A Landscape Archaeological Approach to Accumulative Stone Throwing (AST) in West African Chimpanzees (*Pan troglodytes verus*)

by

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We acknowledge and respect the lək̓ʷəŋən. peoples on whose traditional territory the university stands and the Songhees, Esquimalt, and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

In Boé National Park in Guinea-Bissau, a community of wild Western chimpanzees (*Pan troglodytes verus*) has been observed engaging in a novel, potentially cultural, behaviour, accumulative stone throwing (AST). Individuals habitually throw rocks at particular trees, making AST a unique instance of primate stone tool use in a non-foraging context. Repeated throws at the same location leave conspicuous sites on the landscape; therefore, a landscape archaeological approach permits the cross-temporal study of AST trees as archaeological sites connected to human- and chimpanzee-created aspects of this shared landscape and consideration of the ways these aspects contribute to the significance of certain places to the chimpanzees. By mapping the distribution of AST sites, I determine how landscape features influence the selection of specific locations for AST. AST sites were analyzed with QGIS, using spatial mapping analysis integrating multiple sources of data including chimpanzee space-use, rock and tree surveys, proximity to rivers, chimpanzee resources, human settlements, and topographical features. The presence of food trees, in particular *Ficus exasperata* and *Parkia biglobosa*, has a significant influence on the likelihood of AST site presence. The frequency of indirect signs of chimpanzee activity was also an important predictor, indicating that AST sites are more likely to occur in the territorial core, an area of high chimpanzee use which contains an abundance of nesting sites and reliable food sources. Increasing our understanding of non-human primate behaviour through spatial archaeological approaches can inform archaeological inferences relevant for hominin evolution and the development of cultural behaviours. Given the Critically Endangered status of Western chimpanzees, studying AST may not only expand knowledge about our hominin ancestors, but also provide support for the importance of biological and cultural diversity in chimpanzee populations.

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Chapter 1

Introduction

1.1 Overview

Chimpanzees, one of our closest living relatives, have long been used as a comparative model for the evolution of human behavioural, morphological, and technological evolution (Boesch et al., 2020; Mosquera et al., 2012; Panger et al., 2002; Teleki, 1974). Unfortunately, like other great ape species, their extended life history strategies (Cardillo et al., 2005) make chimpanzees highly vulnerable to anthropogenic impacts such as habitat destruction, disease transmission and hunting (Kühl et al., 2017). Globally, chimpanzees are classified as "Endangered" in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Humle et al., 2016); of the four currently recognized subspecies—the Eastern chimpanzee (*Pan troglodytes schweinfurthii*), the Central chimpanzee, (*P. t. troglodytes*), the Nigeria-Cameroon chimpanzee (*P. t. ellioti*), and the Western chimpanzee (*P. t. verus*)—the Western chimpanzee is at the highest risk of extinction with an IUCN rating of Critically Endangered. Although widespread habitat modification in the Anthropocene threatens chimpanzee survival, they have displayed high degrees of behavioural flexibility in face of changing environmental conditions (Kalan et al., 2020) and have demonstrated an ability to live in proximity to humans (Hockings et al., 2015). Human-chimpanzee sympatry results in changes to chimpanzee behaviour which may include the incorporation of cultivated foods into the diet, shifts in ranging patterns and an increase in conflictual interactions between humans and chimpanzees (McLennan & Hill, 2012). Importantly, the average behavioural diversity indexed by behavioural richness of chimpanzee communities (i.e., social groups) is lower in highly human impacted habitats, including both tool use and culturally transmitted behaviours (Kühl et al., 2019a). This suggests that rare behaviours like accumulative stone throwing are at risk of extinction. Accumulative stone throwing is only found in Western chimpanzees, a critically endangered subspecies, and has been recorded in areas with high human influence (Humle & Kormos, 2011). In this thesis, I combine approaches from ethological studies of primates with primate archaeology, while drawing from theory and case studies from spatial archaeology to investigate accumulative stone throwing from a multi-disciplinary, shared landscape approach to shed light on the larger situational context of this unique behaviour.

1.2 Primatology

Primatology was established in the early twentieth century, with the first research being conducted by psychologists interested in comparing human and nonhuman primate cognition (Kohler, 1925; Yerkes, 1925). It arose from biological anthropology as an interdisciplinary field combining zoology, psychology, and physical anthropology (Rodman, 1999). The study of primates in relation to the development of human societies began with Kinji Imanishi, an ecologist and anthropologist, who began the Japanese tradition of primatological research (Imanishi, 1952). In the late 1950s and early 1960s in the United States, anthropologist Sherwood Washburn and psychiatrist David Hamburg collaborated to study human evolution and contemporary human behaviour through primate research, establishing the utility of a comparative approach (Washburn & Hamburg, 1965a, 1965b). Primatological approaches can provide a basis for genetic, anatomical, and behavioural comparison with humans (Martin, 2002). For example, primatological data can contribute to paleoanthropological questions through the comparison of morphological aspects of skeletal materials. Comparison of humans and nonhuman primates provides insight into human evolution (Baron-Cohen, 2012; Byrne & Whiten, 1992; Martin, 2007), permits testing of general hypotheses in evolutionary biology and ecology (Bowmaker, 1998; Garber, 1987; Terborgh & Janson, 1986), and informs conservation strategies for primates threatened with extinction (Frazier et al., 2021; Galea & Humle, 2022; Hockings & McLennan, 2019). The comparative primatological approach can help create a more comprehensive understanding of human evolutionary biology and behavioural ecology. Although primates are often used as analogues for human culture, the discipline has also seen a turn towards the consideration of non-human primate culture independently of human standards for culture (De Waal, 1999). More recently, an ethnoprimatological approach has developed, which blends the typically objective biological approach of "traditional primatology" with an inductive approach drawn from social anthropology (Malone et al., 2014). It seeks to introduce diverse cultural perspectives and shift away from the Western notions of science from which biological anthropology and thus primatology originated. This shift away from the colonial origins of primatology and biological anthropology is particularly important because primate host countries are not Western countries, and often have a history of colonial occupation by European powers (Waters et al., 2022). By centering the relationships between humans and nonhumans (Riley & Fuentes, 2011), this approach endeavours to minimize the impact of a Western scientific bias on primatological research while emphasizing the shared social and ecological worlds of human and non-human primates (Malone et al., 2014).

1.3 Primate Archaeology

Like its parent discipline, primate archaeology is an interdisciplinary subfield combining traditional behavioural observations in primatology with archaeological methods. Considering both the past and present material record, it offers "a comprehensive comparative and long-term evolutionary framework for understanding the biological, environmental and social contexts of primate behaviour, through analyses of tool making, tool use and the spatially patterned accumulation of refuse" (Haslam et al., 2009, p. 339). Primate archaeologists expanded the traditional anthropocentric definition of archaeology to include the recovery and interpretation of behavioural evidence left by any species. Like ethnoarchaeology, contemporary interpretations of archaeological evidence from primates can be bolstered through behavioural observation to investigate the "evolutionary trajectories of primate behaviour from both anthropocentric and 'primatocentric' perspectives" (Haslam et al., 2009, p. 342). As with primatology, primate archaeology employs comparative studies of organic and lithic technologies used by humans and non-human primates to explore the context of the origin of tool use. Recently, there has been a trend in primate archaeology towards interpreting stone tools versus 'naturally' flaked or used stones, studying the emergence of hominin stone flaking, and identifying which primate species might act as models for early hominin lithic technology and tool-use (Haslam et al., 2017; Proffitt et al., 2016, 2023). Often, primate archaeological research focuses on raw-material selection and transport, tool use, and the resultant forms. Stone has the potential for "controlled formation of acute margins during fracture (that is, detachment of a flake from a larger core), with the degree of control reflecting motor skill and cognitive capacities" (Haslam et al., 2009, pp. 339–340). The characteristics of stone and its durability make it a primary focus of primate archaeology. Primate stone tools, like the hammers and anvils used for nut cracking by chimpanzees, capuchins, and macaques, can develop characteristic use-wear patterns of fractures, pitting and abrasions which provide insight into their handling and use (Arroyo et al., 2021; Mercader et al., 2002; Proffitt et al., 2021). Research into primate stone tool use has identified important implications for understanding the development of hominin stone tool use, as unintentional breakage might be a first step toward the deliberate production of stone flakes (Proffitt et al., 2016). Several factors likely contribute to the independent development of tool use, including the availability of suitable ecological niches, manipulative ability, the intelligence to learn complex skills, and social tolerance in a group setting (van Schaik et al., 1999). Analysis of the spatial patterning of stone tools and seasonal re-use of locations is another major area of study within primate archaeology, as re-use leaves recognizable non-human archaeological assemblages on the landscape (Mercader et al., 2002).

The traditional separation of human-focused archaeological methods from primate behaviour limits our ability to address questions about the evolution of tool use. By combining the two through primate archaeology, we can gain new insight into the origins and development of human behaviour through comparison of non-human primate artifacts, tool, and landscape use to those of early hominins (Luncz, Arroyo, et al., 2022). Primate archaeologists can borrow methods from archaeology (Benito-Calvo et al., 2015), and archaeologists studying humans may be inspired to revisit or rethink previous conclusions (Agnolín & Agnolín, 2023; Patterson, 1983). These comparisons are facilitated by phylogenetic proximity and similarities in morphological characteristics of the hand; among other similarities, early hominins and modern non-human primates share a bipedal posture and comparable forelimb, wrist and hand structure (Kivell, 2015; Tocheri et al., 2008). Due to the durability of material culture, primate archaeology allows us to study behaviour and abilities even if the user is absent or deceased (Luncz et al., 2015). This is particularly useful for wild, non-habituated groups of non-human primates. When study populations may be disturbed by or avoid the presence of humans, less-invasive data collection methods drawn from archaeology such as transect surveys of artifact distributions, proximity to nesting sites, and observations of raw material availability can help answer questions about tool selection and use (Luncz et al., 2017). Primate archaeology also adds time depth to our understanding of primate behaviour, allowing us to identify when tool-use innovation or loss occurred and to track the spread of behaviours (Haslam, Luncz, Pascual-Garrido et al., 2016; Haslam, Luncz, Staff et al., 2016; Proffitt et al., 2016).

1.4 Landscape Archaeology

Landscape approaches within archaeology arose at least as early as the 1920s and have since expanded to consider the landscape not just as a backdrop for material remains, but as “an active and far more complex entity in relation to human lives” (Knapp & Ashmore, 1999, p. 2). The landscape includes not only the natural environment—stemming from traditional considerations of landscape ecology—but the cultural systems that mediate the way people interact with their environments. As a subdiscipline, landscape archaeology emerged in the 1970s (Aston & Rowley, 1974). It deals with “the understanding of archaeological remains (artifacts, sites, and site complexes) in terms of the wider spatial realms (both physical and meaningful) of past human experience” (Denham, 2017, p. 464). Early archaeologists studying landscapes usually had training in other disciplines, often geography or history. Following the general trend in archaeology, it went through its processual era in the 1960s and 70s with an emphasis on explaining the past through scientific theory and systems thinking (Turner et al., 2018). Later, there was a post-processual shift to include social processes and social theory. More recently, landscape archaeology has become focused on the meanings of landscape to its inhabitants (Cosgrove, 1984; Criado Boado & Vázquez, 2000; Fowles, 2010). Landscape archaeology considers the diverse processes at play over different timescales in the landscape as well as the environmental and human aspects of a defined area of land—in this thesis, the non-human, chimpanzee perspective is taken as an inhabitant of the land shared by humans. This draws inspiration from current perspectives on interspecies interactions, including niche construction theory (Laland et al., 2016). When humans and other primates share ecological spaces, they influence the construction of each other’s niches through, for example, habitat modification and hunting on the human side, and seed dispersal and crop-foraging from non-human primates (Ellwanger & Lambert, 2018; Kamilar & Tecot, 2016). Landscape is defined as a “human scale of lived experience” or “an area, as perceived by people, whose character is the result of the action and interaction of natural and/or human factors” (Denham, 2017, p. 464; Turner et al., 2018, p. 1). For the chimpanzees, this would consist of their home range (Chapman & Wrangham, 1993), where topographic features, their behaviour, and human factors shape how they move about in and use their territory.

