to determine the extent of home ranges. Only the indirect signs found within the minimum convex polygon formed by the most distant cameras used by recorded members of a same community were used to include different forest patches as part of the home-range of a particular community.

3.2.4. Permits

All the authorizations required for this study were provided by the Ivorian Government and the managers of the park, the *Office Ivoirienne de Parcs et Reserves*, OIPR. Data in the field were collected in compliance with the guidelines of the *Ministere de l'Enseignement Superieure et de la Recherche* Scientifique and the *Ministere de l'Environement*. We adhered to the legal requirements of Ivory Coast, and respected all of the international laws regarding the protection of fauna, avoiding causing any damage to the animals involved or their habitats.

3.3 RESULTS

3.3.1 Chimpanzee presence and encounter rates

A total of 1713 nests forming 695 groups were found during the preliminary phase (2014-15) in our main study area in the southwest of the park. The mean nest-group size was 2.46 nests (±2.14 SD) with a maximum of 22 fresh nests found together at one site in stratum C.

Over the course of the entire study period (2014-18), we found chimpanzee signs, nests, tools, dung, feeding remains, vocalizations and direct observations in five of the seven strata of our main study area, A, B, C, D and G (Fig. 1). For the first time, we found a permanent chimpanzee population east of the Comoé River within the CNP, in Stratum G. This population has been repeatedly confirmed to be present from 2014 to the present. In 2018, we found a chimpanzee population in the center of the park, on both banks of the Comoé River, although the encounter rate of nests was much lower than in the main study area (Fig. 2, Table 1)

Table 1. Total km walked along recces and transects in every sampling zone, e.g. our main study area in the southwest of the park (only in 2015) and the additional areas prospected in the center (MAB and GAWI-W), in the east and northwest of the park. The km walked include savanna. From the 823 km walked in 2015 in our main study area, 561 km were in savanna. We could not confirm presence of chimpanzees in either in the northwest or in the east of the park.

SAMPLING ZONE	DATES OF SAMPLING	EFFORT (Km of recces & transects)	ENCOUNTER RATE (nests/km)	
MAIN STUDY AREA (SW)	2015	823	2.08	
NW	2016	55	0	
MAB	2018	43	0.07	
GAWI-W	2018	64	0.22	
EAST	2018	52	0	

3.3.2 Nest decay rate

After repeatedly revisiting the 50 nests to total degradation, we found that the mean life of chimpanzee nests at Comoé was 178.74 days (SE 10.83), which is more than double the figure from Taï Forest, which has been used in most previous studies (73.3±4 days, Marchesi et al. 1995). We observed that some nests in *Annogeissus leiocarpus* and *Cynometra megalophylla* survived almost a year, (346 days) which is similar to long survival times found in other dry savanna mosaic areas (Hernandez-Aguilar, 2009).

3.3.3 Nest counts along non-random transects

We found nests in all of the sampled strata of our main study area, except in F, which corresponds to an area close to the park limit, with easy access to humans and affected by poaching for a long time. This is the same area in which Marchesi et al. (1995) and Campbell et al. (2008) did not find chimpanzee traces. In the rest of the strata, encounter rates were very variable, producing quite different densities. The highest density was found in stratum A, but due to the small area of forest in this stratum, we estimated it was home to a relatively small number of weaned chimpanzees. On the other hand, the lowest densities, found in stratum B, the most heavily-forested of all the surveyed strata, produced an estimated count of of 19 weaned chimpanzees due to the large forest area in this stratum (Table 2)

Table 2. Densities and abundances of weaned chimpanzees estimated in our main study area in the southwest of the park (Fig. 1). SCNC along non-random transects was applied in every stratum. In the first column is the area covered by forest in km², in the second, the sampling effort realized expressed in km of transects walked. d stands for the estimated density of weaned chimpanzees in forest (weaned chimpanzee/km² of forest). N is the total number of weaned chimpanzees estimated to inhabit each stratum. Effort represents km of transects walked across the forest.

STRATUM	Forest area (Km ²)	Effort (Km)	d (in forest)	N	95 % CI
А	11.81	6	2.476	29	22-39
В	42.61	14	0.449	19	12-29
С	23.51	13.5	2.094	49	38-63
D	11.85	6.6	1.758	20	13-31
E	9.2	7.3	0	0	NA
F	8.1	5	0	0	NA
G	12.68	9	0.774	10	7-14
TOTAL	119.76	61.4	1.06	127	92-176

3.3.3.1 Densities in forest and in the total area (including savanna)

The 127 (92-176) weaned chimpanzees estimated to inhabit our entire study area gives us a mean density of 1.06 chimpanzees per km² in the forests, but if we consider the total area, including savanna (for which density is practically cero), the mean density would be of 0.14 weaned chimpanzees per km².

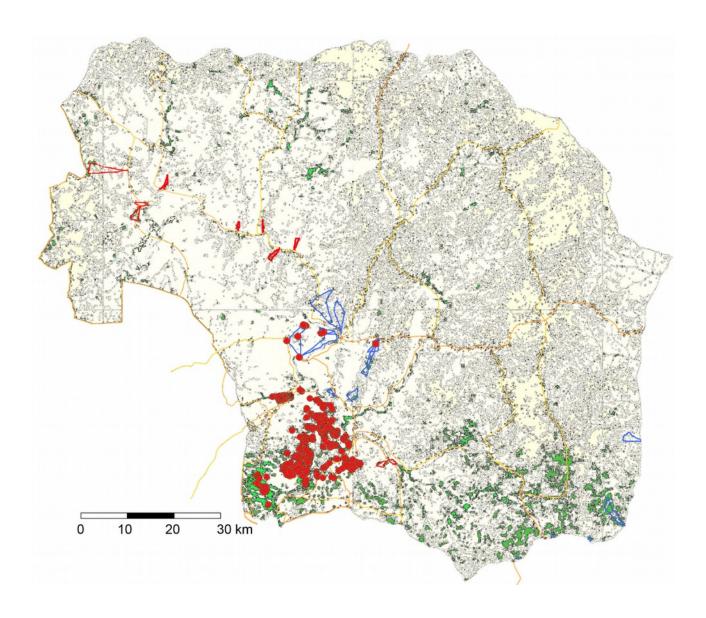


Fig. 3 Distribution map of chimpanzee nests encountered in the CNP. Each dot represents a group of nests. Blue and red lines are the reconnaissance walks done in 2016 and 2018. Yellow lines form the road network of the park, most of which is still inaccessible.

3.3.4 Nest counts along regular transects

We found a total of 78 nests along the 32 km of regular transects with random origin of coordinates placed in strata C and D of our main study area (see fig. 1). Distance analysis, using the half-normal model produced an estimation of 66 weaned chimpanzees (27-160, 95% CI) with a SE of 29.85, for the two strata together. The estimated total density (including savanna) was 0.302 weaned chimpanzees per km² for the combined area of 218.53 km² of strata C and D. The ESW was 22.535 meters.

3.3.5 Nest counts along elephant survey of the park

In 2017, after OIPR teams walked 230 km of transects crossing forested habitats across the entire park. We found only 15 chimpanzee nests, which was not enough to allow us to apply a Distance analysis. These 15 nests were all found our main study area in the southwest, therefore, we cannot confirm the presence of chimpanzees in any additional area of CNP. Taking into account the sampling effort, the result strongly suggests the absence of chimpanzees in most of the northwest quarter and the eastern half of the park.

3.3.6 Camera trap survey

During the entirety of the study period from 2014-18, we accumulated a total of 39615 camera days. We sampled a total of 115 grid cells (13 %) in our main study area containing potential chimpanzee habitat, of which, we recorded chimpanzees in 60, in strata A, B, C, D and G (Fig. 1). We recorded a total of 2326 videos of chimpanzees during the study period, from which we were able to individually identify 123 chimpanzees, including infants. Cohen's Kappa index among the two trained observers was 0.86, which is considered an almost perfect agreement by most authors (Head et al. 2013).

3.3.7 Communities identification, structure and home-ranges

Using consistent association of individuals which never appeared mixed in with those of other communities, we identified a minimum of six communities. The exception is a young female that migrated from Odyssey community to Achean community in 2018. We found that two communities live in strata C, one in D and one in G. We recorded this four communities continuously along the whole study period, while we could only record the communities living in strata A and B during the dry season. Thus, our data are sufficient to allow us to know that the members of communities from the other strata never get in A or B, but we cannot be sure yet if the chimpanzees in these last two strata form only two communities or perhaps more.

We rarely recorded all the identified individuals of a particular community together in the same video. Most often, we recorded individual males and females, females accompanied by offspring and parties of variable size, ranging from three to 23 individuals. Over the four years of recordings, however, individuals belonging to a particular community were never recorded together with those belonging to a different one, with the exception mentioned above,

All of the communities likely contain individuals who have not yet been identified since many images are blurry or distant and the chimpanzees frequently pass far from the

cameras or behind them. We have also observed that while some individuals remain in the core area of their home-range for longer periods, others remain in peripheral areas most of the time, making their detection and identification more difficult. This behavior may be related to their status in the hierarchy of the community.

Table 3. Structure of the known communities, based on the chimpanzees identified from camera traps. The proportions of males, females, adults and juveniles are similar to those of well-known communities in other study sites. * Communities A and K are less well-studied so they may actually include one or more communities each and the percentage of individuals identified is probably still small. # = Number of videos used to identify the chimpanzees in each community. AM is Adult male, AF, Adult Female, ADM, Adolescent Male, ADF, Adolescent Female, Juv. Juvenile and INF is Infant.

COMMUNI TY	STRATU M	NUMBE R OF VIDEOS #	АМ	AF	ADM	ADF	JUV.	INF.	TOTAL IDENTIFIE D
ACHEAN	С	1223	3	8	1	2	5	4	23
TROJAN	С	277	4	8	0	0	5	6	23
Odyssey	D	645	3	7	2	1	4	5	22
AENEID	G	79	1	2	0	0	1	1	5
A*	В	27	3	5	0	0	4	4	16
K*	Α	75	4	12	2	2	6	8	34
TOTAL	ALL	2326	18	42	5	5	25	28	123

3.3.8.1 Estimation of total abundance based on camera-trap results

From the total number of individual chimpanzees identified during the camera-trap survey, 22.76 % were infants who do not make nests. If we add this percentage to the abundance estimations which we produced from SCNC (which only account for weaned chimpanzees who make nests), we would have a total population of around 164 chimpanzees in our main study area in the southwest of the park.

The population detected in the center of the park is not included in the previous calculation, since we lack a reliable estimation for it as well as for the contiguous population still present in the peripheral area of Mont Tingui, former GEPRENAF, outside of the park. Joining together all of these sub-populations, however, could put the total population of Comoé at over 200. We must conduct more accurate surveys of some of these other areas, in the future to be sure.

3.3.9 Habitat selected for nesting

From the 1713 nests that we found during the preliminary phase, 67.6 % (n=1147) were in forest islands, 32.7 % (n=561) were in gallery forests and 0.3 % (n=5) were in savanna close to forest. The few nests found in savanna were always less than 50 m away from the forest and built on big fruiting trees, such as *Parkia biglobosa*.

3.4 DISCUSSION

We began this study with four main questions in mind. We will address the results here, each in turn:

1 Does a sizable chimpanzee population live in the CNP? With this study, we demonstrated the presence of a viable population of savanna chimpanzees inhabiting the CNP, estimated by nest counts in at least 127 weaned chimpanzees (92-176) in our main study area, plus smaller subpopulations in the center of the park, not yet quantified.

2 Can we map the located population?

We mapped the distribution of multiple communities of chimpanzees located during our surveys, mainly concentrated in the southwest of the park, with some additional sparse sub-populations in the center. Despite systematic sampling during the elephant survey and our own quick recces, we failed to locate any chimpanzees outside these areas within the CNP, but we did find, for the first time, chimpanzees living permanently to the east of Comoé river, within our main study area.

3 How many communities of chimpanzees live in the park. What is their group structure? Through analysis of camera-trap videos, we identified 123 chimpanzees belonging to a minimum of six different communities, part of whose structure we described in the results.

4 Which habitats do the chimpanzees use for nesting?

We found that chimpanzees use almost exclusively (1708 of 1713 nests) forested habitats to nest and only nested in savanna when a very attractive fruiting tree was close to the forest edge. They nested in forest islands in two thirds of the cases, while they nested in gallery forest in the other third of the occasions.

This study has revealed that the areas where most of the chimpanzees are concentrated in CNP were not covered by previous surveys, since Marchesi et al. (1995) and Campbell et al. (2008) did their transects close to the park limits. The 2008 survey by WCF/OIPR, using many more transects, detected only a small number of nests in the park because of the systematic regular distribution of transects which happened to cover mainly savanna and only a small proportion of forest (WCF, 2009). Our results are different because we concentrated the sampling effort in the forested habitats. The CNP is vast and we could only thoroughly sample the most promising southwestern corner, while most of the park remains insufficiently surveyed. Nevertheless, the results from the elephant survey and our fast surveys in the east and northwest extremes of the park, suggest that chimpanzees may be absent from the rest of CNP or, if present, in very low densities that make them very difficult to detect.

Previous surveys for chimpanzees in the CNP used the nest decay rates from the Taï NP, which is a humid rainforest. Marchesi et al. (1995), using only 26 nests in Taï, estimated a decay rate of 73.3±4 days. This decay rate is, however, much shorter than

that of the drier savanna-forest mosaic of Comoé, so their results overestimated the real population size. Other authors found much longer nest survival times in savanna-woodland mosaics than the ones found in rainforest (Hernandez-Aguilar, 2009, Stewart et al. 2011). Some studies have reported survival cases of individual nests in savanna-woodland areas surviving up to 427 days (Stewart et al. 2011). The use of our own local nest decay study allowed us to achieve the first consistent estimations for Comoé. These decay rates will be useful for future surveys in similar West African savanna-woodland.

Traditionally, local villagers believed that no chimpanzees lived permanently in CNP east of Comoé River (Fisher et al. 2002, interviews to villagers). This belief, reflected in interviews conducted during previous surveys influenced these researchers' choice of sampling area, and they consistently omitted the portion of the park east of the Comoé River. German researchers working in the area for decades had never observed chimpanzees on the east side, with the single exception being the observation of a lone male chimpanzee in 2000 (Fisher et al. 2002). During the present study we found similar habitats on both sides of the river in our study area, inspiring us to sample the east side of the Comoé as well, which led us to eventually find a resident chimpanzee population there. This experience should lead us to be very cautious when interpreting interviews with locals, since local villagers often answer based on 'common knowledge' and not first-hand experience; sometimes they may have hidden interests or biases. Moreover, the lack of previous survey data should not be taken as proof of the absence of a population, as other studies have demonstrated (Hicks et al. 2014). What remains unconfirmed is the presence of chimpanzees further to the east of the CNP, and in the whole northern half of the park. The results from the elephant survey carried out in collaboration with OIPR suggest that we cannot be optimistic, as no signs of chimpanzees were detected outside of our main study area and the center of the park. The forest cover in the southeast of the park is similar to that in our main study area, but no chimpanzee presence has been confirmed there so far. This may be due to historical reasons, such as more extensive human presence linked to the traditional gold mining, practiced for centuries (interview to villagers). Nevertheless, during our guick surveys of 2018, we found a limited presence in the eastern extreme of CNP of some favorite chimpanzee fruit trees, such as Tamarindus indica, Dialium guineense and Diospyros mespilliformis. Future research on forest structure is needed to elucidate if the habitat quality is a factor determining the peculiar distribution of chimpanzees within the CNP. Therefore, the distribution map produced through modeling by Heinecke et al. (2019b) should be revised in the light of our findings, since there are no potential habitats (only woody savanna) in the whole northeastern quarter of the park and we did not find any chimpanzee traces in the potential habitats surveyed by us in the northwest and southeast of the CNP.

From our results, we cannot tell if the status of the Comoé chimpanzee population has changed much from the last published census (Campbell et al. 2008). Campbell et al. surveyed the Amaradougou, Gansé and Kolonkoko areas to compare with Marchesi's results (Marchesi et al. 1995). These three areas are close to the park limits and are easily accessible by vehicle. Campbell's survey was conducted during the unstable period of the Ivorian politico-military crisis (2002-2011) when there was no law enforcement in the CNP and poachers camped freely across the park. The strong reduction in chimpanzee numbers detected by Campbell when compared to Marchesi's results could be partially attributed to poaching, but also to a change in the behavior of the chimpanzees in response to disturbance, since they could have become more cryptic and moved to parts of their home-ranges further from the park limits, where no transects were walked in both surveys. We could not, however, find any signs of chimpanzees in Kolonkoko, in the northwest of the park, in 2016. No chimpanzee signs have ever been found close to

Gansé (our stratum F), neither by previous surveys nor by us, therefore, this has not changed. On the other hand, the chimpanzee density that we detected in the stratum B, where the Amaradougou transects were walked in previous surveys, is one of the lowest in our study area (0.449 weaned chimpanzees/km² in the forest and 0.16 for the total area of the stratum B), which corroborates Campbell's low densities for these areas. Nevertheless, Campbell et al. (2008) could have underestimated the real size of the chimpanzee population of Comoé, since they did not sample the areas where we found our highest densities.

The strata A, C, D and G of our main study area were not sampled by Marchesi and Campbell and only a few km of transects reached the forests of these strata during the last survey by WCF/OIPR (WCF, 2009). Interestingly, it is in the strata A, C and D where we found the highest density of chimpanzees in the park (Table 2); therefore, the most important population center of the chimpanzees in CNP remained unsurveyed until this study.

The mean density we found in the forest in our main study area, 1.06 per km², is quite low compared to the densities estimated by Marchesi et al. (1995), 5.52 and 4.53, but we must take into account that they calculated these values from just 15 and 3 km of effort respectively, while we walked 61.4 km of transects through the forest to obtain ours. No concrete density value is found in Campbell et al. (2008), although we can compare their nest encounter rate of 0.43 nests/km with our mean encounter rate of 2.08, which is much higher, but still much smaller than the one obtained by Marchesi et al. (1995) of 8.13 nests/km. We may be tempted to assume that the population of Comoé chimpanzees has decreased since 1990, but it is difficult to tell, since the Marchesi et al. (1995) survey in Comoé covered a much smaller area than ours.

When we compare our values with other savanna sites where similar surveys have been conducted, we use our overall mean value which includes savanna areas: 0.14 weaned chimpanzees/km². This value is guite similar to the one obtained by Pruetz et al. (2002) for Assirik in Senegal, 0.13, a quite interesting finding given that this is another old national park, Niokolo Koba, with conditions similar to those found in Comoé. On the contrary, we are far from the densities published by Fleury-Brugiere & Brugiere (2010) for Haut Niger NP, in Guinea, of 0.87 chimpanzee/km², however, this last density is one of the highest reported for savanna chimpanzees and much higher than the 0.05 estimated by Piel et al. (2015) for the Masito-Ugalla Ecosystem, one of the driest chimpanzee habitats in Tanzania. Aebischer et al. (2017) found a density ranging from 0.63 to 1.43 in closed canopy forest of the savanna-forest mosaic in Chimko, CAR, while Hicks et al. (2014) found densities of 0.66 to 2.08 in a savanna-forest mosaic of Northern DRC, which has a relatively high proportion of forest. Interestingly, despite the fact that we usually expect to find higher chimpanzee densities in rainforest, N'Goran et al. (2013) found even lower densities in the rainforest of Taï NP, Ivory Coast (0.087) than the ones we found in Comoé, perhaps because Taï chimpanzees have been decimated by some endemic diseases which are so far thankfully unknown at Comoé (Hoffman et al. 2017).

Even if the villagers around the park are mostly Muslim and besides, they traditionally believe that chimpanzee meat should not be consumed because chimpanzees look like human beings, interviews with villagers suggest that they hunted baboons intensively and sometimes passed off chimpanzee meat as baboon, after smoking and cutting the head and hands. Fischer et al. (1999) suggested that poaching of chimpanzees was low in the CNP based on the absence of remains in poachers' camps; this absence, however, may be explained by the use of chimpanzee bones in traditional medicine, which makes them valuable and gives poachers another reason to hunt them. During our study period, we have not detected a single case of chimpanzee poaching and only three

identified adult males and two infants have stopped being recorded, which could be part of the normal mortality rate under natural conditions. Nevertheless, we cannot discard the possibility of occasional poaching for infant trafficking, even though it would likely be very difficult to hide infants with our present continuous activity and recent improvements of the law enforcement.

The use of regular transects with a random origin of coordinates, required to apply the Distance software, has not proved itself efficient enough to quantify the chimpanzee population of CNP. The partial 2008 survey by WCF/OIPR, which encountered 14 nests on 143.5 km of transects; the survey of 2012 (no chimpanzee traces found on 296 km of transects) and our own results from the elephant survey of 2017, in collaboration with OIPR (15 nests found on 230 km of transects) demonstrated that this method is not adequate in such a vast park with a forest cover of only 9 %. This is almost certainly because, when placed this way, most of the transect length falls in savanna, which is not a preferred chimpanzee habitat, as our results showed. Our higher encounter rates from the 32 km of transects which were densely packed into strata C and D (fig. 1) are certainly due to the fact that we concentrated our sampling effort inside a smaller area with a previously known higher concentration of chimpanzees. We suggest that under the conditions of Comoé, where potential chimpanzee habitat is fragmented into small, unevenly-distributed patches, the quantification of the population requires a concentration of much of the sampling effort into the potential forested habitats with the transects placed in a relatively non-random fashion allowing them to cross the maximum possible lengths of potential habitat. Other authors have successfully used non-randomly placed transects in similar habitats, such as Pruetz et al. (2002) in Senegal or Piel et al. (2015) in Tanzania. The combined use of camera-traps with extensive field surveys has proved more efficient in the detection and quantification of low density chimpanzee populations in vast areas (Head et al. 2013, Aebischer et al. 2017) than the exclusive use of nest counts along transects. Our pioneering use of camera-traps in the CNP produced a great wealth of data. not only useful for achieving abundance estimates and producing distribution maps, but also for understanding the population structure of the chimpanzees along with their ecology and behavior. Our results show that the Comoé chimpanzee communities for which we were able to record hundreds of videos appear to have a similar size (22-23) identified individuals each) to the community size reported for Assirik, Senegal (Baldwin et al. 1982) which has similar environmental conditions. This is also a similar community size to that of Bossou, Guinea (Matsuzawa et al. 2011), although the human influence in this latter site is quite higher, since chimpanzees live around a village and use the plantations. Community size in the habituated groups of Taï forest is usually larger, unless they have been decimated by diseases (Boesch & Boesch-Acherman, 2009). Nevertheless, the group structure of the CNP and Tai chimpanzees is similar, with more than two adult females per each adult male and almost 50% of group members being juveniles and infants. The Gombe chimpanzees in Tanzania have sometimes had similar group sizes following splitting or the impact of epidemics (Pussey et al. 2007). We cannot yet know if we have recorded all of the individuals in the Comoé focal communities, but we confirmed after several years of recordings that individuals from each community only associate with the other members of the same community and were never recorded in the home-range of the neighboring ones, with the exception of a young female that migrated from Odyssey to Achean in 2018. However, the relatively small size of the communities in the CNP could be a natural trait, an adaptation to the scarcity of food resources, as may happen in Assirik (Baldwin et al. 1982). We are currently collecting more data to clarify this point. As of now, we have no indication that any epidemic diseases have impacted the Comoé chimpanzees, although they do have a low prevalence of entero-parasites shared with

humans (Hamilton et al. 2018). We found only one skeleton over the last five years and so far, no sign of chimpanzee epidemic diseases have been found to be present in the CNP (Hoffman et al. 2017, personal communication). Poaching has likely reduced the community sizes over the last decades (Campbell et al. 2008). We know from interviews with villagers that at least six chimpanzees were killed and sold during the period of political instability between 2002 and 2011. If this is the case, a progressive recovery of the numbers in each community could be expected, now that we are able to collaborate with OIPR in ensuring their conservation (Pussey et al. 2007, Campbell et al. 2011).

The West African chimpanzee, the most endangered subspecies of *Pan troglodytes*, has declined by 80 % across the region (Kühl et al. 2017) and by 90% in IC (Campbell et al. 2008) leaving a surviving population of perhaps only 1000 individuals in the country (Heinecke et al. 2019), therefore, the CNP population is surely the second largest remaining in the country, after that of Taï, and, taking into account the progressive reduction of the chimpanzees in Taï due mainly to diseases (Hoffmann et al. 2017) it could sadly become more important for the species in IC in the next decades.

Comoé could become one of the strongholds of West African chimpanzee due to its location in a relatively well-preserved national park. Its interconnection with other remaining populations has not, however, been demonstrated and it may represent an isolated population, which would put it under an even higher threat due to lack of genetic diversity. It has been demonstrated that long term research projects deter poachers from decimating wildlife populations (Pussey et al. 2007, Wrangham & Ross, 2008, Campbell et al, 2011). Continuous surveillance of the chimpanzee territory of Comoé will help to ensure protection of the habitat and all of the precious fauna. Additionally, collaboration between our project and local authorities combined with the gradual improvement of law enforcement efforts have generated a momentum that we are currently using to amplify conservation efforts in the CNP for anti-poaching control and to develop a sustainable long term project that engages local community in the conservation of an emblematic species such as the chimpanzee, providing future opportunities for research and ecotourism.

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CHAPTER FOUR 4 FEEDING ECOLOGY OF COMOÉ CHIMPANZEES

ABSTRACT

Comoé chimpanzees live in a savanna-forest mosaic in Comoé National Park (CNP) and surrounding areas of northeastern Ivory Coast. The habitats they use offer a great variety of food resources but subjected to seasonal changes that can be extreme. Therefore, the availability of food i changes irregularly and some fruits that are abundant one year can be rare the next. Comoé chimpanzees overcome these difficulties using many different food sources. We studied the feeding ecology of these chimpanzees through the analysis of the contents of 362 dung samples collected from the October 2014 to October 2018. We also collected data on feeding signs along more than 4000 km of recces over the same period. We also recorded videos with camera traps and made direct observations confirming the importance of some food sources that are less likely to leave traces in dung samples. Using this combination of methods, we confirmed the consumption of 72 food items. Over the course of one year, we studied the phenology of 400 trees belonging to the main 22 species consumed by chimpanzees, which allowed us to estimate the Fruit Abundance Index (FAI) for that year. We used the FAI to corroborate the use of Ceiba pentandra cambium as fallback food in periods of seasonal fruit scarcity. We found that the consumption of this last resource by Comoé chimpanzees reaches a level found nowhere else. We found that insectivory, especially the dipping of driver ants (Dorylus burmeisteri) is important throughout most of the year. Through the analysis of chimpanzee's tools found using etho-archaeological methods, we investigated as well the seasonal consumption of honey and insects, which we corroborated with the use of camera traps and direct observations. Overall, the Comoé chimpanzees showed a great ability to adapt to their changing environment. This is the first time savanna chimpanzees and their feeding behavior have been studied in Ivory Coast, adding important data that helps to understand the adaptations of savanna chimpanzees in West Africa. The feeding behavior of savanna chimpanzees could be used to develop an enlightening model to help us understand the adaptations that human ancestors might have developed when transitioning from the rainforest to the more open savanna-woodland habitats.

4.1 INTRODUCTION

Although chimpanzees (*Pan troglodytes*) are frequently considered to be ripe fruit specialists (Wrangham et al. 1998)), they are omnivorous, as are most primate species, with the exception of a few specialists, such as gorillas (*Gorilla gorilla*) and colobine monkeys, which are mostly herbivores (Milton & May, 1976), and tarsiers, which are carnivores (Gursky, 2011). However, there can be great differences among the diet of chimpanzees inhabiting different habitats or even among different communities in the same area (Potts et al. 2011).

Savanna chimpanzees actually inhabit mosaics of forested and savanna habitats and usually rely more on the resources obtained from forested patches than from the savanna itself (Duvall, 2008, Bessa et al. 2015, Yoshikawa, 2015, Piel et al. 2017) The exception to this rule could be the chimpanzees that live in the driest and most open savanna habitats of Fongoli, Senegal (Pruetz et al. 2006, Lindshield et al. 2014) and Issa, Ugalla, in Tanzania (Russak, 2013), that have been found to consume more food items from the woodland (equivalent to woody savanna or open forest at other sites) than from the forest itself.

Savanna chimpanzees find their food resources scattered across larger areas. Living in habitats with only a small proportion of forest, they usually live at lower densities (0.01- 0.25 chimpanzees/ km²) and need larger home-ranges than forest chimpanzees to cover the needs of the whole community (Baldwin, 1979, McGrew, 1981, Tutin et al. 1983, McGrew, 1988, Boesch & Boesch, 2002, Russak, 2013, Piel et al. 2017). Chimpanzees at savanna sites have been described to use home-ranges as large as 560 km² in Tanzania (Kano, 1972), although the accuracy of this estimate has been questioned (Baldwin, 1979). Other estimations for the size of savanna chimpanzees home-ranges vary from 250 km² for Assirik, Senegal (Baldwin, 1979), 63-85 km² for Fongoli, Senegal (Pruetz, 2006, Wessling et al. 2018), 85 km² for Ugalla, Tanzania (Piel et al. 2017) and 50.1 km² for Semliki, Uganda (Hunt & McGrew, 2002). It has been observed that estimations of the home-range size using minimum convex polygons increase when the community becomes more habituated and better studied (Pruetz, 2006). On the other hand, chimpanzees living in rainforest have been found at much higher densities (2.9-5.2/ km²) and in much smaller home-ranges, such as 7.8-14.9 km² in Budongo, Uganda (Reynolds, 2005) or 7.9-30.1 km² in Taï Forest, Ivory Coast (Boesch & Boesch-Achermann, 2000, Kouakou et al. 2011), which is possibly due to the higher concentration of food resources (Tutin et al. 1997, Wrangham et al. 1998, Balcomb et al. 2000, Boesch & Boesch-Achermann, 2000, Reynolds, 2005, Nakamura et al. 2012, Piel et al. 2017).

The behavior of chimpanzees and other primates have also been found to be influenced by seasonal fires that burn the savanna grass, which are usually human-made (Tutin et al., 1997, Pruetz and Bertolani, 2009). In Comoé, forest islands represent a refuge from the fire, protecting a wide diversity of fruit species that are of great importance for primates (Mühlenberg et al. 1990).

Forested patches in savanna areas similar to Comoé can provide forest resources even if they are scattered. In the forest of Kibale, Uganda, Balcomb et al. (2000) found a direct relationship between the density of trees producing large, fleshy fruits (> 1.5 cm in diameter) and the density of chimpanzee nests. They found 34 species of trees producing this type of fruit, while in the savanna-woodland site of Fongoli, there were 27 of such species available for the chimpanzees (Pruetz, 2006), although the density of these latter trees was not provided by Pruetz, she suggests similarities in the use of forest resources by Fongoli savanna chimpanzees and by the forest dweling chimpanzees of Kibale.

Previous studies of Comoé chimpanzees were limited to a few nest count surveys and opportunistic observations (see Chapters 2 and 3). Their ecology and diet have never been studied before and we were obliged to study also the structure of the forest and to know the densities of fruiting trees for which only general studies have been previously carried out (Mühlenberg et al. 1990, Hennenberg, 2005).

When we started this study, we assumed that Comoé chimpanzees would likely share ecological similarities with other savanna chimpanzees. Similarly, we expected their diet and habitat use to be comparable to that of other savanna chimpanzees and therefore, we formulated the following hypothesis based on the literature:

Hypothesis 1 Given that savanna habitats are submitted to strong seasonality, we predict that fruit availability will strongly change along the year and that the number of different food items found in dung samples will vary greatly with seasons.

Hypothesis 2 Considering that during some months of the year fruit availability will be very low, we expect Comoé chimpanzees to rely on some type of fallback food during fruit scarcity periods.

Hypothesis 3 Given that Comoé chimpanzees spend much more time in the forest than in the savanna, we expect to find a higher proportion of forest food items than savanna ones in their diet.

Hypothesis 4 Given that many food sources are not readily accessible, especially those associated with insects, we expect Comoé chimpanzees to use tools to forage on insects and insect products.

Hypothesis 5 Given that chimpanzees have been found to hunt mammals in most study sites, we expect Comoé chimpanzees to hunt mammal prey.

Hypothesis 6 Taking into account that the consumption of soil or clay as source of minerals by chimpanzees has been described in the literature of several study sites, we predict that Comoé chimpanzees will consume clay or soil.

Hypothesis 7 Given that savanna chimpanzees are assumed to consume a smaller number of different food items than forest ones, we expect to find the same at Comoé.

Hypothesis 8 Considering that savanna chimpanzees live in habitats where the food resources are more disperse than in the rainforest, we predict that Comoé chimpanzees will have larger home-ranges than chimpanzees living in rainforests, such as the Taï Forest population.

4.2 MATERIALS AND METHODS

4.2.1 Study area

Comoé National Park (CNP) is located in the northeast of Ivory Coast, West Africa. It is the largest national park in the country, covering about 11,500 km2. The park lies in the transition zone between two bioclimatic regions, the more forested and wetter Guinean region and the drier and savanna-dominated Sudanian region. The climate is warm and dry, with an average annual temperature of around 27°C and precipitation around 1090 mm (Hennenberg, 2004), although during the period between October 2014 and May 2019, we recorded an annual mean precipitation of only 925.5 mm and a mean temperature of 26.79° C. Vegetation is composed of a mosaic of savanna and forest, in which forested habitats cover just 9 % of the surface of the park. However, the southern part of the park and especially the southwest, where our study area was located, has a higher proportion of forest cover, 13 %. Forested habitats include gallery forest along the rivers and forest islands which are independent of water courses. The dominating forest habitat is dry forest, with a high proportion of deciduous species that lose the leaves during the dry season such as Annogeissus leiocarpus, Cola cordifolia or Ceiba pentandra. Some forest islands have a semideciduous forest that includes evergreen species such as Cynometra megalophylla, Dialium guineense or Diospyros abissinica. The major rivers are lined by a gallery forest dominated by *Cynometra megalophylla*, while smaller rivers which become seasonally dry are flanked by gallery forest that shares many species with dry forest and some which require wetter conditions, such as Isoberlinia doka, Berlinia grandiflora or Detarium senegalensis. Savanna includes woody savanna, with more than 30 % of tree cover, bushy savanna and a small proportion of open grassland savanna. The vegetation type that other authors have called woodland (Pruetz, 2006, Hicks, 2010, Piel et al. 2017) would be the equivalent of what we call in Comoé clear or open forest, with more than 80 % of tree cover, following the French classification (Lauginie, 2007). For the rest of the chapter, when we speak about savanna, we refer to the mosaic formed by woody and bushy savanna that rarely contains open grasslands and not to the woodland equivalent, following the criteria of Lindshield (2014). Both forested and savanna habitats include several fruit species (See table 1) that are exploited by chimpanzees and the other 11 species of primates present in the park. One of the most abundant and widespread

primate species in Comoé is the olive baboon (*Papio anubis*) which shares the same habitats with the chimpanzees, although uses more intensely the savanna. Counting the primates, at least 152 species of mammals have been detected in the park (Fischer et al. 2002), including forest elephant, hippopotamus, leopard, hyena, buffalo and many other species (see Chapter 2). Other vertebrates include more than 500 species of birds and more than 20 reptiles. We carried out the data collection in our study area in the southwest of the CNP, which covers 900 km² (fig. 1). This area is divided from north to south by the Comoé River, which serves as a barrier for many animals during the rainy season, but becomes easy to cross during the dry season.

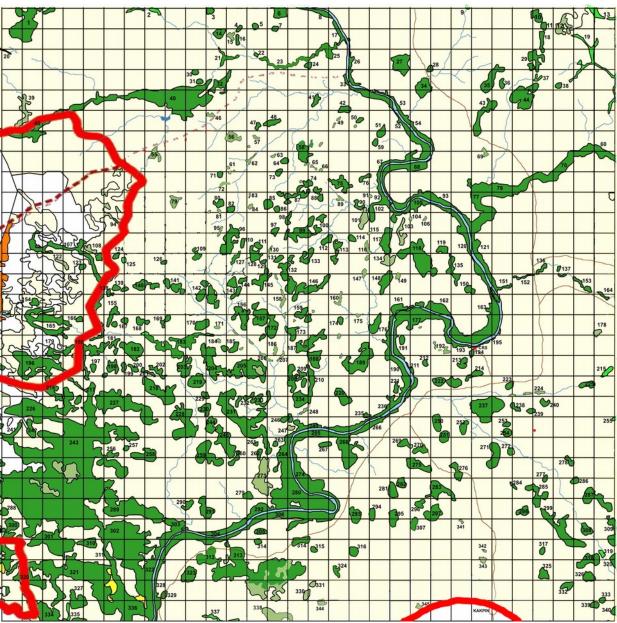


Fig. 1 Distribution of vegetation in our study area in the southwest corner of the CNP. The red lines are the park limits as of 2017. Dark green patches are dense forest and light green ones are open degraded forest (affected by human activity and fire prior the park creation, as suggested by remains of settlements). Blue lines correspond to rivers. The cream background corresponds to savanna habitats. The grid is made up of 1 km 2 cells. The total area is $30\times30 \text{ km} = 900 \text{ km}^2$.

Our study covered the period from October 2014 to May 2019. We lack data from June and July 2015 due to a pause in research, as well as from October 2018, when flooding made our research untenable, but we have weekly data for the rest of the period. We covered the study area with more than 9360 km of reconnaissance marches (recces) and transects (see Chapter 3). Every week, a team of two to six members walked for four days through the different habitats, searching opportunistically for chimpanzee traces, including dung, feeding remains, footprints, tools, nests, direct observations and vocalizations. The locations of all observations were recorded using a handheld GPS.

4.2.2 Meteorological data

Over the course of the entire study period, we collected data on precipitation, maximum, minimum temperature and humidity, using an electronic thermometer and a plastic rain gauge. Mean monthly and annual variables were calculated and compared with data previously recorded in the CRS and with the data available from the closest weather stations of Bondoukou and Dabakalá.

4.2.3 Phenology

From November 2015 to November 2016, we monitored monthly 400 trees belonging to 22 of the fruit species which we had observed to be the most consumed by chimpanzees during the preliminary phase of the project (21 trees and 1 liana). We monitored 20 trees / vines of each species. The trees / vines were selected along permanent transects that covered the home ranges of three different chimpanzee communities. Every month, a team of two persons observed the canopy of the fruiting plants with binoculars and scored the proportion which was covered by young leafs, flowers, buds, ripe fruits and total fruits, using the following broad categories to make the observations more comparable: 0= no cover, 1= up to 25 % cover, 2=26-50%, 3=51-75%, 4= more than 75% (Arandjelovic et al. 2014).