Landscape archaeological research explores how aspects of the landscape become meaningful for its inhabitants, visitors, or viewers. For the chimpanzees, the core versus peripheral areas of the home range can have different significance; the core would include reliable food resources and sleeping sites, while the periphery is a zone of interaction with other communities, requiring patrolling and defense while also potentially including useful resources (Herbinger et al., 2001). Phenomenology, or the “study of the structures of human experience and consciousness” (Johnson, 2012, p. 272) has become associated with landscape studies as a method of understanding the subjective creation and meaning of landscapes. It takes an interest in the body and lived experience, as demonstrated in the work of Tim Ingold (2005, 2007, 2010). Ingold described the temporality of the landscape as something socially experienced by its inhabitants and in a process of continual becoming (Ingold, 1993). The landscape shapes and is shaped by its inhabitants, incorporating the patterns of activities that take place within it into what Ingold refers to as the “congealed form of the taskscape” (Ingold, 1993, p. 162); over time, practices become incorporated into the landscape, “providing sequential evidence of human-environment interactions in the past” (Denham, 2017, p. 465). Habitual use of a location for non-human primate activities like nut cracking (Luncz et al., 2019), nesting (Stewart et al., 2011), or AST (Kalan et al., 2019; Kühl et al., 2016) result in the formation of conspicuous sites on the landscape. Nesting sites and the sticks and leaves used by primates degrade and disappear over time, while the stones used for nutcracking and AST can endure, providing a time depth not available for perishable items. With their characteristic use-wear signs rendering them visible on the landscape, trees used for AST are broadly similar to culturally modified trees in British Columbia and the Pacific Northwest. Culturally modified trees (CMTs) are defined as "trees, both living or dead, that have evidence of traditional or cultural use by First Nations People" (DeRoy et al., 2021, p. 467). Bark stripping is an Indigenous cultural practice, where bark is harvested from red and yellow cedar trees in a way that ensures the tree's survival and is used to make clothing, fish traps, baskets, and many other items (Oliver, 2007). People harvested bark from trees near their settlements but would also travel long distances to collect bark from mountainous terrain. Stands of cedar with the best trees for bark stripping would be returned to, and patterns of harvesting followed pathways outwards from these places. As the same people worked the stands of stripped trees and returned to them again and again, the groves became entangled in webs of family connections, with tree scars acting as a physical manifestation of social practice and generational time (Oliver, 2007).

The distribution of lithics and other cultural artifacts can be analyzed as a visible and durable reminder of activity left on the landscape (Clarkson, 2016). Lithics provide a record of material transport, selection, and the functional role and cultural value of stone artifacts. The accumulation of stone tools gives insight into the frequency of use of a site (Kuhn & Clark, 2015). Stone accumulations can also signify symbolic value of a site, as in the case of human cairns (Mizin, 2013). Primate archaeological research can draw on methodologies developed for archaeological studies of artifact distribution, accumulation, and assemblage composition, as well as association. For example, humans tend to center their activities around unique places, places of practical utility, and around certain features of the environment (Clarkson, 2016), and non-human primates may make similar choices. Although lithics are a common focus of archaeological investigation due to their durability, archaeological approaches are frequently applied to non-lithic materials as well, as evidenced by recent research into plant scarring and the "archaeology of the perishable" (d'Errico & Backwell, 2021; Pascual-Garrido, 2018). New methods to examine the internal and external damage patterns of wooden percussive tools used by primates have been developed (Luncz, Braun, et al., 2022); this represents a significant development in primate archaeology, since much of the tool use of non-human primates is of herbaceous vegetation or wood (Kalan et al., 2020). These techniques could be applied to AST trees, to date the trees or at minimum assess use-wear patterns. Additionally, the analysis of phytolith assemblages in sediments has recently been used to identify dormant oil palm nut cracking sites (Phillips et al., 2022), providing insight into the length of site use and potential for dietary comparison over time.

The chaîne opératoire approach is another useful analytical method adopted by primate archaeologists. It was originally introduced by ethnographers to describe the sequence of traditional crafting and manufacturing techniques but was applied by archaeologists to identify sequential phases of raw stone production in tool production and use (S. Carvalho et al., 2008). In lithic analysis, common stages are raw material selection, blank production, tool production, tool use, recycling or maintenance, and discard. Identifying differences in stone tool use strategies helps us to understand variability and cultural variation between related or neighbouring groups of populations. Finally, primate archaeologists employ use-wear analysis to assess the function of an artifact over its lifetime and the degree of its usage (Carvalho et al., 2008). However, while the chaîne opératoire approach was used in a study by the pioneers of primate archaeology (Carvalho et al., 2008), it has not since been explicitly applied to nonhuman primate tool use.

1.5 Accumulative Stone Throwing

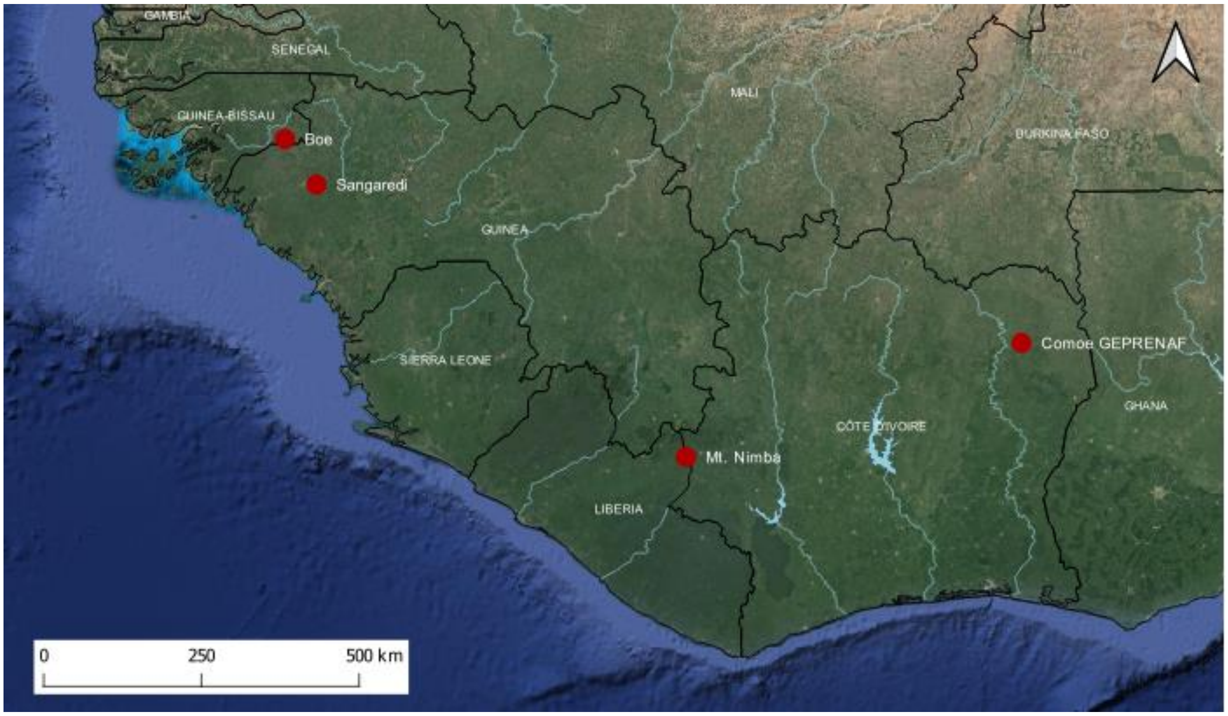
Most instances of stone tool use in primates have been in the foraging context (Gumert et al., 2009; Mercader et al., 2002; Pruetz & Bertolani, 2007; Visalberghi et al., 2007) with few observations in a socio-communicative setting. Accumulative stone throwing (AST) is a unique instance of stone tool use in a non-foraging context, where the stone is thrown at an external object, the tree (Kalan et al., 2019), and performed repeatedly at the same location, leaving conspicuous sites on the landscape. While many have redefined and attempted to clarify and refine the definition of tool use, Beck's (1980) definition has frequently been used as a basis:

> 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 when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool (p.10).

St. Amant and Horton (2008) expanded Beck's definition of tool use to include tools that influence or alter the flow of information between tool users, the environment, and/or other organisms. Examples of this form of tool use include gorillas using sticks to test water depth (Breuer et al., 2005) and apes dragging a branch across the ground as part of a display (Nishida et al., 1999; Schamberg et al., 2017; van Schaik et al., 2003). Following these definitions, AST constitutes tool use because chimpanzees hold the stones just prior to use, are responsible for the effective orientation of the tool, and use of the tool alters the flow of information between the user and other organisms by supplementing auditory signals—the pant hoot and buttress drumming, described later—with an additional audible impact sound. The first direct observations of AST occurred in 2011 at the Sangaredi Pan African Programme temporary research site in Guinea, and it was soon after observed in other Western chimpanzee communities at Boé in Guinea-Bissau, Mt. Nimba in Liberia, and Comoé GEPRENAF in Côte d'Ivoire, shown in Figure 1 (Kühl et al., 2016). A wealth of auditory, visual, and reconnaissance data for this behaviour exists for Boé, created by the Pan African Programme (PanAf) 'The Cultured Chimpanzee' and Kalan et al.'s follow up research (2019). The behaviour has thus far not been observed in any other chimpanzee communities, including at all long-term field sites where chimpanzees have been studied for decades. AST is suggested to be a culturally learned practice due to its limited distribution of the behaviour even within west Africa and the lack of correlation with rock and tree availability (Kühl et al., 2016). In animals, cultural behaviour is defined as being learned from group members and transmitted socially, rather than genetically or developed as an adaptive response to specific ecological conditions (Boesch, 2003, p. 83). It is a distinctive collective practice, so an individual's originating group can be inferred from their socially learned practices. Regional birdsong dialects (Baker & Cunningham, 1985) are an early example of animal culture, and cultural phenomena have been identified in a wide range of taxa (Whiten, 2021), including primates, which show cultural differences in tool use (Luncz et al., 2015), grooming (Perry et al., 2003), and foraging (Samuni et al., 2020). In humans, culture is based on meanings shared between members of the same group, resulting in the development of a mutually recognized symbolic system, such as human language. It remains unclear if nonhuman primates can develop a similar socially shared symbolic system.

Figure 1

Map of Chimpanzee Communities with Observations of AST



Note. Map showing the four chimpanzee communities with observations of AST; Boé in Guinea-Bissau, Sangaredi in Guinea, Mt. Nimba in Liberia, and Comoé GEPRENAF in Côte d’Ivoire. Made in QGIS 3.22. Map data from Google Satellite.

AST sites are defined by the presence of “trees with visible wound marks from repeated impact by rocks and the accumulation of rocks at, or inside, the tree” (Kalan et al., 2019, p. 2). The wound marks created by stone throwing may be fresh, exposing the inner bark, or healed over, creating a knotted scar; both fresh and healed wound marks are visible in Figures 2 and 3.

Figure 2

Example of AST Site

Note. Kalan, A. K. (2017). [Photograph of *Crossopteryx febrifuga* AST tree]. This example shows an AST tree with a hollow cavity, rather than buttress roots. Stones accumulate inside the hollow cavity and at times around the base of the tree.

Figure 3

Example of AST Site

Note. Kalan, A. K. (2017). [Photograph of *Bombax costatum* AST tree]. This tree species has buttress roots which function as mechanical supports or tension elements (Kalan et al., 2019). The stones accumulate in the forks of the buttresses or around the base of the tree.

AST is most frequently performed by adult males and rarely by adult females, though one juvenile was also observed engaging in the behaviour (Kalan et al., 2019; Kühl et al., 2016). It is composed of elements found within the chimpanzees' species-specific behavioural repertoire, specifically stone throwing, buttress drumming, and the ritualized agonistic displays of adult male chimpanzees (Kühl et al., 2016). Stone throwing in chimpanzees was first described by Jane Goodall (1964), who observed male chimpanzees throwing stones directly at people, baboons, and other chimpanzees during agonistic displays but never at trees. Buttress root drumming is considered a long-distance auditory signal, audible over a kilometre away, where chimpanzees will repeatedly hit and slap the trunk and buttress roots of trees with their hands and feet (Arcadi et al., 1998). It is typically performed by adult males, often in association with a long-distance vocalization, the pant hoot, and may contribute to the identification and location of chimpanzees dispersed in the landscape (Babiszewska et al., 2015). Pant hoots and buttress drumming are also commonly observed in the male chimpanzee display (Kalan & Boesch, 2018). During these agonistic displays, male chimpanzees may also throw objects, stones, branches, and the like, but these throws are rarely aimed at individuals (Goodall, 1964).

The frequency and the length of buttress drumming bouts and their association with calls differ between communities, suggesting that social learning may play a role in the development of the signal repertoire (Arcadi et al., 2004); because these signals are integrated into the AST behavioural sequence, this indicates that components of AST may also be socially learned. Kühl et al. (2016) suggest that AST is a socially learned cultural tradition that plays a role in long-distance communication. This hypothesis is supported by Kalan et al.'s (2019) follow-up research, which showed that chimpanzees use tree species that produce more resonant sounds which would be optimal for communication over long distances. Still, it is unclear if AST simply represents an augmentation to the male chimpanzee display, with the addition of targeted stone throwing to enhance sound propagation for long distance communication, or if there may be an alternative explanation such as a symbolic context for the behaviour.