4.2.4 Habitat plots

In order to analyze the structure of the forested habitats, we established a total of 405 vegetation plots along the transects, covering the same home ranges of the three chimpanzee communities in which the phenology fruiting species had been chosen. The square plots measured 20×20 m (400 m 2) and were separated by 100 m. 40 of the plots were established in the woody savanna close to the edge of the forest, where fruit species exploited by chimpanzees can be found. In every plot, we identified, counted and measured the diameter at breast height (dbh) of all the trees / vines above 10 cm in dbh. We also selected a smaller plot of 1 m 2 in the right bottom corner of each plot to identify and estimate the cover of herbaceous species (Arandjelovic et al. 2014).

4.2.5 Fruit Availability Index

We combined the data of the habitat plots and the phenology study to estimate the availability of fruit belonging to these 22 species throughout the year. To calculate the fruit availability index (FAI) we used a formula adapted from Hockings et al. (2009): FAI $\frac{1}{4}$ [S (Pi " Fi)]/[S (Pi " 4)] " 100, where Pi is the basal area of the tree (in m^2 per k^2 , instead cm²) and Fi is the food (flower, fruit, or leaf) score of the tree (0–4).

4.2.6 Faecal samples

During the same period, we collected fecal samples that were taken to the laboratory of the CRS for a detailed analysis of the contents. These samples were

collected throughout the year, but due to differences in the probability of preservation under wet and dry conditions, we found many fewer dung samples during the wettest months than in the dry ones (see table 2). Once in the laboratory, we washed the fresh samples in a sieve with a 1 mm mesh diameter. We identified all particles found in the sample with the help of local experts, when possible, and we kept samples of every element found, for later confirmation of the identification. We classified the particles found into the following categories: seeds, leaf fragments, fibers, insect fragments, hair, meat and wax. For insect identification, we had the support of entomologists contacted by the Max Planck Institute and through Copenhagen University and Freiburg University, for the ants Dr. Caspar Schöning and, for the termites, Prof. Judith Korb and Prof. Rudolf H. Scheffran.

4.2.7 Feeding signs

Along the recces, we recorded all of the feeding signs associated with chimpanzee footprints and/or dung and clear chimpanzee tooth marks. Feeding signs included wadges of fruit, half-eaten fruits, stems, bark, and also social insects nests with tools associated and partially-consumed animals. Identification of plants and animal traces was possible by the experience of local experts, the author himself and the botany Prof. Konan Edouard Kouassi of Felix Hophouet Boigny University.

4.2.8 Foraging tools

In order to to test the hypothesis that the chimpanzees used more tools to forage on non-fruit food sources during periods of fruit scarcity (Yamakoshi, 1998), we recorded the number of the different types of tools found along recces every month for the whole study period. Comoé chimpanzees use tools for different purposes but especially for foraging, including ant fishing, ant dipping, termite fishing and honey dipping tools (see chapter 7 and Lapuente et al. 2016, 2017, 2018 for the definition of chimpanzee tool that we used). The presence of tools associated with remains of the consumed food, was recorded both for the tool use study (Chapter 7) and to complete the data from the dung samples: the remains of most termites and honey rarely appear in the dung (personal observation), so we used the number of tool sites found per month as a proxy of the monthly frequency of every type of tool-assisted foraging.

4.2.9 Direct observations

Given that the Comoé chimpanzees are wild and have suffered from poaching pressure (chapter 2), they usually hide when humans come close. Only in the last year of the study we began the lengthy process of habituating one of the communities. Hence, most of our direct observations were made opportunistically and were not amenable to statistical analysis, but are important complements to the dung study to complete our checklist of food sources. They allowed us to confirm the presence in the chimpanzees' diet of foods that are rarely identifiable in dung samples. We observed the chimpanzees hunting, consuming fruits and using tools to prey upon insects and acquire honey. To avoid stressing the animals and transmitting diseases to them, we kept a distance of more than 20 m between ourselves and the chimpanzees. Nevertheless, the observers carried face masks to prevent the transmission of respiratory diseases in case of closer encounters.

4.2.10 Camera traps

To overcome the difficulties of direct observation, we installed camera traps in hot spots of chimpanzee activity, especially at tool use sites. Chimpanzees habituate to cameras faster than to human observers, so we acquired valuable data from the first

month of the study. We placed the cameras systematically in forest habitats across a sampling grid with 1 km² cells as the sampling unit within which, we selected chimpanzee activity hot-spots. From October 2014 to October 2015 we used 20 Bushnell HD trophy cameras (model 119437). From October 2015 to May 2017 we increased to 80 cameras, of which, the Department of Primatology of MPI-EVAN provided 60 Bushnell HD Agressors. From May 2017 to May 2019, we continued our study using 30 cameras, 12 of which were Browning SPEC-OPS and the remaining were Bushnell HDs. All of the cameras were programmed to record one minute-long videos. The cameras were triggered by the motion of animals which were detected by body heat. When the light was insufficient to record color videos in visible light, cameras recorded infrared black and white videos. The videos allowed us to confirm the consumption of certain foods that were not identifiable from the dung samples, but also to detect the seasonality of foraging for each food source. For more details on the methodology, see Lapuente et al. (2016, 2018, 2019b).

4.2.11 Geophagy: consumption of clay and marle

From the beginning of our study, we found salt-licks (places where several species of animals consume the soil, apparently looking for salts, creating holes in the ground or on cliffs, called "salines" by the locals, who think that the animals obtain salt from them) with chimpanzee footprints. We recorded the presence of 16 salt-licks in which the chimpanzees could potentially consume soil, the same way other animals do. These salt-licks were inside forest patches or close to the forest edge. Other 22 salt-licks were found deep in the savanna, far from routes used by the chimpanzees, therefore, we did not monitored them for this study. We looked for indirect signs of chimpanzee activity at the salt-licks such as footprints, dung or traces of scraping on the soil (tooth or finger nail marks). We placed camera traps in four of the potential salt-licks and monitored them for 36 months in one case and for six months in the other three cases.

4.2.11 Home-ranges

For the estimation of the surface area of the home-ranges of each community, we used a combination of the results of the camera-traps with the evidence recorded of indirect signs, such as nests, dung, tools, footprints and also direct observations and vocalizations. For more details on the methodology behind this approach, please consult section 3.2.3.1.

4.2.12 Data analysis

Because our data had a non-parametric distribution, we tested for differences between means using a Wilcoxon U-test All statistical analyses were realized using R-Studio software. GPS data were analyzed in Quantum GIS and we used this software as well for the calculations of areas and the creation of maps.

4.3 RESULTS

4.3.1 Plant food species

We identified at least 82 species of trees, shrubs, lianas and herbs within the permanent plots and transects installed in the habitats used by the chimpanzees. At least 58 of these species were consumed in one form or another by the apes, as we show in table 1. For some species, chimpanzees consumed just one part of the plant, while for others, such as *Ceiba pentandra*, they consumed up to four different parts.

Table 1. Species identified within the sampled habitats, including life forms and plant parts, consumed by the chimpanzees and source of the data used. DO refers to direct observation, FS to fecal sample, TR to feeding traces and CTV to camera-trap video. NA = not applicable, i.e. we were unable to confirm the use of these species as plant food sources.

Species	Habitat	Life form	Part consumed	Data
Adansonia digitata	Forest/ecotone	Tree	Fruit	DO, TR
Afraegle paniculata	Forest	Tree	Fruit	DO, CTV
Aframomum alboviolaceum	Savanna	Herb	Fruit, pith	FS, TR
Afzelia africana	Savanna	Tree	Pod	DO, CTV
Albizia adianthifolia	Forest	Tree	Pod? Leaf?	FS
Albizia lebbeck	Forest	Tree	NA	NA
Albizia zygia	Forest	Tree	Pod	TR
Alchornea cordifolia	Forest	Tree	NA	NA
Anogeissus leiocarpus	Forest/ecotone	Tree	Leaf?	TR
Antiaris toxicaria	Forest	Tree	Fruit	DO, TR
Balanites grandifolia	Forest	Tree	NA	NA
Balanites wilsoniana	Forest	Tree	Fruit	TR
Berlinia grandifolia	Gallery Forest	Tree	NA	NA
Cassia sieberiana	Forest/ecotone	Tree	Fruit	TR, FS
Ceiba pentandra	Forest	Tree	Fruit, leaf, flower, inner bark	DO, TR, CTV
Celtis integrifolia	Forest	Tree	Fruit, leaf	DO, FS
Celtis subintegrifolia	Forest	Tree	Fruit, leaf	TR, FS
Celtis zenkieri	Forest	Tree	Fruit, leaf	TR, FS
Citrus x aurantifolia	Forest/ecotone	Tree	Fruit	TR, FS
Cola cordifolia	Forest	Tree	Fruit	TR, FS
Combretum molle	Forest	Tree	NA	NA
Combretum nigricans	Savanna	Tree	NA	NA
Combretum spp.*	Forest	Tree	NA	NA
Crossopterix febrifuga	Savanna	Tree	NA	NA
Cynometra megalophylla	Forest	Tree	NA	NA
Daniellia oliveri	Savanna	Tree	NA	NA
Detarium microcarpum	Savanna, ecotone	Tree	Fruit, seed	TR
Detarium senegalense	Forest	Tree	Fruit, seed	TR
Dialium guineense	Forest	Tree	Fruit	DO, FS, TR, CTV
Diospyros abyssinica	Forest	Tree	Fruit	TR, FS
Diospyros mespiliformis	Forest/ecotone	Tree	Fruit	DO, TR, FS
Drypetes chevalieri	Forest	Tree	NA	NA
Drypetes floribunda	Forest	Tree	Fruit	DO, TR, FS
Drypetes gilgiana	Forest	Tree	Leaf	TR
Elaeis guineensis	Gallery Forest	Palm	Fruit	TR
Faidherbia albida	Savanna/ecotone	Tree	NA	NA
Ficus elegans	Forest	Tree	Fruit	TR, FS
Ficus ingens	Savanna	Tree	Fruit	TR, FS
Ficus lyrata	Gallery Forest	Tree	Fruit	TR, FS
Ficus platyphylla	Savanna	Tree	Fruit	TR, FS
Ficus strangler*	Forest	Tree	Fruit	TR, FS
Ficus sur	Forest/ecotone	Tree	Fruit	TR, FS
Ficus thonningi	Forest	Tree	Fruit	TR, FS

Garcinia afzelii	Forest	Tree	Leaf?	TR
Gardenia aqualla	Savanna	Tree	NA	NA
Gardenia erubescens	Savanna	Tree	Fruit	TR
Grewia lasiodiscus	Forest	Tree	Fruit	TR
Isoberlinia doka	Forest/ecotone	Tree	NA	NA
Khaya senegalensis	Forest	Tree	NA	NA
Kigelia africana	Forest/ecotone	Tree	Fruit?	TR
Lannea acida	Savanna	Tree	Fruit, leaf	TR
Lannea welwitchi	Forest	Tree	Fruit, leaf	TR, FS
Lophira lanceolata	Savanna	Tree	NA	NA
Malacantha alnifolia	Forest	Tree	NA	NA
Manilkara multinervis	Forest	Tree	Fruit	DO, TR
Maranthes polyandra	Savanna	Tree	NA	NA
Markhamia tomentosa	Forest	Tree	NA	NA
Milicia excelsa	Forest	Tree	Fruit	TR
Mitragyna inerme/inermis	Savanna/ecotone		Fruit	TR
Monotes kerstingii	Savanna	Tree	NA	NA
Morus mesozygia	Forest	Tree	Fruit	TR
Newbouldia laevis	Forest	Tree	NA	NA
Oncoba spinosa	Savanna/ecotone		NA	NA
Oxianthus racemosus	Forest	Tree	Fruit	DO, FS, TR, CTV
Parkia biglobosa	Savanna/ecotone		Fruit	DO, FS, TR, CTV
Phoenix reclinata	Gallery Forest	Palm	Fruit, pith	FS, TR
Piliostigma thonningii	Savanna/ecotone	Tree	Pod	FS, TR
Pseudocadreta kotschyi	Savanna	Tree	NA	NA
Saba comorensis	Forest/ecotone	Liana	Fruit	FS, TR
Saba senegalensis	Forest/ecotone	Liana	Fruit	DO, FS, TR
Schrebera arborea	Forest	Tree	NA	NA
Strychnos congolana	Forest	Liana	Fruit	TR
Strychnos spinosa	Forest	Tree	Fruit	TR
Tamarindus indica	Forest/ecotone	Tree	Fruit	DO, FS, TR
Tapura fischeri	Forest	Tree	leaf, stem	FS, TR
Terminalia avicennoides	Savanna	Tree	NA	NA
Terminalia macroptera	Savanna	Tree	NA	NA
Tetrapleura tetraptera	Forest	Tree	Fruit	TR
Uapaca togoensis	Savanna	Tree	Fruit	TR
Vitellaria paradoxa	Savanna	Tree	Fruit	FS, TR
Vitex doniana	Forest/ecotone	Tree	Fruit	FS, TR
Ximenia americana	Savanna	Tree	Fruit	FS, TR
Zhana golungensis	Forest	Tree	Fruit	FS, TR
Zanthoxylum xanthoxyloides	Forest	Tree	NA	NA
Ziziphus abyssinica	Forest/ecotone	Liana	leaf	FS, TR

Apart from the identified *Ficus* species in the list, we documented the consumption by the chimpanzees of a number of strangler figs which we could not identify during the study. This was especially the case of fig seeds in the dung. We thus pooled these unknown *Ficus* sp. together into a single group (*Ficus* strangler). We had a similar problem with a number of *Combretum* species (not including *C. nigricans* and *C. molle*), which we were unable to identify. We classified these as *Combretum spp*.

For two of the plant foods listed above we must make some important remarks. *Adansonia digitata*, the baobab tree, is not native to the area but was introduced by humans coming from the North some centuries ago (Interviews to elder). This tree is apparently incapable of propagating itself naturally in Comoé, thus we only found it where it had been planted to mark the creation of a new human settlement, as elder in neighboring villages told us. We found them, in most cases, associated with remains of the ancient settlements within the park. Once the camps and villages were abandoned by, at the latest, 1968, with the creation of the park, the baobabs remained and continued growing slowly, becoming an attractive but scarce and scattered fruit source for both mammals and birds (personal observation).

The lime tree *Citrus x aurantifolia* (popularly called the "citronnier" by the locals), is also scattered and scarce, but associated with gallery forest. The popular explanation for its distribution among the villagers is that it was also a cultivated plant and that elephants consumed and dispersed it throughout the region. This is possible, since we frequently found *C. aurantifolia* seeds in elephant dung, and we know that it is an introduced crop species brought from Asia (personal observation, interviews with elder in the neighboring villages).

Plants that we listed in Forest/ecotone usually grow in forest but frequently appear in the ecotone as well, at the limit between forest and savanna or even colonizing the first meters of savanna from the forest. On the contrary, plants listed as growing in Savanna/ecotone were usually found in the savanna (all types), often in proximity of the forest and occasionally in the ecotone or even within the first meters inside the forest patch. Plants listed as living in gallery forest were found exclusively in the gallery forests, along water courses, while plants listed in forest habitat were found both in forest islands and gallery forests or even exclusively in forest islands.

We confirmed the consumption by chimpanzees of at least 40 food plant species in forested habitats, plus four questionable ones. We confirmed the consumption of 14 food plant species in savanna (combining all types of savanna). We observed (DO, TR, CTV) chimpanzees using savanna species mainly when traveling from one forest patch to the next one, although in many cases, we found them feeding on trees less than 100 m away from the forest edge, after which they returned to the safety of the forest.

4.3.2 Fruit Availability Index (FAI)

The period during which we carried out our phenological study began on the first of November 2015 and finished on the first of November 2016. The study began in the dry season (early November-mid April) and ended with the next wet season (mid April-end of October). Some of the plant species chosen, such as *Drypetes floribunda and Lannea welwitchii*, which we had previously observed the chimpanzees eating, happened to not fruit over the entire year. For the calculation of the FAI, however, we pooled together the fruiting data of all of the 23 species used for the phenological study, thus the weight of a particularly less productive species should not heavily impact the results. We present in table 2 the monthly FAI for each species, highlighting the seasonal differences and the relative weight of each species. As we can see in fig. 2, there was a pronounced peak of fruit availability during the dry season and a zenith with almost no fruit available during several months of the rainy season. The smaller peak of fruit availability at the beginning of the wet season was due mainly to the fruiting of *Cola cordifolia, Parkia biglobosa* and *Vitellaria paradoxa*.

Table 2. Monthly contribution to the FAI of each of the 23 fruiting species used for our phenological study.

Species	Nov. 1	Dec. J	Jan. I	F eb. I	Mar.	Apr.	May .	Jun.	Jul.	Aug.	Sep.	Oct.
Adansonia digitata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.21
Afraegle paniculata	19.24	0.00	0.00	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Afzelia africana	0.00	0.68	1.51	0.12	0.17	0.01	0.10	0.38	0.04	0.00	0.00	0.01
Albizia zygia	0.00	8.71	8.71	9.15	0.87	0.00	6.97	54.89	0.00	0.00	0.00	0.00
Antiaris toxicaria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ceiba pentandra	0.00	0.00	732.30	366.15	137.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Celtis integrifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cola cordifolia	7.37	0.00	0.00	0.00	0.00	42.03	252.21	175.14	14.01	0.00	0.00	0.00
Detarium senegalensis	0.00	8.83	2.21	0.00	0.00	0.00	2.32	1.54	0.00	0.00	0.00	0.48
D. mycrocarpum	36.45	9.94	149.12	173.97	14.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dialium guineense	0.00	0.00	0.00	14.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diospyros abyssinica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
D. mespiliformis	0.00	0.00	0.00	0.00	10.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Drypetes floribunda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ficus ingens	0.00	0.12	0.47	0.37	0.06	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Ficus (strangler)	0.00	23.90	8.96	41.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lannea welwitschi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Parkia biglobosa	3.63	0.00	0.00	0.00	0.00	12.89	32.66	26.13	2.45	2.45	0.00	0.00
Piliostigma thonningi	0.00	2.65	28.67	6.37	0.35	0.18	0.18	4.25	0.00	0.00	0.00	0.20
Saba senegalensis	0.07	0.00	0.00	0.00	0.00	0.00	0.08	0.33	0.00	0.00	0.00	0.00
Tamarindus indica	0.00	73.81	137.78	11.07	2.58	0.00	31.00	7.75	2.58	2.58	0.00	0.00
Vitellaria paradoxa	0.00	0.00	0.00	0.00	0.00	3.45	15.51	17.24	0.00	0.00	0.00	0.00
FAI (all species)	66.77	128.65	1069.72	623.55	167.13	58.56	341.03	287.65	19.09	5.03	0.09	3.89

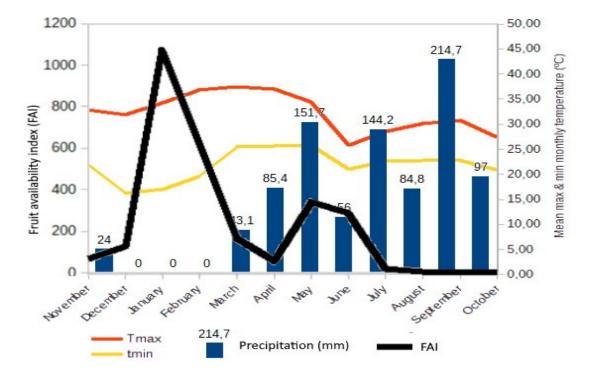


Fig.2 Monthly changes of the combined FAI of the 23 selected fruiting species compared to meteorological variables (precipitation, monthly mean maximum and minimum temperature) for the Comoé region. The data used in the graph correspond to the period from November 2015 to November 2016.

4.3.3 Dung samples

A total of 362 fresh chimpanzee fecal samples were collected over the entirety of the study period for analysis of contents, which is less than 10 % of the dung we observed in the field, but most of the dung found was not fresh enough for analysis or had already been disturbed by beetles; these were discarded from the analysis.

Among the contents identified in the dung samples, we counted particles of at least 35 identified plant species, at least 5 insect taxa, hair and meat of at least 3 mammal species, bones of one frog and multiple unidentified plant fragments and seeds (see table 3). Leaf fragments and fibers were so degraded that in most cases we could not identify them, so we pooled them together in the category of unidentified leaf fragments and unidentified fibers. The exception are the fibers of *Ceiba pentandra* and *Aframomum alboviolaceum*, which were always easily recognizable and still looked like cambium and pith fibers found in the field.

We found that some of the food plants we knew to be consumed by the chimpanzees were underrepresented in the fecal samples, since their seeds were too big to be swallowed, such as *Vitellaria paradoxa*, with spheroid seeds usually above 2.5 cm in diameter. In some cases only the flesh of the fruit (*Detarium senegalense, Balanites wilsoniana*) or the pod (*Tetrapleura tetraptera, Afzelia africana, Albizia zygia*) was consumed, leaving few or no visually recognizable remains in the washed sample. In the case of *Blighia sapida*, only the seed is consumed, but it is a soft seed that is chewed, leaving few recognizable fragments. Similarly, the seed of *Cola cordifolia* is soft, but is also too big to be swallowed in most cases, while the soft *arilum* that covers it is the most eaten part of the fruit, leaving no recognizable traces in dung.

In the case of *Afraegle paniculata*, the seeds are found in the center of a large fruit the size of a grapefruit, surrounded by a gluey substance that the chimpanzees avoid while eating the flesh. This likely reduces the frequency of *Afraegle* seeds occurring in the dung. In most cases we could not identify leaf remains and fibers to the species level, since they were partially digested and degraded quickly, so the relative importance of specific leaves as a food source is not fully reflected in the data of table 3, although the undifferentiated category of unidentified leaf remains and fibers reflects more approximately the relative frequency of these food remains in dung. Among insects, the hard heads of driver ant soldiers (*Dorylus burmeisteri*) always appear in the dung, while termite remains only rarely pass through the gut undigested.

Table 3. Contents of the fecal samples analyzed in the laboratory (n=362). with number of samples in which one or more of a particular kind of food was found and percentage over the total of 362, ordered from the most to the least frequently found.

Species	Type of particle found	Number of samples in which one or more particles was found (n=362)	Percentage of the samples in which one or more particles was found (n=362)
Dorylus burmeisteri	Insect	128	35.36
Unidentified plants	Leaf fiber	125	34.53
Tamarindus indica	Seed	101	27.90
Unidentified plants	Seed	98	27.07
Diospyros mespilifornis	Seed	87	24.03
Dialium guineense (seeds)	Seed	67	18.51
Ceiba pentandra	Cambium fiber	58	16.02
Oxyanthus racemosus	Seed	53	14.64

Saba senegalensis	Seed	46	12.71
Celtis integrifolia	Seed	32	8.84
Ficus spp.	Seed	25	6.91
Liana (unidentified)	Seed	21	5.80
Diospyros abyssinica (seeds)	Seed	17	4.70
Flacourtia indica	Seed	16	4.42
Parkia biglobosa	Seed	13	3.59
Drypetes floribunda	Seed	12	3.31
Aframomum alboviolaceum	Stem fiber	12	3.31
Aframomum alboviolaceum	Seed	9	2.49
Tamarindus indica	Fruit fiber	9	2.49
Phoenix reclinata	Seed	7	1.93
Cassia sieberiana	Seed	6	1.66
Stone (marle)	pebble	6	1.66
Blighia sapida	Piece of seed	5	1.38
Cola cordifolia	Seed	5	1.38
Ximenia americana	Seed	5	1.38
Antiaris toxicaria	Seed	4	1.10
Ceiba pentandra	Bark	4	1.10
Ceiba pentandra	Leaf fiber	4	1.10
Citrus x aurantifolia	Seed	4	1.10
Manilkara multinervis	Seed	4	1.10
Macrotermes subhyalinus	Insect	3	0.83
Meliponini spp.	Wax	3	0.83
Piliostigma thonningii	Seed	3	0.83
Unidentified animal	Meat	3	0.55
Unidentified plant	Bark	3	0.55
Wood (unidentified)	Wood	3	0.83
Adansonia digitata	Fruit fiber	2	0.55
Afraegle paniculata	Seed	2	0.55
Camponotus maculatus	Insect	2	0.55
Cercopithecus lowei	Hair	2	0.55
Beetle larvae (unidentified)	Insect	2	0.55
Lannea welwitchii	Leaf fiber	2	0.55
Piliostigma thonningii	Fruit fiber	2	0.55
Saba comorensis	Seed	2	0.55
Zhana golungensis	Seed	2	0.55
Adansonia digitata	Seed	1	0.27
Albizia adianthifolia	Seed	1	0.27
Cercopithecus petaurista	Hair	1	0.27
Cola cordifolia	Fruit fiber	1	0.27
Ficus ingens	Seed	1	0.27
Frog (unidentified)	Bones	1	0.27
Lannea welwitchii	Seed	1	0.27
Oecophylla sp.	Insect	1	0.27
Pan troglodytes*	Hair	1	0.27
Parkia biglobosa	Fruit fiber	1	0.27
Uvaria chamae	Seed	1	0.27
Vitellaria paradoxa	Seed	1	0.27
Ziziphus abyssinica	Leaf fiber	1	0.27

The hair of chimpanzee*, although it is theoretically possible that it could result from cannibalism, may have been swallowed during grooming, while the hair of monkey species (*Cercopithecus lowei* and *C. petaurista*) the remains of meat and the frog bones were most

likely product of predation. The pebble of marle was not contamination from the ground, but soil consumed by the chimpanzees, as confirmed with videos.

4.3.4 Seasonality in dung contents

The frequency that different food items appeared in the dung varied across the year, revealing the relative importance of different food sources in the different seasons. The maximum diversity of seeds in the dung was found during the dry season, which is in accordance with the results of the FAI. During the same period, fibers of *Ceiba pentandra* cambium, on the other hand, appeared only during the late rainy season, when bark-peeling behavior was also recorded (see chapter 5).

Table 4. Number of dung samples in which each food type was found per month, distinguishing type of particle found.

	Type														
C	of	T	r.l.	Ъ.б	Δ	N #	. т	. T1	A	- C		0-4	NI T	.	1- 4-1
Species found	partic	Jan	Feb 2	Mar	Apr	May	' Jur	ı Jul	y Au	ig S	ept	UCT	NOV 1	Jec 1	
Adansonia digitata	S S		2					2							2
Afraegle paniculata Aframomum	3							2							2
alboviolaceum	F, S	4	. 9)										5	18
Albizia adianthifolia	r, s	4		, 1										J	10
Antiaris toxicaria	S		4		-										4
Bark (unidentified)	В	3		•											3
Blighia sapida	S	J	•							5					5
Camponotus maculatus	I									J		2			2
Cassia sieberiana	S	3	1	. 2)							_			6
Ceiba pentandra bark	В	J	_		•							2	2		4
C. pentandra cambium	F								1	2	16				58
Ceiba pentandra fruit	Ē	4							_	_	10	10			4
Ceiba pentandra leaves	F							3	1						4
Celtis integrifolia	S	6	,					J	_	2	13	8		3	32
Cercopithecus lowei	H	2													2
Cercopithecus petaurista	Н	1													1
Citrus x aurantifolia	S		4	Ļ											4
Cola cordifolia	S							6							6
Dialium guineense	S	5	30) 15	5 5	5	3	2	7						67
Diospyros abyssinica	S	4	. 4	l 1	_							2	3	3	17
Diospyros mespilliformis	S	31	12	2 1	-							6	10	27	87
Dorylus burmeisteri	I	31	15	5 8	3	2	3			3	2	36	6	22	128
Drypetes floribunda	S						4	8							12
Ficus ingens	S	1													1
Ficus spp.	S	7	7	7								4	2	5	25
Flacourtia indica	S									1	9	6			16
Frog bones	В	1													1
Insect larvae	I												1	1	2
Lannea welwitchii	S	1		1	=								1		3

Liana unidentified	S	1	2	11	5								2	21
Macrotermes subhyalinus	I							3						3
Manilkara multinervis	S							4						4
Meat (unidentif. animal)	M		1									2		3
Meliponini	W							1			2		1	4
Oecophila sp.	I	1												1
Oxyanthus racemosus	S	1	13							1	33	2	3	53
Pan troglodytes	Η	1												1
Parkia biglobosa	S, F		1	2	10									13
Phoenix reclinata	S		7											7
Piliostigma thonningii	S, F	4	1											5
Saba comorensis	S		1	1										2
Saba senegalensis	S	7		6	6	8	12	2			1		4	46
Stone	-										2	1	3	3
Tamarindus indica	S, F	33	25	12							1	2	31	104
Unidentified plants	S, F	56	54	15	4	2	3			25	50	19	25	253
Uvaria chamae	S	1												1
Vitellaria paradoxa	S						1							1
Ximenia americana	S			2	3									5
Zhana golungensis	S									1	1			2
Ziziphus abyssinicus	S								1					1
Total		209	193	78	35	20	35	21	14	67	172	74	135	1050

S = seed, F = fiber, H = hair, I = insect, M = undigested meat, B = bone, W = wax and E = fepieces of exocarpum (the exterior cover of a fruit).

4.3.5 Relative importance of savanna vs forest foods

We have to remind here that there is very little proportion of open grasslands in Comoé and when we talk about savanna is either woody savanna or bushy savanna, forming mosaics or gradients with changing tree cover, following the criteria of Lindshield (2014). We do not include in the category of savanna what other authors have classified as woodland.

We have known since 1985 that the Comoé chimpanzees occasionally make use of savanna: recordings made in that year show them crossing the savanna close to forest edge (Galat & Galat Luong, 1985) although the relative importance of this use in their ecology was unknown. We collected from the savanna only 25 of the 362 dung samples analyzed. Nevertheless, the presence of savanna species was detected almost exclusively in dung samples collected in the forest and savanna samples contained almost exclusively forest species (1 of 25 contained savanna species). When we were able to successfully follow the chimpanzees, we observed that, when crossing from one forest patch to another and foraging on savanna trees, they never stayed for longer than one hour in the savanna. Only 12 % of the total of 362 dung samples analyzed contained the remains of savanna species, mainly seeds, but also fibers. The savanna species detected in the dung samples were Parkia biglobosa, Aframomum alboviolaceum, Ximenia americana, Piliostigma thonningii, Ficus ingens and Vitellaria paradoxa, with Parkia biglobosa being the most frequently found (in 14 samples). To this list, we could add some species that are normally found in the forest or ecotone between forest and savanna, but occasionally can grow over old termite mounds in the savanna, such as *Diospyros*

mespilliformis, Tamarindus indica and Saba senegalensis. These are preferred chimpanzee foods, eagerly consumed by the apes, but we obviously are unable to tell from the dung samples whether the fruits were consumed in the forest or the savanna. It is important to point out that on only two occasions did we find evidence of tool-assisted foraging in savanna, less than 200 m away from the forest edge; on both occasions it was for honey-dipping. We never found signs of chimpanzees foraging on insects or vertebrates in the savanna. Although it is possible that they consume animals killed by bushfires, we never found any evidence of this, despite having walked through burnt savanna on numerous occasions. More importantly, we repeatedly found traces of the consumption by chimpanzees of *Afzelia africana* and *Detarium mycrocarpum* fruits, both savanna species that were mostly undetectable in the dung. We found chimpanzee footprints and dung near *D. mycrocarpum* and *A. africana* fruits, and on some occasions tooth marks, but for the latter species, we also made two direct observations of chimpanzees eating this fruit and also obtained camera trap videos (see table 4). Thus, the relative importance of the savanna foods in the diet of the Comoé chimpanzee is likely greater than is reflected in the results from the dung sample analyses. We should remark that all of the savanna fruits we recorded being consumed were eaten during the dry season or, in the case of *Vitellaria paradoxa*, at the beginning of the rainy season.

4.3.6 Camera trap videos

During the study period, 2014-18, we achieved a total of 39615 camera days, covering 115 grid cells across 13% of our main study area of 900 km². We recorded chimpanzees in 60 of these grid cells, with a total of 2326 videos of chimpanzees. From these, we were able to individually identify123 chimpanzees, including infants.

The most recorded foraging events were those related to the tool use: ant-dipping, ant-fishing, termite-fishing and honey-dipping (Table 5). This is likely due to the fact that we were mainly targeting tool-use sites for our general study. Nevertheless, we occasionally recorded chimpanzees eating fruits or pounding them open on natural anvils to eat them afterwards, in particular with the fruit of *Afraegle paniculata*. Of special interest are the 13 videos that recorded 10 adult chimpanzees, from three different communities, carrying savanna fruits into the forest, probably to eat them more comfortably, such as *Afzelia africana* and *Parkia biglobosa*. To carry this last species, we found that chimpanzees stripped off an entire branch containing 10-12 fruits and carried it into the forest in their mouth, sometimes more than 500 m from the tree.



Fig. 3 Chimpanzees carrying savanna fruits into the forest. In the background, Andromaka, from the Trojan community carries a bunch of fruits of *Parkia biglobosa* from the nearby savanna into the forest, while Penelope dips for water in the foreground.



Fig. 4 Adamea, from the Achean community, carries in her mouth a bunch of fruits of *Parkia biglobosa* 200 m deep into the forest, while following a traveling party of chimpanzees.



Fig. 5 Chimpanzees of the Achean community carrying the pods of *Afzelia africana* from the savanna to consume them in the forest. To the left, the female Atenea carries a pod in her hand, to the right, the male Ajax carries a pod in his mouth.

Table 5. Number of videos recorded per foraging-type, distinguishing between those that were tool mediated and those done without tools. Fruit pounding is marked with and asterisk, as the use of an anvil upon which to pound an object, is not usually considered to be tool-use, but it has recently described as percussive technology. The soil was consumed without tools in most cases, but as we describe in chapter 7, chimpanzees in Achean community used leaf sponges to drink clayish water from salt-licks.

Type of foraging recorded	Tool use	Species eaten	Part eaten	Number of videos
Ant-dipping	Yes	Dorylus burmeisteri	Whole insects	100
Ant-fishing	Yes	Camponotus maculatus	Whole insects	2
Termite-fishing	Yes	Odontotermes majus	Whole insects	18
Termite-fishing	Yes	Macrotermes subhyalinus	Whole insects	18
Honey-dipping	Yes	Apis mellifera	Honey	1
Honey-dipping	Yes	Meliponini spp.	Honey	60
Fruit-pounding	*	Afraegle paniculata	Fruit pulp	27
Fruit-eating	No	Afzelia africana	Pod	6
Fruit-eating	No	Parkia biglobosa	Fruit pulp	7
Fruit-eating	No	Oxyanthus racemosus	Fruit pulp	2
Soil-consumption	No*	Clay, marle, clayish water	Portions of soil	98

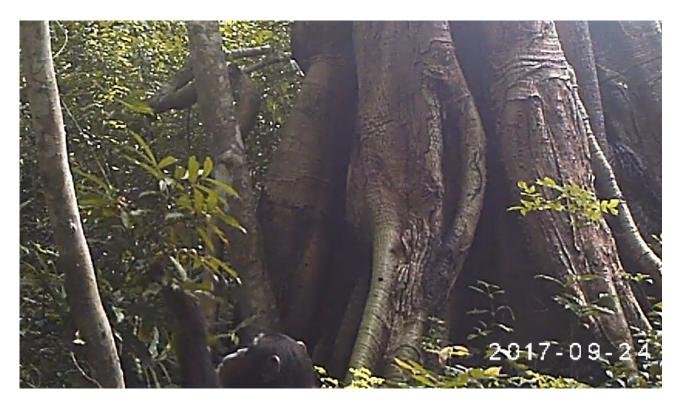


Fig. 6 The subadult female Chriseys, from Achean community, collects and eats the fruits of *Oxyanthus racemosus*. This large shrub was not included in our phenological study, as we were considering only species with more than 10 cm dbh, so its fruiting period during the wet season is not reflected in our estimation of the FAI. Judging, however, by the presence of its seeds in dung samples, direct observations and feeding traces, it provided an important fruit food source during a period of general scarcity.



Fig. 7 This young adult male of Mont Tingui consumes a fruit of *Afraegle paniculata* after pounding it open against a root anvil. The use of an anvil is not usually considered as tooluse, since it is attached to the substrate, although it is now called percussive technology (Hicks et al. 2019b).

4.3.7 Foraging tools

During our study of the Comoé, chimpanzees, we confirmed the use of tools for drinking, foraging and hitting trees in displays. The These apes were proficient tool users, mainly constructing and using stick tools, adapted to every function (table 4). Among the foraging tools, we found stick tools for ant-dipping (the use of tools to extract ants from their underground nests), ant-fishing (to extract ants from tree holes), termite-fishing (to extract termites from their earthen mounds) and honey-dipping (to extract honey from arboreal beehives). In the case of honey, we rarely found tools inserted into the hives of honeybees (Apis mellifera) and only twice found signs of successful honey dipping, such as empty honeycombs on the ground beside tools. We recorded a single video of chimpanzees dipping for the honey of *Apis mellifera*. On the contrary, we frequently found stick tools inserted into the hives of Meliponini spp. stingless bees and at the bases of trees containing stingless bee beehives, and we recorded multiple videos of this type of tool use (see table 4). We detected a certain seasonality in the use of the different types of foraging tools, which may be related to the seasonal availability of the different food sources (Fig. 8). More information about the characteristics, measurements and numbers of different tool types is found in chapter 7.

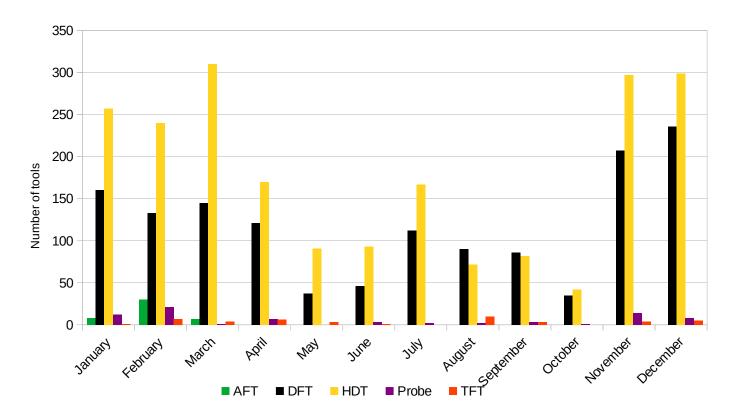


Fig. 8 Total of foraging tools found in the field during the entire study period, separated per month. We can see that the encounter rate of ant-dipping and honey-dipping tools is higher in the driest months (see fig. 1 for precipitation). Ant-fishing tools were exclusively found in the middle of the dry season (January-March), while termite-fishing tools had no clear pattern; perhaps related to the heavy individual rainstorms. Similarly, probes are found throughout the year, since they are used to inspect holes with multiple purposes.