Percussive stone tool use has been identified in Western chimpanzees, *Pan troglodytes verus*, (Boesch & Boesch, 1990; Sugiyama & Koman, 1979), bearded capuchin monkeys, *Sapajus libidinosus* (Falótico & Ottoni, 2016; Fragaszy et al., 2004; Luncz et al., 2016; Ottoni & Izar, 2008), long-tailed macaques, *Macaca fascicularis* (Gumert et al., 2009, p. 200; Luncz et al., 2017; Malaivijitnond et al., 2007), and one group of white-faced capuchin monkeys, *Cebus capucinus imitator* (Barrett et al., 2018). Most stone tool percussion occurs in feeding contexts, as with long-tailed macaques which use hammer and anvil stones to exploit a wide variety of food sources including nuts and shellfish, selecting their tools based on the type of food (Gumert et al., 2009). Like those used for nut cracking, AST stones have characteristic use-wear patterns which makes them identifiable. Laterite is the primary type of rock used for AST; it is a red, brown, or chocolate coloured consolidate of several minerals that forms in humid, tropical areas as a product of weathering (Haldar, 2013). Following an impact, the red un-oxidized interior of the rock becomes visible as shown in Figure 4.

Figure 4

Example of an AST Rock

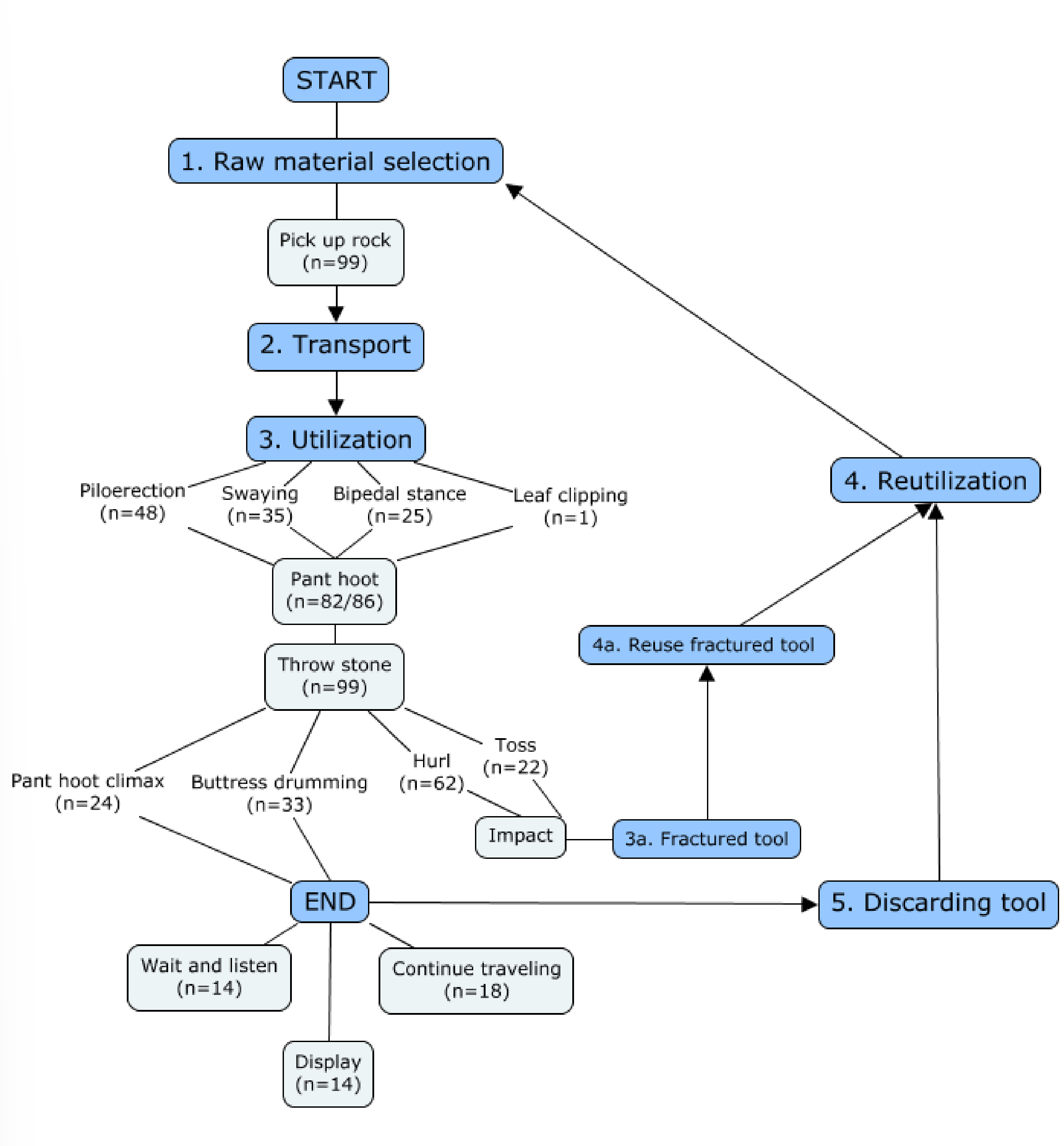
Note. Kalan, A. K. (2017). [Photograph of rock at ASTCROSS2].

1.6 Chaîne Opératoire

Applying the archaeological chaîne opératoire approach to the sequence of behaviours making up AST can provide a concise overview and comparative archaeological framework for situating AST within the broader scope of primate and landscape archaeology. The operational sequence used by Carvalho et al. (2008) to describe chimpanzee nut cracking included twelve phases; "stone selection for tool construction," "tool-function selection," "change tool function," "flake extraction" and "tool playing" were all found not to be relevant to the AST operational sequence and so were excluded. However, Buys et al. (2022) observed an infant banging a small stone on a tree next to the focal AST tree, so it is possible that infants do play with or at least manipulate AST rocks. Kühl et al. (2016) additionally reported a juvenile who similarly banged on the tree in a play-like fashion, suggesting that this could be how young individuals learn or practice the behaviour. The remaining five phases and the behaviours associated with each phase are visualized in Figure 5. Figure 5 combines 63 observations of AST stone throwing from Kühl et al.’s (2016) original description of AST with 36 AST stone throws collected by Kalan et al. (2019) whereby all observations were captured using remote camera trap videos placed at AST sites. Figure 5 therefore includes AST data from all four sites where AST has been observed (Figure 1).

Figure 5

Blending the Chaîne Opératoire Approach with the AST Behavioural Sequence



Note. Total sample size n=99. The blue boxes indicate phases of the AST behavioural sequence following Carvalho et al. (2008) and the white boxes represent detailed behavioural actions observed within a phase if applicable along with the number of throws where it was observed.

In the raw-material selection phase (Phase 1), chimpanzees select a rock to throw (Figure 6). Because the observations were collected using camera traps, chimpanzees were sometimes observed with a rock already in hand. For cases where the rock was picked up on camera, the distance of travel is short—usually 1m or less (Phase 2). Phase 3, utilization, encompasses the majority of the behaviour. Behaviours such as piloerection, swaying, bipedal stance, and leaf clipping often precede the pant hoot vocalization and the throw (Figure 7). Camera trap videos show that stones may be thrown in three ways: a bang, where the rock is repeatedly hit against the tree; a hurl, defined as a directed throw at the tree; or a toss, where the rock is thrown into a hollow of the tree or its roots (Kühl et al., 2016). However, adult chimpanzees at Boé have only been observed to hurl or toss the rocks excluding the two observations of play from young individuals. The impact of the throw produces a sound and may result in the rock fracturing (Phase 3a; Figure 8) (Kalan et al., 2019). Instances of AST are often associated with the pant hoot vocalization, which occurs after or while the individual picks up and manipulates the rock. The throw is usually accompanied by the climax phase of the pant hoot and may be followed by buttress drumming. After throwing the rock, the chimpanzee may wait and listen for a response, engage in a display, or continue travelling. It can be inferred that reutilization of rocks (Phase 4) occurs by tracing the re-use of rocks via consecutive camera trap videos. However, the frequency with which rocks are reused remains to be quantified. The rocks are discarded following the throw (Phase 5).

Figure 6

Chimpanzee Selecting a Rock for AST

Note. Kalan, A. K. (2017). [Screen capture of camera trap video of stone throw at ASTCROSS1]. The chimpanzee holds the rock, selected from several available, prior to the throw.

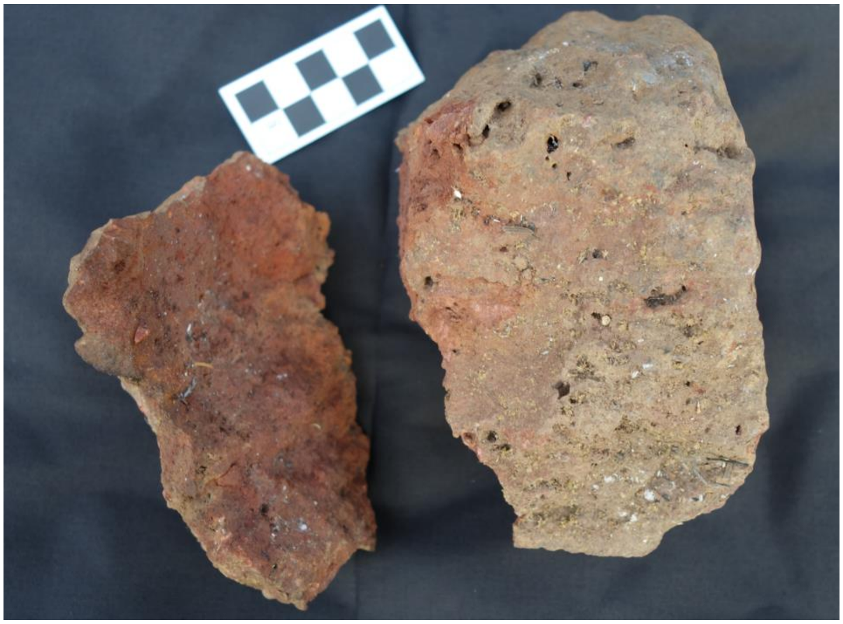
Figure 7

Bipedal Stance Preceding AST Throw

Note. Kalan, A. K. (2017). [Screen capture of camera trap video of stone throw at ASTCEIBA]. An adult male stands bipedally while holding the rock before throwing.

Figure 8

Fractured AST Rock



Note. Kalan, A. K. (2017). [Photograph of AST rock]. After the fracture caused by impact during AST, the unoxidized interior of the rock is visible.

The behavioural sequences for AST and nut cracking share Phase 1, raw material selection. However, while raw materials for nut cracking are selected based on rock type, more information on the availability of different rock types would be needed to determine if chimpanzees preferentially select laterite for AST or if it is simply the most prevalent type of rock in their environment. Chimpanzees select stones for nut cracking tool construction based on certain morphological characteristics, such as weight, that make them suitable for specific functions (S. Carvalho et al., 2008; Luncz et al., 2019); it is so far unclear which, if any characteristics influence chimpanzee rock selection for AST. Unlike nut cracking, where stones can be used as hammers, anvils or wedges, chimpanzees choosing rocks for AST do not need to determine which function a stone is best suited for. In both nut cracking and AST, chimpanzees transport tools from their original position. In Carvalho et al.'s (2008) research on nut cracking, this transportation is influenced by the size of the tool and potentially by individual tool preference, whereas in AST, tools are necessarily transported to the tree. Patterns in tool use are similar between Carvalho et al.'s (2008) observations and AST, with adult males performing the behaviours most frequently, followed by females. However, while juveniles were observed to frequently use and reuse stone tools for nut cracking, no juveniles were observed to perform AST. Reutilization was more difficult to identify for AST than for nut cracking; S. Carvalho et al. define reutilization as "using one tool that another individual selected before during a session" (2008, p. 153), and observed 110 instances of reuse during their twenty-nine experimental sessions. Reuse is easier to observe in their context, because chimpanzees were constantly monitored and remained in the area, and tools were numbered. In camera trap videos of AST, it is more difficult to track tool reuse and reuse of fractured tools outside of consecutive videos. In nut cracking, individuals may unintentionally produce stone flakes, while in AST, stones are more likely to fracture into large pieces. This can be compared to beginning stages of lithic reduction, where large pieces of stone are removed. However, unlike in lithic reduction, stone fracture for the production of suitable smaller pieces to be worked into stone tools is not the goal of AST, but a potential outcome. Patterns of discard differ between the stone tools used for nut cracking and AST; in nut cracking, primates may discard stones if fracture renders them too small to be effective, while in AST, stones are simply left behind after the throw when the chimpanzee moves on. These stones may be reused in later AST events. Analyses of the stones would be required to determine if, like nut cracking, individuals prefer stones of a particular size for AST and discard fractured stones below a certain threshold. Comparing the chaînes opératoires for different behaviours tell us about the strategic choices made by primates selecting resources for those behaviours and comparing behavioural sequences for the same behaviour can provide insight into cultural variation between groups.