4.3.8 Hunting and meat consumption

Besides the hair of Cercopithecus monkeys and bits of undigested meat that we found in the dung samples (see previous section), we found indirect signs of predation, such as the partially-consumed carcass of a red-flanked duiker (*Cephalophus rufilatus*) surrounded by chimpanzee footprints and dung. On one occasion we found numerous hairs of a marsh cane rat (Thrionomys swinderianus) at the entrance of a burrow associated with chimpanzee footprints and two modified sticks which may have been used by the chimpanzees as probes to try extract the cane rat from the hole (see chapter 7 for more details). On one occasion, our team of assistants witnessed a fight between a group of baboons (Papio anubis) and a party of chimpanzees from the Achean community. When they arrived at the spot 15 minutes later, they found the chimpanzees running away from the freshl partially-consumed carcass of a juvenile baboon (Fig. 8). It is worth to mention, that the confrontation between the two primate species occurred at the savanna edge, with the chimpanzees taking the carcass inside the forest afterwards. On another occasion, we recorded with our camera traps what seemed to be the beginning of a hunt by chimpanzees of white-thighed colobus monkeys (Colobus vellerosus) by the male chimpanzees of Odyssey community. In the video provided in the supplementary materials, (vid. 1) two adult male chimpanzees can be seen running along the ground and looking upwards into the canopy while the colobus vocalize loudly in the background (fig. 10).



Fig. 9 Partially-consumed fresh carcass of a juvenile baboon (*Papio anubis*) found by our assistants just after they observed a fight between a troop of baboons and a party of chimpanzees.



Fig. 10 Possible onset of a hunting bout recorded by a camera trap. Two adult males of the Odyssey community run along the forest floor while loud vocalizations of *Colobus vellerosus* sound in the background.

4.3.9 Insectivory

We found evidence of Comoé chimpanzees feeding on insects at the tool use sites, from videos and via dung samples. This was a behavior directly witnessed by our team in 12 occasions. The chimpanzees consumed insects across the whole year and some of the insects, such as the driver ants, were found in more than a third of the dung samples, suggesting that insectivory is very important for Comoé chimpanzees

4.3.9.1 Ants

The insect most frequently found in the dung samples was the driver ant (*Dorylus* burmeisteri), occurring in 35.36 % of the samples (Table 3). This is consistent with the great number of ant-dipping tools and tool sites that we found throughout the year (Fig. 8). As confirmed by videos and direct observations, the chimpanzees used sticks as antdipping tools to extract driver ants from their temporary underground bivouacs. The seasonality of the tool-making also corresponds with a higher frequency of the ant heads found in the dung during the dry season than in the wet season. Along our recces and transects during multiple years of the study, we observed that driver ants moved more actively during the rainy season, forming marching columns and swarms. In the dry season, the ants remained mainly in their underground bivouacs. Interestingly, however, it was in the wet season when the ants were less likely to be consumed: most of the tools associated with ant nests were found during the dry season. Ant-fishing of carpenter ants (Camponotus maculatus) was also quite seasonal. Ant-fishing differs from ant-dipping in that the chimpanzees use tools to extract the ants from tree holes, instead of underground nests. The apes predated upon carpenter ants exclusively during the height of the dry season, from January to March, as documented with videos and tools (see table 4 for number of videos of each behavior). This could be related to the activity cycle of the ants or to the fact that driver ants, that could be a preferred prey with respect to carpenter ants. retreat deep underground during this period and were more difficult to reach. We also found once stick tools associated with a nest of *Crematogaster sp.* ants in a tree hole.

The last ant species we confirmed to be consumed at Comoé via dung samples was the weaver ant *Oecophila cf. longinoda*, which makes nests out of leaves in the tree canopy. I other study sites, the chimpanzees have been observed to roll these nests between their hands and smash the ants (Nishida, 1983, Hicks et al. 2019b). We found this ant in only one dung sample, suggesting that its consumption by the Comoé chimpanzees is infrequent.

It is important to remark that all the above-mentioned examples of ant foraging were recorded or observed in forest and we never found any indirect signs or observed directly the chimpanzees foraging on ants in the savanna. However, we did observe driver ants crossing savanna stretches in columns or even swarms, in proximity of the forest, but as previously stressed, we never observed the chimpanzees foraging on swarms or columns of driver ants, neither in forest nor in savanna.



Fig. 11 Adult female Melantea, from Odyssey community, dips for driver ants (*Dorylus burmeisteri*) in a seasonal nest while the subadult male Laertes and the juvenile male Euriloco closely watch her.

4.3.9.2 Termites

We also confirmed that the Comoé chimpanzees forage on termites with tools. This was based on the tools we found inserted into or lying atop termite mounds, in association with footprints and dung. We also found in one occasion a single termite head, belonging to *Macrotermes subhyalinus*, in a dung sample. Finally, we observed the behavior via camera-trap videos. (Table 5, Fig. 8). We discuss below the reasons why we think termites were so rarely found in the dung despite our other abundant evidence for the behavior. Through these indirect signs and videos, we confirmed that the Comoé chimpanzees target at least two termite species, the above-mentioned *Macrotermes subhyalinus* and also *Odontotermes majus* (see table 4 for the number of videos recorded of each behavior). We also frequently found smashed-open mounds of *Cubitermes sp.* in association with chimpanzee footprints and dung. Although we could not confirm the consumption of this latter species via dung samples or videos, we considered chimpanzees to be the most likely culprit of breaking the *Cubitermes* mounds that we found smashed on root anvils, as we discuss below.

Most of the termite-fishing observations were made in forest, both gallery forest and forest islands. All the videos of this behavior were recorded in forest and only one on 22 termite-fishing events detected through indirect signs occurred in savanna, around 20 m away from the forest edge. Similarly, all of the *Cubitermes* mounds pounded were found inside the forest.



Fig. 12 *Cubitermes sp.* mound pounded open against a root anvil, most probably by chimpanzees. Photo taken in a large forest island in the Odyssey home range the 30th of September 2016.

4.3.9.3 Bees and honey

Even though we never found remains of adult bees or larvae in the dung samples we anayzed, we did find chewed wax on several samples (table 3), which we presume came from the honey-combs of sting-less bees (*Meliponini spp.*). In the 61 videos that we recorded of the behavior via camera traps, the chimpanzees could often be seen swallowing substances attached to the honey-dipping tools. Since they pierced the chambers of the beehive to extract the honey, we can assume that pollen and larvae were most probably extracted together with the honey. We also found on two occasions completely empty combs of *Apis mellifera* associated with freshly used chimpanzee tools, footprints and dung, suggesting that the chimpanzees had eaten all of the contents in the comb, not only honey. It is important to remark that this is the only example of tool use that we found to occur clearly in the savanna, with two cases in Aeneid and Achean communities respectively, in which chimpanzees had been foraging on honey of Meliponini beehives at more than 100 m from the nearest forest.

4.3.9.4 Other insects

We found remains of beetle larvae twice in the dung samples, however, as we discuss below, we may be underestimating the frequency of the ingestion of this food source due to their frequent destruction by digestion. The possibility of dung beetle larvae that had hatched in the dung was discarded, since dung beetles bury the portions of the

dung where they lay their eggs and sometimes they bury even the whole dung. It also takes several days for the larvae to become as big as the ones found and the dung would be completely gone by then, if remained on the surface. On the contrary, the dungs where we found the described beetle larvae were fresh, from the same day.

4.3.10 Possible consumption of giant snails of genus Achatina

We found in five occasions stone anvils on which giant snails of the species *Achatina achatina* and *A. fullica* had been pounded open. We could not confirm that the chimpanzees consumed the snails through videos of camera traps or direct observations, although we did find abundant chimpanzee footprints and dung in one occasion around the anvils, suggesting that the snails were cracked by the apes (see chapter 7 for more details).

4.3.11 Consumption of clay and marle as probable source of minerals

As described in methods, we monitored with camera traps four of the 16 salt-licks that could potentially be used by the chimpanzees, each in a different community homerange. We found chimpanzee traces (footprints) in four of the 16 potential salt-licks, including two of the monitored ones. We recorded 140 videos of chimpanzees in the two salt-licks in which the chimpanzee traces were found. 98 of these videos contained images of the chimpanzees scraping the soil with finger nails or teeth in one of the salt licks and two other videos showed the chimpanzees using leaf-sponges to drink the clayish water accumulated in the salt-lick after a rainstorm (chapter 7).



Fig. 13 Odyssey community: adult male Polifemo scrapes marle and clay with his teeth, while female Anticlea uses her finger nails for the same purpose in a salt lick in a cliff at the river bank in the center of their home-range.

4.3.11 Consumption of Ceiba pentandra cambium as fall-back food

Starting in November 2014, we found a number of *Ceiba pentandra* trees which had been freshly peeled of their bark, with traces of what seemed to be tooth and nail-scraping by chimpanzees. With the use of camera-traps, we confirmed that not only the chimpanzees, but also the baboons peel the bark of these trees, and the chimpanzees were confirmed to eat the cambium exposed (For more details on this behavior, see chapter 5).

We found that the cambium was consumed exclusively during the late wet season and beginning of the dry season, from July to beginning of December, when the fruit availability of the main food tree species was at its minimum (Fig. 2). This suggests that the chimpanzees consumed the *C. pentandra* bark as a fall-back food during times of food scarcity, and when the cambium was full of sap, during the late wet season (we compared the content of water of the cambium in wet and dry season).

We also found that the chimpanzees consumed the flowers, fruit and the young leaves of *C. pentandra* tree at different periods of the dry season, when these different parts of the tree were available, but we never observed bark-peeling or cambium consumption during the period in which they consumed the other tree parts.

4.3.12 Number of food items consumed compared with other study sites

The study of the diet and feeding ecology is usually carried out in most research projects working with wild chimpanzees. Nevertheless, the sampling effort has been very different depending on the projects, which sometimes have different priorities or lack the botanical expertise necessary for the identification of most food items. Nevertheless, the longer a research project has been working, the more detailed is the list of food items recorded. We present here a table with data obtained from the literature describing some ecological variables and the food items recorded for a number of study sites, both in the forest and in the savanna. We completed the table presented by Piel et al. (2017) with the data for the Baffing site, Mali (Duvall, 2008) and our own data from Comoé.

We need to remark that some sites that have been classified as forest in table 6, such as Gombe and Mahale, in Tanzania, despite the high precipitation recorded, contain a high proportion of woodland, relatively open habitats with discontinuous canopy and grass in the understorey. However, the high number of food items recorded in these sites could also be partially explained by the long duration of the studies (more than 50 years) that allowed the list to grow longer with the accumulation of observations.

The 72 food items that we counted for Comoé include the 58 plant parts plus the four species of ants, the three species of termites, the beetle larvae, the honey, the three species of monkeys, the frog and the clay (marle). We could enlarge the list with the inclusion of other species that were probably consumed, such as other two mammal species (*Cephalophus rufilatus* and *Thryonomys swinderianus*), two species of giant snails (*Achatina achatina* and *A. fullica*) and several plant parts that we could not confirm with videos or direct observations, but we will wait for the results of further research to continue completing the list.

Table 6. Environmental variables and number of food items consumed by the chimpanzees at different study sites, including both forest and savanna (modified from Piel et al. 2017. Data for Bafing from Duvall, 2008). Sampling methods distinguish only between direct observation (D) and indirect (I) faecal analysis and feeding remains, although at our site, video recording with camera-traps could be considered the equivalent of the direct observation. Sd means that data were not made available to us for that site.

							Sympatric medium- large	:	Plant	
Dominan habitat	t Study site / Country	Annual rainfall (mm)		annual	Monthly T min °C	Monthly T max °C	mammal species (n)	Diet sample size (n)	species consume d (n)	Samplin g method
	Bossou (Guinea)	sd	sd	sd	sd	sd	sd	sd	200	D
	Budongo (Uganda)	1489±197	3	20-38	sd	sd	15	2641	58	D
	Bwindi (Uganda)	1100-2400	sd	sd	sd	sd	29	187	32	I/D
	Gishwati (Rwanda)	sd	sd	sd	sd	sd	sd	1381	23	ı
Forest	Gombe (Tanzania)	1430-2542	6	sd	19	28	25	807	147	D
Forest	Goualogo (R. Congo)	sd	sd	sd	sd	sd	19	sd	115	D
	Kahuzi Biega (D.R.C.)	sd	sd	sd	sd	sd	sd	7212	110	I/D
	Kibale (Uganda)	1536	5	19.2	12.3	26.6	37	1059	102	D
	La Lopë (Gabon)	sd	6	25.2	26	28	25	1854	132	ı
	Mahale (Tanzania)	1762±125	5-6	20.2	12.3	27	30	sd	198	D
	Semliki (Uganda)	1389±41	5	24.06	20	34	26	72	36	I
	Issa Valley (Tanzania)	1094	6	23.9	11.7	38.7	36	812	77	ı
	Comoé (Ivory Coast)	1090	6	27	15.7	36.12	69	725	72	I/D
Savanna	Kasakati (Tanzania)	962	6	22.1	16.5	26.6	37	7	78	ı
	Mt. Assirik (Senegal)	954±182	7	29	23.1	34.9	27	60	43	ı
	Fongoli (Senegal)	900	7	28.4	17.1	38.9	22	1320	77	I/D
	Bafing (Mali)	1100	sd	sd	sd	sd	sd	71	39	I

4.3.13 Home-ranges

We were able to estimate with some precision the home-ranges of our four most studied communities: Achean, Trojan, Aeneid and Odyssey. We required more data to confirm the limits of the home-ranges of Argonaut and Theogony, which we visited only once per month during the dry season. Nevertheless, we have a rough idea that these communities occupy the gallery forest surrounding the Gondo River and Iberá River, respectively. The latter is the largest forest patch in the entire CNP and even where it is crisscrossed by the Iberá River and its tributaries, it is mostly composed of dry forest. The poaching pressure, however, was higher in this forest during the civil war period according to the local villagers we interviewed. They told us that the villagers of Amaradougou (at the west limit of the park) hunted the chimpanzees, selling the smoked meat with the hands

and head cut off so it could pass as baboon meat. Therefore, we can speculate that the lower chimpanzee density in the Theogony home-range was due to poaching. This could also explain why we found large forest islands, rich in fruit, between the Theogony and Trojan home ranges that had no traces of chimpanzees.

With respect to the chimpanzees inhabiting the special zone of biodiversity of Mont Tingui, we only began surveying this area in 2018, thus, we still lack much knowledge about the seasonal movements of these chimpanzees. Back in 2013, however, we surveyed the area for one week and found many more nests spread out over a wider area than we would later encounter in 2018-19. In 2013, we found no access point for vehicles and villagers apparently rarely entered the zone, while in 2018, cattle herders and gold miners were intensively using the zone, which could explain why the chimpanzees retreated from the forests closest to Amaradougou.

Even for our most extensively-studied home-ranges there are still some areas where we are not certain which community, if any, inhabits them, as we lack camera-trap data and direct observations. These areas are indicated with question marks in figure 13. For the home ranges sizes that we estimated, they ranged from 40 km² for the Trojan community to71 km² for the Odyssey community, with the intermediates being the Achean (52 km²) and Aeneid (65 km²) communities. The average size of the better known homeranges is around 57 km².

Table 7. Area of the home-ranges of the four better known Comoé chimpanzee communities, together with percentage of forest cover in each home range and the number of chimpanzees identified from camera traps.

	Home range area (Km²)	Forest area (Km²)	Forest %	Identified chimpanzees
TROJAN	39.8	19,9	50	23
ACHEAN	52	13,5	26	23
AENEID	65	17,6	26	5
Odyssey	71	18	25	22

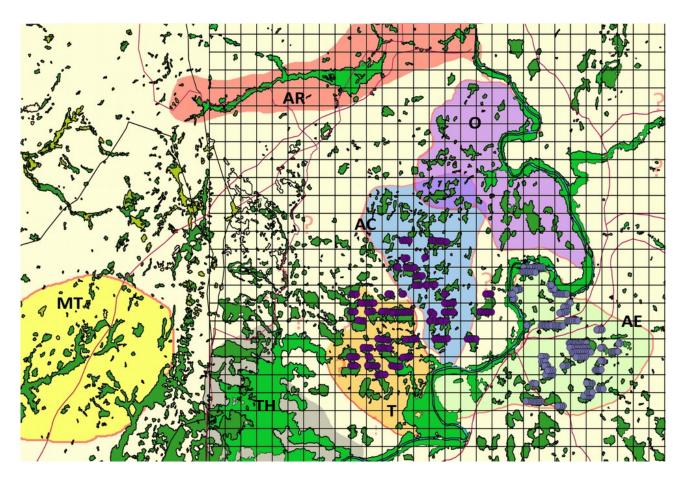


Fig. 14 Estimated home range sizes of the identified chimpanzee communities. Yellow = Mont Tingui, Grey = Theogony, Pink = Argonaut, Orange = Trojan, Blue = Achean, Purple =Odyssey and Green = Aeneid. Only the last four communities were considered for estimation of home range area based on having sufficient data. The purple dots across the Trojan, Achean and Aeneid home-ranges correspond to the positions of the habitat plots used to study the structure of the forest, where most of the phenology trees were chosen.

4.4 DISCUSSION

With this study we aimed to discover more about the diet and habitat use of Comoé chimpanzees, how these aspects varied along the seasons and how they could be compared to other research sites.

We confirmed hypothesis 1, since we found that fruit availability changed significantly across the year, at a minimum during the late rainy season and at a maximum during the late dry season (Fig. 2). Similarly, we found that the variety of food items in the dung samples depended greatly on season, in parallel with the fruit availability, which is logical, since most of the food items found in dung were seeds (Table 4).

We confirmed that during the months of August, September and October, fruit availability was at its lowest and we found that the Comoé chimpanzees relied more heavily then on the consumption of the cambium of *Ceiba pentandra*, which is likely a fallback food during this fruit scarcity period, providing support for hypothesis 2 (see chapter 5 for more details on this behavior).

We found that Comoé chimpanzees spent more time in the forest than in the savanna, and consumed a higher proportion of forest food items than savanna ones in

their diet, supporting our prediction of hypothesis 3. From the 58 different plant food items that we found to be consumed, only eight (13.8 %) were obtained in the savanna. Six of these savanna items were seeds from savanna fruit trees or shrubs that we found in the dung samples. Only the 12 % of all dung samples (n= 362) analyzed contained savanna species. Parkia biglobosa was the most frequently found savanna species. It should be repeated that some species, such as Piliostigma thonningii, Afzelia africana and Detarium mycrocarpum were likely underrepresented in the dung samples because chimpanzees ate mainly the pod, not always swallowing the seeds. This was clearly the case with the latter two species, which never appeared in the dung despite being consumed by the chimpanzees, as confirmed with videos, direct observations and feeding traces. Even if other savanna species were similarly difficult to detect in the dung, a similar proportion of undetectable forest species might be expected, thus not undermining our finding of the much higher proportion of forest over savanna foods in the diet of the Comoé chimpanzees. For instance, the chimpanzees of the Achean community consumed many seeds of Blighia sapida, a forest species during the rainy season, as we directly observed in 20 occasions, but the remains of the seeds were rarely identified in the dung samples. We have not included in this comparison the non-plant food items, which were in most cases obtained in the forest too, such as all the ant species, most of the termites and most of the mammals. The exception would be the baboon that was killed at the forest edge and a single case of termite fishing observed in the savanna, around 20 m away from the forest. Honey was obtained from beehives in forest trees in all but two cases in which we found honey dipping tools in savanna.

As we expected, Comoé chimpanzees used tools to extract insects and insect products from their nests. Therefore, hypothesis 4 was supported by the data. The insects foraged for with tools included three species of ants, two of termite species (three if we include the digging out of *Cubitermes* mounds with sticks). The chimpanzees also collected honey with tools from beehives of several sting-less bees, a behavior that has also been documented at other study sites, such as Mont Assirik, Senegal (Bermejo et al., 1989), Loango, Gabon (Head et al. 2009) and Ngotto Forest, CAR (Hicks 2004) among others. On the contrary, they rarely fed on honey from from honey-bees (Lapuente et al. 2016, Soro et al. 2019), which has been documented at Goualougo, Congo (Sanz & Morgan, 2009), Ngotto (Hicks et al. 2004) and Taï forest, IC (Boesch & Boesch-Achermann, 2000), among others. The availability of insects and insect products was varied seasonally and this was reflected in the seasonality of the tool-use, as reflected in the number of tools that we found per month.

As we expected, Comoé chimpanzees hunted mammal prey, as confirmed by direct observation, feeding traces and hairs and undigested meat in dung samples, which supports hypothesis 5. We confirmed the hunting and consumption of at least three species of primates, *Papio anubis, Cercopithecus lowei* and *C. petaurista*, and a camera trap provided us with footage suggesting the possible initiation of a hunt of *Colobus vellerosus*. We also found chimpanzee traces associated with a freshly-consumed carcass of *Cephalophus rufilatus*. A hair-strewn burrow of *Thryonomys swinderianus* was also suggestive of a possible chimpanzee predation event, possibly even involving the use of tools.

Apart from the mammals, we could confirm the consumption of an unidentified frog species by finding its remains in a dung sample. Comoé chimpanzees probably consumed the giant snails of genus *Achatina*, since on five occasions we found their footprints around anvils used to crack the thick shell of these snails. This behavior has been suggested as well for the chimpanzees of Bili (Hicks et al. 2019a).

As predicted by hypothesis 6, we found that Comoé chimpanzees consumed the soil, specifically the clay and marle that the scraped from salt-licks using their finger nails or teeth. The geophagy, the consumption of soil, has been described in chimpanzees of other research sites, such as Mahale, Tanzania (Nakamura et al. 2015), Kibale, Uganda (Mahaney et al. 2005) or Budongo, DRC (Reynolds et al. 2015). Different authors have suggested that it could be related with the need of salts that could be obtained from the soil or from the dirt of termite mounds (Reynolds et al. 2015) or to help in the digestion of plant foods rich in tanins thanks to clay or minerals that could buffer the toxic effects (Mahaney et al. 2005). We need further research to learn why Comoé chimpanzees consume the clay and clay-rich marle in salt-licks. We did observe from our videos that no carnivore species consumed the soil, whereas many herbivores, from squirrels to elephants did. The species that consumed the soil most often were antelopes and, apart from chimpanzee, the only other species recorded doing it was the baboon. All these species consume some unripe fruit, bark or leaves that can be rich in tanins, although we need more data to confirm that this is the main benefit searched by the chimpanzees when consuming the soil.

We found that the Comoé chimpanzees consume at least 72 different food items, which represents a more diverse diet than those described for some less well-studied savanna sites (Mt. Assirik, in Senegal, Bafing, in Mali and Semliki, in Uganda) but not as diverse as those found in better-studied savanna sites (Fongoli, in Senegal and Ugalla, in Tanzania). The number of food items found to be consumed in Budongo Forest, Uganda, was smaller than that of Comoé; this number, however, is low for forested sites. Well-studied forest (and woodland) sites, such as Bossou, in Guinea (200 items), Gombe (147) and Mahale (198), both in Tanzania, or Kahuzi Biega, in D.R.C. (116), Lopé, in Gabon (136) or Goualogo, in Congo (115) present a longer list of food items and twice as long as at Comoé in some cases (see table 6), suggesting that the hypothesis 7 is supported by our data,

Chimpanzee densities have been found by other authors to range between 2.9-5.2 at rainforest sites such as Budongo or Taï forest, while forest home-ranges can be between 7.8–14.9 km² in Budongo, Uganda (Reynolds, 2005) or between 7.9-30.1 km² in Taï Forest, Ivory Coast (Boesch & Boesch-Achermann, 2000, Kouakou et al. 2011), On the contrary, if we consider the total surface of our study area, including savanna, we found that the home-ranges of the four best known chimpanzee communities in Comoé ranged between 39.8 and 71 km² with a mean density of just 0.14 weaned chimpanzee / km² (see chapter 3). Therefore, our data supports hypothesis 8, since Comoé chimpanzees live clearly at lower densities and have much larger home-ranges than those at forested sites.

Savanna research sites have been described as presenting a more extreme seasonality (Baldwin, 1979, McGrew, 1981, Tutin et al. 1983, McGrew, 1988, Boesch & Boesch, 2002, Russak, 2013, Piel et al. 2017) which poses a challenge to chimpanzees inhabiting them, which suffer higher degrees of thermal, hydric and nutritional stresses (Pruetz et al. 2006, Wessling et al. 2018). Chimpanzees and other primates are known to change their behavior in response to fruit scarcity (Tutin et al. 1997, Wrangham et al. 1998) altering their usual ranging patterns or diversifying their food choices, and in many cases relying on fallback foods that are not a preferential choice in times of food abundance. As we have demonstrated in this chapter, the Comoé chimpanzees are faced with strong changes in fruit availability. This could not be offset with the ingestion of more insect food, since the maximum and minimum availability of both types of food occurred during the same periods. Therefore, Comoé chimpanzees turned to foraging on *Ceiba pentandra* cambium, a type of food that they never consumed during times of fruit and insect abundance (Fig. 2, table 4, chapter 5). Since this period of food scarcity when the

cambium was frequently consumed was the late rainy season, during which many insects are active, we might be surprised that the chimpanzees did not rely as much on insect foods during that period. As a matter of fact, the most-consumed insect, the driver ant (Dorylus burmeisteri), was found to be quite active during that period, usually forming long migration columns or huge amoebic swarms to hunt. We found few tools that could potentially be associated with these particular ant behaviors (five of 1408 tools) and never confirmed it through videos or direct observations. On the contrary, most of the ADTs were found inserted in temporary driver ant bivouacs, which are more common during the dry season. We cannot know if there is a cultural reason that might explain this apparent preference of Comoé chimpanzees to dip for the driver ants in their nest, instead of dipping them along the columns or swarms. The aggressive defensive behavior of the ants could explain this preference. In many study sites the chimpanzees dip for driver ants at the bivouac, like in Gombe, Tanzania (Goodall, 1986) in Taï, IC (Boesch & Boesch-Achermann, 2000), Fongoli, Senegal (Bogart, 2009) or Bili, DRC (Hicks et al. 2019a), although some populations also do so in swarms or trails, like in Ngotto, CAR (Hicks et al. 2005) or Bossou, Guinea (Matsuzawa et al. 2011). We observed in our videos that the Comoé chimpanzees always avoided the ants biting their feet by clinging to branches or vines above the nest or remaining on the ground as far as possible from the nest entrance while reaching towards it with a long ADT. This technique would be clearly harder to implement with a swarm, since the ants move unpredictably across the forest floor and would rapidly climb up to any place where the chimpanzee was, making it hard for the chimpanzees to stay in a safe place while eating. More information on the ant-dipping behavior of the Comoé chimpanzees can be found in Chapter 7.

Similarly, the seasonal behavior of termites, which realize their nuptial flights following heavy rainstorms, means that the chimpanzees mainly consume them with tools at the onset of the rains, during the first half of the rainy season. Just before the flight, termites make the walls of the mound thinner at some points, preparing to open holes through which the winged termites will come out. The galleries close to these thinner spots are full of soldiers which are the objective of the chimpanzees, who scrap the surface of the termite mound with their finger nails and then insert the tools to fish the defending soldiers, this behavior was already described by Goodall (1986) in Gombe, Tanzania (see chapter 7 for more details on termite fishing in Comoé). Honey is also much more readily-available during the dry season, since most of the trees are flowering at that time and the bees of every species are more active. Therefore, the second half of the rainy season, when there was the most precipitation, was coincidental with the scarcity not only of fruit, but also of other alternatives, such as insect foods.

The data we used to produce the FAI has an important limitation. We used the 23 fruit species that we considered to be the most commonly consumed by the chimpanzees at our site, based on the data we took during the preliminary phase. Nevertheless, the methodology that we followed for this particular study (Arandjelovic et al. 2014) limited the species to those with dbh above 10 cm and we found some important plant foods, consumed during the rainy season, such as the shrub *Oxyanthus racemosus* or the herb *Aframomum alboviolaceum* which were not included in the FAI for being smaller. As you can see, however, in the list of food items confirmed to be consumed by the Comoé chimpanzees (table 1), there are many more species for which we could not acquire data from the dung study. *Blighia sapida*, for instance, produced important fruit crops during the rainy season, but their remains in the dung samples were hardly identifiable, since the chimpanzees chewed the seeds. Therefore, the quantity of this species consumed is probably underestimated in the count of dung samples. We observed directly 15 times the chimpanzees of the Achean community spending hours in the canopies of *Blighia* trees,

consuming the fruits. The trees of this species were, however, scattered and scarce, and were quite rare in the home ranges of the Aeneid and Odyssey communities. Thus, the relative importance of this species in the average diet of Comoé chimpanzees is probably quite small. On the other hand, *Ceiba pentandra* was abundant and evenly distributed across all of the chimpanzee community home ranges (see chapter 5), thus, its cambium provides a reliable resource during times of food scarcity.

Foraging on insects was very important for the Comoé chimpanzees, as suggested by the number of tools found and videos recorded. While they foraged on the driver ants (Dorylus burmeisteri) throughout the year, with seasonal peaks and lows, they only foraged on carpenter ants (Camponotus maculatus) during the height of the dry season, when driver ants were less available because they went deeper underground (personal observation). Termite fishing also occurred over the greater part of the year, probably because the chimpanzees practiced this behavior just after heavy rainstorms, when the winged termites were preparing to pop up to the surface. This is the moment when the termite workers make the walls of the mound thinner at some points, making it easier for the chimpanzees to pierce them. We recorded chimpanzees scratching the surface of Macrotermes and Odontotermes mounds with their fingernails and introducing the TFTs in the hole afterwards. Even though termite flights occur at different periods of the year, we witnessed more of them during the first half of the rainy season. Virtually no rain falls during December and January, but a few scattered rainstorms fall in February and March, the late dry season, and sometimes trigger termite flights. In any case, we recorded the termite fishing behavior less frequently than the ant dipping, partly because the TFTs were destroyed by termites within few days after their use but mainly because Comoé chimpanzees did not practice the termite fishing as frequently as the ant dipping.

While we found the heads of driver ants in the dung frequently, it was extremely rare to find termite remains in the dung samples. We only found the heads of *Macrotermes subhyalinus* twice. We confirmed, however, the consumption of *M. subhyalinus* and *Odontotermes majus* via camera trap videos and the remains of *Cubitermes* mounds dug up (chapter 7) or pounded open, suggesting that Comoé chimpanzees also consumed all of these termites, or at least the dirt of the *Cubitermes* mounds. The quitine exo-skeleton of termites is much softer than that of the ants and especially the smaller termites with softer heads, meaning that *Odontotermes* and *Cubitermes* presence could not show up in the dung samples [as appeared to be the case with *Thoracotermes macrothorax* and *Cubitermes* sp. at Bili (Hicks et al. 2019a). This was also observed in Fongoli, where chimpanzees consumed *Macrotermes* termites more often than ants, but the remains were also rarely found in the dung (Bogart, 2009, Lindshield, 2014).

The relative importance of the consumption of other alternative food sources by Comoé chimpanzees, such as meat and giant snails is difficult to evaluate with our data. We confirmed that the Comoé chimpanzees hunt mammals, consume small vertebrates and probably snails, but these foraging activities did not leave as many traces as the fruit or insect foraging, suggesting that the relative importance of the former is much smaller than that of the latter. Interestingly, one of the recorded cases of predation on primates was on the olive baboon (*Papio anubis*), following a fight with a group of these large and dangerous monkeys. Several authors have pointed to the possible importance of the dietary overlap and potential competition between sympatric baboons and chimpanzees (Goodall, 1986, Matsumoto et al. 2000, Nakamura, 2015). The killing of baboons by chimpanzees could therefore be not only a way to get meat, but a way to eliminate a strong competitor, as it has been suggested for similar cases of chimpanzee predation on baboons in Gombe and Mahale, Tanzania (Goodall, 1986, Nakamura, 2015). We confirmed, via dung inspection and direct observation, that baboons consume the most

important fruits consumed by chimpanzees, *Diospyros mespiliformis, Tamarindus indica, Parkia biglobosa* and *Dialium guineense*, although they consumed a greater amount of savanna foods, such as *Ficus ingens, Vitellaria paradoxa* and *Gardenia erubescens*, which were less preferred by the chimpanzees, previous studies on the diet of olive baboons in Comoé support these observations (Kunz & Linsenmair, 2007). Baboons also frequently consumed grass stems and seeds, which were almost never touched by chimpanzees. Baboons are common and widespread in Comoé and clearly outnumber the chimpanzees across all the studied home-ranges, with troops that can have more than 100 individuals, as we confirmed through camera traps and direct observations. They share the same habitats, although the baboons spend more time in the savanna (Nevertheless it is clear that the overlap between the diet of baboons and chimpanzees may lead to competition. More research is needed to better understand the relative importance of this competition.

As reflected in table 6, the diet of the Comoé chimpanzees is better studied than at several other research sites, both in the savanna and the forest, as we collected many more data from direct observations and camera traps as well as from dung samples. However, our data collection is still incomplete and much inferior to those of long term research sites that have been studied for decades. In general, the longer the study, the longer the list of food items recorded (Pruetz et al. 2006), especially when the chimpanzees are habituated and can be followed while foraging, as at Bossou, Gombe or Mahale. Therefore, we would expect that the planned continuation of our study at Comoé will provide many more data about their diet (Boesch & Boesch-Achermann, 2000, Nakamura et al 2012, Piel et al. 2017). Similarly, the more we work in the area, the better is the knowledge of the home ranges and the ranging patterns of these chimpanzees. We can expect to find, in a similar way as at Fongoli, that the known home-ranges should also increase somewhat as we study them for a longer period (Pruetz et al.2006, Lindshield, 2014).

The Comoé chimpanzees show important dietary diversification for a savanna site. They consume a minimum of 72 different food items, including 58 plant species, four ant species, two or perhaps three termite species and other insects, honey from a variety of bees, probably the giant snails of the genus *Achatina* and at least three monkey species. They also likely consume two more mammal species (cane rat and red flanked duiker) and a frog. This is a relatively high number of food items consumed, including a considerable variety of insects and a diverse selection of meat. The Comoé chimpanzees exploit large home ranges with scattered resources and rely on specialized fallback foods when other food sources become too scarce (see chapter 5). All of these features suggest an efficient adaptation to their harsh and extremely seasonal environment, which may provide a good model for the feeding ecology of our last common ancestor (McGrew et al. 1988, (Henry et al. 2012, Wessling et al. 2018).

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CHAPTER FIVE (Article 2)

5 SUSTAINABLE BARK-PEELING OF *CEIBA PENTANDRA* BY CHIMPANZEES OF COMOÉ NATIONAL PARK, IVORY COAST

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ABSTRACT

Wild chimpanzees exhibit great behavioral diversity across Africa, as studies of new populations frequently reveal. Since 2014 we have been using a combination of cameratraps and indirect signs to study the ecology and behavior of the wild chimpanzees in Comoé National Park, Ivory Coast, to better document and understand the behavioral adaptations that help them to survive in a savanna-forest mosaic landscape. We found that Comoé chimpanzees peel the bark of the buttresses of Ceiba pentandra trees to eat the cambium underneath. We confirmed that individuals of all sex/age classes across at least six neighboring communities performed the bark-peeling of Ceiba, and only during the late rainy season and beginning of the dry season, when cambium may represent an important fallback food. Baboons also target the same trees but mainly eat the bark itself. Most of the Ceiba bark peeling wounds completely healed within two years, seemingly without any permanent damage. We recorded chimpanzees visiting trees in early stages of wound recovery but leaving them unpeeled. Only 5.7 % of peeled trees were reexploited after a year, suggesting that chimpanzees waited for the rest to fully regrow the bark before peeling again, thus, using them in a sustainable way. Cambium has been sustainably exploited by many human groups of hunter-gatherers and herders. The observation that similar sustainable bark-peeling behavior evolved in both chimpanzees and humans suggests that it could have an important adaptive value in harsh environments when other food sources become seasonally scarce, by avoiding the depletion of the resource and keeping it available for the scarcity periods.

KEY WORDS

Ceiba pentandra, bark-peeling, chimpanzee, sustainable, savanna-forest mosaic

5.1 INTRODUCTION

The consumption of bark and/or cambium (also called "inner bark", the living wood immediately below the bark through which the sap flows) by many mammal species has been described in different climates and habitats, like brown bears in Siberia (Seryodkin et al. 2017) several ungulate species in Europe (Feher et al. 2016) and African elephants (Ssali et al. 2012, Kassa et al. 2013). In many of these examples, the massive extraction of the bark or cambium, all around the trunk, permanently damages the trees and it is more commonly called bark-stripping, an unsustainable practice that often causes the death of the stripped tree.

Primates, including species of *Lemuridae*, *Indridae*, *Cercopithecidae*, *Pongidae* and *Hominidae*, have long been known to peel and consume the bark and cambium of woody plants (Nishida,1976) and, more recently, in Central and South American capuchin monkeys (Hanson, 2007, Mikisch & Liebsch, 2014). Guenons (Beeson, 1987), barbary macaques (Camperio-Ciani et al. 2001, Van Lavieren & Wich, 2009) and chacma baboons, (Katsvanga et al. 2009, Bigalke & Hensbergen, 2010) unsustainably strip the bark of conifers in forestry plantations and are therefore considered pest species in human-dominated African landscapes. Among the great apes, bark has been reported to be an important fallback food for both orangutans, *Pongo abelli* (Campbell et al. 2011) and gorillas, *Gorilla gorilla* (Rogers et al. 1994) which rely on bark as a fallback food during periods of scarcity.

Eastern chimpanzees, Pan troglodytes schweinfurtii, in Gombe (Goodall 1968) and Issa Valley, Ugalla, (Russak 2013), Tanzania, consume cambium of *Brachystegia bussei* and other unidentified species, by cutting the bark with their teeth and then pulling large stripes of bark with their hands, from which they scraped the bark transversely with their teeth. At Mahale, Tanzania, chimpanzees consume bark and especially the cambium of 31 different tree species in the late rainy season as a response to fruit scarcity (Nishida, 1976, Nishisa & Uehara, 1983). Conversely, Central chimpanzees, P. t. troglodytes, were found to consume little bark or cambium and, in Loango, Gabon, they consumed none, while the sympatric gorillas, G. gorilla, did (Head et al. 2011). Western chimpanzees, P. t. verus, consume the bark or cambium of at least five woody species in Fongoli and four in Mt. Assirik, both dry savanna-woodland mosaic in Senegal (McGrew et al. 1988, Pruetz, 2006), while they consumed 11 different species in the forest habitat of Bossou, Guinea (Matsuzawa et al. 2011). In the dry savanna-woodland of Bafing, Mali, chimpanzees were found to eat at least the inner bark of Pterocarpus erinaceus and probably three additional species (Duvall, 2008). Bessa et al. (2015) found that chimpanzees inhabiting Canthanhez National Park, in Guinea Bissau, consumed fruits, flowers and also bark of Ceiba pentandra, but they did not indicate whether chimpanzees were eating inner or outer bark and they also did not describe how the chimpanzees stripped the bark. Very recently (November 2019) chimpanzees of Fongoli, Senegal, were observed peeling the bark and eating the cambium of two trees of Ceiba pentandra in a very similar way to the one of Comoé chimpanzees (Pruetz, J. personal communication).