The accumulation of rocks with distinctive use-wear patterns in association with trees with characteristic wound marks makes AST a strong candidate for archaeological investigation. Although previous research suggests that AST plays a role in communication and that the acoustic properties of the tree may influence its uses, it is unclear what factors influence individual site selection. The distribution of rock density and the presence or absence of hollow trees did not appear to influence the likelihood of AST site occurrence (Kühl et al., 2016). Kalan et al.'s (2019) survey of AST tree species density revealed that despite there being an abundance in an area—as many as 417 trees per km^2 for *Bombax costatum*, for example—only a fraction are used for AST. The spatial patterning of AST sites may relate to the proximity of high use areas within the chimpanzee home range, such as nesting sites, food trees, and water sources, but this has not yet been investigated.

1.7 Research Questions and Predictions

In this thesis I investigate the spatial distribution of AST sites in the landscape to determine how certain landscape features and resource availability influence the selection of particular locations whilst considering chimpanzee-human interactions. With hundreds of seemingly appropriate trees in the area, (Kühl et al., 2016), what about these specific sites makes them suitable for AST? I ask:

1. Are there any identifiable patterns in the spatial proximity of certain resources, chimpanzee and human space-use, or landscape features to AST sites?
2. Which resources, space use elements, or landscape features influence AST site presence?

I predict that the proximity of chimpanzee specific resources, human activity, landscape features, and the availability of rock and AST tree species in the environment affect the distribution of sites. This prediction is based on research showing that chimpanzees alter their ranging patterns and select nesting places based on topography, vegetation type (Lindshield et al., 2021), food abundance (Doran, 1997; Koops et al., 2013), water availability (Hernandez-Aguilar, 2009) and the presence of predators and humans (Fotang et al., 2021; Stewart & Pruetz, 2013). Additionally, Almeida-Warren et al. (2022) found that nut cracking site selection is influenced by nut tree presence, the availability of raw materials, food tree availability and proximity to nesting sites. The selection of AST sites may similarly be influenced by these predictors. AST sites may be near important resources, such as shade, fruit trees, or water sources, to mark or protect these significant locations, like how *utsjoki*—piles of stones found in northern Finland—mark trails, fishing areas, or remarkable places (Mizin, 2013). In the dry, savanna woodland habitat, sources of shade such as gallery forests and caves may be highly valued alongside water sources for thermoregulation (Pruetz & Bertolani, 2009). During the hottest parts of the day and in periods of low water availability and high temperatures, chimpanzees—particularly lactating mothers—visit caves to alleviate heat stress (Boyer Ontl & Pruetz, 2020; Pruetz, 2007). Research in Kibale National Park indicated that relative chimpanzee densities can be predicted from the abundance of food trees in the area (Balcomb et al., 2000); chimpanzees may visit these areas more frequently, making it more likely that AST sites would arise here by chance or out of a need to communicate with group members in other areas. Sites near human settlements may play a role in chimpanzee communication to avoid or scare off humans or livestock. Although there are no reports describing how chimpanzees might communicate about human presence, human-chimpanzee interactions are becoming more frequent as habitat is converted to agricultural land

(Hockings & Sousa, 2013; McLennan et al., 2019). Chimpanzees communicate about the presence of predators (Crockford et al., 2012), so it follows that they may communicate about the presence of humans if they are perceived as a threat. Additionally, given the communicative aspect of AST, sites might be found near chimpanzee nesting sites, potentially demonstrating their significance for group coordination (Kalan et al., 2019). Buttress drumming patterns and pant hoot vocalizations can communicate the identity of the signaler and are suggested to coordinate the movement of dispersed individuals (Babiszewska et al., 2015; Desai et al., 2022). Alternatively, AST sites may be located on the periphery of home ranges since chimpanzees actively monitor and protect their territories (Watts & Mitani, 2001). In this case, AST sites might play a role in communicating territorial boundaries with members of neighbouring communities. As with behaviours like nut cracking, where tool selection and use are significantly influenced by raw material availability (Luncz et al., 2016), site selection may also be influenced solely by the availability of AST tree species and rock sources in the landscape, rather than aspects of the shared chimpanzee/human environment. These predictions are summarized in Table 1.

Table 1

Variables Potentially Influencing AST Site Presence

	Influence on		
Variable	Ranging patterns	Nut cracking site location	Nesting site location
Resource variables			
Food trees	Balcomb et al., 2000; Doran 1997	Koops et al., 2013	Hernandez-Aguilar, 2009
Water sources	Lindshield et al., 2021		Hernandez-Aguilar, 2009
Raw material availability		Almeida-Warren et al., 2022; Luncz et al., 2016	Lindshield et al., 2021
Nesting sites	Lindshield et al., 2021	Almeida-Warren et al., 2022	
Landscape variables			
Caves	Pruetz & Bertolani, 2009; Boyer-Ontl & Pruetz, 2020; Pruetz, 2007		
Human settlements	Hockings & Sousa, 2013; McLennan et al., 2019; Crockford et al., 2012		Fotang et al., 2021

Note. This table summarizes the references providing support for the influence of the identified variables on AST site presence.

Chapter 2

Methods

2.1 Study Site

The Republic of Guinea-Bissau is a small but ethnically, religiously, and linguistically diverse country located in West Africa, with Senegal to the North, Guinea to the South and East and the Atlantic Ocean to the West (Ferreira, 2004). Its area of 36 125 km^2 includes the islands comprising the Bijagos archipelago (Gippoliti & Dell'Omo, 2003). From sea level, the country's topography rises eastwards to moderate elevations. Mangrove forests follow the coasts and six major estuaries, while closed broad-leaved forests intersect the savanna and small areas of primary forest subsist in the south- and northwest. The climate is warm year-round, with an average temperature of 26ºC, and the country receives between 1500 and 2000 mm of precipitation yearly. Guinea-Bissau gained its independence from Portugal in 1974 and continues to recognize Portuguese as its official language and Crioulo, a Portuguese creole as a national language (Studer, 2019). As a result of long-term political instability following successive coups d'état, Guinea-Bissau is among the world's poorest countries. It is divided into eight administrative regions—Bafatá, Biombo, Bolama, Cacheu, Gabu, Oio, Quinara and Tombali—and one autonomous sector, Bissau.

The Boé sector covers about 3000 km^2 of the Gabu Region in the south-east of Guinea Bissau (Studer, 2019). It contains approximately 75 villages, the biggest being Béli, and houses Boé National Park. The Boé sector has a tropical and dry or savanna type habitat and receives an average of 127 mm of rainfall annually, with most precipitation in July and August (Aladin, n.d.). The average temperature in May, the hottest month, is 28.1°C, but temperatures in March can reach 35°C (*Climate-Data.Org*, n.d.). Savanna woodland type vegetation is predominant due to the shallow soil and lateritic crusts, though forest may develop along rivers where the soil is deep enough and not subject to long-term flooding (Studer, 2019). Habitat fragmentation and loss due to development for agriculture or mining is one of the greatest threats facing chimpanzees in the Boé sector (Kormos & Boesch, 2003). The Chimbo Foundation, a Dutch non-governmental organization, has been active in the Boé sector since 2007 with the aim of conserving chimpanzee habitat and preventing their extinction.

2.2 Study Species

Along with bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*) are one of our closest living relatives (Langergraber et al., 2012). The chimpanzee range extends across equatorial Africa, including a wide variety of habitat types and elevations. The species includes four subspecies: the Eastern chimpanzee (*Pan troglodytes schweinfurthii*), the Central chimpanzee, (*P. t. troglodytes*), the Nigeria-Cameroon chimpanzee (*P. t. ellioti*), and the Western chimpanzee (*P. t. verus*). As a species, chimpanzees are considered Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with the number of mature individuals decreasing (Humle et al., 2016). The Western chimpanzee inhabits rainforest, savanna, scrub forest, and gallery forest habitats in West Africa from Senegal to Ghana, but is thought to be extinct in Benin, Burkina Faso and Togo (Humle et al., 2016; Jones et al., 1996). Like other subspecies, Western chimpanzees live in fission-fusion communities with multiple males and females, where community size and composition can change fluidly based on food availability, presence of receptive females, and community activity (Lehmann & Boesch, 2004). Home range size varies depending on the habitat type, group size, and neighbour pressure, with the largest ranges recorded for chimpanzees living in savanna woodland habitats (Lemoine et al., 2020). Western chimpanzees are designated as Critically Endangered on the

IUCN Red List (Humle et al., 2016). Like other great apes, their low population densities, low reproductive rate, late age of first reproduction and long interbirth intervals make them particularly vulnerable to anthropogenic impacts, including hunting, disease transmission and habitat destruction (Kühl et al., 2017, p. 2). Western chimpanzees are the only chimpanzee subspecies reported to use stone tools regularly, with most research to date focused on stone tool use for nut cracking.

2.3 Boé Chimpanzees

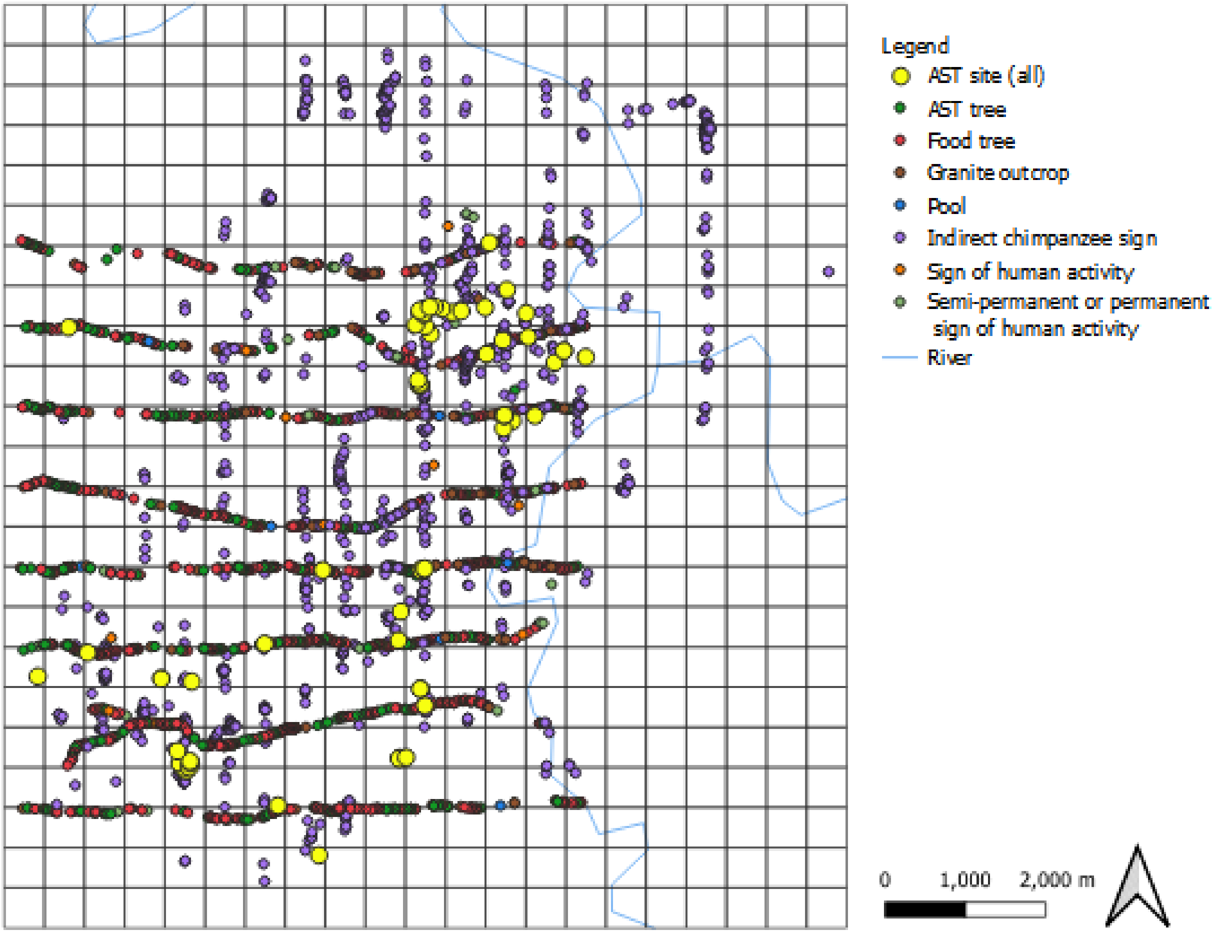
It is estimated that between 600 and 1000 Western chimpanzees remain in Guinea-Bissau (Sousa et al., 2005). There are no habituated chimpanzee communities in the Boé; all behavioural research has been conducted using remote camera-trap videos (Buys et al., 2022; Kalan et al., 2019; Kühl et al., 2016). Chimpanzees in savanna woodland habitat rely on gallery forest found near water sources for nesting sites (Nunes van den Hoven, 2017). In this type of habitat, chimpanzees tend to build nests on hillsides, with a preference for forests, but not forest patches in swamps or at the tops of hills (Hernandez-Aguilar, 2009). Gallery forests also have a higher diversity of tree species, meaning they may provide better access to food sources as well as providing shade during the dry season. Chimpanzee habitat in Boé National Park may overlap with agricultural areas, logging, or temporary settlements. Previous research in the area found that if large trees are available, the chimpanzees can tolerate some anthropogenic impact in their environment (Wenceslau, 2014).