The bark-peeling behavior exhibited by great apes could have also been present in fossil members of *Hominidae* family. Evidence from microwear traces and isotopes found in dental calculus of *Australopithecus sediba* have been interpreted as proof of a diet that included bark or wood, in a similar proportion to the present chimpanzees inhabiting the savanna-woodland mosaics (Henry et al. 2012) although we cannot know the technique used by this Australopithecus to forage on these hard foods. Traditional human bark-peeling is carried out with specific tools that share a resemblance with paleolithic tools made by Neanderthals, leading some authors to speculate about the possibility that

Neanderthals practiced bark-peeling and consumption of cambium of different tree species as identified from paleo-pollen (Sandgate & Hayden, 2015).

On the other hand, modern human hunter-gatherers, such as the indigenous peoples of North America from the Yukon to New Mexico (Blackfeet, Carrier, Gitskan, Kootenais, Okanagan-Colville peoples, among others), or traditional herders like the Saami people in Northern Europe, have peeled conifers, birches, poplars or elm-trees in a sustainable way. These humans peeled only one side of the tree, not cutting the sap flow to the rest, and allowed the bark to fully regrow before re-exploiting it. Therefore, they avoided killing the trees, in order to have a reliable source of cambium during famine periods (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009). This sustainable bark-peeling has been traditionally carried out across centuries and even thousands of years, leaving permanent traces on so called culturally modified trees (CMT) as demonstrated through dendrochronology and archaeobotany (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009). However, the sustainable harvest of cambium as defined for humans by these authors has never been described for other primates, thus, finding an example in chimpanzees is of great importance to help us to understand how the sustainable use of diverse resources could have originated in our common ancestors.

Western chimpanzees (Pan troglodytes verus) are the most threatened subspecies of chimpanzee (Critically endangered, A4bcd, Humle et al. 2016). Their populations have declined by 80 % overall and by 90 % in Ivory Coast alone (Campbell et al. 2007, Kuehl et al. 2017). The wild chimpanzees in Comoé National Park (CNP) had never been previously studied, except for a few censuses (Hoppe Dominik, 1991, Marchesi et al. 1995, Campbell et al. 2007, WCF, 2014) until we started our project in October 2014. In the south west portion of the park we found that this chimpanzee population inhabits a savanna-forest mosaic habitat and presents characteristic behaviors that had never been described in other populations, such as dipping for water with especially long brush-tipped stick tools (Lapuente et al. 2016). This behavior could provide the chimpanzees an adaptive advantage over other animals to use the scarce resources of their dry and harsh environment. They also exhibit a variant of the behavior recently described as accumulative stone throwing (Kuehl et al. 2016). A better knowledge of the special behaviors displayed by Comoé chimpanzees to overcome the difficult ecological conditions of their environment give us insight on the behavioral flexibility and adaptability of savanna chimpanzees, similarly to other special adaptive behaviors observed in savanna in Kharakhena, Senegal (Boyer Ontl and Pruetz, This Issue) or Issa, Tanzania (Hernandez and Reitan, This Issue).

To date, bark peeling of *Ceiba pentandra* for foraging has only been mentioned by Bessa et al. (2015) but never described in detail, neither for humans nor for apes. It has recently been observed in Fongoli, but not published yet (Pruetz, J. personal communication, 2019). When we started our research on Comoé chimpanzees, in October 2014, we found hundreds of long traces (50-150 cm) of bark-peeling on *Ceiba pentandra* buttresses across our study area SW of the park. The traces suggested that the outer bark was peeled in long stripes and then, the inner bark or cambium was scraped from the wounds. Traces appeared especially concentrated in areas where we found abundant and frequent footprints, dung or direct observations of chimpanzee. In addition, elephants, monkeys, and humans were also present in the area and might have been responsible for these traces.

We initiated this study of the bark peeling in CNP with the following hypotheses in mind:

Hypothesis 1: Given that the bark-peeling traces were concentrated in the activity hot-spots of chimpanzees and frequently associated to chimpanzee signs and that

chimpanzees are known to strip the bark of other tree species, we hypothesize that chimpanzees are doing the bark peeling.

Hypothesis 2: Given that the bark-peeling wounds were marked with cuts and scratches that had the aspect of teeth and nail marks, but sometimes looked like made with tools, we propose that the bark was removed to eat the cambium using teeth, hands and maybe tools

Hypothesis 3: Considering that we found many bark-peeling traces on medium sized *Ceiba pentandra* trees after the rainy season of our first year of study, we hypothesize that the bark peeling is selectively done on trees of a limited range of sizes of a preferred species during a particular season.

Hypothesis 4: Assuming that chimpanzees are the animals producing the bark peeling traces and considering that these animals are social and all sex/age classes are known to forage on the same types of food resources, we predict that we will find individuals of all sex/age classes displaying the *Ceiba* bark-peeling behavior.

Hypothesis 5: If the bark-peeling traces consistently appeared in far apart areas occupied by different chimpanzee communities, the behavior would be widespread and not limited to a particular community.

Hypothesis 6: Assuming that the *Ceiba* tree is able to heal the cuts after every bark-peeling, that the tree is not reducing its growth or health and that the animals wait for the wounds to regrow completely the bark before peeling again, the repeated re-exploitation of the resource would be sustainable.

5.2 METHODS

5.2.1 Study site

At more than 11,400km², CNP is the largest protected area in Ivory Coast and one of the biggest in West Africa. It is characterized by savanna-woodland mosaic habitat, with a 9 % of coverage of forest habitats that are more concentrated in the southern half (Mühlenberg et al.1990) and is classified as a very open and dry landscape for chimpanzees, overall (van Leeuwen et al. This Issue). The chimpanzees use mainly the forested habitats: gallery forest, along the rivers and forest islands, not linked to water courses, but growing on plateaus along the interfluvia (Mühlenberg et al.1990, Lapuente et al. 2016). The park is crossed from North to South by the Comoé river, which gives its name to the park. The climate is dry and warm with a mean annual temperature of 27 ° C and precipitation around 1090 mm (Hennenberg, 2005) although in our study site, SW of the park, a mean of 1010 mm was measured from 1993 to 2000 (Fischer, Gross, & Linsenmair, 2002) and 1014 mm during our study period, from October 2014 to December 2017. The dry season lasts from the end of October to the end of April, with only some scattered rainstorms, while the rainy season lasts from May to October, with the highest precipitation peaks in May and September (fig. 2). We established a study area of 900 km² in the south-western corner of the park. Despite being the driest portion of the CNP, it has the highest percentage of forest cover of the whole park (22 %).

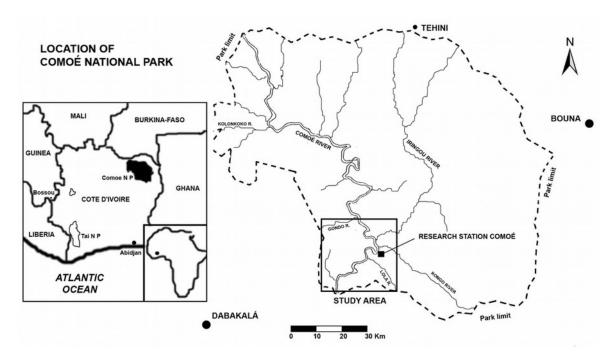


Fig. 1 Study site location

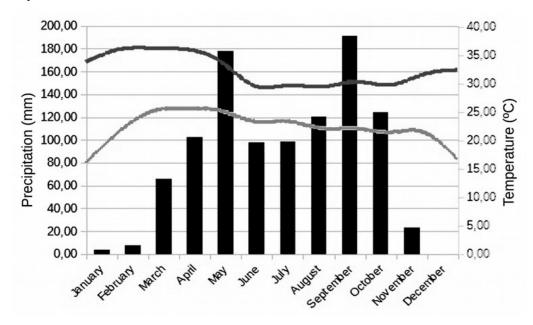


Fig. 2 Mean monthly precipitation (mm) and mean monthly maximum and minimum temperatures (Celsius degrees) during the whole period of study (October 2014-December 2017).

Forested habitats used by chimpanzees in our study area can be divided into five main types, There are two types of gallery forests: semideciduous, dominated by *Cynometra megalophylla*, and deciduous and three types of forest islands: deciduous, semideciduous and liana dominated. *Ceiba pentandra* grows in all of them (Mühlenberg et al. 1990, Hennenberg, 2005). *C. pentandra* (kapok, cotton tree) is a tree in the family Malvaceae, subfamily Bombacoideae. It is native to South and Central America and also to tropical West and Central Africa, where it has been found to grow from the Pleistocene (Maley & Livingstone, 1983, Dick et al. 2007). It can reach more than 70 m tall (Dick et al.

2007) and more than 3 m in diameter with fast growth of up to two cm in diameter per year (personal observation). The tree is most often sustained by big tabular roots or buttresses that can be more than five meters high and wide (personal observation). Young trees are protected by big conic thorns. while upper branches are always protected by abundant thorns. In Ivory Coast (IC) it is a common tree, found across all forested habitats, from rainforest to savanna-woodland (Lauginie, 2007). In Comoé, it is the biggest tree, emerging from the canopy of both forest-islands and gallery forest, at a mean density of 178.35 trees/km², with a mean basal area of 2.97 m²/Ha (methods, below). In this region of Northern IC, traditionally, the wood of medium sized Ceiba trees was used by human populations to make canoes, while older trees were never cut and formerly revered with offerings of pottery or votive stone-axes, since they were thought to contain spirits (local elders, personal communication). The cotton that surrounds the seeds was used to fill mattresses and pillows and the ash from the wood was used to make soap. The leaves are still eaten after cooking (local elders, personal communication). Bark is still occasionally harvested for medicinal purposes, like in other parts of West Africa or abroad, since it is locally believed to be effective as an antidiabetic, antidiarrheic, antibiotic, analgesic, and other ailments (Ueda et al. 2002, Djomeni et al. 2006).

Chimpanzees have also been described to consume different parts of *C. pentandra* trees, across West Africa including flowers and unripe fruits in Fongoli, Senegal (Pruetz, 2006, Lindshield, 2014), leaves, fruits and seeds in Mt. Assirik, Senegal (Luchterhand et al. 1982, McGrew et al. 1988), young leaves and flowers in Bossou, Guinea (Matsuzawa et al. 2011) and fruits and flowers in Tenkere, Sierra Leone (Alp, 1997). Despite having a Ceiba sp. available, Mahale chimpanzees in Tanzania, East Africa, were not observed to consume any of its parts in 50 years of research (Nakamura et al. 2015). West African chimpanzees have been found to use tools to ease the foraging on *Ceiba pentandra*, Alp (1997) described how the chimpanzees in Tenkere, Sierra Leone, used sticks to protect their feet or as seats while eating fruits and flowers on the spiny branches of *Ceiba* trees. Adult male chimpanzees in Bossou, Guinea, cracked *Ceiba pentandra* branches and stripped them of the spiny bark to make hook-shaped tools that they used to reach fruits from a fig tree (Sugiyama & Koman, 1979b).

5.2.2 Data collection

We carried out monthly sampling of four chimpanzee communities' home-ranges: Odyssey, Aeneid, Achean and Trojan (Lapuente et al. 2016) in our study area from October 2014 to December 2017, completing a minimum of 40 km of transects and reconnaissance surveys across a different chimpanzee home-range every week. Aeneid, Achean and Trojan home-ranges were studied in collaboration with the PanAfrican Programme: The Cultured Chimpanzee, of MPI-EVA (Vaidyanathan et al. 2011) from October 2015 to May 2017. We also sampled less intensely two more home-ranges in the northern and western extremes of our 900 km² study area, which were visited once in February 2015 and four times along the dry season of 2016-17. Along the transects and reconnaissance marches we recorded all direct and indirect observations of chimpanzees. such as bark-peeling traces, nests, feeding signs, footprints, tool use sites, vocalizations and dung. For every observation, date, time, habitat type and GPS coordinates were recorded. For all bark-peeling traces detected on C. pentandra along these surveys, we recorded the diameter of the tree trunk above the buttresses, the percentage of the canopy covered by leaves, flowers or fruits, number of the peeling traces or cuts and their relative age. Since we could not know the real age of the traces when we started our study, we classified them into four relative age categories: stage 1, when they appeared freshly or very recently done, with a wet wound and no signs of bark regrowth, stage 2, when the

wound was completely dry and the surrounding bark had started to grow and cover it, stage 3 when the regrowth of bark had completely sealed the wound but the bark was still young, green and thin and wound edges were still visible and sharp and stage 4 when the wound was covered in old thick grey bark and wound edges were also old and covered by bark regrowth (fig. 3). From January 2015 to December 2017, we recorded both peeled and intact C. pentandra trees along transects and reconnaissance marches, and also measuring the above-buttress diameter of intact trees. For those trees that were impossible to measure directly due to gigantic buttresses impossible to climb, we took photos with a measuring tape as reference to estimate the diameter of the bole above the buttresses.

To obtain the density and basal area of the trees in the area, Four hundred and five square habitat plots of 400 m² were placed along regular transects across forest patches included in the home ranges of chimpanzees living both sides of Comoé river, 205 plots west of the river and 200 east. Within the plots, all trees above 10 cm in dbh were counted and identified, obtaining the corresponding densities per species.

Basal area was calculated in m² per Ha applying the formula $BA = \Sigma \frac{\pi. (dbh/2)^2}{10000 \, x \, number \, of \, Ha \, sampled} \, \text{(Arandjelovic et al. 2014)}.$



Fig. 3 Stages of recovery of the bark after bark-peeling of C, pentandra buttresses. 1, freshly peeled buttress, wet from sap and unoxidized, with long strips of hanging bark. 2, traces already dry and with edges of new bark forming. 3, new bark has almost completely covered the wound but it is not yet sealed and the bark is still green and thin in places. 4, thick, old bark completely sealing the wound and with the same color as the rest of the buttresses but the characteristic deformation of repeated bark-peeling (that gives the spine of the buttress the shape of a bunch, with several parallel divisions of the spine) is still visible.

In parallel to the reconnaissance survey (recce) and transect sampling, we systematically placed camera-traps, across our study area in forest habitats using a grid with 1 km2 cells as sampling units within which we selected chimpanzee activity hot-spots (Vaidyanathan et al. 2011, Lapuente et al. 2016). From October 2014 to October 2015 we used 20 Bushnell HD trophy cams (model 119437), from October 2015 to May 2017 we added 60 cameras Bushnell HD Agressor. From May 2017 to December 2017, we continued our study with 30 cameras, of which 12 were Browning SPEC-OPS and the remaining were Bushnell HD trophy cams. All cameras were programmed to record oneminute-long videos. Cameras were motion-triggered with a passive infrared (PIR) sensor. When the light was insufficient to record color videos, cameras recorded infrared black and white videos. The cameras were used to record chimpanzee behavior, tool-use and habitat use, but also to identify individuals. To corroborate the identification, we used double blind recognition: two trained biologists (JL and P. C. Köster) independently identified 86 chimpanzees from six different communities from 2090 videos, by observing individual characteristics such as face and body features, scars, missing ears and balding patterns. Reliability of identifications was further tested with Cohen's K coefficient to measure the percentage of coincidence between independent identification by the two trained biologist (Head et al. 2011, Lapuente et al. 2016). Community structure and limits of home ranges were determined by observing the consistent association between individuals and their ranging patterns with the camera traps distributed across the home ranges. Members of different communities were never found mixed together in four years, but always forming part of the parties of a specific community. Once we confirmed the forest patches that were occupied by each community, we used the minimum convex polygon method to estimate the minimum extension of each home range (Head et al. 2011, Lapuente et al. 2016).

Starting on November 15th 2014, bark-peeling traces were detected in proximity to chimpanzee traces such as nests, footprints and dung. To determine the species producing the traces and the techniques used, we monitored affected trees with cameratraps. From November 2014 to December 2017, a total of 65 different bark-peeling sites were monitored with camera-traps, of which three trees were monitored for the entire sampling period, twelve trees were monitored for two full consecutive bark-peeling seasons and the rest (40) were monitored for one of the three seasons.

When videos of bark-peeling activity were recorded, we measured the length, width and depth of traces and recorded the direction of the cuts with respect to the buttress spine.

To test if the bark-peeling effects were hampering the growth of *C. pentandra* trees, we selected 20 trees with recent bark-peeling traces and 20 untouched ones of similar initial diameters (between 60 and 110 cm). Initial measurement of the bole above the buttresses was done in October 2015 and we measured all of them again in October 2017.

To test if bark thickness was increasing with the age of the trees, we cut portions of 2 x 2 cm of bark from the spine of unpeeled buttresses from 31 trees of different sizes and measured the bark thickness in mm with a gauge. Using the same method, we additionally measured the thickness of the regrown bark over 10 bark-peeling traces of stage 3 wounds to check if the regrown bark was thicker or thinner than the uncut bark.

To determine how long the tree bark took to attain stage 4 of recovery, we selected a small buttress with traces of repeated peeling, including very old (stage 4) traces and we cut it transversely to take a sample that included the whole bark-peeling history of the buttress. After polishing it, we counted the annual growth rings (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009). Dendrochronology has been successfully applied before in CNP (Schongart et al. 2006), both to savanna trees (*Daniellia olivieri*) and forest

trees (*Anogeissus leiocarpus, Diospyros abyssinica*) but not to *Ceiba pentandra*. However, other authors have used growth rings of a very close Neotropical species, *Ceiba speciosa*, for dendrochronology and dendroclimatology (Vasconcellos et al. 2019). C. pentandra growth rings have been found to be prominent also by other authors (Duvall, 2011). Nevertheless, our method should be validated by further studies in Comoé.

5.2.3 Video recordings of bark-peeling behavior

Within the videos that recorded animals peeling the bark of *Ceiba pentandra*, we defined a bark-peeling event as the period in which a single individual animal continuously peeled bark and ate it at the same location and on the same day. If the same individual left the location and returned the next day to peel the same tree, we counted it as a new bark-peeling event. If several individuals were peeling bark at the same time and location, we recorded each of them individually, as separate events, in order to compare the technique and time invested among different species and age/sex classes.

For every individual bark-peeling event, we noted the species peeling the bark, its age/sex class, distinguishing infants, juveniles, adolescents and adults, (Goodall,1968) and the duration of the event in seconds. We also counted the number of cuts made on the bark with the teeth, we noted if the animals pulled off the bark with teeth or hands, if the animals consumed the bark itself or the cambium, the number of scrapes made on the cambium, if the scrapes were made with teeth or finger-nails and if the scrapes were made perpendicular or longitudinal with respect to the spine of the buttress. We estimated the length of cuts from the videos, although most of them were measured afterwards if no later cut had been made on the same spot.

Ethical statement: we used non-invasive techniques for this study, including camera-traps and indirect signs, to avoid causing any unnecessary stress or harm to the wild chimpanzees. All hygienic and security measures were taken to avoid putting animals at risk (Arandjelovic et al. 2014) and all data collection was undertaken under the supervision of park managers, respecting the rules of the park, the laws of Ivory Coast and the International laws on endangered species. All necessary research permits were obtained.

5.3 RESULTS

5.3.1 Videos

Between October 2014 and December 2017, we recorded a total of 8,112 camera days, while monitoring *Ceiba pentandra* bark-peeling sites (with one camera day being 24 hours of continuous monitoring by one camera). Along the whole period, we recorded a total of 12,234 videos in which 44 species of mammals were represented, including eight species of primates (*P. t. verus, Papio anubis, Cercocebus lunulatus, Chlorocebus sabaeus, Cercopithecus lowei, Cercopithecus petaurista, Procolobus verus, Galago senegalensis*), seven species of rodents (*Histrix cristata, Atherurus africanus, Thrionomys swinderianus, Cricetomys gambianus, Funisciurus pyrropus, Heliosciurus rufobrachium, Protoxerus stangeri*), twelve species of bovids (*Syncerus caffer, Tragelaphus euryceros, T. scriptus, Cephalophus sylvicultor, C. niger, C. dorsalis, C. rufilatus, Philantomba maxi, Kobus ellipsiprymnus, K. kob, Hippotragus equinus, Alcelaphus bulselaphus*), ten of small and medium sized carnivores (*Crossarchus obscurus, Ichneumia albicauda, Atilax paludinosus, Herpestes ichneumon, Genetta genetta, G. thyerri, Mellivora capensis, Profelis aurata, Civettictis civetta, Canis adustus*), two of big carnivores (*Panthera pardus, Crocuta crocuta*), pangolins (*Manis tricuspis, M. tetradactyla*), ardvaarks (*Orycteropus*

afer), hippopotamuses (*Hippopotamus amphibius*) and elephants (*Loxodonta cyclotis*) and three species of hogs (*Hilochoerus meinertzeghani, Potamochoerus porcus* and *Phacochoerus africanus*).

5.3.2 Animal species bark-peeling Ceiba

After more than three years monitoring the trees, the only species recorded causing the bark-peeling traces on C. pentandra were chimpanzees and baboons. Of all the remaining species of mammals, only two more primates and two rodent species showed interest in the bark of C. pentandra. We found that guenons (Cercopithecus lowei and C. petaurista), giant pouched rats (Cricetomys gambianus) and squirrels (Funisciurus pyrropus) bit small round portions of bark (less than four cm in diameter) in the thinner parts previously peeled by chimpanzees or baboons, stages 2 and 3. Both chimpanzees and baboons were recorded peeling long stripes of bark of *Ceiba*, but while the baboons consumed mainly the bark itself (N=29 bark only consumption, 6=cambium consumption), the chimpanzees always left the bark aside to consume the exposed cambium (N=38). We recorded 54 videos of baboons and 130 videos of chimpanzees peeling the bark of Ceiba between August and November 2016, representing 35 events for the baboons and 38 for the chimpanzees. These videos were recorded at 14 different sites across the home-ranges of four different communities of chimpanzees (Lapuente et al. 2016). At only two of the 14 sites, both baboons and chimpanzees peeled the bark of the same tree, but at different moments during the same season, with baboons always peeling the bark first and chimpanzees doing it two and three weeks later. From the remaining 12 bark-peeling sites, four were used exclusively by baboons and eight exclusively by chimpanzees. Chimpanzees of all age/sex classes were recorded peeling the bark. Adult female baboons were never recorded bark peeling but baboon adolescent and juvenile females and males of all ages did (table 1).

Table 1. Number and characteristics of the bark-peeling events recorded. Duration of events is given in minutes, although it was measured in seconds. During an event, the primates could make a single or several consecutive cuts in the bark with their teeth. * The length was estimated in the following categories to make comparison easier 1 for <25 cm, 2 < 50 cm, 3 < 100 cm, 4 > 100 cm. For the length estimations, we measured directly the final length of the cut on the tree in our next visit after the event.

SPECIES	SEX/ AGE	NUMBER OF EVENTS RECORDED	MEAN DURATION EVENT (mean N of minutes ± SD)	MEAN NUMBER OF CUTS PER EVENT ± SD	MEAN CUT LENGTH ± SD (*)
	ADF	1	1	1	3
	ADM	3	2.17 ± 0.76	1	2
Pan	AF	11	6.30 ± 3.79	1.72 ± 1.27	3.36 ± 0.50
troglodytes	AM	9	5.89 ± 5.11	1.33 ± 1	3.33 ± 0.70
	INF	7	3.57 ± 2.24	1.14 ± 1.07	NA
	JUV	7	2.29 ± 1.91	1	0.67 ± 0.58
Papio anubis	ADF	7	2.77 ± 2.38	1.57 ± 0.98	1.4 ± 0.55
	AM	8	2.79 ± 2.36	1.5 ± 1.07	2.29 ± 1.11
	INF	1	0.62	1	NA
	JUV	19	2.39 ± 2.49	1.16 ± 0.37	1.33 ± 0.82

Sex/age classes are abbreviated as AF adult female, AM adult male, ADF adolescent female, ADM adolescent male, JUV juvenile, INF infant.

For the infants, we did not consider the length of the cut since they always used the cuts previously made by the adults. We found no significant interspecific or intraspecific differences for the following variables: the duration of the event, mean number of cuts or mean cut length. This equivalence may be related to the small sample size (Mann-Whitney U, p > 0.5) However, mean duration of the event in adult chimpanzees was double the time than that of adult baboons and the mean length of the cuts was also bigger in chimpanzees than in baboons (Table 1).

5.3.3 Technique used

To start the cut, both species used their canines but, while baboons bit small portions of bark from different parts of the buttress spine, chimpanzees, in all the cases, made a transverse first cut of several centimeters in the upper part and, using their hands or teeth, pulled to tear a long stripe of bark, exposing the cambium underneath (table 2). After this initial cut, chimpanzees continued pulling pieces of bark either with hands (22 of 38 events) or with teeth (16 of 38 events). The chimpanzees used their hands to pull the bark significantly more than baboons (W = 462.5, p = 0.002865). See videos 1 and 2 in supplementary materials.



Fig. 4 Left, the adult male Aeneas, the adult female Dido and the juvenile female Juno, from Aeneid community, pull long stripes of bark from a buttress previously peeled multiple times. Right, the adult male Priamo, from Trojan community, scrapes the cambium longitudinally from an open cut with his finger-nails, a technique used exclusively by chimpanzees.

Once the cut was open, the baboons left the bark torn into small pieces around the buttress, while the chimpanzees left long strips rolled at the base of the buttress or lying around. The exposed cambium was also consumed in different ways by each of the species. While the baboons scraped exclusively with their teeth, the chimpanzees always used both their finger-nails and teeth. Most of the scraping made by baboons was transverse to the spine of the buttress (93.2 %), while the chimpanzees scraped mostly

longitudinally (95.1 %) and only made some transverse scrapes at the bottom of the cut, when it was too close to the ground to scrape longitudinally with teeth (4.9 %)(Table 2). The total amount of scrapes per event was similar between both species, but since chimpanzees made much longer longitudinal scrapes, the quantity of cambium obtained was probably higher.

We found stone tools beside 85 of the peeled trees. However, these tools were probably used for stone throwing, since we found stone throwing traces in most of the 85 trees associated with stones and we did not record any tool use in relation to the bark-peeling at any of the sites.

Table 2. Technique used by chimpanzees and baboons to peel the bark of *Ceiba*. Mean number of times per event (± SD) that chimpanzees and baboons used their hands or teeth to pull out bark from the cut. Mean number of times per event that each species scraped the cambium longitudinally or transversely from the cut with their teeth and mean number of times that chimpanzees used their nails to scrape cambium per event.

SPECIES	EVENTS PER SEX/AGE	PULL HAND	PULL TEETH	LONGITUDINAL TEETH SCRAPING	TRANSVERSAL TEETH SCRAPING	NAIL SCRAPING
	ADF (n=1)	1.00	9.00	5.00	0.00	1.00
Pan troglodytes	ADM (n=3)	0.67 ± 1.15	9.67 ± 4.51	7.00 ± 6.56	1.00 ± 1.73	0.33 ± 0.57
	AF (n=14)	4.79 ± 5.90	16.29 ± 16.29	23.57 ± 25.08	0.36 ± 0.93	11.07 ± 17.99
	AM (n=9)	3.11 ± 2.93	11.11 ± 7.09	13.00 ± 9.27	1.22 ± 2.99	5.22 ± 11.61
	INF (n=7)	4.00 ± 8.08	1.57 ± 3.35	18.00 ± 14.51	0.71 ± 1.88	3.14 ± 6.17
	JUV (n=7)	1.14 ± 1.46	0.50 ± 0.84	4.17 ± 4.17	1.33 ± 2.06	3.14 ± 7.44
Papio anubis	ADF (n=7)	0.43 ± 1.13	18.29 ±	0.43 ± 1.13	20.29 ± 12.85	0.00
	AM (n=8)	1.75 ± 2.71	16.63 ±	2.25 ± 4.09	26.38 ± 27.32	0.00
	INF (n=1)	0.00	0.00	0.00	6.00	0.00
	JUV (n=19)	0.63 ± 1.67	11.16 ±	1.39 ± 5.28	14.79 ± 16.75	0.00

AF is adult female, AM is adult male, ADF is adolescent female, ADM is adolescent male, JUV is juvenile and INF is infant.



Fig. 5 Left, an adult male baboon in the home-range of the Achean community bites pieces of bark transversely from a buttress of C. pentandra. Right, a young male baboon scrapes transversely with his teeth from an open C. pentandra cut in the Odyssey home-range.



Fig. 6 Characteristic traces produced by chimpanzees (left) and baboons (right). Chimpanzees made longitudinal, long scrape marks with their fingernails and front teeth and left long stripes of bark at the bottom of the buttress. Baboons bit a piece of bark (top, right) and scraped cambium transversely with teeth, leaving horizontal traces and pieces of bitten bark over the ground (bottom, right)

5.3.4 Bark-peeling season

In 2016, we recorded 73 events of bark-peeling by chimpanzees with our cameratraps, the first one on August 5th 2016 and the last one on November 26th 2016. Counting the *Ceiba* trees that had fresh, stage 1, traces of bark-peeling along transects and recces, we found the earliest signs by the end of the month of June (data from two years) and the latest by mid-December (data from four years). The highest number of freshly peeled trees was found in October and November, over three consecutive years. We never found freshly peeled trees between the months of January and May (dry season). Therefore, we confirmed that this behavior is only displayed during the rainy season and the beginning of the dry season, peaking at the end of the rainy season, when the trees are still full of leaves, and ceasing completely when the trees start producing flowers in mid December.

5.3.5 Bark peeling behavior in other chimpanzee communities over time

The results of the videos shown in tables 1 and 2 demonstrate that chimpanzees of all age and sex classes performed the bark-peeling behavior. These videos were recorded in four different known chimpanzee communities (Odyssey, Achean, Trojan and Aeneid), with most of the individuals already identified (Lapuente et al. 2016). Additionally, bark-peeling traces in *Ceiba* trees were found across the home-ranges of neighboring areas to the north and west where at least two more communities live (communities A, K, Fig.8). New bark-peeling traces have been found every year in each of these home-ranges, in 2016, 2017 and 2018. This widespread distribution and great abundance of traces of all stages suggests that the bark-peeling behavior is common, widespread and probably customary (Whiten et al. 1999) in Comoé chimpanzees.

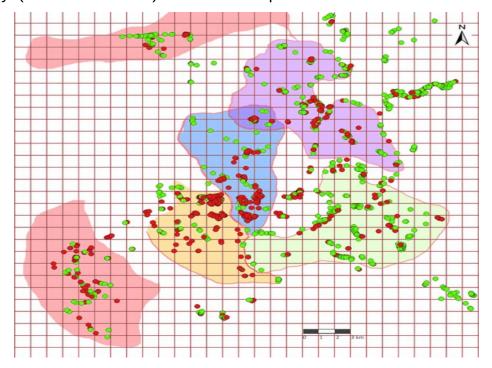


Fig. 7 Map with the distribution of bark-peeling traces on *C. pentandra* (red dots) and untouched *C. pentandra* trees (green dots) across the study area of 900 km2. The colored areas represent the home-ranges of at least six different chimpanzee communities where we found traces of the behavior. Home-ranges were based on data from camera-traps, combined with concentrated signs of chimpanzee presence (nests, tools, dung, footprints, feeding signs and direct observations).

5.3.6 Tree species selection

During the preliminary phase we found a total of 958 trees that had evidence of debarking by animals, of which 857 were *Ceiba pentandra* (89.46 %). The remaining trees of different species were debarked mainly by elephants based on tusk marks, footprints and other traces or by unknown animal species (table 3).

Table 3. Number of trees of different species found with bark-peeling or debarking traces during the preliminary phase (October 2014- May 2015) and animal species causing them.

Tree species	N of trees	Animal species
Adansonia digitata	1	Elephant
Annogeissus leiocarpus	2	Unknown
Antiaris toxicaria	26	Elephant/chimpanzee*
Blighia sapida	2	Elephant
Ceiba pentandra	857	Chimpanzee/baboon
Cola cordifolia	6	Unknown
Dialium senegalense	8	Unknown
Ficus sp.	7	Unknown
Kaya senegalensis	2	Unknown
Lannea welwitchii	44	Elephant
Manilkara obovata	1	Unknown
Tetrapleura tetraptera	2	Elephant
TOTAL	958	·

^{*}Chimpanzees were suspected to peel *Antiaris toxicaria* because some of the traces were very similar to those they made on *Ceiba pentandra*.

5.3.7 Additional uses of Ceiba pentandra by chimpanzees in CNP

Comoé chimpanzees were directly observed consuming fruits, flowers and young leaves, besides the cambium of this species. All the observations of fruit, flowers and leaves consumption where made during the period in which they do not bark peel. Bark-peeling stopped in December, once *Ceiba* trees started flowering (but hadn't produced leaves and fruit yet). By the beginning of the bark-peeling season, the end of June, no more flowers, fruits and few young leaves of *Ceiba* were available. Additionally, we found chimpanzee nests in *Ceiba pentandra* trees four times during the dry season.

5.3.8 Selection of Ceiba pentandra trees for bark peeling

During the entire study period (October 2014-December 2017) we checked a total of 1834 *Ceiba pentandra* trees in our 900 km² study area, 908 of them with bark-peeling traces and 926 with no signs of peeling. We measured or estimated the diameter above the buttresses of 1469 of these trees (708 with bark-peeling traces and 761 untouched). For stage 1 peeled trees, the minimum diameter measured was 22 cm and the maximum 240 cm. The mean diameter of stage 1 peeled trees was 103.93 ± 37.53 cm. Trees with recent peeling traces (stages 1 and 2) had significantly smaller diameters above the buttresses than those with only older traces (stages 3 and 4) (W = 35197, p < 2.2e-16) and untouched trees (W = 114660, p = 1.133e-15).

Table 4. Mean diameter in cm (± SD) in trees with bark-peeling traces of different stages. CBP is the abbreviation for *Ceiba* bark-peeling.

	Stage of recovery of the most recent trace	Mean diameter above buttresses		
	1	103.93 ± 37.53		
CBP stages of	2	110.99 ± 44.54		
recovery	3	121.06 ± 47.06		
•	4	154.86 ± 50.79		

5.3.9 Possible effect of bark thickness

After measuring the thickness of the bark samples from the spine of the buttresses of 31 *Ceiba* trees, we found a significant positive correlation between diameter above the buttresses and bark-thickness (Pearson's cor 0.742356, t = 5.9667, df = 29, p = 1.745e-06).

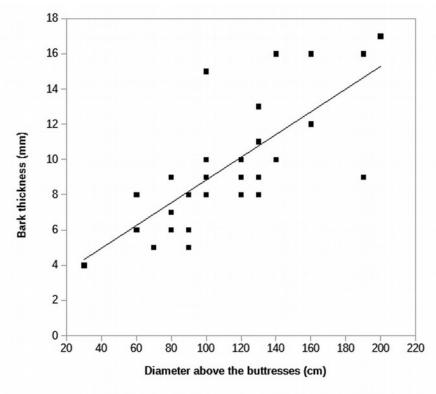


Fig. 8 Pearson's correlation between the thickness of the bark on the spine of the buttress of 31 *Ceiba pentandra* trees and the diameter of the bole above the buttresses.

We found that 86.7% of the previously bark-peeled trees, which were revisited by chimpanzees (n=45), had regrown bark that covered the traces in stage 3 of recovery. We measured ten samples of this green thinner bark from stage 3 traces and we found that it was 4.5 ± 0.97 mm in average. All these data suggest that chimpanzees prefer to peel thinner bark and usually don't target trees above 130 cm of girth, that can have bark 10 to 12mm thick.

5.3.10 Sustainability or damage to Ceiba trees

Of a total of 908 trees with bark-peeling traces over three years, we found only two that fell during strong wind storms. Similarly, six of 926 unpeeled *Ceiba* trees fell after storms. Of the 53 *Ceiba* trees found with freshly peeled (stage 1) traces in 2014 and 2015, four had completely sealed the wounds with bark (passed from stage 1 to 3) one year later and 41 had become stage 3 two years later. Twelve trees took three years to become stage 3, due to very large wounds, with more than 20 cm of width. Only three of these 53 trees were revisited and peeled again by chimpanzees in the next year while 14 were revisited and peeled again two years after the initial peeling, once the bark had regrown and covered most of the wound. In all cases of bark-peeled trees, we found that only the spines of the buttresses had been peeled, which represented less than 5 % of the surface of bark at that level, leaving the rest of the bark around the tree intact.



Fig. 9 Regrowth of bark over bark-peeling traces made by chimpanzees on *Ceiba* pentandra buttresses. Photo A, trace stage 1 photographed in February 2015. Photo B, the same trace one year later. Photo C, *Ceiba* tree heavily peeled in October 2015, this tree had also been peeled in October 2014. Photo D, the same tree in October 2017, all the wounds have been completely sealed by regrown bark.

When we counted the growth rings in the section we cut from a repeatedly peeled buttress, with completely sealed wounds (Fig. 9), we found that this particular buttress had been peeled three times in the last 16 years and that at least eight years had passed since the last peeling.



Fig. 10 Left, transverse cutting of the selected buttress, the aspect of the bark over the stage 4 bark-peeling traces is the same as on the rest of the tree, already grey and fully regrown. Right, aspect of the transverse cut after polishing, the traces of 3 separate bark-peeling events are marked with red numbers from 1 to 3, the growth rings over the last wounds are still clearly visible and correspond to a minimum of 8 years, marked with green numbers. We conducted separate experimental cuts in four buttresses of four different trees, that we checked after three years, finding that, in the conditions of Comoé, there is a visible growth ring forming every dry season on the buttresses of *Ceiba pentandra*.

After comparing the mean growth in diameter of the 20 peeled and 20 unpeeled trees that were monitored between October 2015 and October 2017, we did not find any significant differences in growth (W = 202.5, p = 0.9547) suggesting that the bark-peeling of the buttresses' spines was not hampering the growth of the trees.

Table 5. Mean diameter (\emptyset), in cm, above buttresses in 2015 and 2017 for 20 *Ceiba* pentandra trees that had fresh bark-peeling traces in 2015 (CBP) and 20 that had not (CP). Mean growth in diameter above buttresses in cm. No significant difference in growth was found between the two groups (W = 202.5, p = 0.9547).

	Mean Ø 2015±SD	Mean Ø 2017±SD	Mean growth±SD
CBP (n=20)	80.40 ± 13.52	83.50 ± 13.58	3.1 ± 0.91
CP (n=20)	81.60 ± 13.59	84.80 ± 13.69	3.15 ± 1.09

5.3.11 Sustainable exploitation of *Ceiba* trees by chimpanzees

We found 45 *Ceiba* trees that were peeled repeatedly during the study period, 40 of them were peeled twice and five were peeled three times, once per year. Of the 40 trees peeled twice, 11 (27.5 %) were peeled one year from the first peeling, 19 (47.5 %) after two years and 10 (25 %) three years after the first peeling. In 39 of the 45 revisits (86.7 %) the chimpanzees peeled over previously peeled stage 3 traces, provoking the progressive deformation of the buttress' spine into a bunch shape, with several parallel divisions of the spine (fig. 3). Moreover, from the 908 *Ceiba* trees monitored over the entire study period, 712 (78.4 %) had traces of at least two different recovery stages, indicating that they had been peeled twice. Of these, 485 (53.4 %) had traces of at least three different stages. These data suggest that the chimpanzees in Comoé regularly peel *Ceiba* trees more than once and that they can keep peeling them for many years (Fig. 9).