2.3 Mapping

Using data from fieldwork in 2017 (Kalan et al., 2019), reconnaissance surveys by the PanAf programme, and open-source mapping layers and tools, a plot of the data including relevant landscape features was created with QGIS version 3.22 (Figure 9). These data include chimpanzee space-use from 87 km of reconnaissance transects, rock and tree plot surveys, the location of rivers and other resources significant to chimpanzees, such as food trees and nesting sites (Kalan et al., 2019, PanAf 2013), as well as signs of human activity and the location of human settlements and plantations (Kalan et al., 2019). Open-source resources include water courses (United Nations Office for the Coordination of Human Affairs, 2022), administrative boundary layers (*GADM*, 2022) and the OpenStreetMap plugin.

Figure 9

Plot of Study Area Showing the Locations of Observations of Each Variable



Note. The overlayed grid cells are 500m-by-500m. The variable 'AST site (all)' includes observations of active AST sites as well as old sites.

2.4 Spatial Analyses

DeRoy et al. (2021) use a spatially explicit multi-criteria evaluation (MCE) framework to predict the suitability of trees for cultural modification. The selection of trees for bark stripping depends on multiple environmental and cultural factors (DeRoy et al., 2021). Like culturally modified trees, the suitability of individual trees for AST also likely depends on multiple variables, albeit for a nonhuman animal. In the MCE framework, several criteria or predictor variables with potential contributions to the suitability of a given outcome are compared against one another to determine their relative influence. This project applies the inverse of their approach, starting with known AST sites to identify potential influential variables given their distribution rather than using variables to predict site occurrence. Predictor variables include the proximity of AST sites to chimpanzee specific resources, such as food, water, and nesting sites, landscape features, and human settlements, as well as indirect signs of chimpanzee habitat use and the availability of rocks and AST species of trees (7 species: *Bombax costatum*, *Ceiba pentandra*, *Pterocarpus erinaceous*, *Crossopteryx febrifuga*, *Cola cordifolia*, *Treculia africana* and *Markhamia tomentosa* (Kalan et al., 2019)). Drawing inspiration from spatial analyses in landscape archaeology (Gilda, 2019), a systematic grid coordinate system was created by superimposing 500m-by-500m cells over the map (Figure 9). This scale is relevant to AST due to its association with long-distance communication; the pant hoot vocalization is audible over one kilometer away (Arcadi et al., 2004). However, the sound may degrade more quickly in the open savanna landscape than in a closed forest environment (Kalan et al., 2016). This scale is also more appropriate than a 1x1km grid for the distribution of AST sites as impact sounds are unlikely to travel as far as pant hoots (Kalan et al., 2019), and it optimized the spatial resolution and number of AST sites in the sample. Within this grid, each cell represents a datapoint, providing critical information about the landscape and AST sites. I determined the centroids of each grid cell and joined the data layer to the grid layer to produce counts of each variable summed per grid cell. Table 1 contains the complete list of variables considered in this project and defines the groupings used in each model. Similar variables were grouped due to the small sample sizes of certain variables and their similar function or use on the landscape; variables quantifying indirect chimpanzee signs were lumped together (total n = 2296), as were variables for ephemeral signs of human activity (total n = 19) and semi-permanent and permanent human signs (total n = 25).

In R v. 4.2.1 (R Core Team, 2022), the presence or absence of AST sites within a given grid cell was modeled as a function of several variables using two generalized linear models (GLMs) with binomial error distribution and logistic link functions. Both models consider the response variable, presence of AST sites (yes/no) as a function of the relevant predictors, using the summed count of presence/absence per grid cell (Table 1).

$$\mathrm{AST\ sites\ y/n} \sim \mathrm{AST\ trees}\ + \mathrm{food\ trees} + \mathrm{granite\ outcrop} + \mathrm{river} + \mathrm{pool}$$

The second model considers AST site presence as a function of aspects of the shared chimpanzee/human landscape.

$$\begin{aligned}\mathrm{AST\ sites\ y/n} \sim\ & \mathrm{indirect\ chimpanzee\ observations} + \mathrm{human\ activity} \\ & + \mathrm{human\ permanent\ and\ semipermanent\ signs}\end{aligned}$$

Table 2

Categorization, Names, Descriptions, and Types of Variables Impacting AST

Variable category	Variable name	Description	Sample size	Type
		Model 1: Resource availability		
AST relevant data	Old AST	Trees with multiple healed wound scars	42	Binary
	Active AST	Trees with fresh wound scars and rocks with fresh impact marks or observations of AST	14	Binary
Resource availability	Food tree	Observations of food trees	1492	Discrete
	AST tree	Observations of AST tree species	794	Discrete
	Granite outcrop	Observation of rock source, also includes inselbergs	110	Discrete
Landscape features	River	Presence of river	27	Binary
	Pool	Observation of water source	13	Discrete
		Model 2: Shared landscape		
Indirect chimpanzee observations	Nests	Observation of nests	1981	Discrete
	Chimpanzee dung	Observations of dung	29	Discrete
	Chimpanzee feeding remains	Evidence of feeding (fruit skins, wadges, kernels, broken branches with fruits eaten)	286	Discrete
Human permanent and semi-permanent signs	Human path	Observation of path	4	Discrete
	Road	Observation of road	10	Discrete
	Temporary settlement	Location of settlement	6	Binary
	Plantation	Location of plantation	5	Binary
Human activity	Hunting	Observation of hunting	4	Discrete
	Waste	Observation of human waste (garbage, etc.)	3	Discrete
	Noise	Direct observation of noise from human activity	3	Discrete
	Cattle	Direct observation of cattle	8	Discrete
	Logging	Direct observation of logging	1	Discrete

Note. Table showing the grouping of variables into the components of each model, as well as a description of the observations included in each variable. Variables are of two types: binary variables concerning presence/absence data, and discrete variables. While discrete variables are summed for each grid cell, binary variables like “Old AST” and “Active AST” are only represented as 0 or 1, signifying “absent” or “present” respectively. The sample size for “River” refers to the number of units where a river passes through the grid cell.

Each model has two variants: one, considering only active AST sites (n=14) and one including old AST sites in addition (n=67). Active sites are defined as those with trees with fresh wound scars and rocks with fresh impact marks indicating recent use, or with observations of AST from camera trap videos. Old AST sites are characterized by trees with multiple healed wound scars, but rocks may no longer be present or may not have clear impact marks on them. This approach supplements the low numbers of active sites and provides potential insight into temporal differences in site selection. The models do not consider AST site multiplicities within single grid cells; instead, they use AST site presence and absence. Although some grid cells include multiple sites, all grid cells are reduced to binary presence/absence data for the active AST and AST site variables. The sample sizes of active AST (n=11) and all AST (n=28) per grid cell are thus reduced due to the spatial distribution of sites.

The resource availability category includes all variables pertaining to the presence of chimpanzee-relevant materials in the landscape. The frequency of food trees is predicted to influence the presence of AST sites, given that chimpanzees have been observed to alter their ranging patterns to exploit food sources (Balcomb et al., 2000; Hernandez-Aguilar, 2009). While some tree species are both used as a food source and for AST, these species were included in the AST tree variable because separating them out into a new category would artificially inflate the variation of the model by duplicating the effect of AST and food trees, i.e., to avoid pseudoreplication. The variables “AST tree” and “granite outcrop” relate to the material aspect of AST; without a tree of one of the seven AST species and a potential source of rocks, the behaviour is much less likely to occur. “Landscape features” refers to other important chimpanzee resources. Rivers and pools represent additional categories of important chimpanzee resources because chimpanzees cannot survive on metabolic water during the dry season (McGrew et al., 1981).

Therefore, like food trees, water sources may also represent significant locations within the territorial range. The indirect chimpanzee observations category encompasses variables contributing to the visualization of chimpanzee activity and habitat use on the landscape. A territory is defined as “an area and its resources, such as food, mates or breeding sites that is defended against conspecifics” (Herbinger et al., 2001, p. 144). The use of the territory differs across its range depending on ecological and social factors, resulting in the differentiation of a core area from bordering areas where territories of neighboring groups overlap (Herbinger et al., 2001). In dry, mosaic, savanna woodland habitats, chimpanzee territories are larger and shaped differently than those of forest chimpanzees; instead of a polygonal shape, they have fingers extending outwards from the core along the gallery forest tracts which follow water courses (Suzuki, 1969). The large size and non-standard shape of these territories can make it difficult to locate territorial boundaries, particularly for unhabituated communities. By calculating the density of chimpanzee signs across an area from the number of indirect observations, the location of high use areas can be determined to create an image of the territorial range. Researchers can use nest sights, opportunistic observations, and material remnants such as feeding remains to estimate chimpanzee occurrence and territory size (Hernandez-Aguilar, 2009) in association with other indirect variables such as chimpanzee dung and feeding remains. Indirect chimpanzee observations are therefore considered a proxy for territory use, whereby high frequencies of indirect signs may correspond to core areas of the territory. Direct chimpanzee observations were not included in the models for this thesis as all the available data came from camera traps at active AST sites. The human activity variable category includes temporary signs of human activity, such as hunting, waste, noise, cattle, and logging, while semi-permanent and permanent signs of human activity are grouped in the corresponding category. Human population growth and the conversion of forest to agricultural land for the cultivation of rice, cassava, beans, and cashews reduces and isolates ranging areas and can result in resource competition through crop raiding (Hockings & Sousa, 2013). Chimpanzees and humans may come into contact on roads, in cultivated areas and on the edges of forest fragments, facilitating disease transmission and creating the potential for negative interactions and hunting. Human variables are included in Model 2 in order to consider the influence of landscape sharing on the occurrence of AST; because chimpanzees actively monitor and protect their territories (Watts & Mitani, 2001), AST sites might occur near areas of human activity as a method of communicating with group members to avoid or scare off human intruders.

2.5 Model Specification and Fitting

Generalized linear models were fit with the function 'glm' from the package lme4 (Bates et al., 2015). To facilitate comparison through standardization, variables were z-transformed to a mean of 0 and standard deviation of 1. GLMs assume the independence of responses, the absence of influential cases, and the absence of collinearity (Dunn & Smyth, 2018). Cook's distance was used to check for influential cases within the predictor variables (Maximum values for Cook's distance: resource model = 0.34, all AST resource model = 0.16, landscape model = 0.20, all AST landscape model = 0.27). Low values for Cook's distance indicate that there are no influential cases present. DFBETA was used as an additional method of assessing the influence of individual observations; no models included absolute values for DFBETA greater than 1, indicating that none of the observations were influential. Variance Inflation Factors (VIFs) were used to check for multicollinearity between the predictor variables. Different threshold cut-off values for VIFs exist; here, the threshold cut-off is set to be 4, although others may use even higher thresholds of up to 10 (Menard, 1995). Using this threshold, all models show acceptably low amounts of collinearity. (Max VIFs: active AST resource model = 2.78; all AST resource model = 3.11; landscape model = 1.01; all AST landscape model = 1.24).

After running each model, likelihood ratio tests of the full-null model comparison were performed via an ANOVA to test the effect of the predictors while also accounting for the number of predictors. The likelihood ratio test for each model was significant (Resource model $p < 0.0001$; all AST resource model $p < 0.0001$; landscape model $p = 0.0019$; all AST landscape model $p < 0.0001$), so individual predictors were additionally evaluated based on the AIC criterion using the function 'drop1' to determine which comparisons were significant. The results of the single term deletions for each model were consistent with the results of the original GLMs. The pseudo-R^2 statistic was calculated to evaluate the predictive power of each model by comparing its deviance to the deviance of the null model (Resource model = 0.30, all AST resource model = 0.16, landscape model = 0.14, all AST landscape model = 0.13).

2.6 Spatial Autocorrelation

When modeling geographic data, the increased correlation of points in proximity disrupts the assumption of independence; non-spatial models can thus be less precise and have higher type I error rates than spatial models (Mets et al., 2017). Accounting for spatial autocorrelation avoids the artificial reduction of variance and inflation of covariate effect size. The results of each model were checked for spatial autocorrelation using the Moran's I test function in the R package 'spdep' (Bivand, 2022). Moran's index describes "the strength of the correlation between observations as a function of the distance separating them" (Crase et al., 2012), which helps address uncertainty about this. When spatial autocorrelation was observed to be significant, a Moran eigenvector filtering function ('ME' in the package 'spatialreg' (Bivand et al., 2021)) was used to determine the subset of vectors to be added to the models to account for spatial autocorrelation in the results of these models.

Chapter 3

Results

3.1 Resource Models

The results of the non-spatial GLM for active AST sites indicated that AST sites are more likely to occur when in proximity to food trees (n = 483; OR = 3.16; 95% CI 1.67 to 6.57; p = 0.001; Table 2). While spatial autocorrelation (SAC) was not significant for the active AST model (Moran's I = -0.00635, p = 0.579), it was significant when considering all AST sites (Moran's I = 0.140, p < 0.0001). In the spatially controlled for model of all AST sites, the effect of food trees remained significant (n = 483; OR = 2.70; 95% CI 1.69 to 4.52; p < 0.0001; Table 3). The odds ratio gives the probability for the presence of active AST sites given a one-unit increase or decrease in a predictor's coefficient. In the tables reporting the results of the GLMs, odds ratio values with an asterisk represent an inverse relationship between the response and predictor; for example, a one-unit increase in the number of AST trees present decreases the likelihood of active AST site presence by 1.89. Plots of active AST sites and all AST sites against the number of food trees are shown in Figures 10 and 11, respectively, to visualize the relationship between the number of food trees and the probability of AST site presence. In these plots, the blue line represents the logistic regression curve, the gray shaded area represents the standard error associated with the regression line, and the points represent the number of food trees in a given grid cell. The points have values of either zero or one because of the structure of a binomial model; AST sites are either present, 1, or absent, 0. When there are four food trees present in a cell, there is a 50 percent greater probability of an AST site being present.

Table 3

Results of the Resource Model for Active AST Sites

Predictor	Odds ratio	Percent probability (%)	95% CI	p
AST trees	1.89*	0.89*	0.17 to 1.15	0.173
Food trees	3.16	2.16	1.67 to 6.57	< **0.001**
Granite outcrop	2.03	1.03	0.8 to 4.95	0.121
River	1.72*	0.72*	0.03 to 5.24	0.676
Pool	1.10*	0.10*	0.05 to 4.27	0.924

Note. Bolded values indicate a significant result. Odds ratio values with an asterisk represent an inverse relationship between the response and predictor. These conventions apply to Tables 4, 5, 6 and 8 as well.

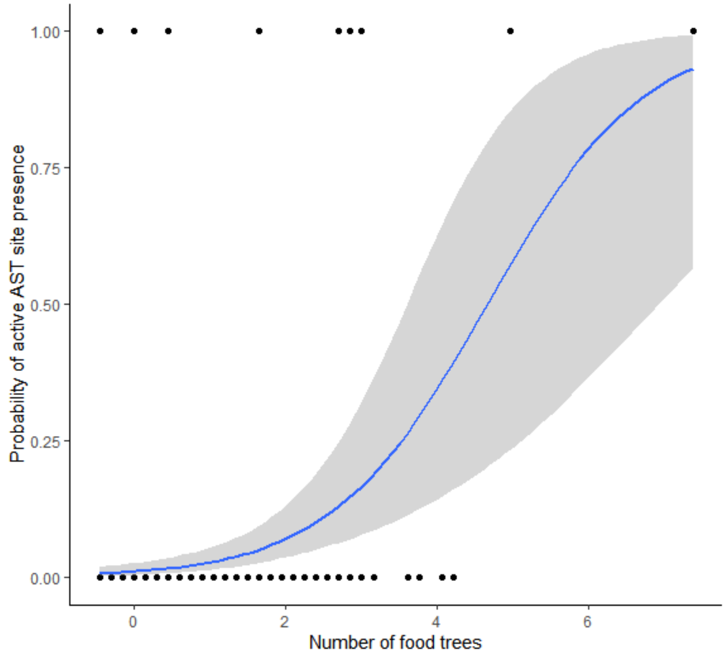
Table 4

Results of the Resource Model for All AST Sites for Non-Spatial and Spatial Models

Predictor	Odds ratio	Percent probability (%)	95% CI	p
		Non-spatial model		
AST trees	1.43*	0.43*	0.38 to 1.15	0.205
Food trees	2.70	1.70	1.69 to 4.52	< **0.0001**
Granite outcrop	1.23	0.23	0.61 to 2.36	0.537
River	2.00*	1.00*	0.06 to 2.44	0.447
Pool	2.38*	1.38*	0.02 to 1.95	0.390
		Spatial model		
AST trees	1.72*	0.72*	0.29 to 1.05	0.0986
Food trees	2.82	1.82	1.64 to 5.17	< **0.001**
Granite outcrop	1.25	0.25	0.57 to 2.52	0.552
River	1.69*	0.69*	0.06 to 3.23	0.592
Pool	1.00	0.00	0.06 to 4.64	0.999

Figure 10

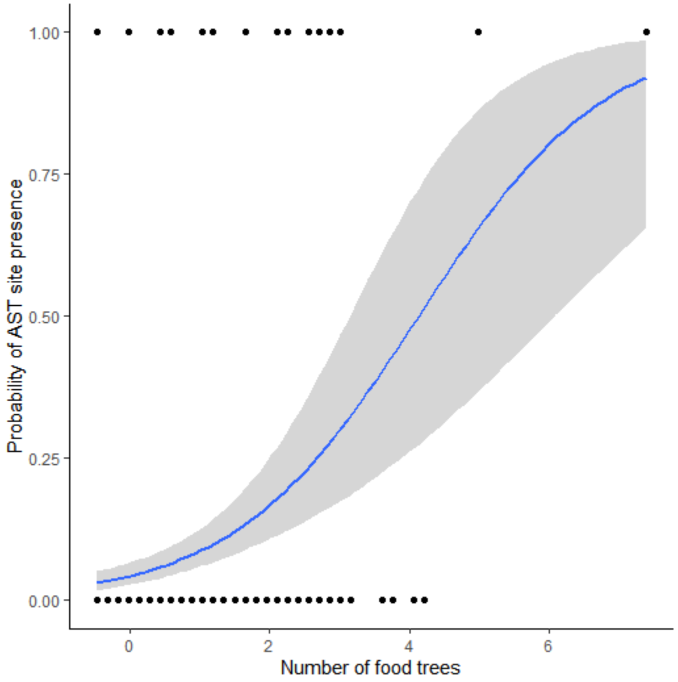
Probability of Active AST Site Presence Against the Number of Food Trees



Note. The linear regression line (blue) shows a positive relationship between the number of food trees and AST site presence. The gray shaded area shows the standard error of the regression line, and the black dots represent observations of the variable on the x-axis. The same conventions apply for all subsequent figures in this chapter.

Figure 11

Probability of AST Site Presence (Active and Old) by Number of Food Trees



To determine if a particular species of food tree was driving this pattern, post-hoc GLMs for the effects of the number of food tree species on AST site presence were carried out for both active (active AST ~ species 1 + species 2 + …) and all AST (AST ~ species 1 + species 2 + …) sites. A simplified model was fit including the counts per grid cell for individual food tree species (Table 4) and excluding the nonsignificant predictors. The influence of food tree species with more than ten individuals present in the entire dataset and the species present in the top ten highest frequencies were assessed in the post-hoc analyses (Table 5). All tree species described as significant here had a positive effect on the presence of AST sites. In models considering all tree species with more than ten individuals, the effect of *Ficus exasperata* was significant. When considering only the top ten tree species, the effect of *Parkia biglobosa* was significant. Accounting for SAC, the *Khaya senegalensis* and *Lannea velutina* were additionally significant. However, the active AST model where the influence of *Ficus exasperata* was significant had relatively high VIF values for *Cordyla pinnata* (VIF = 4.12), *Lannea velutina* (VIF = 4.51), *Ficus exasperata* (VIF = 4.39), and *Pachystela pobeguiniana* (VIF = 4.49). The model including all AST sites had a high VIF value for *Ficus sur* (VIF = 4.39). High VIFs indicate that in these models, multicollinearity inflates the variance for these variables meaning that there may be high levels of interdependence among the predictors (Thompson et al., 2017). One strategy used to address high VIF values is to sequentially remove the covariate with the highest VIF until all VIFs are below a pre-selected threshold (Zuur et al., 2010). However, these tree species are included due to their measured frequency in the landscape; given that the threshold cut-off value of 4 is generic and arbitrary—many authors suggest that a VIF threshold of 8-10 is acceptable—the results can still be considered but should be taken with a degree of caution.

Table 5

Ranking of Food Tree Species by Frequency Within the Study Area

Ranking	Abbreviation	Number of individuals
1	*Parkia biglobosa*	266
2	*Cordyla pinnata*	215
3	*Erythrophleum guineense*	183
4	*Lannea velutina*	183
5	*Sorindeia juglandifolia*	118
6	*Sterculia setigera*	71
7	*Daniellia oliveri*	64
8	*Prosopsis africana*	63
9	*Dialium guineense*	47
10	*Khaya senegalensis*	42
11	*Ficus exasperata*	37
12	*Piliostigma thonningii*	37
13	*Elaeis guineensis*	35
14	*Spondias mombin*	30
15	*Detarium senegalense*	28
16	*Pachystela pobeguiniana*	13
17	*Ficus sur*	12

Table 6

Results of the Resource Model for All AST Sites for Non-Spatial and Spatial Models

Predictor	Active AST			All AST			
	Tree species with frequency ≥ 10	Top 10 tree species		Tree species with frequency ≥ 10		Top 10 tree species	
	Without SAC*	Without SAC	SAC	Without SAC	SAC	Without SAC	SAC
	p	p	p	p	p	p	p
Parkia biglobosa	0.12	**0.018**	**0.0250**	0.075	0.080	**0.05**	**0.035**
Cordyla pinnata	0.83	0.29	0.19	0.31	0.052	0.89	0.11
Erythrophleum guineense	0.45	0.55	0.23	0.77	0.80	0.37	0.058
Lannea velutina	0.12	0.41	0.24	0.26	0.054	0.12	**0.037**
Sorindeia juglandifolia	0.32	0.10	0.068	0.70	0.056	0.77	0.23
Sterculia setigera	0.91	0.31	0.26	0.12	0.51	0.20	0.62
Daniellia oliveri	0.38	0.60	0.84	0.74	0.47	0.96	0.90
Prosopsis africana	0.21	0.66	0.70	0.66	0.70	0.63	0.95
Dialium guineense	0.39	0.36	0.17	0.70	0.14	0.92	0.090
Khaya senegalensis	0.11	0.053	**0.045**	0.53	0.09	0.40	0.28
Ficus exasperata	**0.0067**	-	-	**0.0050**	**0.0022**	-	-
Piliostigma thonningii	0.80	-	-	0.54	0.49	-	-
Elaeis guineensis	0.74	-	-	0.76	0.29	-	-
Spondias mombin	0.92	-	-	0.42	0.81	-	-
Detarium senegalense	0.89	-	-	0.24	0.27	-	-
Pachystela pobeguiniana	0.45	-	-	0.071	0.21	-	-
Ficus sur	0.73	-	-	0.95	0.33	-	-

**Note*. This model did not indicate any spatial autocorrelation therefore only the model without SAC is shown.

3.2 Landscape Models

The landscape model considered the presence of AST sites as a function of the frequency of indirect chimpanzee signs, signs of human activity, and human semi-permanent and permanent structures. Due to the large standard error (SE = 576.89) and low sample size (n = 19) for the human activity variable in the active AST model, these measures were included with counts of human semi-permanent and permanent signs for both the non-spatial and spatial landscape models relating to active AST. Non-spatial GLMs indicated that the frequency of indirect chimpanzee observations has a significant positive effect on the presence of all AST sites (n = 483; OR = 1.81; 95% CI 1.36 to 2.42; $p = 0.0001$; Table 5). Combining the two human variables for the models including all AST sites did not affect these results. SAC was significant for both the active AST model (Moran's I = 0.0423, $p = 0.0326$) and when considering all AST sites (Moran's I = 0.134, $p < 0.0001$). In both spatial models, the effect of indirect chimpanzee activity remained significant (Table 6; Figures 12 and 13).

Table 7

Results of Non-Spatial Landscape Model GLMs for Active and All AST Sites

Predictor	Odds ratio	Percent probability (%)	95% CI	p
		Active AST		
Indirect chimpanzee signs	1.81	0.81	1.36 to 2.42	< **0.0001**
Human activity	1.14*	0.14*	0.25 to 1.28	0.661
		All AST		
Indirect chimpanzee signs	1.90	0.90	1.50 to 2.44	< **0.0001**
Human signs	1.05*	0.05*	0.44 to 1.30	0.807
Human semi-permanent and permanent signs	1.28*	0.28*	0.32 to 1.27	0.451

Note. Bolded values indicate a significant result. Odds ratio values with an asterisk represent an inverse relationship between the response and predictor. These conventions apply to Table 8 as well.