We recorded three videos of three different adult females and one adult male inspecting the buttresses of four different *Ceiba* trees and then looking up towards the canopy and then leaving the spot without peeling. We also recorded four adult females and one male in four different videos, checking the buttress and the canopy and then starting to bark-peel, Moreover, we recorded two sequences of videos of the same group of chimpanzees checking the buttresses of a specific *Ceiba* tree and leaving afterwards but the same group returned exactly one year later to the same tree and bark-peeling (Fig. 10, video 3 in supplementary materials).

In 100% of cases, the only part peeled of the tree was the spine of the buttresses, which represented on average less than 5 % of the total surface of the bark at that level of the tree such that most of the sap would continue to flow without interruption.



Fig. 11 Left, adult female Dido, from the Aeneid community checks the buttresses of a *Ceiba pentandra* in November 2015. This tree had already been peeled in November 2014 and the traces are stage 2 of recovery in the video-capture of the left. Dido left after inspecting the tree for 42 seconds. Right, Dido returned exactly one year later to the same tree and peeled all the buttresses. In the video-capture, we can see that the bark-peeling traces of 2014 had become stage 3 by November 2016, two years later.

5.4 DISCUSSION

With this study, we confirmed that both chimpanzees and baboons peeled long strips of bark from the spine of the buttresses of *Ceiba pentandra* to consume the cambium underneath. Furthermore, we found that this harvesting activity was sustainable, since the trees healed the peeling wounds, usually in two years and with no obvious decrease in survival or growth. Finally, we observed that chimpanzees waited for the bark to regrow before re-exploiting the trees. The high availability of the resource, high density of *Ceiba pentandra* within the large home ranges of the chimpanzee communities, helped to the sustainability of the re-exploitation. Even though guenons and rodents were recorded creating small round holes in the bark, only baboons and chimpanzees were recorded peeling the bark of *Ceiba* in more than three years. *Ceiba* represented 89.46 % of the bark-peeled trees, suggesting that this foraging behavior could be more important in Comoé, maybe as a fallback food, than other forms of bark or cambium consumption by chimpanzees in other study sites (more comparative research is needed to demonstrate this). Through the videos, we confirmed our hypothesis that the behavior was exhibited across all chimpanzee age/sex classes and studied communities in Comoé.

The videos confirmed that both teeth and hands are used by both chimpanzees and baboons to pull bark strips from the cuts. Videos also showed that both species scraped the cambium with their teeth to eat it, but only baboons were recorded eating portions of bark and only chimpanzees were recorded using finger-nails to scrape the cambium and eat it. We never recorded the use of tools to cut the bark or scrape the cambium. Therefore, our second hypothesis is partially supported by the data, confirming the use of teeth and hands but not of tools to remove the bark and eat the cambium.

During the entire study period, including three complete rainy and dry seasons, we found that all the fresh traces were made during the late rainy season and beginning of the dry season on *Ceiba pentandra* trees with a mean diameter of 103.93 cm. Ceibas below 50-60 cm of diameter are usually covered by big thorns and have poorly developed buttresses, making bark-peeling much more difficult. Ceibas above 120 cm in diameter usually have bark thicker than 1 cm, making more difficult to cut the bark with teeth. These data support our hypothesis that chimpanzees peel preferentially the bark of younger *Ceiba* trees.

The season when the behavior was displayed seems to be when fruit is scarce (Lapuente et al. unpublished data), suggesting that Ceiba cambium might be an important fallback food for both chimpanzees and baboons in Comoé during this period, although this study did not explicitly test the fallback hypothesis and more research is needed. Multiple species of mammals strip the bark from different species of trees around the world to feed either on the bark itself or the cambium underneath (Feher et al. 2016, Servodkin et al. 2017, Ssali et al. 2012). In most cases, these mammals cause serious damage to the trees, known in forestry as bark-stripping, which often kills the tree. Most of these animals are considered pests that destroy forestry plantations or natural forest stands. This is also the case of most African primates that strip bark, for instance, barbary macaques in Morocco and Algeria are threatening the last wild *Cedrus atlantica* forests by bark stripping during dry periods. It has been hypothesized that the main driver of this destructive behavior could be to obtain moisture for the bark as the macaques lack access to good water sources during the bark peeling periods (Camperio-Ciani et al. 2001, Van Lavieren & Wich, 2009). The destructive bark-stripping caused on pine plantations by blue monkeys in Malawi and by chacma baboons in Zimbawe and South Africa is also considered a pest behavior by some authors (Beeson, 1987, Katsvanga et al. 2009, Bigalke & Hensbergen, 2010). In these cases, the reduction of natural habitats and food resources and the

intrusion of anthropic landscapes such as the exotic pine plantations has been cited as the main cause for the destructive behavior in periods of food scarcity.

Scarcity of alternative food sources has been interpreted as the most probable reason why the great apes rely on bark or cambium as a fallback food, especially during the rainy season, as in the case of orangutans (Campbell et al. 2011), gorillas (Rogers et al. 1994) or chimpanzees (Goodall 1968, Nishida, 1976, Nishida & Uehara, 1983, Pruetz, 2006). In the case of humans, the use of inner bark in extreme climates, such as areas close to the arctic circle is also interpreted as an emergency food in times of scarcity, like early spring, and historic accounts support this interpretation (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009). However, while most mammals, including monkeys and great apes, cause serious damage and even death to the trees with bark-stripping, human hunter-gatherers and herders harvested the cambium of trees in a consciously sustainable way, by peeling only a section of the trunk that never completely severs the flow of sap through the xylem (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009).

The chimpanzees of Comoé National Park also appear to peel the bark during periods of food scarcity (Lapuente et al. unpublished data), but they only peel the bark of the spine of buttresses of *Ceiba pentandra*, leaving the rest of the tree intact. Usually, *Ceiba* trees have very large buttresses or tabular roots, with a surface of several square meters of bark each side of the buttress (personal observation). The strips that Comoé chimpanzees peeled, rarely arrived to the bole of the trunk and they never peeled the space between buttresses. This selective peeling of a non-vital part of the bark, allows sap to continue to flow uninterrupted and thus, the trees do not show any sign of deterioration. We cannot say if the chimpanzees are conscious of the importance of peeling only a small proportion of the bark for the survival of the tree. It is probable that they only peel the spine because it is more accessible, both to perform the initial cut with their teeth and to scrape the cambium with their teeth, Nevertheless, the technique they use allows the tree to easily recover.

On nine occasions, chimpanzees were recorded visually inspecting the buttresses, leaving them unpeeled on four occasions and proceeding to peel in five other occasions. This suggests that the chimpanzees may be able to tell when the buttress is ripe to peel and that they do not peel the buttress until the wounds of previous peelings are at least stage 3 of recovery, with a thin green new bark covering them almost completely (video 3, supplementary materials). As a result of this behavior, trees can be peeled repeatedly for several years (at least 16, fig. 9) as we confirmed by counting that 53.4 % of trees had been previously peeled on at least three different occasions.

The great abundance of *Ceiba pentandra* trees in the home-range of Comoé chimpanzees and the very small proportion of dead trees with bark-peeling traces, similar to the proportion of dead untouched trees, suggests that the damage caused by *Ceiba* bark-peeling is not producing any extra mortality in the trees. We questioned Pruetz, J. about the mortality caused by chimpanzees peeling the bark of *Pterocarpus erinaceus* and *Ceiba pentandra* in Fongoli. She explained that the branches of *Pterocarpus* peeled by chimpanzees died, although, as far as she knew, they hardly ever ate the bark on the trunk to the point that it killed the entire *Pterocarpus* tree. About *Ceiba*, Pruetz said that the chimpanzees were eating the bark of the lower part of the trunk of young *Ceiba pentandra* trees, which might kill the tree, depending on how it reacted, although they had not circled the whole trunk of the two trees found in November 2019 (Pruetz, J. personal communication).



Fig. 12 Chimpanzees of Fongoli (Senegal) were observed to peel two young *Ceiba pentandra* trees, for the first time, in November 2019. The aspect of the bark-peeling traces and the technique used to scrape the cambium was, apparently, the same as in Comoé. Baboons have not been observed peeling the bark of *Ceiba* in Fongoli yet, *Ceiba pentandra* is relatively rare in Fongoli, although we do not have data on density or basal area. Pruetz, J. personal communication. Photo by Pruetz, J.

Back in Comoé, the results of monitoring 20 peeled and 20 untouched trees for two years did not show any significant difference in the diameter growth rate. We have not found any reference in the literature consulted about mortality caused to bark-peeled trees by chimpanzees in other research sites, but smaller species can die if the bark is stripped all around the bole, like it happens with the cited cases of *Cercopithecidae* monkeys, bears or elephants (Beeson, 1987, Camperio-Ciani et al. 2001, Van Lavieren & Wich, 2009, Katsvanga et al. 2009, Bigalke & Hensbergen, 2010, Ssali et al. 2012, Feher et al. 2016, Seryodkin et al. 2017).

All these data support the hypothesis of total recovery of the trees after the peeling and suggest that this behavior is a sustainable exploitation of this very valuable resource that can probably be carried out for generations.

Very old trees, with diameters of more than two meters above the buttresses had very old traces in many cases, suggesting that the behavior has been ongoing, possibly for several decades, but this point has not been tested yet because it would require

destructive sampling. However, traces of all recovery stages have been found in hundreds of trees all across the home-ranges of at least six different chimpanzee communities, in an area of 900 km², suggesting that the behavior is widespread and established in the area.

The videos show chimpanzees of all age/sex classes bark-peeling, often with juveniles and infants doing or trying to do it beside their mothers, suggesting that the behavior could be customary, passed from one generation to the next, possibly being an important part of the local culture of Comoé chimpanzees. Cultural behaviors in other study sites have been found to provide also solutions for the challenges of living in very hot and dry savannas (Boyer Ontl and Pruetz (This Issue), Lindshield et al. (This Issue), and Wessling et al. (This Issue).

The fact that sustainable bark-peeling was an important form of obtaining fallback food also for human hunter-gatherers even in recent prehistory (Niklasson et al. 1994, Prince, 2001, Ostlund et al. 2009) and the possibility that bark-peeling was also important for Neanderthals (Sandgate & Hayden, 2015) and Australopithecus (Henry et al. 2012) suggests that this behavior of Comoé chimpanzees could be a good model for the sustainable exploitation of alternative resources and fallback foods by human ancestors.

The density of Ceiba trees in Comoé, with a mean of 178.35 trees/Km², and the mean basal area of 3.05 m²/Ha are much higher than the density and basal area found in similar habitats in Benin, with 9-57 trees/Km² and 0.038 to 0.115 m² / Ha respectively (Sokpon et al. 2011). This relatively high abundance provides a potential fallback food that is probably very important (Lapuente et al. unpublished data) for the survival of these chimpanzees in the harsh and unpredictable environment of the park. Ceiba pentandra is common all across West and Central Africa, but only in Cantanhez NP, Guinea Bissau (Bessa et al. 2015), Fongoli, Senegal (Pruetz, J. personal communication) and Comoé, chimpanzees have been found to peel the bark of this species and only in Comoé we have described this behavior, which could be an adaptive response to the particular ecology of the park, where the savanna-woodland mosaic contains a significant percentage of forest (9-13 %) where Ceiba can thrive. In Fongoli, where the same kind of bark-peeling that we found in Comoé has been very recently observed (November 2019), Ceiba pentandra is relatively rare, so this behavior could not produce an important fallback food for chimpanzees, while the abundant *Pterocarpus erinaceus*, which they seasonally peel every year could (Pruetz, J. personal communication). Comoé chimpanzees ability to exploit this resource has probably helped them to occupy habitats that would be otherwise marginal. Savanna chimpanzees are presented with special challenges by their demanding habitat, with seasonal extremes and great fluctuations in the food availability (Lapuente et al. unpublished data), Ceiba bark peeling is one of the survival strategies developed by the savanna chimpanzees of Comoé.

However, even if the result of the behavior of the Comoé chimpanzees produces a sustainable exploitation of the resource, there could be phytochemical changes in the contents of sap and bark, either defensive or nutritional, that could be influential in the timing of the bark peeling. Further research is needed to fully understand the peculiar form of exploitation of this resource by Comoé chimpanzees. The knowledge of this particular behavior, with its ecological and cultural importance is of key importance to plan adequate conservation measures which are so necessary to preserve the critically endangered Western chimpanzee.

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CHAPTER SIX (Article 3)

6 FLUID DIPPING TECHNOLOGY OF CHIMPANZEES IN COMOÉ NATIONAL PARK, IVORY COAST

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ABSTRACT

Over a 6 month period during the dry season, from the end of October 2014 to the beginning of May 2015, we studied tool use behavior of previously unstudied and non-habituated savanna chimpanzees (*Pan troglodytes verus*) living in the Comoé National Park, Ivory Coast (CI). We analyzed all the stick tools and leaf-sponges found that the chimpanzees used to forage for ants, termites, honey and water. We found a particular behavior to be widespread across different chimpanzee communities in the park, namely, dipping for water from tree holes using sticks with especially long brush-tip modifications.

Using camera traps, we recorded adults, juveniles and infants of three communities displaying this behavior. We compared water dipping and honey dipping tools used by Comoé chimpanzees and found significant differences in the total length, diameter and brush length of the different types of fluid-dipping tools used. We found that water dipping tools had consistently longer and thicker brush-tips than honey dipping tools. Although this behavior was observed only during the late dry season, the chimpanzees always had alternative water sources available, like pools and rivers, in which they drank without the use of a tool. It remains unclear whether the use of a tool increases efficient access to water. This is the first time that water dipping behavior with sticks has been found as a widespread and well-established behavior across different age and sex classes and communities, suggesting the possibility of cultural transmission. It is crucial that we conserve this population of chimpanzees, not only because they may represent the second largest population in the country, but also because of their unique behavioral repertoire.

Keywords

Western chimpanzee (*Pan troglodytes verus*), tool use, fluid dipping, brush tipped tool, water-acquisition

6.1 INTRODUCTION

Chimpanzee tool use has been the subject of systematic study since the 1960s (Goodall, 1968, Jones & Sabater Pi, 1969, Nishida, 1973, Sabater Pi, 1974), revealing regional and local variations that have been argued to be similar to culturally transmitted practices in humans (McGrew, 1992, Whrangham et al., 1994, Boesch & Tomasello, 1998, Whiten et al. 1999, 2001). Western chimpanzees have been found to have several tool use behaviors unknown in other chimpanzee populations, such as nut cracking, studied since the 1970s both in the Tai Forest, CI (Boesch & Boesch, 1990), and Bossou, Guinea (Matsuzawa et al., 2011), and the hunting of Galago spp. with spears in Fongoli, Senegal (Pruetz et al., 2007). More recently, Kühl et al. (2016) documented accumulative stone throwing in Western chimpanzee communities of Guinea-Bissau, Guinea-Conackry, Liberia and Ivory Coast, where chimpanzees habitually bang and throw rocks against trees, or toss them into tree cavities, resulting in conspicuous stone accumulations at these sites. Fluid dipping behavior is defined as the use of a probe to extract fluids such as honey or water from cavities (Boesch & Boesch, 1990, Wrangham et al. 1994, Whiten et al., 1999, 2001). Honey dipping with probes is a guite widespread behavior, found in West African sites in Ivory Coast (Boesch & Boesch, 1990), Senegal (Bermejo et al., 1989) and Nigeria (Sommer et al., 2012, Dutton & Chapman, 2014), many Central African sites (Bermejo et al. 1999, Hicks, 2005, Sanz & Morgan, 2007, 2009, Boesch et al., 2009), as well as East Africa (Goodall, 1968, Watts, 2008, Gruber et al. 2009). The use of probes to dip for water, however, has only been described in Kibale (Wrangham et al., 1994) with the occasional use of chewed stems of *Aframomum*, and more recently, in a playing context by immature Mahale chimpanzees (Matsusaka et al. 2006). In both cases, the behavior was not habitual or customary, but only present in a small number of individuals.

The use of sponges, made by folding or chewing leaves to collect water from ponds, streams or holes in trees has been reported in many chimpanzee communities across Africa (Goodall, 1968, Sugiyama, 1995, Whiten et al., 1999, 2001, Matsusaka et al., 2006, Sanz & Morgan, 2007). Matsuzawa et al. (2003) found, however, that the Western chimpanzees of Bossou occasionally produced a local variant of leaf sponging behavior, by dropping leaf-sponges into tree holes too narrow to access by hand and then retrieving them with the help of sticks. This behavior, defined as 'push-pull', has been seen only rarely at other sites (Sugiyama, 1995, Toonoka, 2001, Matsusaka et al., 2006).

Chimpanzees inhabiting savanna-woodland mosaics and dry environments have been studied more closely in East Africa (Goodall, 1968, Nishida, 1973, Wrangham, 1994, Hunt, 2002), while in West Africa, the only area where long term studies in this type of habitat have been carried out is SE Senegal (i.e. Fongoli and Mount Assirik) (McGrew, 1981, Tutin et al., 1983, Pruetz et al., 2007) and more recently in Gashaka-Gumti, Nigeria, for P. t. ellioti (Dutton & Chapman, 2014). As a result of behavioral adaptations to dry habitats and extreme seasonality, savanna chimpanzees are reported to exhibit seasonal changes in their movements across home-ranges, which are linked to water availability, migrating and concentrating around the scarce water sources during the peak of dry season (Baldwin et al., 1982, Tutin et al., 1983, Duvall, 2000, 2008, Hunt & McGrew, 2002, Pruetz & Bertolani, 2009). Other chimpanzee behaviors linked to water in some of these areas include digging wells in order to filter water (Hunt & McGrew, 2002, Galat et al., 2008, Bogart, 2009) as well as bathing in ponds, probably to cool down (Pruetz & Bertolani, 2009). In Tongo, DRC, which is an especially dry environment located on top of a lava flow with no access to surface water, chimpanzees drink from tree holes using moss sponges and dig up and consume tubers as probable alternative source of water (Lanjouw, 2002). Although water is a limiting factor for chimpanzees, they are able to adapt to living

in marginal habitats as long as they have access to some water source on a daily basis (Duvall, 2000, Pruetz & Bertolani, 2009)

Even though chimpanzees in the Ivory Coast (CI) have been studied since the 1970s in the Taï Forest and surrounding areas (Boesch & Boesch, 1990, Hoppe-Dominik, 1991), in the rest of the country, in particular in the Comoé National Park located in the northeast, research on chimpanzee has been limited to a few general censuses (Hoppe-Dominik, 1991, Marchesi et al., 1994, Campbell et al., 2007) and occasional observations {Fischer & Gross, 1999), nevertheless, feeding ecology of other primates, such as baboon (Papio anubis), has been thoroughly studied in Comoé (Kunz & Linsenmair, 2010). Prior to our work, nothing was known about the distribution, ecology and behavior of the Comoé chimpanzees, which inhabit a mosaic of differing savanna types, gallery forest and forest islands. It has been argued that savanna-woodland mosaics represent one of the environments in which human ancestors appear to have lived during much of the first 6 million years of their evolution (Cerling et al., 2011, Henri et al., 2012). Human ancestors probably found the same tool materials and faced problems in these habitats similar to those modern chimpanzees face, such as water and food scarcity. The technological solutions developed by wild chimpanzees to confront the challenges of this environment can provide a model for early technological adaptations of hominins (Wynn et al., 2011).

Chimpanzee populations are threatened, due to factors such as poaching and habitat destruction (Campbell, 2008, Hicks, 2010) and with the extinction of local communities we may lose critical information on behavioral variability and technological adaptations present in great apes. Comoé chimpanzees live in a changing environment, where water passes from being abundant during the rainy season to be scarce and unevenly distributed during the dry season. Considering that chimpanzees in other study sites have been found to mofify their behavior to adapt to dry environments (Baldwin et al., 1982, Tutin et al., 1983, Duvall, 2000, 2008, Lanjouw, 2002, Hunt & McGrew, 2002, Pruetz & Bertolani, 2009), we expect that Comoé chimpanzees developed behaviors to confront their dry savanna-woodland environment. Accordingly, we test the following hypotheses:

- 1 Assuming that chimpanzees modify their behavior to confront savanna-woodland dry conditions, we expect to find evidence of adaptive tool-use behavior produced by Comoé chimpanzees.
- 2 Assuming that tool technology in wild chimpanzees is spread by social transmission, we expect water dipping behavior to be common and widespread across the studied chimpanzee communities.
- 3 Assuming that tools used by chimpanzees are specific to a particular task, we test the hypothesis that tools produced by Comoé chimpanzees to collect water are different in dimensions and structure from those made to dip for and harvest honey.
- 4 Given the evidence that the chimpanzees produce tools with long brush-tips specifically to dip for water, we expect a direct correlation between brush length and amount of water absorbed.
- 5 Considering that water is a less dense fluid than honey and longer brush tips will be needed to absorb enough water per dip, we expect water dipping tool brush-tips to be longer than honey dipping tool ones.

6.2 METHODS

6.2.1 Study area

Comoé National Park is a protected area covering 11,500 km² located in the NE of Ivory Coast (Fig. 1). Savanna habitats cover 91% of the park, with the remaining area consisting of gallery forest and forest islands, which serve as the main chimpanzee habitat (Muhlenberg et al., 1990).

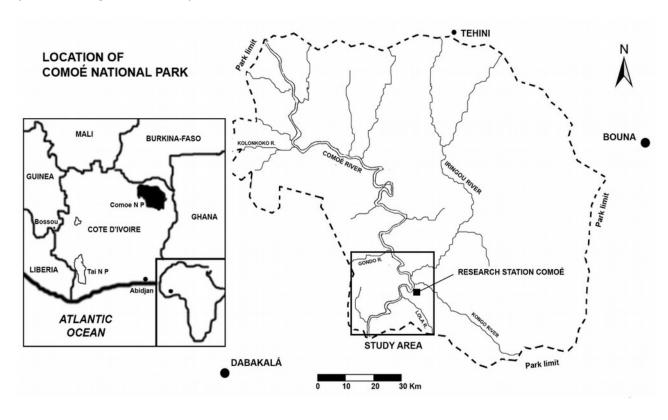


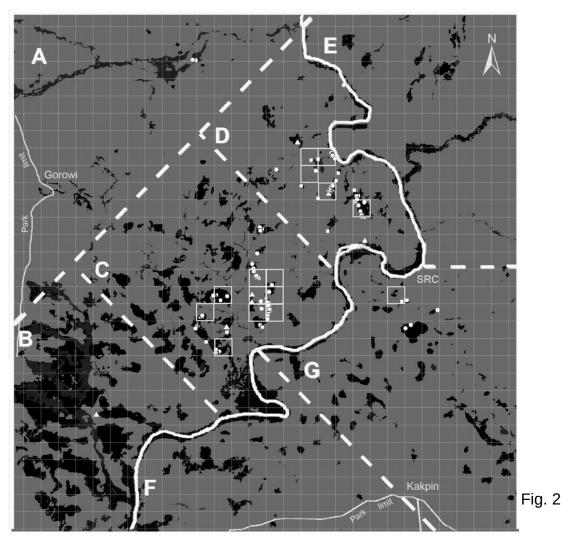
Fig. 1 Location of Comoé National Park and our study area, SW of the park.

Comoé's tropical climate is warm and dry, with a mean temperature of 27° C and an average annual precipitation oscillating around 1090 mm (Hennenberg, 2005), based on data from two meteorological stations located 74 and 109 km respectively from the center of the study area. Our own measurements of rainfall at the Comoé Research Station, averaged 1010 mm during the period between 1993-2000 (Fischer et al., 2002). The dry season lasts for 6 months from November to April, with virtually no precipitation in December and January, and scattered rainstorms during the rest of the dry season. Total average precipitation during the dry season is around 100 mm (Fischer et al., 2002). The Comoé River divides the park from N to S, and most of the park's known chimpanzee population resides to the west of the river. A network of tributaries crisscrosses the park, but most become completely dry or only retain small puddles of water during the dry season.

In addition to chimpanzee, we confirmed the presence of nine of the 14 species of primates that Fischer et al. documented in 2002, including baboon (*Papio anubis*), patas monkey (*Erythrocebus patas*), white naped mangabey (*Cercocebus lunulatus*), Lowe's monkey (*Cercopithecus lowei*), lesser spot-nose monkey (*Cercopithecus petaurista*), green monkey (*Chlorocebus sabaeus*), Demidoff's galago (*Galagoides demidoff*), Senegal

galago (*Galago senegalensis*) and common potto (*Perodicticus potto*). Regarding large predators at the site, the presence of lion (*Panthera leo*) has not been confirmed after 2002, but leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) are common (Henschel et al. 2010, personal observations). In the Comoé River and its main tributaries, West African crocodyle, *Crocodylus suchus* and slender-snouted crocodyle *C. cataphractos* are still present (personal observations).

We chose a 900 km² study area in the SW sector of the park because it covers most of the range in which chimpanzees had been detected in previous surveys (Hoppe-Dominik, 1991, Marchesi et al.,1994, Campbell et al., 2008), and also because Würzburg University has established the well-equipped Research Station Comoé (RSC) in the core of this study area, considerably improving logistics and sample analysis in the field. In order to facilitate behavioral sampling, we divided the area into 7 strata or sampling blocks with areas ranging from the 88 km² (block D) to 165 km² (block A). The forest cover ranged from the 15 % in blocks A and E to the 49 % in block B.



Distribution of fluid-dipping sites found across the study area. The area covers 900 km², divided into grid cells of 1 km² each (white squares). Blocks C and D were the most intensively sampled, but we visited most of the forest patches in the study area. In the map, black and dark-grey patches represent gallery forest or forest-islands. The highlighted grid cells are where we recorded videos of chimpanzees. Triangles represent water dipping sites using only sponges, circles represent water-dipping sites using sticks or sponges and squares represent honey-dipping sites.

6.2.2 Data collection and analysis

From October 29th 2014 to May 9th 2015, we sampled the 900 km² study area with 823 km of reconnaissance walks (recces) and transects. Since the population status and distribution of the Comoé chimpanzees was largely unknown at the beginning of this study, we first concentrated on localizing activity 'hot spots' including nesting areas, tool use sites and promising places for camera trapping due to the presence of fresh signs of chimpanzee activity and tool use. In order to maximize the number of chimpanzee-related observations, we conducted a stratified sampling program focusing on forested habitats (gallery forest and forest islands), although we also crossed long stretches of savanna (of the 823 km walked, 611 were in savanna) along which we recorded all chimpanzee observations.

Since this research was carried out within the framework of a larger project, which had as one of its main objectives to find chimpanzee communities suitable for long-term study, we devoted more sampling time (80% vs 20%) to the communities found in the strata closest to Research Station Comoé. Thus, we dedicated six weeks to sampling block C, six weeks to D, two weeks to E two weeks to G, and only one week to block A and one to B (See Fig 2). A team of 3-4 persons (the first author, two local assistants and from April to May a Master student) walked slowly (estimated walking speed of 1.5 km/h) along reconnaissance routes and transects using a GPS Garmin 62st and a Suunto A-10 compass. All tool-use related observations were made ad-libitum. We also recorded all direct and indirect observations of chimpanzee activity (i.e feed, foraging, rest, social interact, travel, tool use), food sources (fruits, leaves, beehives, vertebrate and invertebrate prey, drinking spots), habitat (gallery forest, forest island, woody savanna, bushy savanna, grass savanna), presence of mammals and evidence of human activity such as poaching, ilegal logging, old settlements, fishing, rangers patrols or tourism. We paid special attention to chimpanzee tool use sites (places where chimpanzees had been using tools, leaving the used tools behind). We recorded GPS coordinates and following standard etho-archeological methods (McGrew et al., 2003, McGrew et al. 2007, Hernandez-Aguilar, 2007, Sommer et al., 2012), we photographed each tool in situ, measured the distances of the tools to the tree holes, distances of the plants used as toolsource to the point of use, height and dimensions of the tree holes. We considered chimpanzee tools those sticks which presented clear signs of modification such as removed branches, leaves and sometimes bark and clear use-wear signs such as blunt or frayed ends. Recently-used stick tools (those that weren't covered with mold, degraded, with parts missing, or partly eaten by termites) were collected and taken to the CRS for further analysis. We defined fluid-dipping sites as tool use sites where we determined that either water or honey had been extracted with sticks. This was based on documenting fluid traces such as water, honey, wax or mud (coming from the bottom of tree holes containing water), as well as the presence of bees or hive remains in tree holes, and whether the tools were found inserted or not into water or bee holes. Whenever possible, we inspected the content of the tree hole, measured its depth, height and diameter and the presence/absence of water. In the laboratory, we labeled each tool, photographed and measured total length, brush tip length, and proximal and distal diameters. Using an experimental approach, we used a precision scale (accurate to 0.01 gm) to weigh the amount of water absorbed in 50 water dipping tools used by chimpanzees.

In November 2014, we set out 20 Bushnell HD trophy cams (model 119437), targeting mainly potential tool use sites, but also areas where it would be easy to identify individual chimpanzees, such as natural bridges. Cameras were placed using a systematic design across a grid of sampling cells of one km², covering the areas with the highest concentration of nests and/or tool use sites, as well as cells in which we had made direct

observations of chimpanzees, within the home-ranges of three neighboring communities. Over the course of the study, we shifted 14 of the cameras within the same cell to focus on temporal activity 'hot-spots', defined as places where tool use signs were very recent and abundant and moved 6 cameras between cells, following the seasonal movements of the chimpanzee groups. The cameras were programmed to record 60 second videos, 24h/day, recording infrared videos when dark. One camera was lost to elephants a month before the end of the study.

In order to identify the individual chimpanzees in the videos, we used double blind recognition: two trained biologists (the first author and P. C. Köster) observed the videos independently. To further corroborate the accuracy of the identifications, we contrasted the results with observation of 50 sample videos by two untrained students. We tested the reliability of our identifications using Cohen's K coefficient to measure the percentage of coincidence between independent identification by the two trained biologists. For the tooluse videos, we considered both episodes (defined as the sequence of fluid dipping, from the moment that one chimpanzee arrives at the fluid dipping site and starts the tool use, to the moment it leaves the site (Tonooka, 2001) and bouts (defined as each individual fluid dipping action, i. e. every time the chimpanzee introduced the tool in the cavity, extracted the fluid and consumed it) (Sanz & Morgan, 2007).

We carried out data analysis using the free software R-Studio. We generated maps and carried out the spatial analysis using Quantum GIS. Since the data for tool length, tools per site and brush tip length did not follow a normal distribution, we used the Mann-Whitney test to look for significant differences between the means. We used Kruskal-Wallis test when testing differences between all tool types at a time.

We obtained estimations of community and party size from standing crop nest counts and camera trap videos and community and party composition from camera trap videos.

Data collection in the field was in compliance with the guidelines of the Ministere de l'Enseignement Superieure et de la Recherche Scientifique, adhered to the legal requirements of Ivory Coast, and the American Society of Primatologists principles for the ethical treatment of primates.

6.3 RESULTS

We found signs of permanent chimpanzee presence, including repeatedly used nesting and tool-use sites, in five of the seven sampling blocks. In the other two blocks, we found some older scars left by chimpanzees on trees resulting from stone throwing behavior (Kühl et al. 2016), but no nest or stick tools. Based on estimates from nest counts on transects, we found larger chimpanzee communities in blocks A, C and D than in B and G. Based on individual identification from camera trap videos, we found well structured chimpanzee communities composed of all sex/age classes in blocks C and D (we estimated a minimum of 54 and 20 weaned individuals respectively from standing crop nest counts). We estimated around 30 weaned chimpanzees in block A, 15 in block B and 10 in G. In blocks B and G. chimpanzee communities may have been smaller as a result of heavy poaching during the civil war that ended in 2011. As confirmed by the distribution of fresh nests and cells where videos were recorded, during the dry season, the most thoroughly-studied chimpanzee communities in blocks C, D and G moved from scattered forest islands after these had dried up to the gallery forests which retained pools of water for a longer period. Over the whole dry season, though, the chimpanzees continued visiting forest islands, to forage fruits, insects and honey.

During the 6 month of sampling period, we found a total of 876 stick tools, including ant-dipping tools, termite-fishing tools, probes and fluid dipping tools used both for honey

and water. We also found 83 leaf-sponges, as well as abundant stone tools. In this paper, we focus our analysis only on the fluid-dipping tools, paying special attention to the water-dipping tools.

We found water dipping sticks (WDT) in four of the sampling blocks (Fig. 2, table 1), while we found honey dipping tools in three. These tools were always associated with tree holes containing either water or colonies of stingless bees (*Meliponini*). All the stingless bees found had their hives in tree holes and never in the ground or branch surfaces. Although we systematically checked all the trees containing honey-bee (*Apis mellifera*) colonies, we never found any tool or signs of exploitation by chimpanzees.

A total of 283 water dipping sticks (WDT) were found at 77 water dipping sites, of which we confirmed revisits by the chimpanzees to 12. Two hundred and eighty nine honey gathering tools (HDT) were found at 38 different sites. Leaf-sponges were found at 18 sites, six of which also included water dipping sticks. Sponges were found only in three of the sampling blocks, and in block B, only sponges and no water dipping sticks were found (it should be pointed out that in block B sampling effort lasted only one week). Sponges were found exclusively in or around those tree-holes which were wide enough to allow the introduction of a chimpanzee's hand (diameter >8 cm). Stick tools, by contrast, were more frequently found associated with holes too narrow for a chimpanzee's hand (175 WDT in holes with a diameter range between 1.5 and 8 cm), although they were found in wider holes as well (108 WDT in holes with diameter between 8-34 cm). We never found sponges associated with honey hives. As we confirmed later with videos, chimpanzees used either sticks or sponges to dip for water from holes that were wide enough. Videos confirmed that sponges were produced using the well-known techniques of chewing or folding the leaves in the mouth prior to use.

Table 1. Number of fluid dipping tools found per sampling block.

	Α	В	С	D	G	Total
Honey-dipping sticks (HDT)	0	0	137	107	45	289
Water-dipping sticks (WDT)	7	0	198	70	8	283
Leaf-sponges	0	7	59	17	0	83

We found that among the 11 tree species that contained water dipping sites, 70% of the holes were in *Dialium guineense* and 12% were in *Cynometra megalophyla*. These also were among the most frequent species of the 9 trees at which honey dipping tools were found (39% = D. guineense, 13% = C. megalophyla), although 16% of honey dipping

sites were located in *Albizia adianthifolia* trees. Holes containing honey do not need to be as impermeable as those containing water, since bees are capable of sealing them with wax. Therefore, beehives can be built in trees were water could not otherwise be retained.

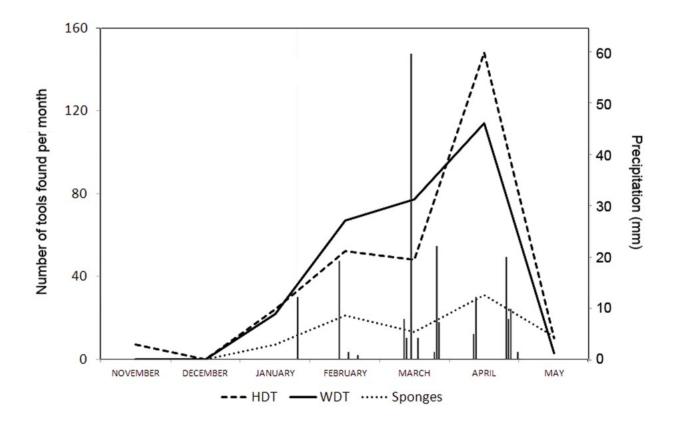


Fig. 3 Number of fluid dipping tools found per month and precipitation. There was no precipitation between the end of November and the end of January. Precipitation (vertical bars in the graph) was recorded at the CRS, but we have no data for November, which had 6 days with rainfall. Sampling in May lasted only until the 9th. The peak in the use of honey dipping tools (HDT) may be related to the flowering of savanna trees, which is at its maximum in March, allowing meliponine bees to produce more honey in April



Fig. 4 A tool assemblage (HDTs) representing a probable tool set. It was found in sampling block G at a honey dipping site which had been exploited earlier that day. All 15 tools were fresh, with remains and/or smell of honey and/or wax on their tips, but we do not know if they were used by one or more chimpanzees. The Meliponini beehive was in a fallen tree. We acquired at this site one video of a juvenile reusing a tool which had been left behind in the hive entrance. The second HDT from the top and the two at the bottom had brush tips of ordinary length and were considered honey collector

Even though all the WDT and sponges were found during the second half of the dry season (from the end of January to May), when the small rivers were dry, there were still water pools remaining alongside riverbeds, and knuckle and footprints revealed that these were used by chimpanzees. Five of the water dipping sites were located alongside the large Comoé River, which always carried abundant water, and chimpanzees were seen drinking from this large river on one occasion. The use of WDTs peaked during the driest part of the season at the beginning of April, and was already in decline at the study's end at the beginning of the rainy season in May (Fig. 3). Between the end of November 2014 and the end of January 2015, there was no precipitation, but small rivers in the core of the chimpanzee territory contained some water until January 15th. Despite the rainstorms in the late dry season, the pools present in the beds of small rivers continued shrinking due to evaporation and the repeated visits of large mammals; thus, by the end of April there were few and small pools in the riverbeds (only 5 in block C and 3 in block D). Trees, however, continued to have water in their holes, and thus provided an alternative source of water for the chimpanzees.

6.3.1 Tool characteristics

Both at water and honey dipping sites, we found that 26% (N=152) of stick-tools had been modified only minimally (the branches and leaves had been removed and the tips cut off). However 74% of all fluid dipping stick-tools (N=620) were more extensively modified, with the bark removed and brush tips fashioned on one or both of the ends. As revealed by camera trap videos, chimpanzees produce brush tips by chewing the tip of the stick to loosen the fibers. Sixty three per cent of the HDTs had brush tips (N=188) while 83 % of the WDTs had them (N=232).

Tool assemblages found at honey dipping sites were significantly larger than those found at water dipping sites, $(6.44 \pm \text{SD}\ 5.42\ \text{HDT}\ \text{per}\ \text{site}$, with a maximum of 19 tools per site for honey vs. $3.32 \pm \text{SD}\ 3.55\ \text{WDT}$ per site with maximum of 21 tools per site for water; U=1002.5, PP < 0.002). While honey assemblages appeared in most cases to be the product of a single episode (see Fig. 4), videos confirmed that, in five of 7 cases, water tools represented an accumulation of several days' (two to five days) episodes of tool use by multiple individuals. We found sticks without brush at 79 % of the honey dipping sites (N= 38 sites, mean number of tools without brush per site= $2.7\pm\ \text{SD}\ 2.99$ tools) but only in $32.47\ \%$ of water dipping sites (N=77 sites, mean number of tools without brush per site= $0.66\pm\ \text{SD}\ 1.35$ tools), suggesting that this kind of tool was part of a tool set (2 or more types of tools used sequentially to achieve a task) more probably in the case of honey dipping than water dipping.