Table 8

Results of Spatial Landscape Model GLMs for Active and All AST Sites

Predictor	Odds ratio	Percent probability (%)	95% CI	p
		Active AST		
Indirect chimpanzee signs	1.66	0.66	1.23 to 2.22	< **0.001**
Human activity	1.15*	0.15*	0.22 to 1.37	0.752
		All AST		
Indirect chimpanzee signs	1.90	0.90	1.50 to 2.44	< **0.0001**
Human signs	1.05*	0.05*	0.44 to 1.30	0.807
Human semi-permanent and permanent signs	1.28*	0.28*	0.32 to 1.27	0.451

Figure 12

Probability of Active AST Site Presence by Number of Indirect Chimpanzee Signs

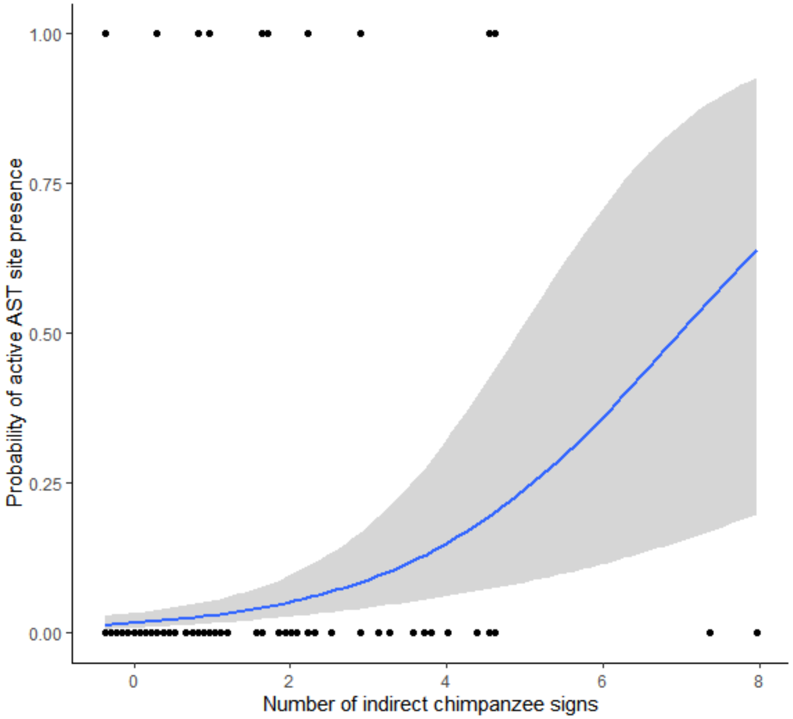
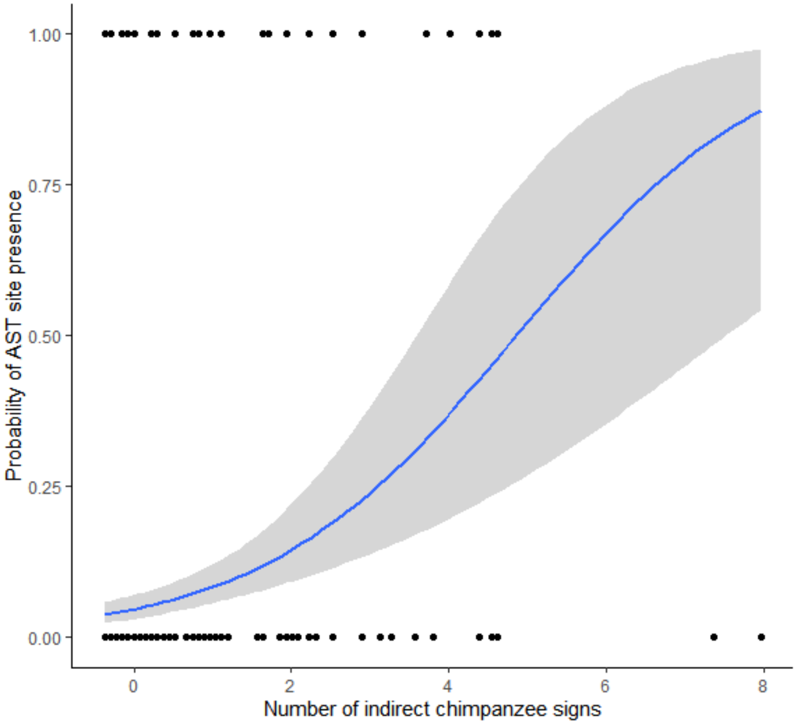


Figure 13

Probability of AST Site (Active and Old) Presence by Number of Indirect Chimpanzee Signs



Note. The linear regression line (blue) shows a positive relationship between the number of food trees and AST site presence. The gray shaded area shows the standard error of the regression line, and the black dots represent observations of the variable on the x-axis. The same conventions apply for all the figures in this chapter.

To determine which of the indirect chimpanzee signs were contributing to the variable's effect on AST site presence, a post-hoc GLM was carried out for active AST (active AST ~ nests + dung + feeding remains) and all AST (AST ~ nests + dung + feeding remains) sites by fitting a simplified model including the counts per grid cell for each predictor. For active AST sites only the frequency of nests was significant with a positive effect on AST site presence ($p = 0.0157$; Figure 10) with SAC being insignificant (Moran's I = 0.028, $p = 0.104$). For all AST sites with the model including SAC (Moran's I = 0.115, $p < 0.0001$), feeding remains were significant with a positive effect ($p = 0.0124$; Figure 14) and nests remained significant ($p = 0.0155$; Figure 15).

Figure 14

Probability of Active AST Site Presence Against the Number of Feeding Remains

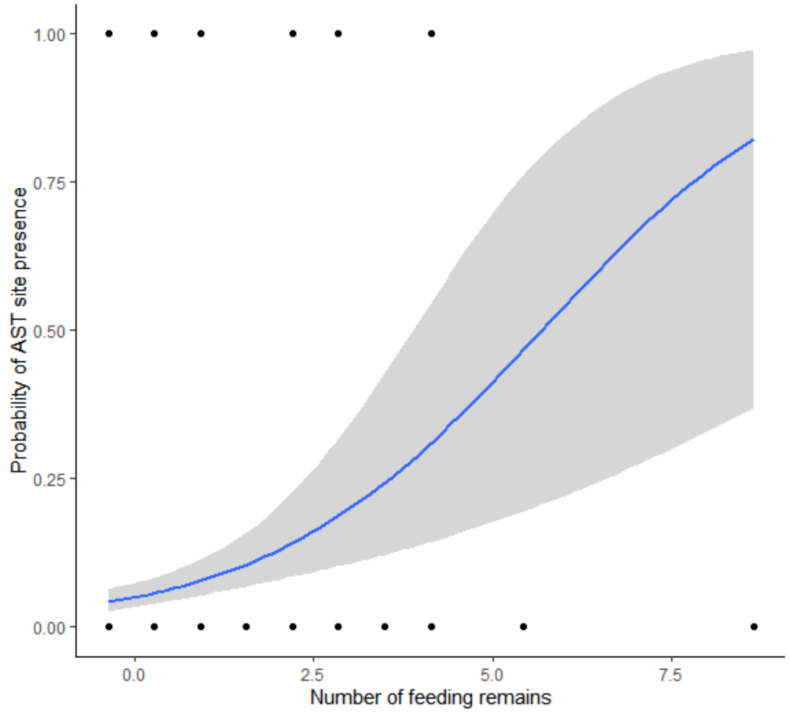


Figure 15

Probability of AST Site (Active and Old) Presence Against the Number of Nests

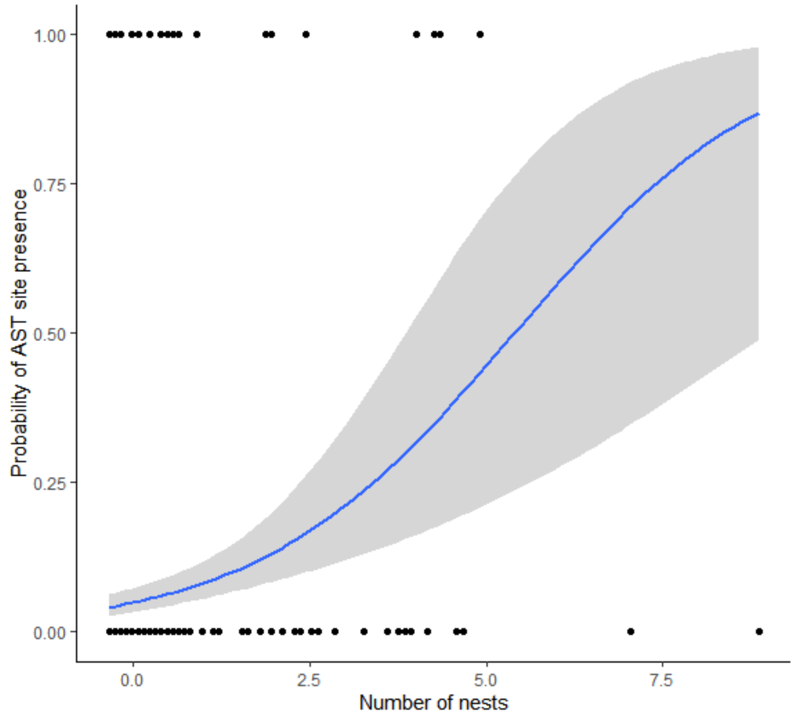
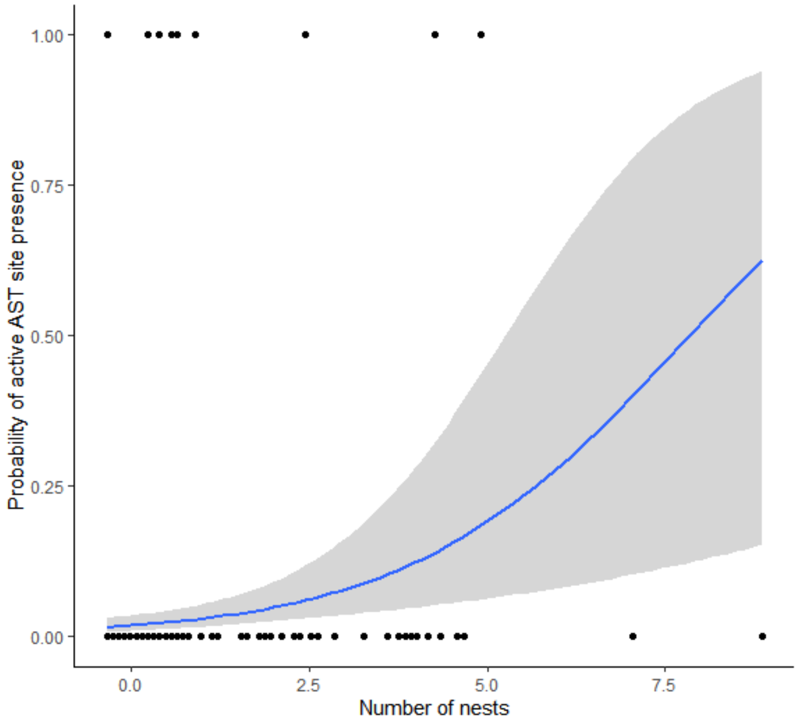


Figure 16

Probability of AST Site (Active and Old) Presence Against the Number of Nests



Chapter 4

Discussion

4.1 Resource Model

The results across multiple models suggest that AST sites are more likely to occur in areas with high frequencies of food trees. This is consistent with predictions based on chimpanzee ranging patterns showing that the availability of food sources influences chimpanzees' use of their territory, including where they nest, i.e., sleeping sites. *Ficus exasperata* was not included in models considering only the top ten species because of its low frequency in the landscape (n=37 trees in the study area), but its significance in the models where it is present suggests that it, along with *Parkia biglobosa*, is one of the two species most strongly influencing AST site occurrence. These two species are both important for different reasons. *Parkia biglobosa* is a predictable and reliable food source in this habitat, occurring in the highest frequency in the study area (n=266) and fruiting reliably in the second half of the dry season (Arbonnier, 2004). Its seeds' high protein and lipid contents make them nutritionally and energetically valuable (Bertolani & Pruetz, 2011), and the fruit pulp is rich in sucrose (Houndonougbo et al., 2020). Given that the effect of *Ficus exasperata* is significant in the models where it is included while *Parkia biglobosa* is only significant in the models without *Ficus*, *Ficus exasperata* is likely the food tree with the strongest effect. *Ficus* species are well documented to be an important food for chimpanzees (Duvall, 2008; McGrew et al., 1988; Pruetz, 2006; Tweheyo et al., 2004) and constitute a preferred food source (J. S. Carvalho et al., 2015) despite their unpredictable fruiting schedule. Even when other species are available, *Ficus* fruit are selectively consumed by Western chimpanzees (J. S. Carvalho et al., 2015). *Ficus* produce large fruit crops, with *F. exasperata* as one of the highest producing species (Tweheyo

& Lye, 2003). Chimpanzees in Issa, western Tanzania and in the Taï National Park, Côte d'Ivoire, have been observed nesting near fruiting *Ficus* trees, suggesting that their preference for this food source affects chimpanzees' ranging patterns (Hernandez-Aguilar, 2009; Janmaat et al., 2014). It follows that AST sites may be more likely to occur near *Ficus exasperata* as chimpanzees adjust their range to exploit this preferred food source.

Engaging in AST near fruiting *Ficus* trees may serve to mark or communicate the location or availability of fruit to other group members through the pant hoot vocalization and impact sound that accompany the AST throw. Pant hoots have been shown to communicate information about environmental features, including the availability of food (Notman & Rendall, 2005), to attract group members to food sources, and to maintain contact with and locate other parties (Marler & Hobbett, 1975; Mitani & Nishida, 1993). Chimpanzees arriving at food trees often produce food calls (Kalan & Boesch, 2018) but may also pant hoot to inform socially important individuals about food availability (Bouchard & Zuberbühler, 2022). Given its potential for long-distance communication through the inclusion of the pant hoot, buttress drumming, and impact sound, the results suggest that AST plays a similar role in that it may strengthen social relationships and attract distant individuals to areas with high frequencies of valuable food sources.

The inverse relationships between AST site presence and AST tree species frequency and river and pool presence contradict the predictions made for these variables, albeit these effects were not significant. AST sites were predicted to be positively influenced by the number of trees of AST species in an area. Instead, AST sites were less likely to occur in locations with high numbers of AST trees. This result could be due to the high frequency of certain AST tree species in the environment. Kalan et al. (2019) recorded 1640 *Pterocarpus erinaceous* trees per square kilometer. The wide availability of AST tree species contrasted with the low sample size of AST sites could therefore limit the influence of AST tree availability on AST site selection. AST sites may be less likely to occur near rivers or pools due to interspecies interactions. Boyer-Ontl and Pruetz (2014) observed chimpanzees, baboons, warthogs, and mongoose calmly drinking together from a permanent water source. The reliability of the river could mean that competition for and defense of water sources is not necessary, and agonistic behaviours like those included in the AST behavioural sequence could even hinder calm interspecies sharing of water sources. Additionally, research shows that chimpanzees have accurate, Euclidean mental maps of their territory and can navigate directly to food resources from different directions (Normand & Boesch, 2009). Similarly, chimpanzees may remember the location of permanent water sources; this may be common knowledge within the community, so AST sites may not be necessary for facilitating group coordination in this case. Further research could be conducted to assess the influence of these variables in studies focusing only on AST sites, rather than broader landscape wide effects.

4.2 Landscape Model

Mapping indirect signs of chimpanzee presence provides a non-invasive, cost-effective method for determining ranging and grouping behaviour (Hansen et al., 2022; Kalan et al., 2016). By locating areas with a high density of indirect chimpanzee signs such as nests, feeding remains and dung, hotspots of chimpanzee activity can be identified (Kouakou et al., 2011). The results of the landscape model suggest that AST sites are more likely to occur in areas of high chimpanzee activity and appear to be in parts of the territory that chimpanzees use most. It is important to note that the numbers of indirect chimpanzee signs are a result of the accumulation of signs over a long period of time, even years; because it is unclear which came first—the high chimpanzee activity in the area or the AST site—the results imply correlation, not causation.

Core areas, which include reliable food resources and sleeping sites, may be more heavily used, although bordering areas may include useful resources as well. Chimpanzees tend to spend the majority of their time in core areas of the territory (Herbinger et al., 2001; Wilson et al., 2007); AST sites in areas with high levels of chimpanzee activity may therefore be located within the core. Post-hoc tests revealed that the frequency of nests has the greatest effect on AST site presence, with feeding remains being additionally significant. This is consistent with predictions based on territory use, as core areas contain an abundance of nesting sites where chimpanzees can safely sleep. Additionally, the AST tree species *Pterocarpus erinaceus* and *Cola cordifolia* are important for chimpanzee sleeping nest construction, with *Pterocarpus erinaceus* especially preferred (Ndiaye et al., 2018). However, AST trees were never observed with nests. *Pterocarpus erinaceus* and *Cola cordifolia* are also food tree species, enhancing their importance for chimpanzees (Arandjelovic et al., 2014). Since chimpanzees have been observed to produce loud calls most frequently in the safety of the core of their territory (Wilson et al., 2007), AST sites may also occur more often in these areas due to the loud nature of the behaviour. Their association with nesting sites and the territorial core suggests that AST sites may play a role in group coordination and communication among dispersed individuals, rather than in territorial defense or marking. However, due to the nonstandard shape of chimpanzee territories in the savanna habitat, territorial defense cannot be ruled out completely; AST sites in the core may still provide an additional way for chimpanzees to announce their presence to intruders or neighboring communities. Although none of the human impact variables had a significant influence on AST site occurrence, the inverse relationship between AST site presence and human activity could be because chimpanzees avoid human settlements. If, as suggested by the results of the models, AST sites are more likely to occur in the territorial core, interactions between humans and chimpanzees could be too rare and unpredictable for an AST site to arise and be habitually used.

Combined, the results of the resource model and the landscape model are complementary in regard to the significant influence of food trees and chimpanzee indirect signs on AST site presence. The abundance of food trees in an area can be used to predict relative chimpanzee density (Balcomb et al., 2000), and areas of higher chimpanzee use will exhibit increased densities of indirect chimpanzee signs, including feeding signs. In Budongo Forest, Uganda, chimpanzee sub-group sizes have been observed to be highest in trees with wide crown diameter and ripe fruits, indicating that food species like *Ficus* have both nutritional and social importance (Tweheyo & Obua, 2001). *Parkia biglobosa* is also one of the eight tree species Western chimpanzees in the Kedougou region of southeastern Senegal use to construct sleeping nests (Ndiaye et al., 2018). The connection between food trees, indirect chimpanzee signs, and territory use indicates that AST sites are likely to occur in the territorial core, near important food sources and sleeping sites.

Given the significant influence of food trees and sleeping nests on AST site presence, AST sites could represent important places in relation to food sources for the chimpanzees, or could have a potential culturally symbolic, socially learned and community derived value. Superficially, AST sites are reminiscent of stone piles used in both ancient and contemporary societies to mark special sacred and secular places on the landscape, relating a physical place to real or mythical events (Mizin, 2013). Additionally, while the definition for ritual in animals varies, AST could be considered a ritual behaviour because it lacks a clear, immediate utilitarian purpose. The production of a sound does not preclude a potential ritual purpose, because ritual behaviours can be communicative and involve the particular use of sounds or even music, for humans (Jackson, 1968). It also incorporates elements from the behavioural repertoire (Perry & Smolla, 2020) and consists of a predefined sequence "of action characterized by rigidity, formality and repetition" (Legare & Nielsen, 2020, p. 1). It also involves attentional focus on the rock being thrown and the targeted tree. Ritual behaviours confer adaptive functions and/or provide psychological or cultural solutions to problems related to living in a group setting (Legare & Nielsen, 2020). While group living is desirable as it decreases the risk of predation, permits the coordinated care of offspring and facilitates technological innovation through social learning, it requires that group members be able to identify one another, ensure commitment to the group, cooperate and maintain cohesion (Legare & Nielsen, 2020; Watson-Jones & Legare, 2016). In nonhuman primates, ritualized behaviours are "stylized, attention-getting and often repetitive interactions" (Dal Pesco & Fischer, 2018, p. 8) which help to foster and maintain cohesion and bind group members together; for example, the ritualized greetings exchanged by male baboons involve non-aggressive, species-specific signals which can buffer aggression and/or reinforce social bonds (Dal Pesco & Fischer, 2018; Whitham & Maestripieri, 2003). However, the definition of human ritual also includes symbolic and procedural components; according to the minimal 'ape' definition of ritual proposed by Tennie and van Schaik, rituals "consist of socially shared, symbolic feature(s) that are created via actions and/or results that require copying" (2020, p. 3). It is unclear if AST must be transmitted by copying stereotypical actions, which transmits know-how, or if it can be shared through non-copying social learning mechanisms like peering or begging, which can sufficiently pass on cultural knowledge such as know-where, know-when, and know-what (Motes-Rodrigo & Tennie, 2021). Future longitudinal studies could further examine the symbolic aspect of AST as well as the social learning and transmission of the behaviour within the community.

Conclusion

This research explored the influence of resources, landscape features, and human activity on AST site selection. Variables including the availability of rocks, AST tree species, food tree species, and water sources, indirect observations of chimpanzee activity, and temporary and semi-permanent or permanent signs of human activity were analyzed for their influence on AST site presence in Boé National Park. The results of the resource model indicate that food trees, in particular *Ficus exasperata* and *Parkia biglobosa*, have a significant influence on the likelihood of AST site presence. The landscape model suggests that the frequency of indirect chimpanzee signs is another important predictor of AST site presence, with proximity to nesting sites as the primary important variable and feeding remains secondary. These results support the overall conclusion that AST sites are more likely to occur in areas of high chimpanzee use; namely the territorial core which includes an abundance of nesting sites and reliable food sources. It remains unclear if the likelihood of AST site occurrence in this area is by chance—chimpanzees being more likely to engage in AST in areas they frequent—or as an additional method of communication with group members in other parts of the territory. Future research could investigate the acoustic dimensions of pant hoots produced during AST to determine how these calls compare to pant hoots produced in feeding contexts to examine a potential acoustic association of AST sites with important food sources (Notman & Rendall, 2005). The strong association of AST sites with *Ficus exasperata* trees—a rare, unpredictable but preferred fruit source—may indicate that AST site selection is not only limited to the core (Janmaat et al., 2014). In an unhabituated community with a large range like the Boé chimpanzees, following individuals to determine ranging patterns is not an option, and tracking devices are largely considered invasive and unethical for great apes (Hansen et al., 2022). Fecal genotype extraction could provide insight into ranging and grouping behaviour for savanna woodland chimpanzees at Boé. Spatial clustering of genotypes can help identify communities and sub-group/party associations (McCarthy et al., 2015), which would facilitate the identification of boundary and core areas. Research relating to chimpanzee ranging patterns in savanna woodland environments is particularly important as it can provide insight into early hominin adaptation to highly seasonal dry, hot, landscapes (Lindshield et al., 2021).

Increasing our understanding of non-human primate behaviour and stone tool use through primate archaeology can inform archaeological inferences relevant for hominin behavioural and cultural evolution. Here, the application of the archaeological chaîne opératoire approach to the AST behavioural sequence provided an overview of the behaviour and a framework for the comparison of AST with nut cracking, an example of stone tool use in a foraging context. Sequences of tool use can act as guides reflecting the strategic choices and underlying mental organization that inform tool use (S. Carvalho et al., 2008). Identifying the pattern of tool use for AST at Boé also creates a basis for comparison of this sequence with the behavioural sequences carried out by chimpanzees in the other three communities known to perform AST. These comparisons could provide insight into potentially culturally derived variations in the behaviour between communities. The lack of transparent site selection criteria or an obvious utilitarian purpose for AST suggests that AST sites—and AST as a behaviour—may have a cultural or symbolic value. Accumulations of stone artifacts created by humans can indicate important resources or suggest that a certain place has a significant history (Clarkson, 2016). Dating AST sites to determine how long they have been in use or aging the impact scars on AST trees could provide time-depth to this behaviour, like what has been shown for hammer and anvil stones used for nut cracking occurring over thousands of years (Falótico et al., 2019). The results of this project provide a first indication that AST sites are associated with significant resources for the chimpanzees, but further research using carefully designed field experiments should test symbolic aspects associated with the sites themselves and the potential meaning they may hold.

Furthermore, studying AST and other rare behaviours has implications for great ape conservation. West African chimpanzees are designated as Critically Endangered (Kühl et al., 2017); human-caused habitat degradation threatens chimpanzee survival, putting rare behaviours at risk of disappearance either by population decline or by inhibiting cultural transmission (Kühl et al., 2019b). Chimpanzees have very high levels of population specific behavioural variation, and many of their behaviours are socially learned and therefore considered cultural (Kalan et al., 2020). The development and maintenance of cultural behaviours depends on innovation, diffusion, and vertical and horizontal transmission, all of which are vulnerable to environmental disturbance. The disturbance hypothesis states that in anthropogenically altered environments, cultural behaviours may disappear not only due to extinction, but also as a result of resource depletion or a breakdown in opportunities for social learning (van Schaik, 2002). Habitat loss, degradation and fragmentation reduce population size, gregariousness and long-distance dispersal which weakens transmission. An integrative approach to conservation that considers behavioural diversity in addition to population size and trends can help protect both genetic and behavioural diversity, both of which are essential for non-human primate survival in a changing environment (Hockings & McLennan, 2019; Kalan et al., 2020; Kühl et al., 2019a, 2019b). The study of AST can therefore expand our understanding of our hominin ancestors while providing support for the conservation of chimpanzee biological and cultural diversity.

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