Fig. 5 Sample of different water dipping sticks (WDT), with long, very long and extremely long brush tips. Tools h, i and j have the fiber-sponge tips described in the text. Tools a and h were used one after the other by adult male Hector (see Video 1 in Supplementary Materials)

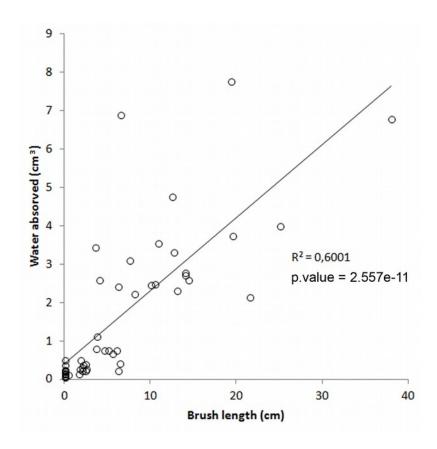


Fig. 6 Correlation between brush length and water absorbed. Weight of water in grams is equivalent to volume in cm³ or milliliters. The dispersion of some points is due to differences in the diameter of the sticks: the bigger the diameter, the more water was collected.

Tools that we classified as honey-perforators or probes, based on blunt or frayed tips and the absence of brush tip, were significantly longer than honey collectors, but not significantly thicker (Table 2). In contrast, the WDTs without brushes were shorter (although not significantly: U= 6341, P= 0.4224) than the ones with brushes. Based on three cases observed in the videos, it is likely that these later tools were selected by juveniles.

Table 2. Measurements of fluid dipping tools found. Mean total length \pm SD, proximal diameter \pm SD (measured at the most heavily-worn tip) and Brush- tip length \pm SD for the 4 types of stick tools that we found at honey and water dipping sites. WDT are water dipping sticks. Differences between tool types were tested with U Mann-Whitney test. Honey collectors were significantly longer than brushed tipped WDT (U= 17217, P < 0.0008) and brush tips of honey collectors were significantly shorter than those of brushed tipped WDT (U= 24965.5, P < 0.0006)

	Number of tools (N)	Total length (cm)	Proximal diameter (mm)	Brush-tip length (cm)
Probable honey probe/perforator	101	59.34 ± 25.88	6.20 ± 1.97	-
Honey collector	188	56.76 ± 21.39	5.92 ± 2.02	4.29 ± 2.9
WDT without brush	51	48.42 ± 20.17	5.64 ± 2.02	-
Brush tipped WDT	232	51.06 ± 19.39	5.59 ± 2.12	5.81 ± 4.67

Brush-tipped HDTs (e.g. honey collectors) were significantly longer than brushed tipped WDTs (U= 17217, P < 0.0008). HDTs without brushes (e.g. honey probes) were longer than any of the other tool types (Kruskal-Wallis chi-squared= 18.9641, P < 0.0003). This may be due to the bees choosing deeper holes as a defensive strategy, but we were unable to measure all of the beehive holes, since they were sometimes inaccessible to us. Beehives for which we could acquire accurate height measurements were significantly higher (N= 14, 6.27 \pm SD 4.54 m) than water holes on trees (N= 32, 2.15 \pm SD 2.73 m, U= 52, P < 0.00004). We found a weak positive correlation between water tree-hole depth and WDT total length (P= 0.002, R²=0.135). This may result from the fact that chimpanzees sometimes used long tools (N=11) in shallow holes and short tools in deep wide holes (N=13).

As we confirmed by camera trap videos and examination of the tools, the chimpanzees used the same technique to modify the tools with teeth or hands for both types of fluid dipping tools. This included; 1 Detaching the stick from a tree, vine or shrub with the hands, 2 Reducing the tool's length with hands and/or teeth, 3 Removing the leaves and branches with hands and teeth, 4 Producing a brush tip with the teeth. Some tools were further modified: 5 Removing completely the bark with hands and teeth, 6 Modifying the length after first use with hands and/or teeth, 7 Producing a second brush tip on the opposite end with teeth. The chimpanzees sometimes made an additional modification when producing especially long brushes (> five cm long) by repeatedly chewing the tip during use (see Video 1 in Supplementary Materials). We found that this latter form of modification was more frequent in WDT (46 % of brushes) than HDT (28 % of brushes). Seventeen percent of the water dipping brushes were >10 cm long, with a maximum recorded length of 38 cm (see figures 4 and 5).

WDT brushes (mean length of $5.81 \pm SD \ 4.67$ cm) were significantly longer than honey collector brushes (mean length of $4.29 \pm SD \ 2.9$ cm) U= 24965.5, P < 0.0006 (Table 2). In 51 cases (18% of all WDT brushes), chimpanzees produced a fiber-sponge at the tip of the WDT by repeated chewing. (fig. 5).



Fig. 7 The adult female Cassandra introduces a WDT with her right hand. She retrieves it and holds it with left hand while drinking. Video capture, March 24 2015

6.3.2 Tool efficiency experiment

In order to test the relationship between brush length and water absorption, we introduced in the laboratory 50 WDTs, which had been used by chimpanzees, into a container full of water (depth 15 cm, width 10 cm) 10 WDTs were selected from each of five brush-length categories (1^{st} = No brush, 0 cm, 2^{nd} =0.1-2.5 cm, 3^{rd} = 2.6-5.5 cm, 4^{th} = 5.6-11 cm, 5^{th} = 11.1-38 cm). After dipping, we weighed the water absorbed (see methods). We found a significant positive correlation (R^2 = 0.6001, P = 2.557e⁻¹¹) between the length of the brush and the amount of water absorbed.

Fiber-sponge brush tips were always longer and had finer and more detached fibers which made them more absorbent than ordinary brush tips (See fig. 3). A sample of 15 ordinary brush tips used in the absorption experiment (mean length $2.88 \pm SD 1.36$ cm) absorbed a mean of $0.77 \pm SD 0.9$ ml of water, while 15 fiber-sponge tips ($16.8 \pm SD 7.5$ cm) absorbed a mean of $3.68 \pm SD 1.7$ ml, five times more water per dip (W = 15.5, P < $9.6 e^{-06}$).



Fig. 8 The juvenile male Laertes dips for water in a 1.5 cm wide hole at the base of a *Dialium guineense* tree. While drinking, he chewed the tip, finally producing a medium sized 4 cm long tip. He peeled all of the bark from his tool in order to make it fit in the narrow hole. Video capture, April 21 2015.

6.3.3 Camera-trap videos

We recorded 267 videos of chimpanzees using 20 cameras over a 6 month period, of which 110 were tool-use videos. Seventy six of the tool use videos were of fluid dipping behavior, of which 39 included water dipping with sticks, three showed honey dipping with a stick, and the remainder (N=34) were of leaf-sponge use. This small number of honey-dipping videos may be explained by the low revisit rate (we checked honey dipping sites periodically and only two were revisited, and on only one occasion, in more than 6 months of censusing) and the fact that the greater average height of honey sites (6.27 \pm SD 4.54 m for beehives vs 2.15 \pm SD 2.73 m for water holes) complicated the installation of our cameras. In the sponge use videos, we recorded two adult males, 6 adult females and five juveniles drinking with leaf-sponges. We recorded one adult male, five adult females, one juvenile and one infant using WDTs. The honey dipping videos were of one juvenile and two adult females.

In addition, we recorded 14 videos of chimpanzees checking waterholes in trees, presumably to see if there was any water left, with three adult males, five adult females, four juveniles and three infants looking inside the holes or probing into them with discarded stick tools. We never observed in any of our videos a chimpanzee using its hands to gather water from tree holes, while four different monkey species were recorded doing so, baboon (*Papio anubis*), Lowe's monkey (*Cercopithecus lowei*), lesser spot-nose monkey (*Cercopithecus petaurista*) and white-naped mangabey (*Cercocebus lunulatus*).

6.3.4 Drinking technique

Based on the videotapes (N=38), we were able to determine that the technique used by the chimpanzees to drink using sponges did not differ from that reported for chimpanzees at other sites: leaves were collected from the immediate vicinity, then introduced in the mouth and chewed (73.5 %) or folded (26.5 %) to make them absorbent. Next, the chimpanzees dipped the sponge repeatedly into the water, taking it to the mouth, sucking it with the lips or pressing it between the lips and teeth. In three holes of depth exceeding 60 cm and diameter greater than 12 cm, the apes introduced their arm up to their shoulder into the hole to reach the water with the sponge. The water dipping technique included sticks which were always chewed before use, to prepare brush tips, and then repeatedly chewed producing long brushes or fiber-sponges during the water dipping episode (N=35). Sticks were torn off from saplings and fashioned by detaching branches, leaves and bark while the chimpanzees were on the ground at the base of the tree hole. In four cases, videos revealed that tools were prepared at a distance (10 to 20 m) and transported to the site. In other 12 cases, we found remains of the tool preparation (detached leaves, broken saplings) up to 60 m away. We also found 25 tools that had not been detached from plants present within 10 m of the water dipping site. In 93 of the 111 water dipping bouts recorded on video, the tip was chewed after drinking and before reintroduction into the hole. The chimpanzees would keep the tools inside the tree holes for 2-10 seconds, moving them slowly up and down to soak up the water. When repeated more than 10 times, the repeated chewing produced very long brushes or fiber-sponges (see Video 1 in Supplementary Materials).



Fig. 9 The adult female Andromaka drinks using a brush stick (WDT) that she carried already prepared to the site in her mouth, while the adult female Cassandra uses her sponge to drink at the same hole, which is wide enough to introduce her hand. The infants of both mothers observe the scene while playing. Video capture, April 25 2015.

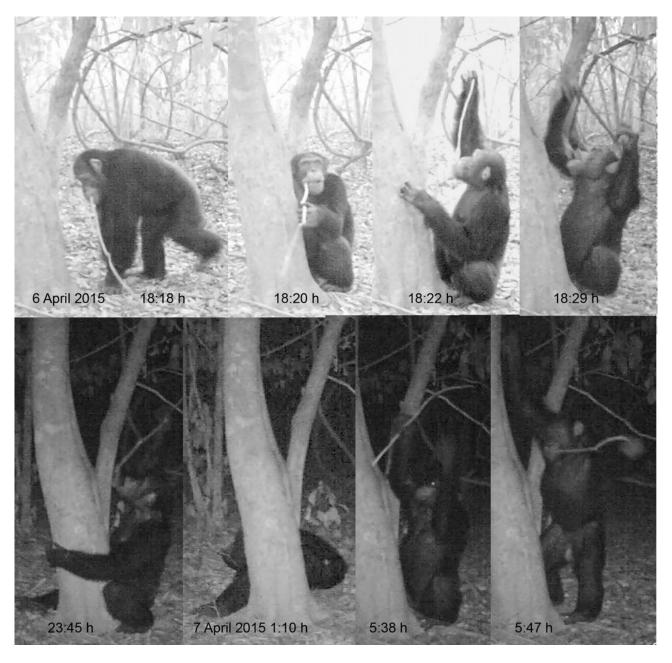


Fig. 10 The adult male Hector brings WDT-h after abandoning WDTa (see Fig 6). He chews the tip to produce a brush and then starts drinking. He introduces the tool mainly with his left hand, retrieving it with his right one, but sometimes switches hands. He stays drinking at the site for 12 hours, spending the whole night drinking and sleeping briefly beside the tree (6th frame). Nocturnal activity has been recorded in very few opportunities. Captures from video 1 (see supplementary materials)

6.4 DISCUSSION

In this research, we examined tool-use behavior in a population of savanna chimpanzees inhabiting a seasonally water restricted environment by testing several hypotheses related to tool dimension, manufacture technique, function, as well as whether tool-use and manufacturing techniques were limited to a particular community or common across several local populations. Previous studies indicate that savanna-living chimpanzees modify their behavior, habitat use and territorial movements to adapt to

water scarcity by moving in large mixed parties within their home ranges and concentrating around water sources during the dry season (Baldwin et al., 1982, Tutin et al., 1983, Duvall, 2000, 2008, Hunt & McGrew, 2002, Pruetz & Bertolani, 2009). Similarly, Comoé chimpanzees also moved within their ranges, as videos and fresh nests demonstrated, concentrating their activities during the dry season to forest patches that were within a radius of two km of the remaining pools in smaller rivers and used tools to obtain water and honey from tree holes during the late dry season. These chimpanzees were found to avoid the large river Comoé, where human activity (poaching, illegal fishing) is concentrated and where larger mammals such as monkeys, buffalos, antelopes, hogs, leopards and hyenas go to drink. Unlike savanna chimpanzees both in Senegal (Galat et al., 2008) and Semliki-Toro, Uganda (McGrew et al., 2007) who dig wells in the sand surrounding dirty pools of water, apparently to filter it, we never found signs of well digging at Comoé N. P., despite the fact that by April, the remaining pools were small and stagnant.

In this research, we tested the following hypotheses:

1 If Comoé chimpanzees develop tool-use behaviors to confront their dry savanna environment then we expect to find evidence of adaptive tool-use behavior produced by these chimpanzees particularly during periods of water scarcity.

We found 283 stick tools (WDTs) used by the Comoé chimpanzees to obtain water from tree holes during the late dry season. 175 of these WDTs were used in tree holes too narrow for a chimpanzee's hand to be introduced, thus the tools allowed the chimpanzees to obtain water from otherwise inaccessible sources. The tools were found during the late dry season, when other water sources were scarce, which supports our hypothesis.

2 Assuming that tool technology in wild chimpanzees is learned by watching others, then we expect water dipping behavior to be common and widespread across the chimpanzee communities under study.

The 283 WDTs were found distributed across four different sampling blocks that contain the home ranges of at least four different chimpanzee communities. We also recorded 39 videos of individuals of all sex/age classes using the WDTs. This evidence supports our hypothesis, suggesting that water dipping behavior with stick tools is common and widespread among Comoé chimpanzees.

- 3. Assuming that tools used by chimpanzees are specific to a particular task, we test the hypothesis that tools produced by Comoé chimpanzees to collect water (WDT) are different in dimensions and structure from those made to dip for and harvest honey (HDT). The mean total length of 289 HDT found during this study was significantly longer than the mean total length of 283 WDT (U= 17217, P < 0.0008). Sixty three per cent of HDT had brush tips, while 83 % of WDT had them. Forty six per cent of WDTs had long brush tips (>5 cm) vs 28 % of HDTs. Thus, WDTs were found to be different in dimensions and structure from HDTs, supporting our hypothesis.
- 4 Taking into account that chimpanzees produce tools with long brush-tips to dip for water, we expect a direct correlation between brush length and amount of water absorbed. We carried out an experiment measuring the water absorbed by a sample of 50 WDTs and found that there is a significant correlation between brush length and water absorved (R²= 0.6001, P = 2.557e⁻¹¹), thus, our hypothesis was supported by the result.
- 5 Considering that water is a less dense fluid than honey and longer brush tips are needed to absorb enough water per dip, we expect WDT brush-tips to be longer than HDT ones. The mean brush length of the 188 brush-tipped HDTs (4,29 \pm 2,9 cm) was significantly shorter (U= 17217, P < 0.0008) than the mean brush length of 232 brush-tipped WDTs

 (5.81 ± 4.67) , thus supporting our hypothesis.

Sugiyama (1995) found in Bossou a similar seasonal pattern to the one found in our study, with the chimpanzees using sponges to drink from tree holes during the dry season. In other study sites, both savanna and forest chimpanzees drink from tree holes using moss, grass, leaf-sponges or leaf spoons (Goodall, 1968, Tonooka, 2001, Matsusaka, 2006, Watts, 2008). These special drinking techniques appear to be adaptive solutions to conditions of reduced or unpredictable water availability during periods of the year or during dry years (Lanjouw, 2002). Clearly, the use of stick tools gives Comoé chimpanzees the ability to access water resources in narrow tree holes that would otherwise remain unavailable. The abundance at Comoé of *Dialium guineense* and *Cynometra megalophylla*, both tree species which produce abundant tree holes capable of retaining water, may have been a factor facilitating the development of the WDT technology. We don't know yet if these species are abundant in other study sites with similar habitats, future comparative research between sites could clarify the importance of this ecological factor.

The development of this behavior in Comoé may have been facilitated by the presence of rainstorms that fill the tree holes with water during the period of highest water scarcity, the late dry season. Matsusaka (2006) also speculates about the possible role that climate change and reduced water availability could have played in the recent appearance of this behavior at Mahale, although in that case, only juveniles have shown the behavior in playing context, and they do not produce elaborated tools, but simple sticks.

We found that fluid dipping using sticks and sponges is common and widespread among the Comoé chimpanzees. While honey dipping with tools and drinking with leafsponges are well known in chimpanzees, and are customary or habitual behaviors at many study sites across Africa (Goodall, 1968, Bermejo et al., 1989, Sugiyama, 1995, Bermejo et al., 1999, Whiten et al., 1999, 2001, Matsusaka et al., 2006, Sanz & Morgan, 2007, 2009, Watts, 2008, Boesch et al., 2009, Gruber et al., 2009, Dutton & Chapman, 2014), water dipping with sticks is extremely rare and has only been described for juveniles in a play context at Mahale, not being neither customary nor habitual at this site, but of recent appearance (Matsusaka, 2006). Although Wrangham once observed a Mahale chimpanzee chewing a stem of *Aframomum* sp. to dip for water, this is not habitual or customary behavior at the site and he describes these tools as stem sponges (Wrangham et al., 1994, Whiten et al. 2001). Goodall (1968) described the use of grass leaves to dip for water at Gombe, but after repeated chewing, these grasses were used more like a sponge. Our findings at Comoé represent a more developed and frequent expression of the behavior. The brushed tipped WDTs produced at Comoé can, therefore, be considered a new variety of specialized tools, which is widespread in this population and adapted to a particular task. We have documented 77 water dipping sites and 283 WDTs distributed across the home ranges of at least four different chimpanzee communities. Based on 39 videos of chimpanzees of different age classes and sexes from neighboring communities dipping for water with sticks, we feel this represents a habitual or customary behavior in Comoé chimpanzees. Nevertheless, further research is needed to confirm this point.

6.4.1 Possible origin of the use of brush-tipped sticks to drink

Sticks with brush tips are widely used by chimpanzees all across Africa, as honey collectors (Bermejo et al., 1989, Bermejo et al., 1999, Sanz & Morgan, 2007, 2009, Boesch et al., 2009, Watts, 2008, Gruber et al., 2009, Dutton & Chapman, 2014) and for the termite fishing in some Central African sites (Sugiyama, 1985, Sanz & Morgan, 2007). Comoé chimpanzees also proficiently and extensively use brush-tipped honey collectors,

we can therefore formulate the hypothesis of a probable extrapolation of the brush-tipped sticks use from honey to water acquisition, that probably required little cognitive effort, since beehives and water holes often occur in the same trees species and chimpanzees frequently use probes to explore tree-holes across their range.

Bossou chimpanzees solved the problem with the push & pull technique, retrieving leaf-sponges with sticks from tree holes (Sugiyama, 1995). We cannot discard the possibility that Comoé chimpanzees may use the push & pull technique as well, because although we never recorded the behavior on video, we found sponges and sticks together at six tool sites.

It appears, however, that the extrapolation of honey dipping with brushed tipped collectors to water dipping is not that obvious for chimpanzees, since it has not been observed anywhere else, despite its clear utility, making water in narrow holes available, although the exact combination of ecological factors that could have favored the appearance of the behavior at Comoé could be absent in other sites.

At the Goualogo and Loango research sites in Central Africa, the chimpanzees have been observed to use tool sets for honey gathering, with the following sequence of tools: 1. thick sticks as pounders to open the hard protective wall of the beehives; 2.enlargers to make holes wider; 3. probes to measure the depth of the honey; and 4. collectors with brush tips to gather the honey (Brewer & McGrew, 1990, Boesch et al., 2009, Sanz & Morgan, 2009).

Given that *Meliponini* beehives in Comoé N. P. are only protected by thin wax walls, they are easy for the chimpanzees to perforate (personal observation). We suggest, therefore, that many of the honey tools without brush tips could have been used as perforators or probes whereas the tools with brush tips were collectors. If this is correct, then most of the groups of tools found at honey gathering sites were probably tool sets (I. e. assemblages of several different types of tools used one after the other to achieve a goal), as most of them had been found freshly used probably following a single episode of honey dipping (although we don't know if by a single individual or several at the same time).

We have found that the WDTs produced by Comoé chimpanzees are significantly different in dimensions and absorption capacity from HDTs, which indicates specialization. Further research is needed to determine if the production of brush-tipped tools, the extrapolation of their use to different contexts and the additional improvement of longer brush-tipped fiber sponges qualifies for a case of cumulative culture. Comoé chimpanzees have successfully tackled the challenging environmental conditions of their harsh habitat not only by generalizing the use of brush sticks to both honey and water, but developing a new variety of brush tool with a specially-modified tip which increases the effectiveness of the tool. It appears to be habitual or customary at Comoé, observed in all age and sex classes, although we need further research to confirm it. We consider the water dipping with brush-tipped WDT behavior of the Comoé chimpanzees as a new type of tool-use behavior.

From all the data collected up to now we cannot yet conclude if making and using WDTs to drink water is more a choice than an ecological need, habituating the chimpanzees and evaluating the relative importance of water consumption from the different sources will allow us to answer this question in the future. The water-acquisition technology of Comoé chimpanzees represents a new set of chimpanzee traditions. Our study demonstrates the importance of carrying out detailed studies of threatened and isolated chimpanzee populations. Without these kind of studies, we will lose forever the opportunity to discover fascinating cultural variations and unique adaptations that could provide with important clues to better understand human evolution. Tool use gives

chimpanzees a clear advantage in water acquisition with respect to any other sympatric animals. Exclusive access to key resources through tool use could also have spurred increased rates of cultural evolution in our own ancestors. We must preserve and study the Comoé chimpanzees not only because they can provide us with important clues about our evolution, but also because they probably are the second largest population in Ivory Coast and the only known viable population of savanna chimpanzees remaining in the country. We are just scratching the surface in our understanding of this population with its extraordinary behavioral and cultural richness.

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CHAPTER SEVEN 7 TOOL REPERTOIRE OF COMOÉ CHIMPANZEES, NORTHEASTERN IVORY COAST

ABSTRACT

Chimpanzees produce and use tools all across Africa. Each particular population, however, has developed a local culture that includes the use of different combinations of tools for foraging as well as social behaviors and self-maintenance. We detail for the first time the particular tool assemblage produced by Western chimpanzees (Pan troglodytes verus) inhabiting the savanna-forest mosaic in the Comoé National Park (CNP) and surrounding areas. We found that the Comoé tool repertoire presents many differences from that of chimpanzees living in forested habitats in the nearest well-studied areas, including Taï in West Ivory Coast and Bossou in Southern Guinea.. It is also guite different from the tool traditions of Western chimpanzees living in similar savanna-forest mosaic habitats such as Mt. Assirik and Fongol, in Senegal, as well as Nigerian-Cameroonian chimpanzees in Gashaka-Gumpti, Nigeria, or those living in Central and Eastern Africa. We found significant differences in the characteristics of tools produced by different communities from within the same population of Comoé chimpanzees, suggesting the existence of subcultures between neighboring groups. The rich tool repertoire of these chimpanzees allows them to adapt to their harsh, extremely seasonal environment by exploiting resources that would remain unaccesible without tools and forms part of a local culture, different from those of the chimpanzees living in other parts of Africa. Our results expose the rich and complex traditions of the Comoé chimpanzees, but also contribute to evidence of the diversity of tool use behaviors across different populations of chimpanzees.

7.1 INTRODUCTION

According to some early theories of human evolution, the key development that led our ancestors to diverge from other primates was the making and use of tools (Oakley, 1956). This line of thinking was referred to as 'man the toolmaker' and stated that while other animal species were content to eat what they could access with their mouths or limbs, only humans modified and used objects to acquire otherwise difficult-to-access items. Later we began to use these tools to modify our very environment, creating our own adaptive niche. This line of thinking, though, had developed without detailed knowledge of the natural lives of our closest living relatives.

The first scientific observation of tool-use in wild chimpanzees (*Pan troglodytes*) was made by Jane Goodall in Gombe, Tanzania, in 1960, after she witnessed chimpanzees using stick tools to dip and fish for ants (Goodall, 1964). At that time, mainstream anthropology considered tool-making and tool-use to be exclusively human behaviors. When Goodall's supervisor, the anthropologist Louis Leakey, learned about her findings, he said his famous phrase: «now we have to redefine tool, redefine man or accept the chimpanzees as humans». Since then, similar discoveries of tool-use in Sumatran orangutans, *Pongo abelii* (van Schaik et al. 1996), long-tailed macaques, *Macaca fascicularis* (Gumert et al. 2009), tufted capuchins, *Sapajus apella* (Ottoni & Mannu, 2001) bearded capuchins, *Sapajus libidinosus* (Spagnoletti et al. 2011a) and white-faced capuchins, *Cebus capucinus imitator* (Barret et al. 2018) have shown that tool use has developed multiple times within the Order Primates.

Much has been learned since then about tool-use in free-living chimpanzees across Africa: the four subspecies of *Pan troglodytes* have all been found to make and use tools (Goodall, 1968, Sabater Pi, 1974, Bermejo et al. 1989, Boesch & Boesch 1990, McGrew,

1992, Wrangham, 1994, Whiten et al. 1999, 2001, Hicks et al. 2005, Pruetz et al. 2007, Watts, 2008, Matsuzawa et al. 2011, Nakamura et al. 2015). Tool-use behaviors are quite diverse in chimpanzees, and have been argued to form part of cultures (Whiten et al. 1999, 2001). The making and use of tools, so widespread in wild chimpanzees, is however extremely rare or even absent in the wild in other closely related African apes, such as bonobos, *Pan paniscus* (Gruber et al. 2010, Furuichi et al. 2014) and gorillas, *Gorilla gorilla* (Kinani & Zimmerman, 2014)). Tool-use has been observed in one population of free-living Sumatran orangutans (*Pongo abelii*, formerly *P. pygmaeus*), but it seems to be less frequent and diverse than in the chimpanzees (Fox et al. 1999).

Chimpanzee tool repertoires can be very rich or quite poor. Eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Ngogo, Uganda, for example, have a very limited toolkit; they use leaves to clean themselves and very rarely leaf-sponges to soak up water and stick tools for honey-dipping (Watts, 2008). The Sonso community in Budongo, Uganda has an even simpler one, with one single foraging tool, the leaf-sponge (Gruber et al. 2012). Curiously, chimpanzees living in a similar habitat in Gombe, Tanzania, have been found to use a great variety of tools, including stick or grass tools to acquire ants, honey and termites. These apes also throw stones as part of noisy displays or aimed throwing, and use leaves or stems to drink water from tree-holes (Goodall, 1964, 1968). Not far to the south, Mahale chimpanzees do not use tools to prey upon driver ants as they do at Gombe, despite those ants being common there (McGrew 1992). Also in Tanzania, in the dryer savanna habitat of Ugalla, indirect evidence indicates that the chimpanzees may dig with sticks for the underground storage organs (USO) of plants (Hernandez-Aguilar et al. 2007).

Central African chimpanzees (*Pan troglodytes troglodytes*) were already described to use specialized stick tools to forage on termites in the 1960s (Sabater Pi, 1974) and more recently, other authors described the use of complex tool sets to forage on ants and termites in Goualogo, Congo (Sanz et al. 2007, 2009, 2010, 2013). They also use clubs to open arboreal beehives on b (Hicks et al. 2005, Boesch et al. 2009) and from underground beehives (Estienne et al. 2017). Brush-tipped termite tools, tool sets, and honey-clubs may represent potential large-scale 'behavioral realms' in Central Africa (Hicks 2019a).

Pan troglodytes ellioti, the Nigerian-Cameroonian chimpanzee, formerly known as *P.t. vellerosus*, was described to make and use stick tools to forage on ants and honey in Gashaka, Nigeria (Schöning et al., 2007, 2008, Sommer et al. 2012). The chimpanzees of this same subspecies were described to use stone hammers and root and stone anvils to crack *Coula edulis* nuts in Ebo, Cameroon (Morgan, 2006) on the basis of indirect signs.

West African chimpanzees (*Pan troglodytes verus*) are well known as the chimpanzees who have entered the Stone Age. Multiple populations are known to crack open nuts (*Coula edulis, Panda oleosa, Sacoglottis gabonensis, Detarium senegalense, Parinari excelsa* and *Elaeis guineensis*) with stone hammers against an anvil; this behavior has been documented in Sierra Leone (Whitesides, 1985), Liberia (Anderson, 1983) Guinea (Humle & Matsuzawa, 2001, Carvalho et al. 2009, Matsuzawa et al. 2011) and Western Ivory Coast, where the Taï Forest chimpanzees use both stone and wooden hammers to crack open the nuts of five tree species (Boesch et al. 1990, 1994, 1998). With the possible exception of Ebo, Cameroon (Morgan, 2006), no clear evidence of nutcracking with tools has been found to the east of the Sassandra River in any of the other chimpanzee subspecies.

Nut-cracking is not the only tool-use behavior described for Western chimpanzees, which have shown to produce diverse tool repertoires in different sites. For instance, chimpanzees in Tenkere, Sierra Leone use stepping and sitting sticks to avoid *Ceiba pentandra* spines when feeding on the fruits and stick tools to forage on ants (Alp, 1993,

1997). Chimpanzees in Bossou, Guinea, in addition to cracking open oil palm nuts (*Elaeis guineensis*) with stone tools, dip for honey and ants with sticks, fish for ants and termites, drink from tree holes with leaf-sponges, scoop algae from ponds using stems of herbs or sticks and practice the pestle-pounding, using the stem of palm leaves to dig holes in the crown of the oil-palms and drink the sap (Matsuzawa, 2011). Curiously, chimpanzees living in the nearby community of Seringbara, also in Guinea, do not use hammers and anvils to crack nuts, scoop for algae or practice the pestle pounding, but use wooden and stone cleavers to fracture big fruits of *Treculia africana* (Koops et al. 2010). Other chimpanzees in the neighboring area of Mount Nimba, do crack nuts, but prefer *Coula edulis* over *Elaeis guineensis*. Researchers did not find an ecological explanation for these differences, suggesting the possibility of cultural differences (Humle & Matsuzawa, 2001, Humle, 2003b, Matsuzawa et al. 2011). Chimpanzees in the further site of Bakoun, Guinea have been found to routinely fish for algae in ponds, using stick tools, a similar behavior to the algae scooping observed in Bossou, that could be a widespread behavioral pattern (Boesch et al. 2017).

Taï Forest chimpanzees also use stick tools to dip for ants and for honey, as well as to extract marrow from bones and to whisk flies (Boesch, 1990, 2013, Whiten et al. 1999). While the Western chimpanzees described above inhabit mostly rainforest, the only savanna chimpanzees whose tool behavior had been previously described are those from Senegal. AtMont Assirik, a savanna site with similar conditions to those of Comoé, Bermejo et al. (1989) reported the use of stick tools to fish for termites and to dip for honey, they also interpreted that chimpanzees pounded open fruits of baobab (*Adansonia digitata*) using stone anvils and hammers from indirect signs, although later, McGrew et al. (2003) challenged this interpretation and suggested that these chimpanzees only pounded the fruits on stone anvils, using the same etho-archaeological methods. At the nearby Senegalese site of Fongoli, these savanna-living chimpanzees also use sticks to fish termites and to dip driver ants (Bogart, 2009), as well as fashion spears to hunt bushbabies (Pruetz& Bertolani, 2007). So far no definitive evidence of nut-cracking using a hammer has been documented at these savanna sites.

The tool use behavior of the Comoé chimpanzees has never been studied before, although Boesch et al. (1994) did look for traces of nut cracking there during a general survey across Ivory Coast. His team, only walked a few kilometers of transects in areas close to the park limit (see chapter 3) and found no traces of nut-hammering, therefore, no tool use had ever been described for Comoé chimpanzees before we started our work (Lapuente et a. 2016). Given that we knew we would be documenting for the first time a new chimpanzee material culture, we began our research with the following basic questions:

Do the Comoé chimpanzees produce and use tools?

Which types of tools do they use and for which purpose?

We constructed the following hypotheses:

- 1 Considering that chimpanzees across all Africa have been found to produce and use tools, we predict that Comoé chimpanzees will make and use tools
- 2 Taking into account that in CNP there are abundant stones that could be used as anvils and hammers and that there are two potential nut species that could be cracked (*Detarium senegalense* and *D. mycrocarpum*) we expect to find evidence of nut-cracking in Comoé.

3 Considering that the ecological conditions of Comoé are more demanding than those of the rainforest, with intense seasonal droughts and more extreme temperatures, we expect to find some tool-behaviors that help the chimpanzees to survive in these harder conditions of Comoé.

4 Since chimpanzees at other study sites have shown the capacity of making specialized tools for different tool-uses, we predict that, if Comoé chimpanzees make tools for different uses, these tools will be significantly different in dimensions and/or structure.

7.2 MATERIALS AND METHODS

7.2.1 Study site

The CNP is the largest protected area in Ivory Coast and one of the largest in West Africa, covering close to 11500 km². The park, found in the transition zone between the Guinean and Sudanian bioclimatic regions, is dominated by savanna habitats, including open grassland and savanna woodland, with only a 9 % of the area covered by forested patches, mainly along rivers. A major river, the Comoé River crosses the park from the north to the south. This river becomes crossable by foot during the dry season at many points. It is fed by a number of tributaries which during the dry season can disappear or be reduced to puddles. Yearly precipitation is around 1090 mm and the annual mean temperature is around 27°C (Hennenberg, 2005), although during our five-year study period (October 2014-October 2019), we recorded an annual mean precipitation of only 925.5 mm and a mean temperature of 26.79° C.

At the beginning of our research project, we initially selected a study area covering 900 km² in the southwestern corner of the CNP. This area includes most of the known range of chimpanzees in the park. In 2018, we also began studying the adjacent area out of the park formerly known as GEPRENAF, which changed its status to become the present Special Zone of Protection of Biodiversity of Mont Tingui. Our entire study area is covered by a mosaic of savanna and forest, with around 13 % covered in forest. The chimpanzees used mainly the forested habitats, which can be classified in two main categories: gallery forests and forest islands, subdivided in deciduous and semideciduous (see Chapters 1 and 4 for more details). Sympatric fauna includes 11 species of primates, all of which could potentially be prey items for chimpanzees, including the threatened white-thighed colobus (*Colobus vellerosus*) and white-naped mangabey (*Cercocebus atys*), as well and the abundant widespread olive baboon (*Papio anubis*). Forest elephants (*Loxodonta cyclotis*) share the area with large carnivores such as leopards (*Panthera pardus*) and hyenas (*Crocuta crocuta*). In total, more than 150 mammal species have been identified in the area (Fischer et al. 2002).

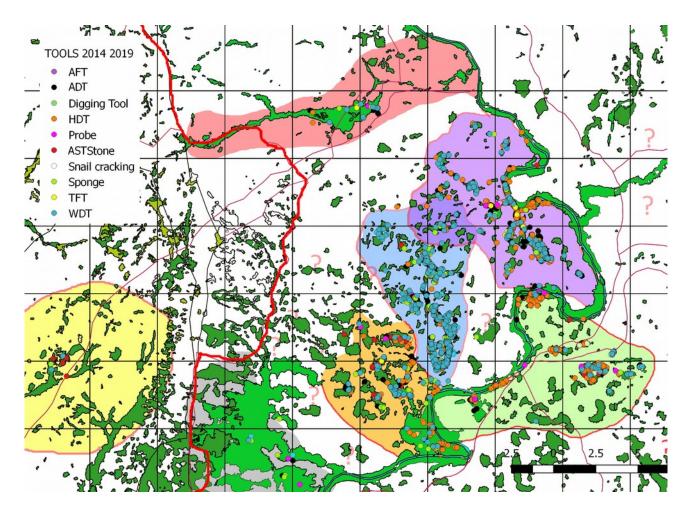


Fig. 1 Map of the study area SW of the park. Dark green patches are forest, while the white area represents savanna. The grid cells measure 4×4 km. The red continuous line crossing from North to South are the 2017 western limit of the Comoé N. P. Left of this line is the Special Zone of Biodiversity of Mont Tingui. Shaded areas of different colors represent the known home-ranges of the studied chimpanzee communities: pink= Argonaut community, yellow = Mont Tingui, grey = Theogony, orange = Trojan, blue= Achean, purple = Odyssey and green = Aeneid. The dots represent the locations of the tools found during the study period, and often overlap one another in the areas of higher chimpanzee tool-use (hot-spots).

7.2.2 Tool identification

We followed one of the most widely used definitions of tool, the one proposed by Beck (1980): "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself". To distinguish used stick tools from the thousands of random sticks that were lying on the forest floor, we checked tool candidates for modifications produced by chimpanzees, tooth marks on the ends, stripping of lateral branches, leaves and sometimes bark, blunt or frayed fibers at the end and dirt or wear (including water, mud, honey or wax) on the sticks. We noted any associated chimpanzee footprints, dung or nests. We also checked the nearby vegetation for stripped branches or leaves and looked for association with insect dwellings or any other potential tool-use site. We did not consider as tools sticks that had no modification or traces of use, even though we later

observed in our videos that infants sometimes used these unmodified sticks when imitating their elders.

In the case of stones used as potential tools, we only considered those that bore traces of use, such as remains of bark or vegetable tissues transferred from impact against a tree, smeared mud presumably from the chimpanzee's hands or weathered areas caused by strikes. We only considered the most recently-used stone tools, since we found many other stones which resembled older tools, but to be cautious we did not include them in this study to avoid possible misinterpretations. We also looked for unnatural stone accumulations that could have resulted from the accumulative stone throwing (Kühl et al. 2016). Within the set of potential stone tools, we studied nut-cracking in Taï NP before working in Comoé and was thus familiar with the wear this behavior produced on stones. We looked for stones with strike marks or depressions caused by repeated hits against nuts and anvils, if used as hammers, and roots or stones with scars of repeated hitting and pits, if used as anvils. The main nut available in the CNP was Detarium senegalense, which is cracked in the Taï forest, IC (Boesch & Boesch, 1990) and possibly in Tiwai, Sierra Leone (Whitesides, 1985), although we also looked for potential nut-cracking of the softer nut *D. mycrocarpum*.

We identified the type of tool use when we found tools inserted into the place of use, such as the underground or arboreal ant nests, arboreal beehives, termite mounds or water holes in trees, but also when lying on the ground, besides underground or tree nests, water holes, beehives. We also attributed the tools to each of these uses when we found them on the ground, at the base of trees where there were clear signs of use for water drinking, honey-dipping or ant harvesting, such as stains caused by the rubbing of animals' body parts, wet tips of the tools, honey dripping from the holes or smell of honey at the tip of the tools. Tools used to harvest ants were also recognized when found lying on top of the ants' nest, associated with chimpanzee footprints or dung. We tried to confirm the use of every tool type with camera-traps, as we explain below.

7.2.3 Reconnaissance walks and transects

Over the duration of the study period, from October 2014 to July 2019, we walked more than 4525 km of reconnaissance walks (walks following a GPS bearing that cross the prospected area, referred as recces from now on) and more than 200 km of linear transects crossing the forest patches used by the chimpanzees. During our walks, we used a handheld GPS to record the coordinates of all of the tools we found. We used ethoarchaeoogical methods (McGrew et al. 2003), noting the position of the tools within each tool-use site, using a measuring tape to measure the dimensions of the tools, distances to the point where the tool had been used and taking photos of the original placement of every object.

We took all of the freshly-used tools which we found between October 2014 and October 2017 to the laboratory in the Comoé Research Station, for detailed measurements and classification. Following that date, in order to avoid interfering with the chimpanzees' learning processes by reusing tools, we left the tools in place at the tool sites, recording data without touching them, to avoid the potential transmission of diseases.

7.2.4 Direct observations

The Comoé chimpanzees are wild, have been submitted to poaching pressure and usually hide when humans approach. Only during the last year of the study did we begin the lengthy process of habituation of one of the study communities (see Chapter 2). Hence, most of our direct observations of the apes were made opportunistically. Although these observations were non systematic, we were able to confirm the consumption of

foods rarely identifiable in the dung samples. We observed the chimpanzees hunting, consuming fruits and using tools to consume insects and honey. We made all of these observations keeping a distance of 20 m or more to avoid stressing the animals and transmitting diseases, moreover we carried face masks to prevent the transmission of respiratory diseases in the case of accidental closer encounters.

7.2.5 Camera traps

To overcome the difficulties of direct observation, we installed camera traps in hot spots of chimpanzee activity, especially in places where tools had been used. Chimpanzees habituate to cameras more quickly than to human observers, allowing us to record valuable data from the first month of the study. We placed the cameras systematically in forest habitats across a sampling grid with 1 km² cells as the sampling unit, within which we selected chimpanzee activity hot-spots. From October 2014 to October 2015 we used 20 Bushnell HD trophy cameras (model 119437). From October 2015 to May 2017 we increased up to 80 cameras, of which the 60 provided by MPI-EVAN were Bushnell HD Agressor cameras. From May 2017 to May 2019, we continued our study with 30 cameras, of which 12 were Browning SPEC-OPS and the remaining were Bushnell HDs. We programmed all of the cameras to record one minute-long videos. The cameras were triggered by the motion of animals with temperature different from background. When the light was insufficient to record color videos in visible light, we set them to record infrared black and white videos. The videos allowed us to confirm the tooluses inferred from the tools investigated through etho-archaeological methods, to confirm the consumption of certain foods which were not identifiable in the dung samples. They also allowed us to investigate possible seasonality of foraging for each food source. For more details on the methodology, see Lapuente et al. (2016, 2018) and Chapter 4.

7.2.6 Data analysis

We conducted all statistical analyses using R-studio software. The data had non-parametric distribution, thus we tested for significant differences between the means using Wilcoxon U-test. We analyzed GPS data and created the maps using Quantum GIS.

7.3 RESULTS

7.3.1 Videos from camera-traps

During the study period, we accumulated 43,712 camera-days (number of days that cameras were working multiplied by the number of cameras functioning each day), during which time we recorded a total of 2621 videos of chimpanzees from seven different communities. Of these videos, 1134 contained scenes of tool-use (1243 if we consider percussive technology on objects attached to the substrate, such as tree-buttresses or anvils: Table 1).

We used the videos not only to confirm the tool-use which we had inferred indirectly via the tools and tool-sites, but also to analyze the techniques used and to observe which members of the community used the tools and how frequently. This allowed us to determine if the behaviors could be classified in the cultural categories established by Whitten et al. (1999); "(1) customary, for which the behavior occurs in all or most ablebodied members of at least one age-sex class (such as adult males); (2) habitual, for which the behavior is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (3) present, for which the behavior is neither customary nor habitual but is clearly identified".

Table 1. Number of videos of tool use recorded, including of percussive technology, not generally considered to be tool-use (the use of objects attached to the substrate or tree-drumming). Number of communities refers to those communities from which we obtained videos corresponding to the different tool types. The actual number of communities where the behaviors have been observed indirectly through tools and tool-sites is in all cases higher, as we can see in the corresponding sections below.

BEHAVIOR	Objective	Tool use site	Number of videos	Number of communities
Water-dipping tool	Drink water	Tree hole	530	6
Leaf-sponge	Drink water	Tree hole	383	6
Leaf-sponge (clayish water)	Drink clay-filled water	Salt lick	2	1
Honey-dipping tool	Forage on honey	Beehive in tree	65	4
Ant-dipping tool	Forage on driver ants	Underground nest	93	3
Termite-fishing tool	Forage on termites	Termite mound	38	2
Ant-fishing tool	Forage on carpenter ants	Nest in tree hole	2	1
Accumulative stone throwing	Display by males	Tree with big buttresses	18	2
Buttress drumming	Display by males	Tree with big buttresses	80	4
Aimed throwing (stone or branch)	Display by juveniles	Any place	3	2
Fruit pounding	Forage on hard shelled fruits	Stone or root anvil	29	2
Total			1243	7

7.3.2 Number and types of tools found

Throughout the study period, we confirmed a total of 6426 tools, including both stick and stone tools. The stone tools which use we could confirm were all used to hit the buttresses of trees in the context of male displays. We found a few stones that seemed to have been used as hammers to crack big snails (*Achatina fullica*) or hard-shelled fruits (*Strychnos spinosa, Afraegle paniculata*), but we cwere unable to confirm their use through videos or direct observation. Among the stick tools, we identified tools used for ant-dipping, ant-fishing, termite-fishing, honey-dipping, water-dipping and multi-purpose probes. Stick tools for honey could be classified into different types, forming parts of tools sets. Ant-dipping tools were in most cases of the same type, but a few of them were specialized for poking the ants in deep underground nests, which we describe below. On two occasions we found digging-sticks with clear traces of use, but we could not confirm them via videos or direct observations. We also found a great number of leaf-sponges, used mainly to drink from tree-holes full of water but also to drink clayish water from ponds in salt-licks.

Table 2. Number and types of tools found during the study period. AFT = ant-fishing tool, ADT = ant-dipping tool, HDT = honey-dipping tool, ASTs = stones used for accumulative stone throwing, TFT = termite fishing tool and WDT = water-dipping tool. The hammer stone tools and the digging stick are marked with asterisks, as we failed to confirm their use via videos or direct observations; we thus consider them to be probable tools awaiting confirmation.

Type of tool	Number
AFT	45
ADT	1408
Digging Tool*	2
Fruit-cracking hammer*	16
HDT	2120
Probe	74
ASTs	69
Snail-cracking hammer*	1
Leaf sponge	787
TFT	44
WDT	1861
Total all tools	6426

7.3.3 Ant-fishing tools (AFT)

We found a total of 45 AFT, both inserted into the narrow holes of arboreal ant nests or lying at the base of trees with ant nests. We found a group of five tools projecting from a *Crematogaster sp.* ant nest, and the rest of the tools at three different nests of carpenter ants, *Camponotus maculatus*, corresponding to a total of seven events of ant fishing, in two different chimpanzee communities (Achean and Odyssey). We further confirmed this type of tool-use via camera trap videos as detailed in the corresponding section below. The technique used to extract the ants, as recorded in the videos, was more similar to that observed to fish termites than to the one used to dip driver ants, despite the apparent ferocity of the carpenter ants. The tools were made from thin branches from nearby vines and shrubs. They were on average shorter than any other stick tool and only slightly thicker than termite fishing tools, but the latter were made mainly from softer materials, like herbs (Table 5).



Fig. 2 Capture from a video of the adult male Achilles, from the Achean community, fishing for *Camponotus maculatus* ants at their nest in a tree hole, using a short, thin and flexible AFT. His adopted juvenile male Diomedes watches.

7.3.4 Ant-dipping tools (ADT)

We found 1408 ant-dipping tools (ADTs) used to extract driver ants, *Dorylus burmeisteri*, from their underground nests. Most of these ADTs were made from long, thin and flexible branches of nearby vines and shrubs, but were significantly thicker and much longer than ant-fishing tools (Table 5). These ADTs were similar in characteristics to the ADTs found in other research sites, such as Gombe stream (Goodall, 1968, Schönning et al. 2007, 2008). In the 100 videos recorded for this behavior (table 5 in Chapter 4) we confirmed the use of these tools by all the sex/age classes of the chimpanzees in the Achean, Odyssey and Aeneid communities. The chimpanzees consumed the ants using both the ant-dip-wipe (manually wiping the ants off the tool) and ant-dip-single (wiping directly the ants with the mouth off the tool) techniques, described in Whiten et al. (1999).

7.3.4.1 Goads, a new type of tool used for foraging on driver ants

In four occasions, we found very long, thick tools, ,the largest tools made by Comoé chimpanzees. These tools had been inserted into *Dorylus burmeisteri* nests in association with several normal ADTs. In one of the cases, four of these large tools were deeply inserted in the hole, while three more were lying around it. In our interpretation, these tools had been used to poke the ants that had gone deep underground during the dry season. The chimpanzees appeared to have used these tools to provoke the ants to emerge, and then used smaller ADPs to dip them. We have named these larger tools goads and we partially confirmed their use through video, as we detail below. Further research is needed to confirm this as part of a potential tool set. In video 2 of the supplementary materials, a juvenile from Odyssey community can be seen removing one of these tools from a driver ant nest, while a second one remains inserted.



Fig. 3 Ant dipping tools found at an underground nest of *Dorylus burmeisteri*, *and* arranged by the first author in groups by type. In the center of the picture are five of the large tools used to poke the ants deep underground, which we called goads. We found these tools inserted in the main entrance of the ant nest to a depth of 40 cm. The goads had been stripped from surrounding saplings. In the upper right corner, 17 normal ADTs can be seen, much thinner and shorter, made from flexible vines found near the ant nest. These tools were used to dip for the ants coming out of the nest after deep poking, by inserting them in the hole and moving them slowly up and down. All the tools had been used in the same event, suggesting sequential tool use. The measuring tape is 1.5 m long.



Fig. 4 Video-capture of adult females Ktimene and Circe, from the Odyssey community, accompanied by their offspring, dipping with long, thin tools for driver ants (*Dorylus burmeisteri*) in an underground nest. They are clinging from branches to avoid the bites of the ants at their feet.

7.3.5 Digging tools

We only found two examples of potential digging tools over the entire study period and we could not obtain any camera-trap footage or direct observations of their use. We found both tools associated with uprooted *Cubitermes sp.* mounds, surrounded by chimpanzee footprints. The tools had apparently been used to dig up the underground part of the termite colony. Taking into account that we thoroughly prospected our study area for five years, we think this type of tool is rarely used, or at least, is used much less frequently than all the other stick tools described in this paper.



Fig. 5 Potential digging-stick tool found beside an uprooted *Cubitermes sp.* mound. To the left, the remains of the termite mound and the excavated soil was around the base of the mound. To the right is the tool, measuring 49 cm long and 1.5 cm in diameter (the one beside the measuring tape). The pointy tip (to the right) was dirty with soil and blunt from use. What appears to be another thinner stick on top is actually a root that comes out of the soil.

7.3.6 Honey dipping tools (HDTs)

We found a total of 2120 HDTs in five of seven chimpanzee communities. We found only six of these tools at three beehives of honeybees (*Apis mellifera*), of which, three were projecting from holes in the hives and the others were found lying at the base of the tree. We found 124 beehives of honeybees, some of them very accessible, which had not been exploited. On the other hand, we found more of 2000 stick tools at the beehives of *Meliponini* stingless bees, suggesting that the honey of these relatively inoffensive bees was the preferred type for the Comoé chimpanzees. The species of stingless bees found were *Meliponula ferruginea, Meliponula togoensis, Meliponula bocandei, Hypotrigona gribodoi*, nesting exclusively on trees, only H. gribodoi was not found exploited by chimpanzees (Soro et al. 2019).

On a number of occasions we encountered apparent tool sets: several types of tools used sequentially at the same site to extract honey. The thick and long ones may be perforators; the thinner and longer ones may be probes used to check the depth of the honey chambers; the flexible ones with brushes on their tips were likely collectors, to dip into the honey and then bring it to the mouth (Chapter 6). In some cases, we also found very short tools with brushes that were likely used to gather the honey dripping around the tree hole, since they were too short to reach the honey chamber in the respective beehives. If indeed this represents the combination of all these different types of tools, used sequentially in a single event, then it would be a tool-set (Boesch et al. 2009). To access narrow cracks at 8 beehives, the chimpanzees had split longitudinally 27 tools to flatten them. Of the total of HDTs we measured, 73.9 % had brushes corresponding to different types of collectors, while 10.4 % had a second brush in the opposite tip. We distinguished at least four types of tools used sequentially during honey-dipping events: perforators, used to make a hole through the protective wax wall of the beehive, probes,

used to test the depth of the honey chamber, collectors, long tools ($51,39 \pm 21,41$ cm) with brushes at their tips, used to collect the honey once the chamber was pierced and swabs, very short tools (< 10 cm) with brushes at their tips, apparently used to collect the honey dripping around the tree hole where the beehive was. For a more detailed description of HDTs, please see Chapter 6.

HDT was the only type of tool for which we confirmed its use in savanna. On two occasions we found HDTs inserted into *Meliponini* beehives in savanna, less than 200 m from the nearby forest. One of these tools had been made on the spot using a dry grass stem. The use of a grass stem as a tool is quite exceptional for Comoé chimpanzees, since over five years we only found one honey dipping tool made from herbaceous materials in five years.



Fig. 6 Example of a tool-set used by the chimpanzees of the Aeneid community to extract honey from a stingless beehive. From top to bottom, we can see a **swab**, a very short collector probably used to gather honey dripping down the exterior of the tree; a **collector with two brushes**, probably used to collect the honey when the beehive was still full; a thick and pointy **perforator** used to make a hole in the wax wall of the hive; a long thin **probe** used to test depth; and two longer **collectors**, used to extract the honey from the bottom of the beehive. This photo was taken in the laboratory of the CRS, prior to measuring all the tools.



Fig. 7 Video-capture of adult female Circe, from the Odyssey community, dipping for honey in a *Meliponini* beehive (the entry hole can be seen close to the chimpanzee's right wrist) while her infant watches. She has introduced the tool deep into the hole and licks the tip after extracting it.

7.3.7 Investigatory probes

We found a total of 74 tools that we classified as investigatory probes, meaning that the tools had been used to inspect holes or objects, without an obviously attempt to forage on the prey species described above. We confirmed that these probes were tools based on signs of modifications and traces of use. Most of these probes were inserted into the holes of trees or were found abandoned on used paths, but in neither of those cases we were unable to link them to any of the other known uses. In at least one case, we think the tool was used to poke into the burrow of a rodent, the cane rat (*Thryonomys swinderianus*) to force it out of its burrow. We found abundant dorsal hair of the rodent around the burrow (easily recognizable for this species) and chimpanzee footprints and traces on the ground with the aspect of rubbing of chimpanzee's legs and arms, suggesting a struggle. Chimpanzees are known to prey on this species at other study sites (Uehara 1997).



Fig. 8 A probe found at the entrance of the burrow of a cane rat (*Thryonomys swinderianus*). We found abundant hair of the rodent around the burrow (dorsal hair of this species is very recognizable) and chimpanzee footprints, suggesting some struggle. Chimpanzees are known to predate on this species in other study sites, Uehara (1997).

7.3.8 Termite fishing tools (TFTs)

We found only 44 termite-fishing tools (TFTs) at 27 sites, in three communities, which were the thinnest in average of all the tool-types, but were longer than the AFTs. Twelve of these tools were made from twigs or the stems of herbaceous unidentified plants and the rest of very thin and flexible vines. The difficulty of preservation of such soft materials may explain the small number of these tools that we found. As we observed that termites "attacked" and devoured the tools inserted in the termite mound or left on top of it, we assume that an important percentage of the tools disappeared before we could observe them. The termites consumed by the chimpanzees with the tools were *Macrotermes subhyalinus* at three of the sites and *Odontotermes majus* at all the rest, species for which we obtained video confirmation. *Cubitermes sp.* were probably consumed after pounding open the mounds on root or rock anvils and twice were associated to digging tools, although we never found TFTs linked to this latter species. As shown by our camera trap videos, the chimpanzees generally sat atop of the termite

mound while termite fishing, unlike how they behaved when dipping for driver ants. Camera traps also revealed some details of the fishing technique (see Figure 9).



Fig. 9 A Video-capture of an adult female, Aerope from the Achean community, fishing for *Macrotermes subhyalinus* using a thin, flexible TFT. She holds the tool against the back of her right wrist while pulling it through her lips with her left hand.

7.3.9 Water dipping tools (WDTs)

We found 1861 WDTs during the study period, made of sticks which had been torn from tree branches or shrubs, stripped of their lateral branches, leaves and sometimes bark (see chapter 6). In the 85.37 % of cases, at least one of the tool tips had been modified by chewing it, to create an absorbent brush that was significantly longer than those made for HDTs, reaching sometimes more than 25 cm (Table 3, Lapuente et al. 2016; Chapter 6) while in 10.85 % of the tools, a second brush had been fashioned at the other tip.

This specialized type of tool has only been found t Comoé (Lapuente et al. 2016; Chapter 6) and it is present in all the studied chimpanzee communities. We recorded videos, in six of these communities, of chimpanzees of all sex/age classes using these tools along the whole study period (Table 5) suggesting that it is a cultural behavior in those communities.



Fig. 10 Video-capture of the subadult male Menelao from the Achean community, drinking water from a tree hole in a *Dialium guineense* using a WDT with a long brush. He puts the head close to the hole to move the tool faster from the water to his mouth. He made this short WDT to handle it more precisely, as the tree hole was full of water.

7.3.10 Leaf sponges

We found 787 individual leaf-sponges which we interpreted as having been used by the chimpanzees to drink water from tree holes. These sponges were made of leaves stripped from nearby trees, and which had been put in the mouth and chewed (73.5 %) or folded (26.5 %) prior to use, to make them more absorbent. The technique used to fold the leaves between the teeth and the lips was similar to the one described at Bossou by Tonooka (2001). As confirmed by a combination of video with measurements of the tree holes made at the same site, leaf-sponges were used only when the diameter of the tree hole was wide enough to pass the hand or the arm and the depth not superior to the total length of the arm. We found, however, that in many tree holes wide enough to use the leaf-sponges, water-dipping sticks were used as well, suggesting that the use of one or the other tool was more of a choice than a necessity (Lapuente et al. 2016; Chapter 6). Sponges were on average constructed using a mean of 19.39 leaves ($SD = \pm 14.72$).

As for plant species used, a total of 110 sponges were analyzed, of which, 15 contained a mixture of two or more plant species (up to four) (Table 4). The species most frequently used was *Tapura fischeri*, found to make a third of the sponges, although this reflects more the abundance of this species in the understorey of the forest than selection by the chimpanzees (tested in the study of habitat plots detailed in chapter 2).



Fig. 11 Examples of leaf-sponges: one folded (left) and two chewed (right). Size is a mouthful.

Table 4. Species composition of the leaf sponges we analyzed in the laboratory of CRS.

Leaf species	Number of sponges containing the leaf species	Proportion of the total (%)
Celtis integrifolia	4	3.6
Combretum molle	3	2.7
Dialium guineense	3	2.7
Diospyros abyssinica	11	10
Drypetes floribunda	3	2.7
Drypetes gilgiana	6	5.5
Grewia sp.	12	10.9
Lannea welwitschii	2	1.8
Malacantha alnifolia	2	1.8
Rhabdophyllum affine	1	0.9
Saba senegalensis	1	0.9
Tapura fischeri	36	32.7
Unidentified	13	11.8
Uvaria chamae	8	7.3
Zahna golungensis	5	4.5

7.3.11 Leaf sponge to drink clay-filled water from salt licks

A special case of leaf-sponge use in Comoé was the use of sponges to suck water from clay-filled ponds formed after storms in salt licks, most probably to obtain the salts dissolved in the water. We found six sponges used for this purpose and obtained two videos of the behavior. This is the only case in which we found chimpanzees using sponges to acquire water not stored in trees. The same behavior was observed in

Budongo, Uganda (Reynolds et al. 2015) where the authors suggested that clay was consumed for minerals and also for detoxification.



Fig. 12 Video-capture of an adolescent chimpanzee from the Achean community using a sponge to drink clay-filled water from a drying salt lick.

7.3.12 Fruit cracking hammers and anvils

Like the digging tools, we found only indirect signs that suggest the use of stone hammers to crack open hard-shelled fruits, such as those of *Afraegle paniculata* and *Strychnos spinosa*. At eight sites, we found 12 stones ranging from 500 to 2000 grams encrusted with dirt (possibly smears from the chimpanzees' hands), along with the remains of smashed fruit shells attached, beside cracked fruits. In Figure 6 (next page), we can see the remains of one of these possible hammer stones, in this case a schist. The hard shell of the fruit is visible in the upper left corner and some seeds are still attached to the stone. Traces of wear from use are visible on the edges of the stone and what may be dirt smears from a chimpanzee hand can be seen in the center. The tool was close to large rocks of the same kind of stone, used as anvils, as denoted by the impact marks from striking and the depressions used as pits for the placement of fruits. The area was full of cracked hard shells of the fruit with traces of impacts at the eight sites. We heard hammering sounds in four occasions, but these could not be distinguished from sounds produced by pounding the fruit against an anvil.

We could not confirm the use of the stones as hammers through camera traps, but we did record videos of the chimpanzees using larger stones or roots as anvils to pound open the fruits. In the majority of definitions of nonhuman too-use, anvils are not considered to be tools as they are attached to a substrate. (discussed below). As we also discuss below, smaller stones may have been used occasionally as anvils, although this is improbable, as larger, more appropriate anvil stones were found nearby and the weathered edges of the stones suggested that they have been used for hitting in different angles. We need further research to confirm the use of stone hammers as tools in Comoé.



Fig. 13 A Schist stone apparently used as hammer to crack the hard shell of a fruit of *Strychnos spinosa*, a small tree of the family of *Rutaceae*. The photo was taken without touching the stone, which remained in its original position.



Fig. 14 Video-capture of a chimpanzee juvenile from the Trojan community pounding open an *Afraegle paniculata* fruit on a laterite stone anvil. The young chimpanzee needed more than thirty hits to open the fruit. Adults could achieve the task in two or three hits. In this case, the anvil stone is clearly attached to the substrate.

7.3.13 Accumulative Stone Throwing

We used here the term 'accumulative stone-throwing' (AST), which was coined by Kühl et al. (2016) for the behavior of hitting trees with stones, as part of a display frequently by adult males. At Comoé, however, we found few examples of stone accumulation around tree buttresses and none of accumulation inside hollow trees: the stones were used more frequently to bang against buttresses, instead of being thrown, as suggested through direct observation (3 events) and sound of other 7 events.. The 69 stones found at 33 sites did not have many characteristics in common. They were schists, quartzites or lateritic stones, depending on the availability in the area. The stones always had traces of recent use, such as weathered edges from the hits, stains of sap or remains of bark attached and were only counted if they were found close to a tree with clear traces of hits. We found many more stones that apparently had been used further in the past, since all traces were dry and old, but we did not consider these older stones for this study, only the recently used ones. Stones ranged from 120 to 11800 grams, although we also recorded a video in which an adult male threw a tiny pebble to the tree (less than 30 grams). On twelve occasions, we found stones that had been placed by the chimpanzees into holes on fallen trunks or behind other trees, with respect to the target tree, suggesting the will to hide them from their peers (figure 15). The maximum accumulation of used stones that we found under one tree was 16. We recorded on film an adult male of the Mont Tingui community throwing a large schist stone against the buttress of a Cola cordifolia tree. The stone, weighing more than 11000 grams, may have been carried from a river bed more than 500 m away, since there were no other stones on the forest floor in that area. The stone was thrown several times per day against the tree and left beside it (Figure 16)



Fig. 15. A quartzite hidden into a hole on a fallen tree. Chimpanzees of Achean community apparently placed this stone into the hole in the log (left) close to a living tree which had strike marks. To the right, the same stone is shown taken out of the hole by the author, showing clear recent traces of hitting (clear spot in the upper part, showing the broken quartzite color).



Fig. 16 Video-capture of an adult male of the Mont Tingui community throwing a large schist stone against the buttress of a *Cola cordifolia* tree which has marks of dozens of strikes.

7.3.14 Drumming

Although not strictly tool-use, the Comoé chimpanzees, like in other populations across Africa, regularly used tree buttress for their drumming displays. This consisted of repeatedly hitting the buttresses of large trees with their hands and/or feet to make noise as part of a ritualized display. It was almost always performed by adult males. Our camera traps recorded 45 events of drumming, involving adult males of the Achean, Trojan and Odyssey communities. While the males of Achean and Odyssey communities used either hands or feet to hit the buttresses, the four males of Trojan community only used feet (14 videos). We also directly witnessed three events of drumming. We recorded one video of a mixed party in which juveniles drummed lightly (play-drummed?) on a buttress that was in the way of the party's path. During this incident, one of the females also struck the tree with her foot (to speculate: was she perhaps demonstrating the behavior to the infants?). Interestingly, regular drumming has the same ritual phases as the accumulative stone throwing: the warming-up phase, when the chimpanzee rocks his body back and forth while emitting a deep pant-hoot call, frequently piloerecting (erecting the body hair), then jumps towards the buttress and hits it with hands and/or feet and finally leaps away, usually screaming. The AST phases are the same, but instead of using hands, the chimpanzee throws a rock against the buttress.

7.3.15 Aimed projectile throwing

Apart from the accumulative stone throwing, where stones were used in a very precise context which often led to them being accumulated beside the target tree, we recorded several instances of projectile throwing, using objects in an improvised fashion. In three cases, projectiles were thrown towards the camera trap by juveniles apparently as

part of a display (Table 5). Upon receiving no reaction from the camera, the behavior ceased. On two of these occasions, the projectile was a branch and on one it was a stone. In the latter case, the thrower was a juvenile male, who had found the stone lying on the spot. He later picked it up later and threw it again. He finally lost interest in the camera and continued foraging (Figure 13).



Fig. 17 A Video-capture of a juvenile male from the Mont Tingui community throwing a stone aimed at the camera trap.

7.3.16 Snail cracking hammer and anvilln

In June 2017, in the Aeneid community's range, we made a single indirect finding of what may have been a hammer used for cracking five African giant snails (*Achatina achatina* and *A. fullica*) in association with chimpanzee footprints. We also found 17 broken snail (*Achatina achatina* and *A. fullica*) shells accumulated around 3 laterite stone anvils, which still had fresh traces of hitting and chimpanzee footprints around.



Fig. 18 Two examples of possible stone anvils used for cracking big snails. To the left, snails were *Achatina fullica*, to the right, *A. achatina*. We can see the traces of impact in the center of the schist stone (left picture) and at the top of the laterite stone (right picture). The accumulation of shells indicates that they were probably transported to the anvil.

7.3.17 Possible absence of nut-cracking

We could not confirm the existence of nut-cracking behavior in the CNP, neither through direct observation nor video recording, although we found 12 potential sites where nuts of *Detarium senegalense* may have been cracked. These sites included three potential stone anvils (one with a potential stone hammer associated), and nine possible root anvils, three of these had potential stone hammers associated). Except for two cases associated with freshly broken *D. senegalense* nuts, the traces that we found were relatively old. We found two sites that initially looked like possible nut-cracking sites of *D. mycrocarpum* next to a chimpanzee trail in savanna, but we cannot rule out the nuts may have been cracked open by the teeth of baboons. We do not consider any of these ethoarchaeological indices sufficient to confirm the presence of this behavior in an area where it is supposed to be absent. We would need further research to confirm the potential presence of this behavior, as discussed below.



Fig. 19 One of the possible nut-cracking sites found in the CNP, close to a *Detarium* senegalense tree. At this relatively old site we found three possible schist hammers weighing between 2.4 and 3.7 kg, and a root anvil that had traces of impacts and pits.

7.3.18 Seasonality of tool-use

We pooled together the data of all the fresh tools found in the field from October 2014 to September 2019 and calculated the monthly mean number for each type of tool. Figure 20 is a representation of the data for the four most commonly-produced types of tools, HDT, WDT, ADT, as well as leaf-sponges, for which we were able to calculate monthly means. We must note, however, that we only found AFTs (not included in the figure) in the middle of the dry season (January, February) and TFTs predominantly during the first half of the wet season (May-July) although we found a few after heavy rainstorms, probably related to the termite flights which occurred then.

We can see in Figure 20 that the four types of tools were produced all year around, with some peaks and lows, that can be partially explained in relation to meteorological variables and their consequences in the availability of the resources foraged. Even if some fresh HDTs were found every month, the majority were found during the dry season (November-March), when most trees were flowering and the production of honey by all types of bees was lower. During the rainiest months (August-October) bees were observed to be much less active, suggesting that honey production was also the lowest in these months. Despite the high frequency of swarms of driver ants that we recorded every year in the rainy season, the production of ADTs was not maximum at this time of the year. On the contrary, we observed more fresh ADTS at the beginning of the dry season

(November, December), when driver ants began forming temporary underground nests, but still were active on the surface

Since both WDTs and sponges were produced to dip for the rainwater accumulated in tree holes, but we did not find a higher production of these tools in months with higher precipitation; on the contrary, we observed that the production of both types of tools decreased during the period of the highest precipitation, August-October and was higher during the dry season, November-May. We observed that during the rainiest months, water frequently accumulated in the depressions of the trees and the seasonally dry rivers were full of water, we recorded with our camera traps chimpanzees drinking directly with their mouths both from tree holes and from rivers, meaning that they did not need as many drinking tools from August to October. We found a low mean number of drinking tools in March, while it was highest in February and April (statistics on these comparisons will be provided in a future publication. We observed every year, however, that all the tree holes became dry by the second half of March, making drinking tools worthless; the chimpanzees were forced to drink from the Comoé River during this period. We observed that chimpanzees more frequently used sponges when the large tree holes were still full of water in June, July and December) while stick WDTs were increasingly used when water level in tree-holes was lower, making it more difficult to reach it with a sponge. Nevertheless, we recorded and observed chimpanzees making and using sponges and WDTs simultaneously at the same tree-hole, suggesting that there was a cultural aspect influencing the choice of WDTs even when they were not necessary. The pattern of increased rates of tool-use during the months of highest availability of the tool-foraged resources and not during the periods of food scarcity supports opportunity hypothesis. rather than necessity (Sanz & Morgan, 2013).

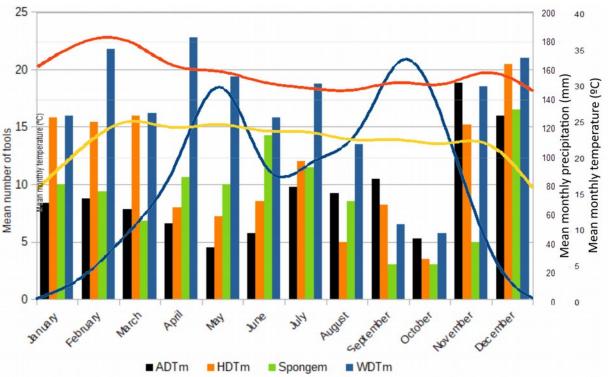


Fig. 20 The mean number of fresh ADT, HDT, WDT and sponges found monthly from October 2014 to May 2019. These numbers are compared with the mean monthly meteorological variables, precipitation (blue line) and maximum and minimum temperatures (red and yellow lines respectively). The four types of tools were found throughout the year, although their use greatly decreased during the rainiest months.

7.3.19 Tool specialization

Of the 5553 stick tools documented in the field, we took sample of 2614 tools to the laboratory in the CRS for thorough measurement. The remainder of the tools found were left untouched in the field, measured via photos of them taken beside a measuring tape. In this section, we compare the measurements of the sample stick tools, which present clear differences in length, diameter and structure, suggesting that chimpanzees made them specifically for each use.

We compared those tools that had more similarities, such as TFT with AFT or HDT with WDT, testing significance of differences with Wilcoxon U-test. We also compared the Goads with the regular ADTs, to test if these were two clearly different types of tools, used as set during the same act of insect predation. The differences between the several types of tools used for honey dipping will be the object of a separate study (Chapter 6; Lapuente et al. 2016), thus, instead of separating them into different categories here, we pooled them together in the general HDT tool type.

Table 5. Mean measurements (±SD) of the sample of different types of tools taken to the laboratory (n). Diameter was measured at the thickest point. Brush length was measured from the point were teeth marks were visible and fibers detached.

TOOL TYPE	n	Diameter (cm)	Length (cm)	Brush length (cm)
AFT	26	$0,2 \pm 0,08$	$31,57 \pm 14,89$	0
ADT	558	$0,44 \pm 0,22$	$61,88 \pm 18,18$	0
Goad	18	$0,93 \pm 0,64$	$126,33 \pm 26,18$	0
HDT	1276	$0,73 \pm 0,37$	$51,39 \pm 21,41$	$3,43 \pm 11,63$
Probe	49	$0,52 \pm 0,22$	$61,04 \pm 27,05$	1
TFT	25	0.2 ± 0.06	$38,95 \pm 18,05$	0
WDT	662	$0,63 \pm 0,21$	$47,27 \pm 18,89$	$5,75 \pm 19,97$

The most similar types of tools in structure could be the HDT and the WDT, since they both frequently have brushes in their tips and are used to dip for fluids. Even though their mean total length is apparently similar, we found that they were significantly different (W = 471870, p-value = 1.302e-05) as it was their diameter (W = 5e+05, p-value = 4.809e-12). The length of the brush is clearly different, being the brush of the WDT much longer (W = 313270, p-value < 2.2e-16). This results confirm the differences found by Lapuente et al. (2016), suggesting that they are different, specialized tools.

As we explained above, the tools made to fish termites and carpenter ants are very similar in size, flexibility and materials, although only for TFT we found tools made with herbaceous materials. Even if TFTs are longer than AFT in average, we did not find a significant difference, probably due to the small sample size (W = 174, p-value = 0.05228). The same can be said about the diameter of AFT and TFT, which is almost identical (W = 166, p-value = 0.02089). and probes are very similar in diameter, although significantly different (W = 5724, p-value = 0.0007626) while their mean length is identical (W = 3465.5, p-value = 0.5879) which suggests that chimpanzees cut both types of tools to the same length probably for safety, as we discuss below.

On the other hand, tools used (possibly as a set) during the same ant-dipping context, such as the goads and the ADTs showed very clear differences. Goads averaged more than twice as the length of ADTs W = 9697, p-value = 7.995e-13) and were more than twice as thick as the regular ADTs (W = 8569.5, p-value = 1.646e-08). This suggests that goads are specialized tools probably complementing the ADTs as part of a tool set.



Fig. 21 A selection of stick and stone tools used by the Comoé chimpanzees with the author (1.70 m) as a size reference. Stones used in AST are above the author's head. rTo the author's right are four goads, and then, on the upper right side, ADTs, below, TFTs, lower left side HDTs, Right from the goads, four probes and the rest are HDTs and WDTs.

Table 6. Number of studied communities in which we observed direct or indirect evidence of the different tool—use or percussive technology-. We included sex/age classes of individuals filmed by camera traps performing the behaviors and number of communities (in parenthesis) in which the behavior has been confirmed to be customary, habitual or present.

BEHAVIOR	Communities with direct and/or indirect observations of behavior (n)	Communities behavior recorded in camera traps videos (n)	Sex/age classes	Degree of expression of the behavior
Water dipping tool	7	6	All	C (6)
Leaf sponge in tree hole	7	6	All	C (6)
Leaf sponge in salt lick	1	1	Adults and Adolescents	+(1)
Honey dipping (Meliponini)	6	4	All	C (4)
Honey dipping (Apis mellifera)	2	1	Adolescents	H (1)
Investigatory probe	6	3	All	C (3)
Ant dipping	6	3	All	C (3)
Termite fishing	4	2	All	C (2)
Ant fishing	2	1	Adult males and juveniles	H (1)
Accumulative Stone throwing	7	2	Adult males	C (2)
Drumming	7	4	Adult males*	C (7)
Aimed throwing (stone or branch)	1	2	Juveniles	H (2)
Fruit pounding (stone or root anvil)	4	2	All	C (2)
Fruit pounding (stone hammer + stone or root anvil)	2	0	Unknown**	+
Termite mound pounding (stone or root anvil)	: 5	0	Unknown**	+
Snail cracking (stone anvil and hammer)	4	0	Unknown**	+
Termite digging with stick tool	2	0	Unknown**	+

(C) customary, for which the behavior occurs in all or most able-bodied members of at least one age-sex class (such as adult males); (H) habitual, for which the behavior is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (+) present, for which the behavior is neither customary nor habitual but is clearly identified". Numbers in parentheses correspond to the number of communities in which the behavior has been confirmed to have those levels of expression.

Regular drumming (*) was usually performed only by adult males, with one exceptional case described in Section 7.3.14. (**) We recorded fruit pounding only against anvils with no hammer. We only found indirect evidence for hammer use, snail and termite mound pounding and termite digging, thus, we do not know which sex/age classes might have carried out these potential behavior.

7.4 DISCUSSION

When we started this research, the only thing known about the tool-use behavior of the Comoé chimpanzees, was that Boesch et al. (1994) found no signs of nut-cracking in the 30 kilometers of transects they covered in 1991. We now can give a full description of multiple tool-use behaviors, some of them described for the first time in any chimpanzee population and many of them shared by multiple chimpanzee communities in Comoé.

As expected, we found that, like chimpanzees in many other study sites, the Comoé population has an extensive tool-use repertoire, with at least thirteen different tool-use behaviors: We confirmed with videos of camera traps, direct observations and indirect signs water dipping behavior using specialized stick tools, dipping for driver ants, fishing for Camponotus sp. and Crematogaster sp. ants, termite fishing of Macrotermes and Odontotermes, the use of stick tools to dip for honey, the use of leaf-sponges to drink from tree-holes and the use of leaf-sponges to drink clay-filled water from salt-licks. We additionally found 74 stick tools that we classified as investigatory probes, which the chimpanzees used to inspect holes and objects and, on two occasions, apparently used sticks to dig the base of *Cubitermes sp.* termite mounds (based on indirect signs). We also recorded Comoé chimpanzees on video hitting stones against buttresses (AST behavior) and engaging in aimed stone-throwing. They may have used stone or root anvils to pound open hard-shelled fruits, Cubitermes mounds and Achatina snails (which has also been described for the Bili-Uéré region (Hicks et al. 2019a), possibly on occasion using hammers to crack the fruits and the snails, although as at Bili-Uere, we only found indirect signs for these behaviors. On the contrary, we did confirm in video the percussive technology of pounding open fruits of Afraegle paniculata on stone and root anvils. The number of different tools could further be subdivided if we consider that they used tool sets for honey-dipping, where we could provisionally distinguish perforators, probes, swabs and collectors and they also used sequentially two types of tools for ant-dipping with a longer and thicker goad to agitate the ants and then shorter sticks to dip them, as partially confirmed by videos in both cases and by multiple indirect signs. Sequential tool use for ant dipping has been described before for Goualogo, Congo (Sanz et al. 2010), although in that case the first tool was an enlarger, used to make the hole bigger before the use of the regular ADT. A similar tool set has also been described at Seringbara, Guinea, based exclusively on the interpretation of indirect signs via etho-archaeological methods. In this latter case, the thicker tools were interpreted as having been digging sticks, used to excavate the ant nest before using the wands for ant dipping (Koops et al. 2014). This interpretation was based on the remains of dirt attached at the tip of the tool and blunted

fibers, which we did not find on our goads. Further research on these tools is required before we can confirm that they are part of a tool set.

On the other hand, tools used for the extraction of honey in Comoé seem to be part of a tool set, similar to those described at Gashaka (Fowler et al. 2011), Loango, Gabon (2009) or Bili (Hicks et al. 2019). Although in other regions of Africa, stingless bees protect their beehives with very solid walls or build them underground, we never found any such hives. Meliponine bees at Comoé make nests consisting of simple wax walls in the cracks and holes of trees, making it easy for the chimpanzees to pierce them using relatively thin stick tools (Soro et al. 2019, personal observation). The probes that they use to test the depth of the honey chambers are not different from investigatory probes used for other purposes, but in the context of the honey extraction, they are part of a tool set, as the collectors and swabs used afterwards. This sequential use of specialized tools to achieve a final goal requires more cognitive complexity (Boesch et al. 2009).

Contrary to our expectations, we failed to find definitive evidence of nut-cracking with hammers at Comoé, although we found possible indirect evidence for it. Thus we are unable to expand the nut-cracking behavioral realm to Comoé, although we cannot rule it out either. This accords with the results of Boesch et al. (1994). After five years of study, we neither recorded the behavior with the camera-traps nor we observed it directly. We found only twelve possible nut-cracking sites and only two of them had recent traces of a few cracked *Detarium senegalense* nuts. The nuts of this species split open naturally when dry, but this is a clean straight split (Boesch & Boesch, 1990). The nuts that we found were forcefully cracked when still wet, leaving fracture edges that were identical to those *D*. senegalense nuts cracked by chimpanzees in Taï (personal observation). We could think that some of the sympatric animals of Comoé chimpanzees could crack the hard nuts with their teeth when still wet, for instance, giant hogs or wart hogs, but we did not find footprints or any other traces of these animals in proximity of the cracked nuts. This nut species is only rarely cracked at Taï, compared to other nuts species (Boesch & Boesch, 1990), and it could be only rarely cracked at Comoé as well. In the case that Comoé chimpanzees would be cracking Detarium senegalense, they could also do it occasionally and not habitually. Although we know similar tool-use sites from nut-cracking areas and indirect signs have been used to describe tool-uses in different sites across Africa (Bermejo et al. 1989, McGrew et al. 2003, Hernandez-Aguilar et al. 2007, Gasperik & Pruetz, 2011) we decided that further research is needed to confirm this behavior in Comoé. Thus, our data did not support our second hypothesis.

With respect to our third hypothesis (Considering that the ecological conditions of Comoé are more demanding than those of the rainforest, with intense seasonal droughts and more extreme temperatures, we expect to find some tool-behaviors that help the chimpanzees to survive in these harder conditions of Comoé) we found that, although the Comoé chimpanzees produce their most frequently-used tools (ADT, HDT, WDT and sponges) over the entire year, they produced them more frequently during the dry season and less during the late rainy season. This seasonality appeared to be related more to the availability of the resource than to the necessity of using them. Nevertheless, the Comoé

chimpanzees are the only known population of the species to produce stick WDTs with long brushes, which allow them to exploit water accumulated in narrow and deep tree-holes which are inaccessible for any other animals. This technology provides them with an exclusive advantage that helps them to obtain water when there is the highest need (Lapuente et al. 2016). We consider, thus, that our third hypothesis to be supported by our data because Comoé chimpanzees do have tool uses that help them to thrive in their dry, seasonal environment.

We measured a large sample of tools in the laboratory at CRS and found significant differences in their characteristics, indicating that Comoé chimpanzees make specialized tools, WDT, HDT, ADT, AFT, TFT, investigatory probes, goads, digging sticks, which supports our fourth hypothesis. Similar criteria to distinguish between different tool types have been applied in other sites (Sanz & Morgan, 2007, Boesch et al. 2009; Hicks et al. 2019a).

The Comoé chimpanzees, like many other populations in West Africa, pound stones against the buttresses of trees to produce resonant sounds as part of their displays. Thus they appear to be part of the Accumulative Stone Throwing tradition described by Kühl et al. (2016). The function of this behavior is not yet clear, although it likely serves a communicative purpose. Chimpanzees in Boé, Guinea-Bissau, have been found to throw stones preferentially against those trees that produced more resonant sounds, especially trees with large buttresses (Kalan et al. 2019). This may also be the case in Comoé, since chimpanzees in our study site throw stones against some of the same species, such as *Cola cordifolia*.

The Comoé chimpanzees produce a great variety of tools that helps them to survive in a seasonal and relatively unpredictable environment. This rich tool repertoire forms part of an exclusive culture, and complements other site-specific behaviors including the sustainable bark-peeling of Ceiba pentandra (see Chapter 5). The fact that most of the tool use behaviors are customary and common to several communities in the area suggest that they are part of a widespread set of traditions partially unique to the region (Whiten et al. 1999, 2001). Other parts of this repertoire, even with probable technical peculiarities, are, however, shared with other West African populations (i.e. AST, honey dipping, ant dipping, termite fishing especially with those of savanna-woodland areas. AST has been found in savanna dominated areas, except for Mount Nimba, in Liberia (Kühl et al. 2016) while nut-cracking has been found so far exclusively in forest dominated areas (Boesch et al. 1994), curiously, both behaviors are stone oriented and exclusively found in West Africa up to date. We could speculate that the West African chimpanzees are more stoneoriented than those of other areas, although the use of stones for AST or nut-cracking does not happen in all the West African populations. We need more research to try to understand why these chimpanzees use more stone tools than others. We can find similarities between the tool uses of Comoé chimpanzees and those of other comparable savanna sites, such as Mont Assirik or Fongoli, both in Senegal. Some of them, suhc as ant dipping or termite fishing are common tool uses (Pruetz, 2006, Bogart, 2009), many others are original and exclusive of each of these sites, such as the use of spears to hunt

Galagos in Fongoli and the habitual use of specialized WDTs in Comoé. More research is needed to find out if these originalities are better explained by accidental independent inventions or by more subtle environmental differences. It is extremely important to preserve this population of chimpanzees with their rich culture, not only because they are probably the only viable savanna chimpanzee population remaining in Ivory Coast, but also because their culture could help us to understand better how our own ancestors adapted to similar savanna-forest mosaics and harsh seasonal conditions..

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CHAPTER EIGHT

8 CONCLUSIONS

This dissertation sums up an important part of the work completed by the author over the past five years in the context of the Comoé Chimpanzee Conservation Project,. During this study period, my team and I have worked hard to learn all we could about the current status, distribution, ecology and behavior of the chimpanzees (Pan troglodytes verus) that live in Comoé National Park and neighboring areas. As a result of our work, partially presented in this dissertation, we confirmed that there was an important sustainable population of chimpanzees in the park, mainly inhabiting the southwest sector. We also confirmed, for the first time, that chimpanzees live permanently to the east of the Comoé River and we mapped the distribution of this population across the park. We studied the diet of these apes, finding that they were feeding mainly on fruits, both from savanna species and forest ones, but also on insect and mammal prey. Importantly, we found that they depended heavily on the cambium of *Ceiba pentandra* as a fallback food during periods of fruit scarcity. We described for the first time how the chimpanzees, advertently or inadvertently, were practicing sustainable bark-peeling of this tree. We also found that these chimpanzees make and use specialized stick tools with extra long brush tips to dip for rainwater in tree holes, a behavior that is exclusive to Comoé. We described the impressive variety of tool-use and percussive behaviors expressed by these chimpanzees, including the use of stick tools, stone tools and objects attached to the substrate to obtain resources from their environment or as part of their social displays.

When we started our work in October 2014, very little was known about these chimpanzees, apart from their presence in the park (GTZ, 1979, Hoppe-Dominik, 1991, Marchesi et al. 1995, Fischer et al. 1999, 2002, Campbell et al. 2008). Even that presence itself had been challenged in the reports of the last surveys, carried out prior to our arrival (WCF, 2009, 2010, 2012). During our rapid survey of 2013 for MPI-EVAN, our hopes had risen that we might still find a modest chimpanzee population surviving in the park (Lapuente et al., unpublished data). A few weeks after we started our work in 2014, we had confirmed the presence of a significant population and a some months later, we had enough data to tell us that this population was sustainable. The data presented in this dissertation provide the most precise population estimate ever obtained for the Comoé chimpanzees. We estimated via nest counts a minimum count of 127 weaned chimpanzees (92-176, 95 % CI) in our main 900 km² study area in the southwest of the park. To this figure, we must add the 22.76 % (estimated from camera trap video data) of infant chimpanzees who do not yet make nests, raising the estimation for this area to around 164. Given that we also found that an additional population lives at the center of the park (although at low density) and that at least one community survives in the contiguous Special Zone of Biodiversity of Mont Tingui, the total of the continuous population may represent over 200 chimpanzees. This probably makes the chimpanzee population of Comoé the second largest population remaining in Ivory Coast, following that of Taï Forest. It is also the only sustainable population of savanna chimpanzees remaining in the country, which makes them a special priority for conservation.

Our extensive transect and recce surveys has allowed us to construct the most precise distribution map of the Comoé chimpanzees to date. For the first time, we confirmed the presence of a chimpanzee community living to the east of Comoé River. The home range of this small community (10 weaned chimpanzees estimated by nest counts) which we named Aeneid, was located exclusively to the east of this river, which acts as a

barrier between them and the other three communities to the north and west: Odyssey, Achean and Trojan. We also found more chimpanzee nests and dung to the east of Comoé River at the center of the park, but we cannot yet confirm if this is a stable resident population, since it is possible for the chimpanzees to walk across the river at many points during the dry season. Our recce walks to the northwestern and eastern extremes of the park, revealed no traces of the chimpanzees. More recently, during a survey for large carnivores, we also collected additional data from these areas (which have not been included in this dissertation) confirming that, despite the availability of potential habitat, no signs of chimpanzees have been found in the parks' northern and far eastern sectors.. Sadly this probably means that a population that formerly inhabited the northwestern sector, specifically in the area of Kolonkoko (Marchesi et al. 1995, Campbell et al. 2008), has probably been wiped out during the past 15 years. We have reasons to suspect that the chimpanzees of Kolonkoko were victimes mainly of the pet trade by foreigners working in that area, but this is still under investigation.

Although we found some structural differences between the forests of the northwestern and eastern sectors of the CNP and those inhabited by chimpanzees in the southwest, like the absence or rarity of six of the chimpanzee's preferred fruit trees, but we have so far conducted no detailed research on potential ecological factors that might limit the distribution of chimpanzees in the park. We hope to investigate this further in the future. We found that the Comoé chimpanzees use mainly the forested habitats of the park, which cover only around the 9 % of the CNP. The southwest area, where our studies were centered and where most of the remaining population of chimpanzee still thrives, has about 13% forest cover. Only a very small proportion of nests was found in savanna (0.3 %). We found traces of the chimpanzees in savanna mainly where they crossed from one forest patch to the next, which we confirmed using camera traps and direct observations. Additionally, the fact that only 12 % of the dung samples analyzed contained savanna food items, with the seeds of only six savanna species out of the 72 food items confirmed in the chimpanzees' diet, suggests that the grassland and woodland mainly serves as a place of travel and an occasional source of food. Given, however, that these chimpanzees cover long distances walking through their home-ranges daily (we confirmed at least 12 km through camera trap videos), and that an estimate 60 % of this walking period is through savanna, they appear to spend a significant part of their time in or near this habitat.

Among the 72 different food items that we confirmed to make up the diet of pthe Comoé chimpanzees, we found 58 plant species, four ant species, two or possibly three termite species, honey from both sting-less bees and honeybees and some other insects, such as beetle larvae. Additionally, they hunted at least three monkey species, probably two more mammal species and a frog, they also likely pounded open and consumed snails of the genus *Achatina*. We compared these results with the diet of chimpanzees in other study sites and we found that we confirmed a number of food items comparable to that of long term savanna sites such as Fongoli (Senegal) or Ugalla (Tanzania). We have also tentatively confirmed the hypothesis that savanna chimpanzees cover a smaller list of food items than forest chimpanzees, although further years of study will confirm this.

One of the characteristic ingredients of the diet of these chimpanzees is the cambium of *Ceiba pentandra*, which they exploit in a sustainable way. Effectively, they peel the bark of the spine of the buttresses of trees of this species, exposing the cambium underneath, which they. They never peel the bark around the bole of the tree, allowing its complete recovery in just two years, which makes the exploitation sustainable, since they peel repeatedly the same trees for many years, without killing them or obviously hampering their growth. The apes consume the cambium only during the late rainy season, when there is a great scarcity of fruits. Thus, we suggested that this resource acts

as a fallback food for Comoé chimpanzees. This is a novel behavior that is customary to several of the chimpanzee communities in Comoé; only during the final phases of the writing of this dissertation (November 2019) was the behavior observed as well at Fongoli, another savanna site in Senegal, but it is apparently a much more rare behavior there (Jill Pruetz, personal communication).

Another behavior that is exclusive to the Comoé chimpanzee and which we have described for the first time in our 2016 paper (Lapuente et al. 2016) and in this dissertation is the making and use of specialized stick tools to drink water from tree holes... The chimpanzees produce a very long brush at the tip of these tools that helps them to obtain water even from very deep and/or narrow tree holes, out of the reach of other animals. These chimpanzees also use leaf-sponges to drink water, as do the chimpanzees at most other study sites, and they used sponges to drink clayish water from salt-licks, perhaps in an attempt to obtain salts diluted in the water. They also used sometimes sponges and brush sticks simultaneously at the same tree hole, suggesting that the use of the water dipping sticks is a choice. Although a few anecdotal cases of using herb stems and twigs to access water have been described before in Tanzania (Wrangham et al. 1994, Matsusaka et al. 2006), the behavior at Comoé is customary or habitual in multiple communities and appears to be an enduring component of their culture. These tools were found to be similar in structure to the brush-tipped honey dipping tools that they also produce, but significantly different in dimensions. This suggests that an extrapolation of the fluid-dipping behavior from honey to water may explain the origin of this particular technology. In this case it may represent a case of cumulative culture.

We also described in this dissertation the full set of tool-use and percussive technology behaviors that we have found in the Comoé chimpanzees to date. They use a variety of stick and stone tools both for foraging and social displays. Among the stick tools that we described are ones used for ant-fishing(*Camponotus maculaturs, Crematogaster sp.*), termite-fishing tools (*Macrotermes subhyalinus* and *Odontotermes majus*) and ant-dipping (*Dorylus burmeisteri*); for the latter, the chimpanzees appear to have devised a newly-described type pf tool used to poke the driver ants, which we have termed a goad. The goad seems to be part of tool set. Tools used to forage on honey, mainly that of stingless bees (*Meliponini*) and occasionally of honey-bees (*Apis mellifera*), include tool-sets of up to four different types of tools: perforators, probes, collectors and swabs. Their tool repertoire also includes the above-mentioned water dipping tools and leaf sponges.

In addition to stick and leaf tools, the Comoé chimpanzees used stones as tools, like a number of other populations of Western chimpanzees, they frequently pounded or hurled stones against trees. This behavior, described as Accumulative Stone Throwing by Kühl et al. (2016), appears to be a crucial part of the male display, alternative to rhythmic drumming sequences against tree buttresses. The Comoé chimpanzees practiced aimed throwing of stones and branches, as confirmed by camera traps for juveniles. Indirect evidence indicates that they also probably use stone hammers to crack open hard-shelled fruits and giant African snails (genus *Achatina*), although this has yet to be confimed. Likewise, we could not confirm the cracking of nuts of *Detarium senegalense* with hammers. Percussive technology is definitely present, with the chimpanzees pounding open hard-shelled fruits against root or stone anvils (confirmed through camera trap videos) and likely *Achatina* snails and d termite mounds of the genus *Cubitermes* (as seen at Bili-Uéré (Hicks et al. 2019a).

The great variety of tool uses of Comoé chimpanzees is part of a rich culture with some exclusive behaviors that helps them to thrive in the harsh seasonal conditions of Comoé. We opened with this dissertation the path for a deeper knowledge of the tool-use and its ecological importance in Comoé, but much is left to study. As we slowly progress in

the habituation process of one of the groups of these chimpanzees, we realize that there are many aspects of tool-use and other behaviors that need further research. Following the chimpanzees during their daily activities will allow us to observe many unpredictable behaviors that the chimpanzees do not complete in a particular spot or are done only occasionally. This is another important research line that is open for the future.

As a product of the work presented in this dissertation, we have accumulated a fundamental knowledge about the status, distribution, ecology and behavior of Comoé chimpanzees. We have established the base for future more detailed research that should be carried out also by new students. In addition to aiding our understanding of behavioral diversity in another population of our close relative *Pan troglodytes verus*, our research has provided population assessment tools, essential for the conservation of this population. We have created a protocol that can be used to monitor the status of chimpanzees here and in nearby regions. Using periodical surveys, we have provided OIPR information about the movements of poachers and the entry routes for illegal activities into our study area: poaching, gold mining and fishing, that should be better controlled by authorities in the future. We have installed a permanent research presence in the area, made up of rotating teams of local assistants, researchers and volunteers, which we hope will prevent poachers from coming close to the chimpanzees. Our survey system will allow us to continue working within the home-ranges of several chimpanzee communities every month. We have planned the next steps for the maintenance of a long term research and conservation project, including the installation of a strict health protocol to prevent the transmission of diseases to the apes as they become more habituated to humans. Our steadily increasing knowledge about the ecology, habitat use, movements and behavior of these chimpanzees can be directly applied to the conservation and management of this population living in the quite particular environmental conditions of Comoé.

By preserving this population of chimpanzees, which shares some behaviors with nearby chimpanzee populations but has also developed its own unique traditions to deal with the seasonal water and food scarcity, we will not only contribute to the conservation of this subspecies, the most threatened one (critically endangered, CR, IUCN), we would also preserve their culture. By preserving enough habitat to support their large home ranges, we will at the same time be protecting many other sympatric animals, such as elephants, leopards, golden cats, white-thighed colobus, white-naped mangabeys, and black-bellied pangolins. We cannot afford to lose such an invaluable opportunity to conserve and study these chimpanzees, who likely inhabit a similar habitat to that of our own ancestors, and thus have so much to teach us about our own species' place in Nature,



Fig. 1 Adult male Jason of the Argonaut community holding the rearguard position while crossing the savanna with a mixed party, a typical defensive behavior shown by adult males when escorting a group. This group of chimpanzees was crossing from a forest island where they had slept the night before to move into a patch of gallery forest where they would spend the day foraging. Jason is looking backwards, as if he is considering the place they just they left behind, before venturing towards the group's next destination.

APENDIX I

FILES WITH ALL THE IDENTIFIED CHIMPANZEES IN THE MOST STUDIED COMMUNITIES

These files contain the images and information about all of the individual Comoé chimpanzees which we have positively identified. The communities may be larger, as estimated from nest counts. Some individuals may remain unidentified for a number of reasons, i.e. they could resemble other identified individuals, they may be shy, or they could spend more time lo in marginal areas of their home ranges. Despite this remaining uncertainty, after five years of work and 2621 videos recorded, we can assume that the main structure and most representative individuals of every community are included in these files.

AENEID COMMUNITY

This is the smallest community at Comoé, which has its home range to the east of Comoé River. After an intensive sampling between November 2015 and April 2017, using up to 40 cameras to survey them, we were unable to record more than 80 videos and we could identify only five individuals, including the adult male Aeneas and two mothers with their dependent offspring. The high poaching pressure in their range, the proximity of the Kakpin Village n and the easy access of humans into the area via a road crossing it may have reduced this community to its present size. It was unlikely, however, to have ever been large, given that the villagers thought that chimpanzees did not live east of Comoé River and only one male chimpanzee was seen once in the area by researchers prior to our work (Fischer et al. 1999).

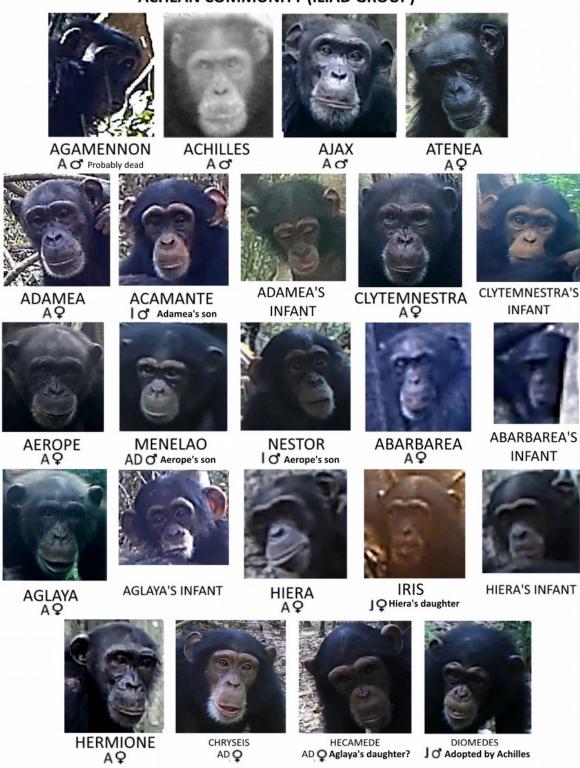
AENEID GROUP



ACHEAN COMMUNITY

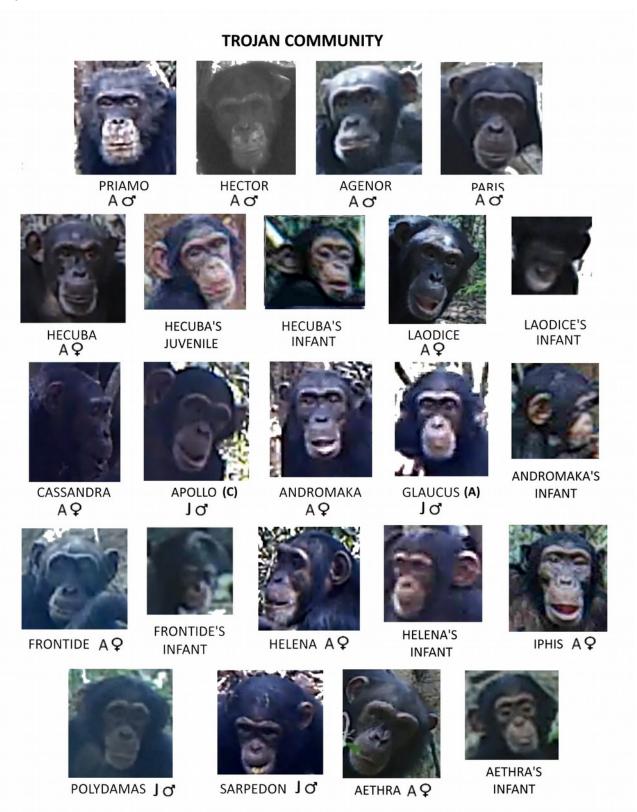
When we began our work, we mistakenly thought that the Achaens and the Trojans formed a single community, but later confirmed they were two. One adult male from this community, Agamenon, is probably dead, as we stopped recording him in 2015. Adult male Ajax was the alpha male ever since. Adult females Adamea and Aerope had new infants by 2019 which have not been included here. This is the most recorded community, with 1430 videos, due to their calm and curious behavior.

ACHEAN COMMUNITY (ILIAD GROUP)



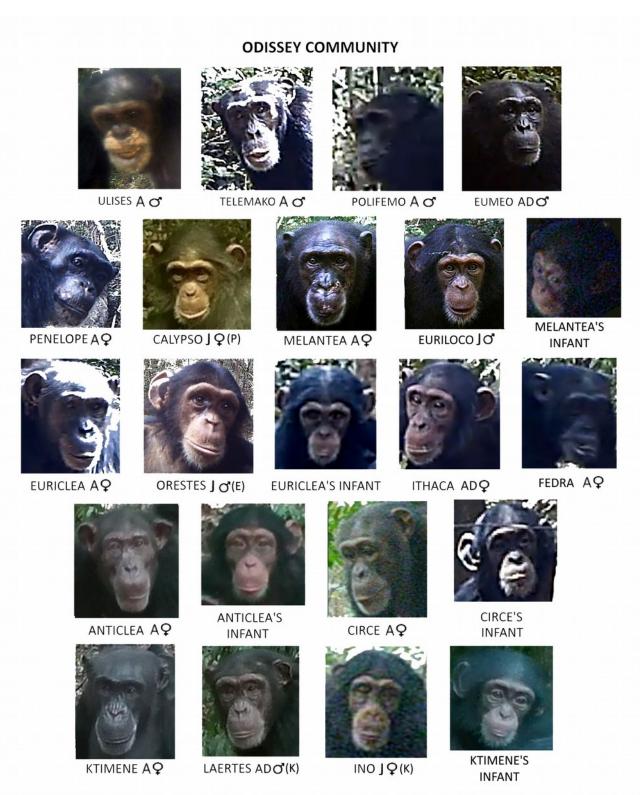
TROJAN COMMUNITY

Formerly considered to be part of the same community as the Achean, we know now that they have distinct ranges with no overlap. This is the community with the largest number of adult males (except for less studied Argonaut one). Priamo was the alpha until 2018, when Paris took over. Recording this community has proved more challenging, we only have 314 videos.



ODYSSEY COMMUNITY

This is the original community we focused on during our study. New infants have recently been born to Euriclea and Anticlea. Adult males Ullyses and Telemako have not been recorded since 2016, but they may have been peripheralized when Polifemo took over as alpha male in that year. We recorded 609 videos, so far.



ARGONAUT COMMUNITY

This community has been less intensely studied than the previous ones, with only one week per month of surveys during the dry season and three cameras covering some parts of their large long home range. We have now managed to identify at least 34 individuals, including four adult males, but the community is probably larger. We have recorded 101 videos by now.



Some chimpanzees of the Argonaut community recorded on May 2018. Individuals in the background are water-dipping with stick tools.

THEOGONY COMMUNITY

This is one of the least-known communities and it is probably smaller than the Achean, Trojan and Odyssey communities. They inhabit the largest forest patch in the CNP, big enough to hold perhaps two communities of forest chimpanzees. The close proximity of the villages of Amaradougou and Gorowi and the high poaching pressure in this area, however, leads to these chimpanzees being extremely shy and may have reduced their numbers. Nevertheless, we managed to record 27 videos using just four cameras during the dry season. We have identified 16 individuals, including three adult males.



A small group of chimpanzees of the Theogony community startled by the camera trap. These chimpanzees are shy, interacting with the cameras less frequently than others and being less predictable in their behavior and movements, due to the great extension of the forest in which they live..

MONT TINGUI

We do not know yet if these chimpanzees belong to one or more communities. We began studying them only in 2018, mainly during the dry season. We have recorded at least four different adult males and several mothers with offspring. Like the Theogony community, they are quite shy, likely due to the frequent presence in the area of poachers, gold miners and cattle herders. The latter are also destroying their habitat by burning the gallery forest in the dry season to produce pasture for their cattle. All of these factors make these chimpanzees more difficult to record. By now, we have obtained 60 videos from four camera traps.



Mont Tingui chimpanzees. An adult male is staring at the camera trap with a juvenile in the background. These chimpanzees are spread out in large patches of gallery forests and may form several communities, although a large part of their former range has been seriously disturbed by human activities and the chimpanzees appear to have deserted it.

APPENDIX II

List of behaviors detected in the different known chimpanzee communities

(Achean, Trojan, Odyssey, Aeneid, Theogony, Argonaut) and less studied populations of Comoé (Mont Tingui, to the west, out of the park and Gawi, in the center of the park). Detailing the confirmed degree of expression of the behavior (C = customary, H = habitual, + = present, - = not yet found) and the method of confirmation (D = direct observation, I = indirect signs, V = video from camera-trap).

BEHAVIOR	Achean	Trojan	Odyssey	Aeneid	Theogon y	Argonaut	Mont Tingui	Gawi
Water-dipping tool	C (D/I/V)	C (D/I/V)	C (D/I/V)	C (I/V)	C (I/V)	C (I/V)	+ (I)	-
Leaf-sponge (water from tree hole) Leaf-sponge	C (D/I/V)	C (D/I/V)	C (I/V)	C (I/V)	C (I/V)	C (I/V)	+ (I)	-
(clayish water from salt-lick)	+ (I/V)	-	-	-	-	-	-	-
Honey-dipping tool (Meliponini)	C (I/V)	C (I/V)	C (I/V)	C (I/V)	+ (I)	+ (I)	-	-
Honey-dipping tool (Apis mellifera)	+ (I/V)	-	+ (I)	-	-	-	-	-
Ant-dipping tool	C (D/I/V)	C (I/V)	C (D/I/V)	C (I/V)	+ (I)	+ (I)	-	-
Termite-fishing tool	H (D/I/V)	+ (I)	H (I/V)	-	-	-	-	-
Ant-fishing tool	H (I/V)	-	+ (I)	-	-	-	-	-
Accumulative stone throwing	+ (I)	+ (I)	+ (I/V)	+ (I)	+ (I)	+ (I)	H (I/V)	-
Buttress drumming*	C (D/I/V)	C (I/V)	C (I/V)	+ (I)	+ (I)	+ (I)	+ (I)	-
Aimed throwing (stone or branch)	+ (V)	-	+ (V)	-	-	-	+ (V)	-
Fruit pounding (stone or root anvil) Snail pounding	+ (I)	C (I/V)	+ (I)	+ (I)	+ (I)	+ (I)	H (I/V)	-
(stone hammer + stone or root anvil) Termite mound	-	-	+ (I)	+ (I)	-	-	-	-
pounding (stone or root anvil)	+ (I)	+ (I)	+ (I)	+ (I)	+ (I)	-	-	-
Ceiba bark-peeling Ground nest	C (D/I/V) + (I)	C (I/V) -	C (I/V) + (I)	C (I/V)	+ (I) -	+ (I) + (I)	+ (I) -	+ (I) -

^{*} In the case of buttress drumming, we marked as indirect observation (I) the unmistakable sound produced by this behavior.

APPENDIX III

FIELD WORK PHOTOS OF THE COMOÉ CHIMPANZEE CONSERVATION PROJECT



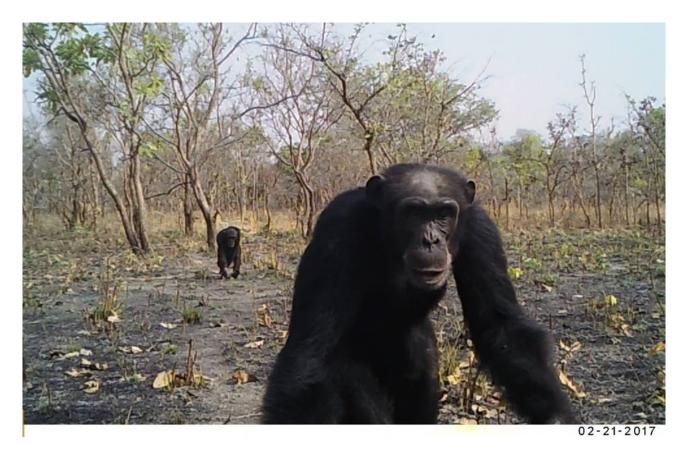
The original CCCP field team in 2014, from left to right: Ibrahim Kouamé, Juan Lapuente and Paco Kouamé.



Greeting the traditional authorities of Kakpin, the village from which we hired our local project assistants.



The field team in April 2015, with the first Master's student Aymeline Eveno. From left to right, Ibrahim, Aymeline, Juan and Paco.



Adult male Ajax and adult female Hermione, from the Achean community, cross the savanna some weeks after the setting of fires by humans, in February 2017.



Training course for the OIPR rangers, demanded by the OIPR itself, at the CRS on identification of local fauna.



Buffaloes moving through the in savanna woodland during the rainy season. The Comoé buffaloes are mostly hybrids, presenting mixed characteristics of the forest (*Syncerus caffer nana*) and savanna (*Syncerus caffer brachyceros*) subspecies.



The field team in November 2015, from left to right: Edouard, Ibrahim, Juan, Paco and Arouna.



The juvenile male Orestes, from the Odyssey community investigates the camera trap using a water dipping tool that he was carrying around.



A training course for the OIPR rangers at the CRS, on the use of camera traps.



Students Anna Hilbert and Shawn Jensen Reed cross the Comoé River following assistant Moussa Ouattara at the end of the 2016 dry season. River can be was much lower.



A group of roan antelopes (Hippotragus equinus) in the savanna near the Iringou River.



Heading northwards through the park in a CRS car. It took us three days to cross the park from south to the north due to the terrible state of the abandoned roads. We used this trip to do rapid recce surveys in the northwest looking for signs of chimpanzees in May 2016.



The team crossing the savanna following the bushfires of January 2017, heading to Camp Nord. From left to right, Sylvain, Paco, Kuma, Ibrahim, Juan.



The author arriving at the CRS with equipment provided by MPI-EVAN. Prof. Linsenmair and Lakado welcome the new arrival.



The field team at the beginning of 2016. Left to right: Sylvain, Paco, Aurelie, Moussa, Juan, Ibrahim, Danielle, Marion, Arouna



Forest elephants (*Loxodonta cyclotis*) drinking from the same tree-hole used by the chimpanzees to dip for water.



The team crossing the Comoé River during the early rainy season of 2018, Moussa holds onto the rope while Peter, Sylvain and Paco sit in the raft.



Sunset over Mount Daliego (Mont Chimpanzé), within the home range of the Odyssey community. This is the only mountain worth of that name in our main study area.



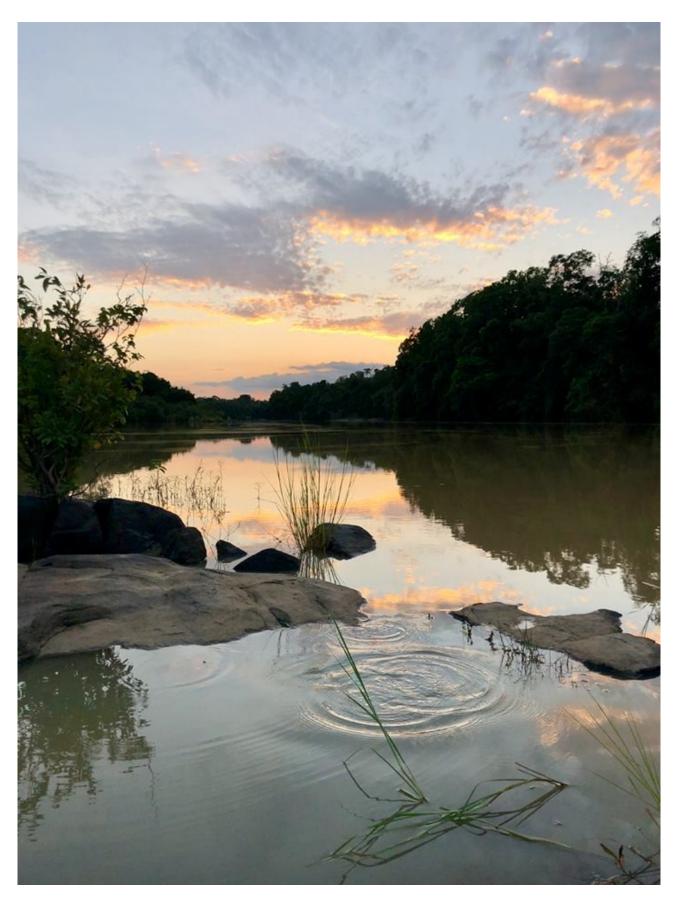
Adult female Melantea, from the Odyssey community, drinks water from an extremely narrow tree-hole using a WDT, while her son Euriloco follows her example.



Some of the research team members in 2017. From left to right, Sylvain, Paco, Juan, Angèle, Prof. Linsenmair, Arouna, Ibrahim and Sara.



A leopard (*Panthera pardus*) recorded by one of our camera traps at one of the most frequently used water dipping sites of the chimpanzees.



Sunset over the Comoé River next to the CRS.



The research team at the beginning of 2018. Standing, from left to right, students Kavel and Didier, assistants Arouna, Paco, Aimé, Ibrahim, students Bryndan, Isabelle, Johanna, assistant Moussa, Squatting, from left to right: student Tchynio, assistant Abou, the author, Juan, student Angèle, assistant Sylvain and student Ryhanna.



Assistants Ibrahim and Paco checking one of the camera traps and changing the SD card. The author personally trained all of the assistants and students participating in the project.



Students Peter Carty and Angèle Soro crossing through the tall "elephant" grass that covered the savanna during the rainy season. Work during this time of the year was extremely demanding due to the frequent rain, the difficulty of crossing the swollen river, the tall grass and the abundant and obnoxious tsé-tsé flies.



Student Avery Maune helping to measure and classify the chimpanzee tools at the CRS.



Training course in 2017 for OIPR rangers on biomonitoring techniques, line transect surveys and data collection.



Field team members at the team end of 2016. From left to right, Moussa, Ibrahim, Angela, Juan, Arouna, Sylvain and Paco.



Hippopotamus amphibius grazing on the dry riverbed of Comoé River during the peak of the dry season of 2018.



Night life at Camp Nord with some of the students. From left to right, Johanna, Angèle, Kavel, Juan, Bryndan, Ryhanna and Isabelle.



Chimpanzees of the Achean community drinking at one of their favorite trees.



Project field assistants project learning to collect samples for genetic and isotope analysis.



The team crossing the savanna at the beginning of the rainy season in 2017.



Odyssey community: Penelope crosses a natural bridge with her daughter Calypso on her back, followed by Euriclea, carrying her son Orestes.



Research team members in April 2019. From left to right, the family of the author, Pamela Köster, Sigrid and Sofia Lapuente, the author, assistants Sylvain Kouamé and Aimé Kouamé, students Pierre Chopin, Hortense Lemerle and Josef Haisch, assistants Ibrahim Koamé and Arouna Dabila.



The author's daughters: Sigrid holds a baboon skull and Sofia holds a chimpanzee skull. They represent the potential future of research and conservation.